PLEISTOCENE POLLEN ANALYSIS AND
BIOGEOGRAPHY OF THE SOUTHWEST [*]

PAUL S. MARTIN,[1] PETER J. MEHRINGER, JR.[1]

WEST OF the 100th meridian, south and west of the Central Rockies, and east of the Sierra Nevada of California lies the desert region of the United States. Most of the deserts fall within the Basin-Range Province, which, except near the Lower Colorado River, lies above 300 m elevation. The Basin-Range Province extends into the Great Basin to the northwest, to the Colorado Plateau on the north, and to the High Plains on the east. Relative relief is great, reaching 4,500 m between the bottom of Death Valley and the top of Mt. Whitney, California, 140 km to the west. In addition to extreme climatic diversity caused by physiography there are major regional differences in mean annual temperature and in seasonal distribution of rainfall. The Great Basin is a high, cool desert with largely winter precipitation, the Mohave Desert somewhat lower and warmer, the Sonoran the lowest and hottest with an important summer-rainfall component, and the Chihuahuan higher and cooler with biologically significant rainfall mainly in the summer season.

Following its acquisition by the United States after the war with Mexico, over 100 years ago, intensive geological and biological surveys of the Southwest began under various agencies of the federal government. By the start of the 20th century most of the higher animals and plants of the region were known to science. But even in these groups new species continue to be discovered occasionally, for example the vertebrates *Salmo gilae* Miller (1950), *Plethodon neomexicanus* Stebbins and Riemer (1950), *Gerrhonotus panamintinus* Stebbins (1958), and the oak *Quercus ajoensis* Muller (1954). That parthenogenesis was only recently discovered in the whiptail lizard, *Cnemidophorus*, is a further illustration that much remains to be learned regarding even the "well-known" terrestrial vertebrates.

Ecological studies of the major animal-plant communities in the San Francisco Peaks of Arizona led to the concept of life-zones, which Merriam (1890) divided into Alpine, Subalpine, Hudsonian, Canadian, Neutral, Piñon Zone, and Desert Area. Similar life-zone descriptions in many desert mountains followed, with emphasis in recent years on the detailed pattern of individual species distribution (see Lowe, 1964; Whittaker and Niering, 1964). While the major biotic zones are now familiar to most ecologists, detailed ecological studies of certain distinctive environments of the Southwest are seldom seen in print. These environments include the margins of playa lakes (Potter, 1957), the natural cienegas and undissected floodplains of the desert grassland (Martin, 1963a, p. 23), the spring mounds of southern Nevada (Mehringer, in press), and the ice caves of New Mexico (Lindsey, 1951). Limnology, a more flourishing field of research in the arid Southwest than one might imagine, has been thoroughly reviewed by Cole (1963), who includes bogs, basin-range playas, meteoritic pits, volcanic lakes, mountain lakes (unglaciated), ox-bows, deflation basins, and solution basins in his inventory of the more important natural sediment traps.

The sizable although locally vanishing areas of natural desert in the Southwest offer excellent opportunity for studies of vegetation dynamics. For example, by photographic comparison Hastings and Turner (in press) show a retreat of mesquite, blue palo verde, and creosote bush from their lower range limits and an upward advance of these and other shrubs into the desert grassland during the last 60 years. The authors consider climatic change to be a major cause.

General accounts of the vegetation in parts of the arid Southwest may be found in Lowe (1964), Shreve and Wiggins (1964), Benson and Darrow (1954), Hastings and Turner (in press), Munz and Keck (1949), and Jaeger (1957). Some of the basic problems encountered in relating present to past vegetation through fossil-pollen counts are exposed in papers by Potter and Rowley (1960), Hafsten (1961), Hevly *et al.* (in press), Dixon (1962), Martin (1963a), Maher (1963), and King (1964). The short, superior summary by Malde (1964) covers, from a geologist's viewpoint, recent developments in the study of Late Pleistocene environments since man's arrival in western North America.

THE DEVELOPMENT OF POLLEN ANALYSIS IN ARID AMERICA

Despite its limitations, the fossil-pollen record is an especially revealing technique in the study of Pleistocene biology, and much of our account will focus on recent developments in this field. In the Southwest the use of pollen analysis in paleoecology can be traced to Laudermilk
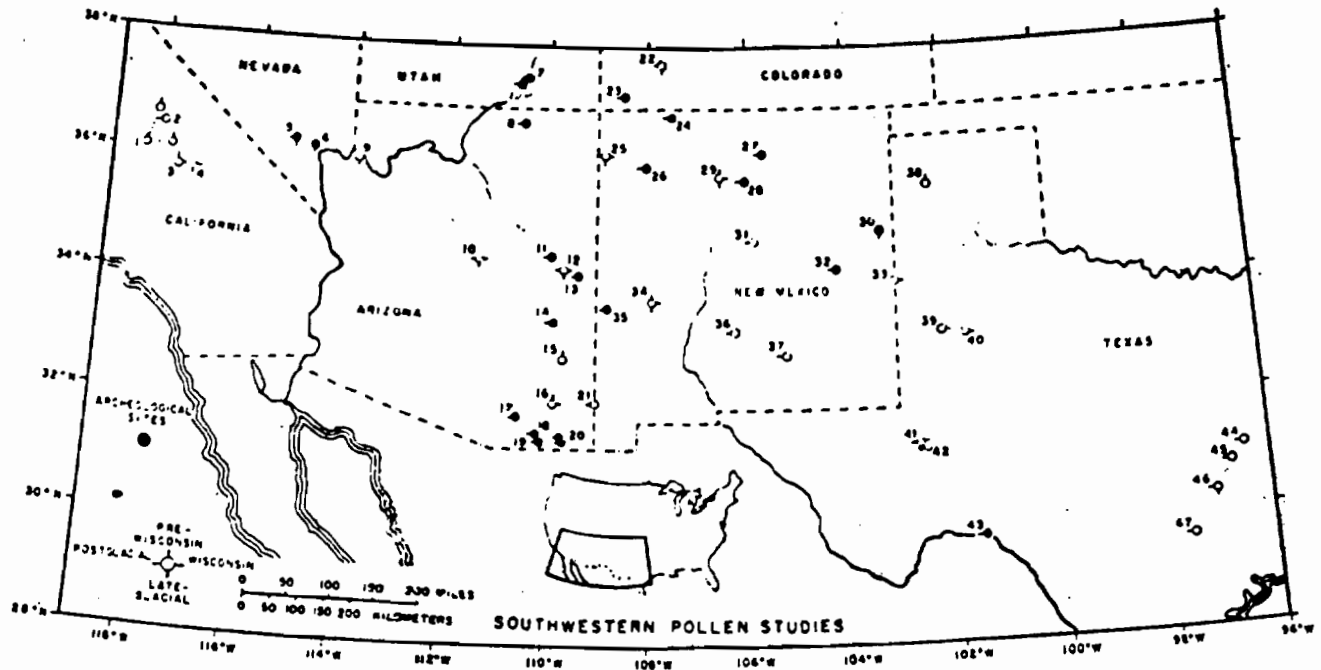
Figure 1. Pleistocene pollen-stratigraphic areas in the Southwest. Numbers refer to areas and bibliographic sources given in Table 1.

and Munz (1934), who illustrated various pollen grains in coprolite of the Shasta ground sloth. An early effort at postglacial pollen stratigraphy, made at the instigation of Ernst Antevs, was that of Sears (1937), who prepared a simple diagram of pollen in alluvial samples found near Kayenta in northern Arizona. The discovery that pollen occurs in sediments from dry lakes (playas) in the Southwest (Sears and Clisby, 1952; Clisby and Sears, 1956) revealed an extraordinarily rich source of fossil pollen in beds once considered largely devoid of organic remains (Tolman, 1909, p. 160). In cave earth Anderson (1955) encountered *Zea* among the pollen associated with archaeological materials. Pollen analysis of the present decade continues to be based on the study of alluvium, playa lake clays, cave earth (including coprolite), and fill of archaeological sites, plus some newly discovered sources such as the buried organic mats and wind-blown silt of spring mounds (Mehringer, in press), and the soil profile of mountain forests (King, 1964).

But each of these environments of deposition has its own effect on the pollen record, and climatic change is not the only major variable that can alter the pollen content of sediments. For example, Tertiary microfossils are a serious contaminant of Pleistocene alluvium in Wyoming (Rohrer and Leopold, 1963). Pollen of *Sarcobatus, Ephedra,* and other xerophytes is carried in dust storms from the desert into conifer-rimmed mountain lakes (Maher, 1963), while tree pollen, notably pine, accounts for as much as 40% of the pollen in certain desert soils. Although pollen is abundant in coprolite, it is greatly affected by phenology and feeding habits of the animal under study. Much remains to be learned about the fossil "pollen pool" and about its most effective use in arid-land paleoecology. Plant macrofossils are needed to supplement the pollen record. A promising

and recently discovered source is the content of desert pack-rat middens which may contain seeds, twigs, and bone cemented with urine and enduring largely intact for over 40,000 years (Wells and Jorgensen, 1964).

All but eight of the Pleistocene pollen stratigraphic records shown in Figure 1 are based on analyses published in the present decade or still in manuscript, making it impossible to develop perspective in our review, which seems destined by the rapid growth of the field for unplanned obsolescence. While the palynological literature of the Southwest is still small enough to summarize easily, the same may not be said for the biogeographic literature, which is voluminous. In the conviction that a major advance in Pleistocene studies of the Southwest over the past decade has been the growth of pollen analysis, we have chosen to stress this part of the fossil record. But there is much to expect from future studies of plant macrofossils, diatoms, mollusks, vertebrates, and other common Pleistocene fossils. The special insight of the taxonomist with a taste for biogeography continues to be worth close attention from all students of the Pleistocene.

DIVISIONS OF THE PLEISTOCENE

The Southwestern fossil-pollen record can be divided into three clearly marked periods: pre-Wisconsin (Sangamon and older), Wisconsin (12,000-70,000 before the present), and postglacial (12,000 years ago to date). Because of the formidable regional variation in climate, vegetation, and therefore in local pollen rain, a detailed Pleistocene chronology of the Southwest will require far more than the 50-odd diagrams reviewed by us at this time (Fig. 1). Certain major guidelines for future study are at hand, and the more obvious features of the Southwestern pollen record can be identified. For example, the dominant Pleistocene

pollen types to be expected in most sediments include the following groups: (1) cheno-ams (Chenopodiaceae plus *Amaranthus*), (2) Compositae (separable into *Artemisia*, short-spine, and long-spine types), (3) grasses, (4) wind-

pollinated trees, especially pine, followed by either spruce, oak, or juniper, depending on location and history of the deposit.

PRE-WISCONSIN PLEISTOCENE

In their pioneering study on the San Augustin Plains, Clisby and Sears (1956) perceived that a major change in pollen content clearly associated with continental glaciation could be found in that part of their core associated by radiocarbon dating with Wisconsin glaciation. The Wisconsin beds can be characterized by a maximum of pine and spruce pollen and are thought to reflect invasion of the arid San Augustin Plains by spruce and other boreal conifers.

The extraordinary feature of Clisby and Sears' record is not the fact that a spruce invasion occurred but that it happened only once. Evidence of a pre-Wisconsin descent of boreal forest into the part of San Augustin Plains now occupied by juniper grassland was not found in deeper parts of the San Augustin Plains core (Clisby et al., 1957; Clisby, written communication), sampled to a depth of over 300 m. Periodic changes in vegetation types that might be assigned to relatively cold versus relatively warm climates through four or more separate glacials are not obvious.

No other playas in the Southwest have been studied to so great a depth as the San Augustin Plains. From pluvial Lake Cochise in southern Arizona the upper 20 m of a 42-m core reveals Wisconsin-age pine parkland and woodland within a region currently dominated by desert grassland and mesquite. Below 20 m grass pollen dominates those strata that contain pollen (Martin, 1963c). Pine-dominated strata are absent, and the pre-Wisconsin pluvial environment shows none of the attributes of the Wisconsin-age beds.

Samples from pluvial Lake Bonneville in two separate drill cores supplied by A. J. Eardley of the University of Utah have been studied to a depth of 30 m; the pine-spruce curves are summarized in Figure 2. Radiocarbon dates of full-glacial age lie at or slightly above the zone in which pine pollen is found in greatest abundance. Presumably, the Wisconsin extends to a depth of 12 m. The zone between 12 and 16 m, in which pollen is not present, is thought to represent an interglacial. Beneath it fossil pollen again marks what should be a glacial, but the maximum in pine pollen (including some spruce) seen at the top of the Wendover core does not reappear.

A drill core from China Lake, California, contains sterile horizons to a depth of 6 m, where pollen of sedge and cattail is associated with a C^{14} date of $28,500 \pm 4,300$ (A-451) on carbonate of the fresh water mussel *Anodonta oregonensis* (P. E. Damon, written communication). Strata lacking pollen again appear between 12 and 16 m and may represent the same sterile zone found in Lake Bonneville. Unlike the record from most Southwestern playas, *Picea* (spruce) is very rare relative to fir in the China Lake core, and there is no reason to believe this boreal tree migrated south along the Sierra Nevada during the Wisconsin (see Adam, 1964, p. 15). Problems and possibilities in correlating playa-lake drill cores are shown in Figure 2.
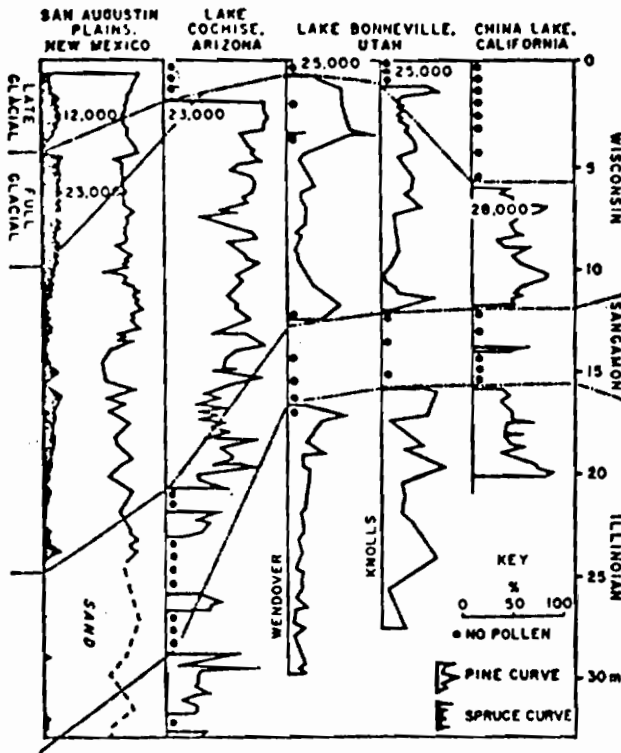
Figure 2. Provisional correlation of Pleisto-
cene drill cores from Southwest-
ern playa lakes. San Augustin
Plains record is that of Clisby and
Sears (1956) and Clisby (unpubl.);
other records are from Martin
(1963c; unpubl.).

Most Early Pleistocene and Tertiary lacustrine or alluvial outcrops in Arizona contain little pollen (Gray, 1960). An exception are three short drill-core samples from the Safford Basin in southeastern Arizona, considered to lie below late Blancan and Irvingtonian vertebrates at the 111 Ranch (Gray, 1961). The fossil counts contain more tree pollen (especially Cupressaceae, *Pinus,* and *Quercus*) and *Artemisia* than do modern pollen-rain samples from the region, thus suggesting a cooler or wetter climate and presumably Early Pleistocene pluvial conditions. A correlation with Nebraskan or pre-Nebraskan glaciation is possible. Of considerable biogeographic interest is pollen of *Ostrya* (24 records in about 4,000 determinations) and of *Ulmus* (5 records in 4,000 determinations).

Pollen analysis of a Blancan-age lake near Channing, Texas, by Harbour (Kirkland and Anderson, 1963) indicates over 50% *Artemisia* pollen, far more than is found in the region today and comparable to the high frequencies of *Artemisia* in the Rich Lake Interpluvial (Zone D of Hafsten, 1961). Further evidence of climatic change is seen in the fossil-leaf record, of which about half consists of *Quercus.* All the oaks are deciduous species presently found either east or west of the fossil locality. Other leaves include *Salix, Populus, Morus,* and *Ulmus,* thus establishing beyond doubt a more westerly occurrence of elm (*Ulmus*) in the Late Pliocene or Early Pleistocene.

Presently, the center of abundance for trees found in the Rita Blanca fossil beds is at least 400 km to the east in a much more mesic part of Texas. However, regions shedding high quantities of *Artemisia* pollen today lie to the west, and a mixing of central Texan with Northern Plains elements seems required by both fossil-pollen and leaf records.

An Early Pleistocene pollen record from California in the southern Sierra Nevada and adjacent Owens Valley is claimed by Axelrod and Ting (1961). If their conclusions are correct the deposits predate a 2,000-m uplift of the Sierra Nevada when species of trees not presently found in southern California extended southward along the Sierra. Their interpretation seems discordant with recent potassium-argon dates of Pliocene age for the surface under study (Dalrymple, 1963) and with the glacial chronology of the Sierra Nevada (Sharp and Birman, 1963, p. 1085). But it is possible that major tectonic activity occurred in the Pleistocene and that this will complicate geologic-climatic dating of certain beds.

While both the Safford, Arizona, and Rita Blanca, Texas, deposits contain evidence of cooler and moister conditions than characterize those areas today, they do not equal the dramatic change seen in the Wisconsin full-glacial. As the latter event occurred through only a relatively small part of the Wisconsin, perhaps no more than 6,000 years, it is possible that Early or Middle Pleistocene changes of comparable magnitude will eventually be found. Admittedly, the absence of a well-marked cold-wet Illinoian in the San Augustin Plains or in the shorter cores from Lake Cochise and the Great Salt Lake Desert does not match current climatic interpretations from other regions. For example, from their Savanna de Bogota core in Colombia, van der Hammen and Gonzalez (1960, p. 305) conclude that the next-to-last glacial, the Riss, was very cold with a greater displacement to vegetation zones than is seen in the Würm-Wisconsin. Such a record has yet to be found in the Southwest, making pre-Wisconsin climatic correlations very difficult.

THE WISCONSIN GLACIAL

If unequivocal climatic correlations between continental glaciation and Southwestern pollen stratigraphy cannot be demonstrated for the Early and Middle Pleistocene, correlations within the last glaciation are more promising and can be supported in some cases by radiocarbon dating.

According to Flint (1963) the last glacial began approximately 70,000 years ago, reached a maximum 20,000 years ago, and ended by 8000 B.C. An estimated age of 70,000 years appears reasonable for the Wisconsin portion of drill cores from San Augustin Plains, New Mexico (Clisby and Sears, 1956), Lake Cochise, Arizona (Martin, 1963c), Lake Bonneville, Utah, and China Lake (see Fig. 2) and Searles Lake, California. Despite major fluctuations in the ice margin, presumably accompanied by climatic changes that would be felt in arid regions, there was no warm interval during the last 70,000 years that could be considered as a true interglacial.

In the Texas High Plains the Rich Lake Interpluvial (22,000 to 32,000 years ago) was characterized by high pollen frequencies of grass and *Artemisia,* with small amounts of *Ephedra,* oak, and cheno-ams. According to Wendorf (1961, p. 130), the pollen and invertebrate data

indicate a climate slightly cooler and possibly more moist than today's. It is quite likely that this interval corresponds in age to the Clear Creek fauna near Dallas, Texas (Slaughter and Ritchie, 1963), carbon-dated at 29,000 years and showing an easterly movement of small mammals now found in central and west Texas, plus a southerly penetration of the bog lemming *Synaptomys*. A decline in pine pollen older than the full-glacial occurs at Tule Springs (Mehringer, in press). These events argue for an interstadial of relatively mild climate immediately preceding the full-glacial and corresponding to the Plum Point interstadial (Flint, 1963) and the Paudorf oscillation of the European Pleistocene.

Southwestern pollen profiles containing horizons that by radiocarbon dates or on other grounds can be assigned to the interval between 17,000 to 23,000 years ago are designated in Table 1 by an asterisk. Within the Mohave Desert at Searles Lake this was a time when woodland occupied a region presently dominated by creosote bush, white bur-sage, and various species of saltbush (Roosma, 1958). Within another part of the Mohave Desert at Tule Springs (Fig. 5a), Nevada, woodland or possibly yellow-pine parkland is represented in sediments of full-glacial age (Mehringer, in press). Radiocarbon dates show that juniper and other trees and shrubs were growing 600 m below their present lower limits near Frenchman Flat at various times from >40,000 to 7,500 years ago (Wells and Jorgensen, 1964). In the Great Basin the pollen record from Great Salt Lake indicates a maximum of pine and spruce, with very little *Artemisia* or other Great Basin desert shrubs, just below sediments dated as 20,000-24,000 years old. Within the Colorado Plateau, Bent (1960) and Bent and Wright (1963) record a subalpine woodland of spruce and *Artemisia* at Dead Man Lake in the Chuska Mountains, while Whiteside (1964) found a similar dominance of spruce and *Artemisia* in sediments from a small lake behind the Mogollon Rim of central Arizona. Both areas have been dominated by ponderosa pine through most of postglacial time.

In a drier area at lower elevation on the north side of the Mogollon Rim, Hevly (1962, 1964a, 1964b) found pollen of pine and spruce similar to the pine-spruce fossil record recorded by Clisby and Sears in the San Augustin Plains. Hevly's pine-spruce maximum lies stratigraphically beneath a radiocarbon date of $7,300 \pm 110$ years (A-256). Clisby and Sears' spruce maximum can be directly related to radiocarbon dates of $23,070 \pm 650$ years (Y-1053). Today both areas are dominated by juniper grassland.

At the bottom of shallow soil profiles, 10 cm or less in depth, in the Sandia Mountains of New Mexico, King (1964) found spruce pollen percentages equivalent to those in the modern pollen rain of the Sandias at higher elevations, in one case implying an 810-m vertical descent of spruce-fir forest. The Sandia profiles are undated; in the absence of an accompanying increase in *Artemisia* they differ from Wisconsin-age deposits in the Chuska Mountains and along the Mogollon Rim. In view of the abundant opportunity for post-depositional alteration of pollen percentages in a soil, it is hard to believe that they do not represent a mixture of pollen rains of different ages. Differential destruction could also account for the apparent increase in spruce with depth. But King's provocative discovery should encourage further interest in the meaning of pollen in the soil profile, and his detailed analysis of the modern pollen rain contained in moss polsters is an important contribution to that neglected subject.

South of the Colorado Plateau in the desert grassland, 20,000-year-old sediments from Lake Cochise, Arizona, are almost exclusively composed of pine pollen with very small amounts of spruce and grass (Martin, 1963c). In west Texas Hafsten records a similar maximum of pine and spruce at about the same time, with very few or no other pollen types represented during the Tahoka pluvial. One radiocarbon date of 17,000 years from Rich Lake indicates full-glacial age. Suspicion that the extremely high pine counts might represent a type of pinyon-juniper woodland (Jelinek, 1962) is not borne out by modern pollen-rain studies in the Sangre de Cristo (Dixon, 1962) and the San Juan Mountains (Maher, 1963). The pine-dominated Tahoka pluvial seems to contain too much spruce pollen and too little juniper to represent a pinyon-juniper woodland. Admittedly macrofossil evidence is badly needed.[2]

Hafsten's pine-spruce Pollen Zone C from the Texas High Plains may be reflected in Potzger and Tharp's (1947) diagram from Patschke Bog in east Texas. The bottom of their profile at 22 ft contains almost 50% pine pollen, with a few percent spruce, in an area in which the postglacial pollen record is dominated by grass and oak with an extremely low frequency of pine. Subsequent work in the east Texas bogs has failed to confirm the initial pine dominance (Potzger and Tharp, 1954; Graham and Heimsch, 1960), but the later studies may not have included sediments of equivalent age.

From what is known of the Southwestern pollen record, especially the localities listed in Table 2 or marked by an asterisk in Figure 1, we have projected a vegetation map for 20,000 years ago (compare Figs. 3 and 4). The result is clearly a first approximation. Furthermore, absolute reliance on radiocarbon dates as criteria for establishing full-glacial age can be hazardous in view of the apparent ages of 17,000 to 25,000 years on *living* aquatic plants in Montezuma Well, Arizona (Damon, Haynes, and Cole, 1964). Fortunately, the Montezuma Well anomaly is a special case related to unusual geochemical and topographic circumstances. For more detailed discussion of procedure, C^{14} dates, and an earlier version of the full-glacial vegetation map, see Martin (1964).

A major difficulty in constructing Figure 4 was the problem of the Sonoran Desert. The sediments from Ventana Cave, in the heart of the Sonoran Desert of southern Arizona, has been carbon-dated at the level of volcanic debris at $11,300 \pm 1,200$ years (Damon and Long, 1962, p. 240). Apart from the hazards involved when climatic inference is based on large Pleistocene vertebrates—to be discussed later—the date indicates that the associated

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[2] P. V. Wells has uncovered wood of pinyon, juniper, and *Berberis* of full-glacial age in pack-rat middens of the Big Bend region, Texas (UCLA 785, 18, 750 ± 360, see Radiocarbon, v. 7). The region today is part of the Chihuahuan Desert; it falls within the area mapped as pinyon-juniper woodland on Figure 4.

TABLE 2

Modern and Full-glacial (17,000-23,000 B.P.) Vegetation in Arizona, New Mexico, and West Texas
(NAP = non-arboreal pollen)

Present environment	Location and source	Elev. in m	Pollen rain in percent		Dominant vegetation	
			Modern	Full-glacial	Modern	Full-glacial
Cool montane conifers	1. Potato Lake, Ariz. (Whiteside, 1964)	2,340	Pine-65 Grass-20	Spruce-25 Pine-15 *Artemisia*-20	Ponderosa pine forest	Subalpine spruce-woodland
	2. Dead Man Lake, N.M. (Bent, 1960)	2,640	Pine-70 NAP-25 Spruce-tr.	Spruce-8 Pine-30 *Artemisia*-50	Ponderosa pine parkland	Subalpine spruce-woodland
Cool grassland	3. Laguna Salada, Ariz. (Hevly, 1962)	1,000	Pine-20 Juniper-25 NAP-50	Spruce-7 Pine-50 *Artemisia*-10	Juniper-grassland	Spruce-pine forest
	4. San Augustin Plains, N.M. (Clisby and Sears, 1956; Clisby *et al.*, 1962)	2,000	Pine-20 Cheno-ams-60 Composites-5	Pine-85 Spruce-13 Fir-1	Blue grama grassland-saltbush	Spruce-pine forest
Warm grassland	5. Pluvial Lake Cochise, Ariz. (Martin, 1963c)	1,260	Pine-20 NAP-70	Pine-98 Spruce-1	Mesquite-grassland	Pine parkland
	6. Rich Lake, Tex. (Hafsten, 1961)	1,100	Pine-15 NAP-85	Pine-90 Spruce-8	Short grass plains	Pine parkland (with spruce?)

fauna will not shed much light on what the Sonoran Desert was like at the height of continental glaciation. The claim for grassland in the area at the time appears based largely on the abundance of horse bones in both the conglomerate and volcanic debris (Colbert in Haury, 1950, p. 137). But the fossil-pollen content of a sample of volcanic debris

(Fig. 6) is similar in proportions to pollen counts of the soil surface of the Sonoran Desert near Tucson and is unlike pollen counts from the desert grassland of southeastern Arizona. Furthermore, the assumption that fossil horses are reliable indicators of grassland loses its validity if one considers the present range of thousands of burros
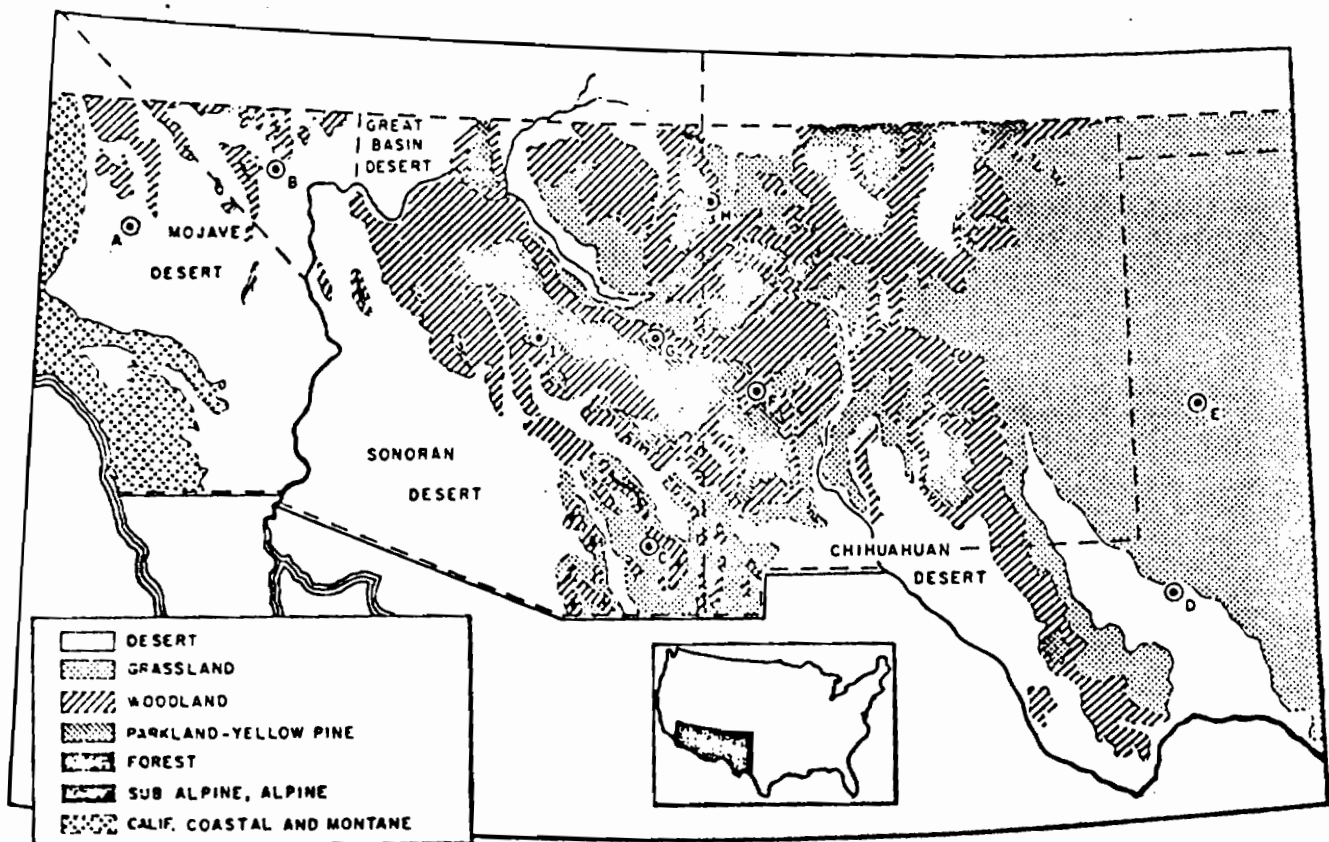

Figure 3. Modern vegetation of the Southwest, based on Shantz and Zon (1924).
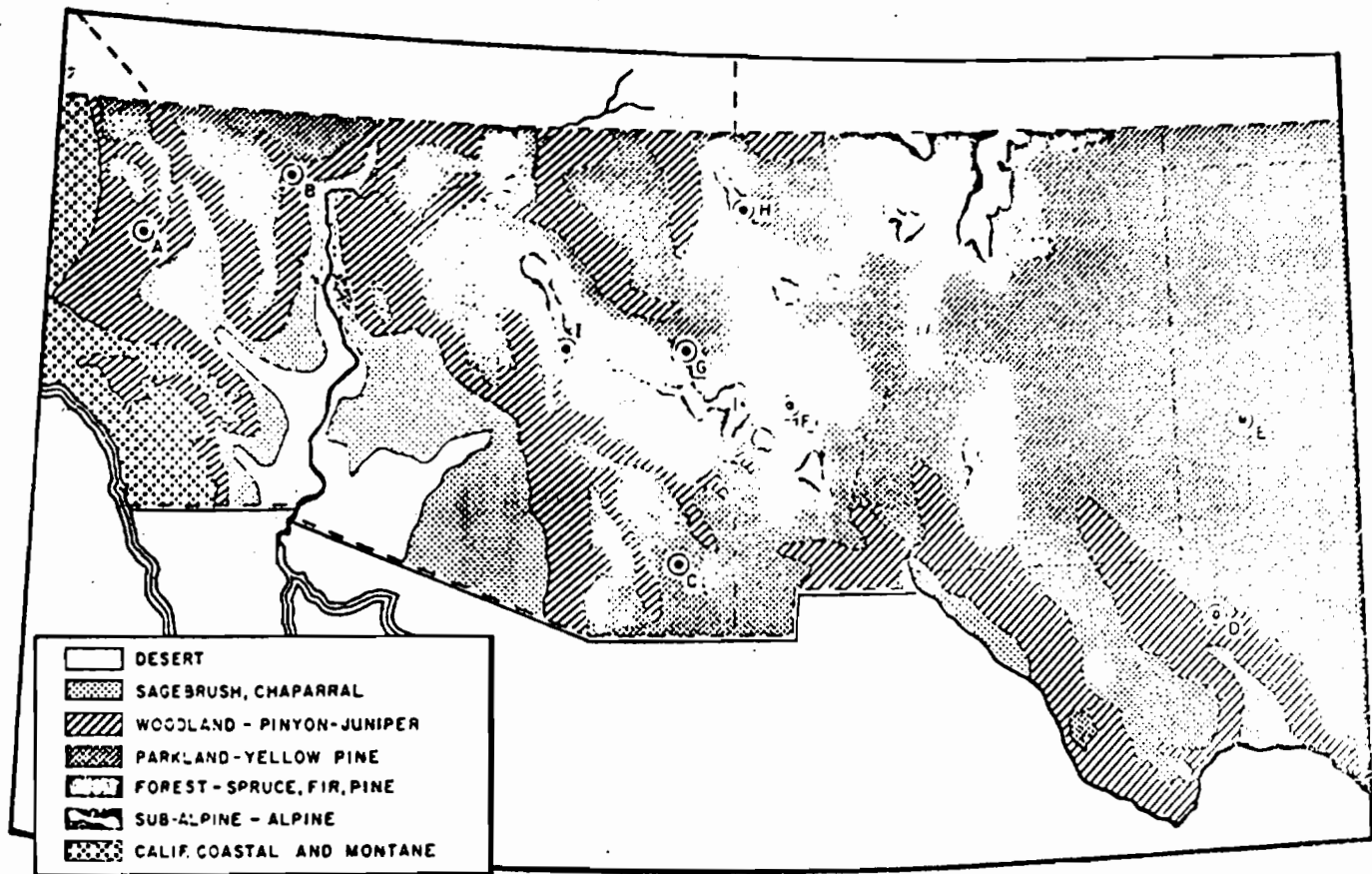
Figure 4. Full-glacial vegetation of the Southwest 17,000-23,000 years ago, based mainly on carbon-dated fossil-pollen spectra from (A) Searles Lake, (B) Tule Springs, (C) Pluvial Lake Cochise, (D) Crane Lake, (E) Rich Lake, (F) San Augustin Plains, (G) Laguna Salada, (H) Dead Man Lake, (I) Potato Lake. See Table 1 for bibliographic sources.

and horses living wild in the Mohave Desert, one of the least grassy parts of western North America.

Despite the fact that the Sonoran Desert was probably in its present position 11,000 years ago, it seems equally likely that it was displaced by earlier full-glacial climatic changes which caused pine parkland to invade the desert grassland and caused woodland to spread through the Great Basin and Mohave Deserts. The plant communities to be expected in the Sonoran Desert 20,000 years ago would be sagebrush and chaparral, with creosote bush persisting along the lower Colorado River. At the same time, applying the expected 900 to 1,200 m of vertical displacement to certain species of the Sonoran Desert creates a peculiar difficulty. Even if sea level were 100 m lower at the time, it appears that any major drop in vertical range would have submerged many desert plants in the waters of the Gulf of California.

This hypothetical fate would not be a hazard in the case of the emblem of the Sonoran Desert, the saguaro (*Cereus giganteus*), which exceeds 1,200 m in its present vertical range, but it would be in the case of those Mexican species that do not enjoy great vertical amplitude, as the cardon (*Cereus pringlei*), boojum (*Idria columnaris*), and the arboreal caper (*Forchammeria watsonii*). Backed against the arid tropics of Sinaloa, with the Sierra Madre Occidental

blocking retreat to the west and with Great Basin chaparral and sagebrush presumably invading from the north, Sonoran Desert plants may have been hard pressed. Hopefully, pollen studies around the Gulf of California begun by Auriel Cross and his students at Michigan State University will uncover the location of Sonoran Desert species 20,000 years ago.

THE POSTGLACIAL, 12,000 B.P. TO PRESENT

On the basis of the pollen-stratigraphic evidence we have chosen to place the beginning of the postglacial in the Southwest at about 12,000 years ago. Thus the early part of our postglacial would fall within late-glacial time of the eastern United States, which is climatically quite distinct from the postglacial of that area (Deevey and Flint, 1957). In the Southwest the last glacial-pluvial pollen records are C[14] dated between 13,000 and 12,000 B.P. There follows a rapid change to pollen spectra resembling more closely those of the rest of the postglacial than of the full-glacial. This rapid change seems to correspond in time to the Two Creeks ice recession of classical Wisconsin glaciation (Broecker and Farrand, 1963). Carbon-dated pollen evidence for a rapid vegetation change in the Southwest at the beginning of the postglacial (*i.e.* from glacial moist-cool
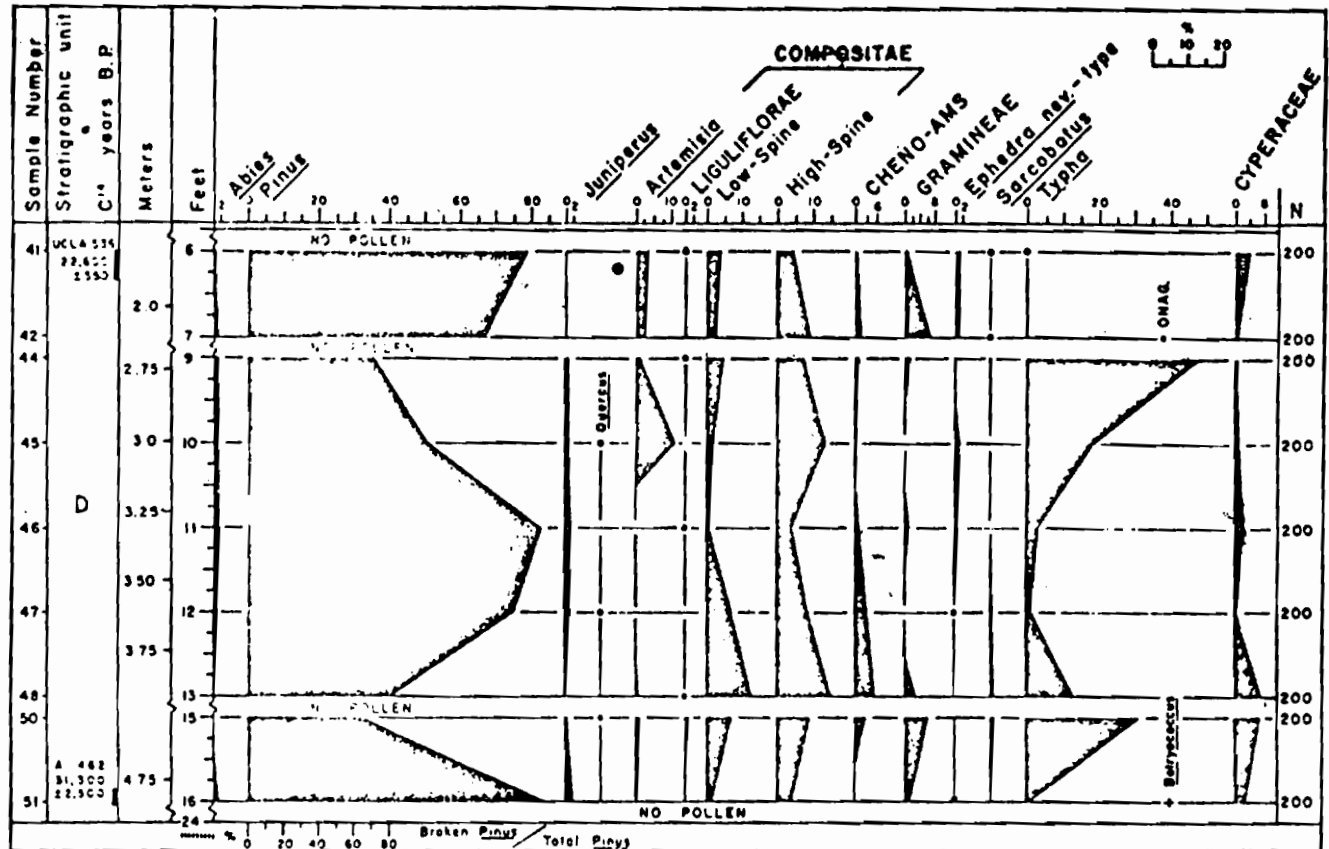
Figure 5a. Pollen diagram (pollen profile II) from Tule Springs, Nevada, showing a full-glacial record from lake beds. The changes in *Pinus* and *Typha* pollen are thought to be the result of fluctuating lake levels which may or may not be related to climatic change (for a discussion of the Tule Springs diagrams see Mehringer, in press).

conditions to postglacial drier-warmer conditions) is apparent in the pollen records from Tule Springs, Nevada (Fig. 5b; Mehringer, in press), Potato Lake, Arizona (Whiteside, 1964), San Augustin Plains, New Mexico (Clisby and Sears, 1956), and Crane Lake, Texas (Hafsten, 1961).

In southeastern Arizona, pollen spectra from the Naco, Ventana Cave, and Lehner Early Man sites (Fig. 6) show that by 11,000 years ago the vegetation was similar to today's (for a discussion of the carbon dating of these sites see Haynes, 1964). At the Lehner site the postglacial beds, dating from about 11,200 years ago, contain fossils of mollusks that are found there now. An older stratigraphic unit, separated from the postglacial beds by an erosion surface and C[14] dated at 11,600 ± 400 B.P. (A-47S, Damon, Haynes, and Long, 1964), contains fossils of snails which live today only in the higher mountains of southern Arizona (Mehringer and Haynes, in press).

While there is every reason to expect late-glacial oscillations of the type so familiar to pollen stratigraphers in temperate latitudes, some claims for their existence in the Southwest appear to be based as much on expectation as on evidence. And in view of the recent revision in the long-accepted correlation of the Two Creeks interstadial of the Great Lakes with the Alleröd of western Europe, based on careful stratigraphy and radiocarbon dating (Broecker and Farrand, 1963), the facile naming of an undated pine

fluctuation in the Southwest as correlative with some particular late-glacial fluctuation in Europe or eastern North America seems to us questionable. If worldwide changes are to be hypothesized, the Southwestern pollen record is in accord with the evidence of Broecker et al. (1960) for an abrupt change in climate close to 11,000 years ago.

The pollen record of the last 10,000 years shows intriguing but at most minor changes. In east Texas the organic material of spring seeps appears to be mainly of postglacial age. Graham and Heimsch (1960) found little change in fossil content of a 4.6-m profile. In high-altitude lakes of the southern Colorado Plateau the postglacial pollen record also seems relatively stable (Bent and Wright, 1963; Maher, 1961; Whiteside, 1964). A more variable postglacial record is that of Hevly (1964a), who recognizes five postglacial zones and develops the concept of "sensitive sites" as necessary in uncovering postglacial vegetation shifts of 150-300-m amplitude.

In the Texas High Plains, Hafsten divided his postglacial Pollen Zone A into four parts, based on minor fluctuations of cheno-ams, composites, and pine. Major fluctuations in the first two types characterized floodplains of southern Arizona, where Martin (1963a) proposed a four-part floodplain chronology with two composite and two cheno-am maxima. In the case of the Lehner site, counts made exclusive of cheno-ams and composites (Fig. 6) re-
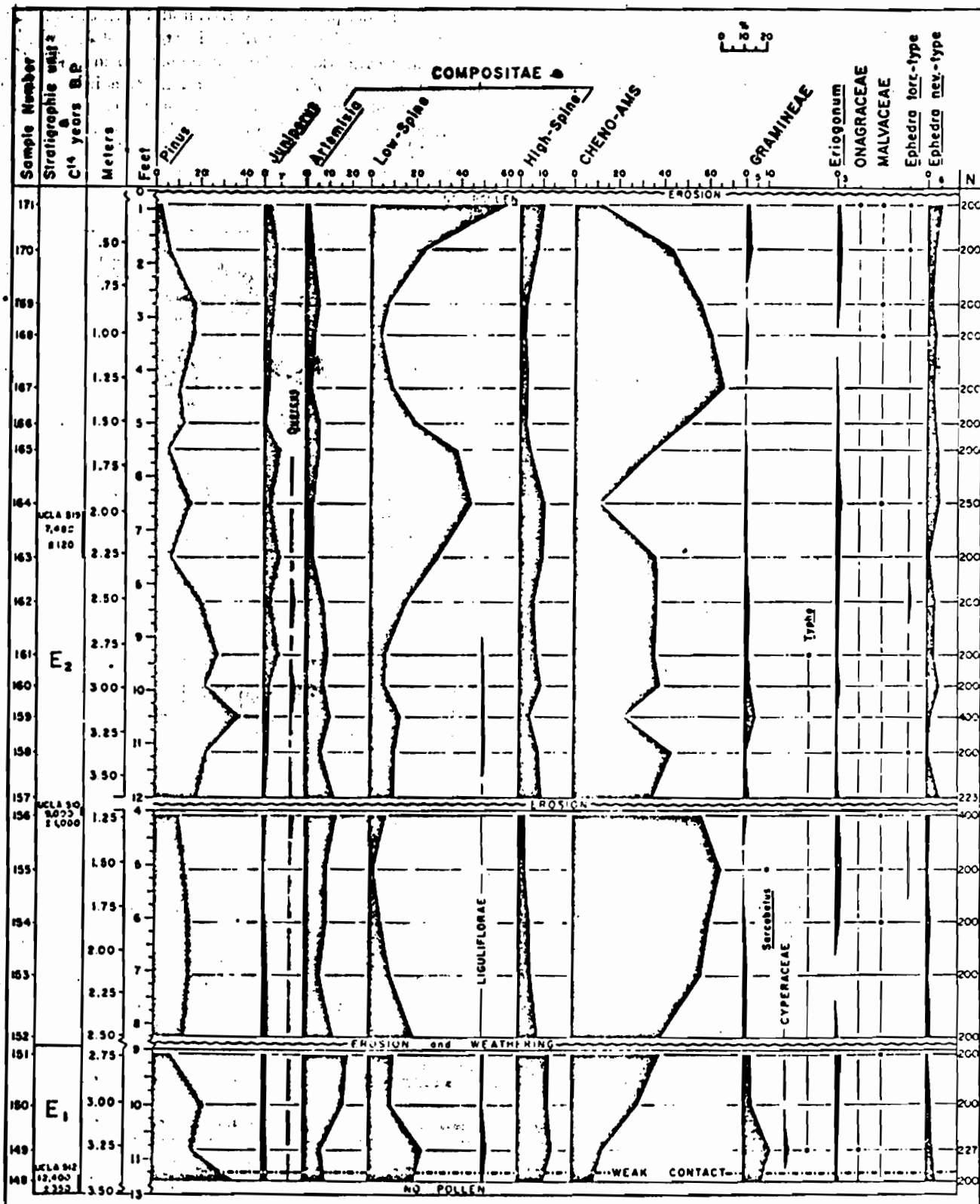
Figure 5b. Pollen diagram (pollen profile IV) from Tule Springs, Nevada, showing a postglacial, alluvial pollen record dominated by NAP. The upper two samples are placed between 6,000–7,000 B.P. on geologic evidence and show pollen spectra similar to the modern pollen rain in the Mohave Desert at the site. The lower samples approach the modern pollen rain of the Great Basin Desert environment.

culminating in a grass-dominated record showing little change. The changes in composite and cheno-am proportions that are conspicuous in most pollen records from the desert grasslands of Arizona are thought to represent local edaphic conditions accompanying erosion (cheno-am dominance) or alluviation (short-spine Compositae dominance) along floodplains (Martin, 1963d, p. 49).

Before the development of Southwestern pollen analysis

a climatic model proposed by Bryan and Antevs was widely adopted—a model that attributed arroyo cutting, calichification, and extinction of large mammals to mid-postglacial hot, dry climates. Evidence for a reduction in tree pollen and a maximum in grass and cheno-am pollen can be found in the mid-postglacial of Wyoming (Hansen, 1951), central Colorado (Pennak, 1963), southern Colorado (Maher, 1961), northern Nevada (Sears and Roosma, 1961), possibly
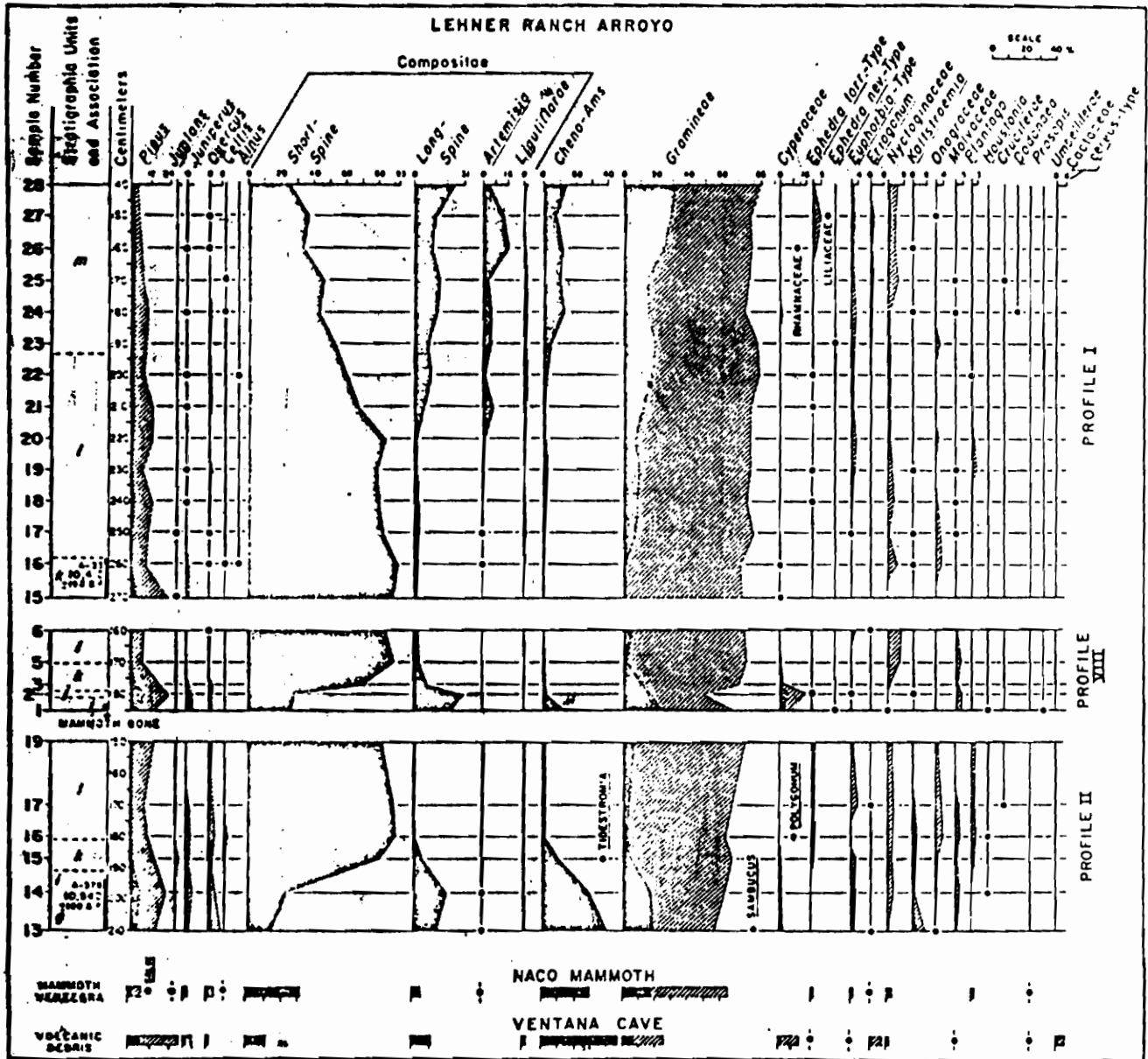
Figure 6. Pollen diagram from the Lehner Ranch Arroyo (Haury et al., 1959) and single samples from the volcanic debris layer of Ventana Cave (Haury, 1950) and from dirt adhering to a vertebra of a mammoth from the Naco Site (Haury et al., 1953).

The Lehner pollen diagram shows portions of three pollen profiles from pre-Altithermal-age beds (Antevs, 1959). The solid portion of the diagram represents the first count (200 grains), which includes all pollen types. The lined portion indicates the second pollen count (100 grains), excluding cheno-ams and composites. The dots (·) indicate less than 1% of a pollen type in the first count or less than 2% in the second count. Both counts are plotted to the same scale and are read from the zero percent line at the left (Mehringer and Haynes, in press).

southern Nevada (Mehringer, in press), and northern Arizona (Hevly, 1964a). How much "drought" is to be read into the records may be less important than establishing whether there was a shift in seasonality, with summer storminess partly compensating for a decrease in winter precipitation (see also Malde, 1964, p. 127).

Along the Mexican border the Antevs-Bryan climatic model of drought as a cause of arroyo cutting has not been substantiated by evidence of marked aridity in the mid-postglacial pollen record (Martin, 1963a). There it is possible that under the influence of the Mexican monsoon the Altithermal actually may have been a time of greater precipitation, at least in summer, rather than of drought. Carbon-dated pollen records falling within the Altithermal (4,000 to 7,500 years) are few, but three gleaned from a total of 13 carbon-dated pollen spectra of postglacial age show slightly higher numbers of either pine or grass pollen, with some ponding evidenced by hygric pollen types (Martin, 1963b). Near the Pecos River in Texas, Johnson (1963) also found a pine rise during the archaic and suggested wetter conditions during the "Altithermal" of that area.

Because of the nature of relative numbers an increase in pine pollen is by no means absolute proof of an increase in growth of pine trees, and under a circumstance in which local pollen production is reduced, conceivably as a result of unfavorable climatic conditions, there could be a *relative increase* in the amount of pine pollen received at the site of deposition. The interpretation of slight changes in pine-pollen frequencies in fossil-pollen records from the arid Southwest presents problems yet to be resolved. In areas of varying relief where coniferous forests are separated from deserts by a thousand or more meters in elevation but by only a few tens of kilometers in distance, a high percentage of wind-blown pine pollen may be found in the modern pollen content of desert soils (Mehringer, in press; Hevly *et al.*, in press). The relative frequency of pine pollen *increases* with the reduction in plant cover as one enters the desert (see Martin and Gray, 1962, Fig. 1). This is also true in areas remote from montane forest. For example, the soil surface of the Sonoran Desert at Yuma, in southwestern Arizona about 110 km from the nearest coniferous forest, contains a higher percentage of pine pollen than do soil surface samples of the desert grassland of southeastern Arizona, which is surrounded by mountains with coniferous forests.

Thus an increase in pine-pollen percentages in an alluvial pollen record from the desert grassland (Martin, 1963a) might mean either an expansion of local forests and more moist conditions, as Martin supposed, or a reduction in local plant cover, the result of drought. Whatever later discoveries may reveal, there is yet no clear evidence from the floodplain pollen record that suggests "deserts on the march" or an Altithermal climate in southern Arizona and New Mexico that was appreciably hotter and drier than today's.

Many pollen studies in the Southwest can be associated with archaeological excavations (see Fig. 1). Pollen occurs in trash mounds, in subterranean ceremonial rooms (kivas), in buried floors of Pueblo rooms or pithouses, and in cave earth. Alluvium contains a pollen record less easily related to man's activities, but some alluvial sites contain corn (*Zea*) pollen, verifying its presence in the Southwest 2,000 or more years ago (Martin and Schoenwetter, 1960) and suggesting its cultivation behind stone walls constructed as check-dams (Byers and Martin, in press). Pollen of *Cucurbita*, both *pepo* and *moschata-mixta* types, commonly appears in prehistoric sites and human feces, while pollen of beans (*Phaseolus*) and cotton (*Gossypium*) is seldom found. Other pollen types found in abundance only around archaeological sites and thus considered of economic significance—although the plants themselves may not have been cultivated by prehistoric man—include Rocky Mountain beeweed (*Cleome*), cactus (especially *Opuntia*), *Agave*, and Liliaceae. Prehistoric human feces are highly variable in pollen content; they may contain large numbers of pollen grains of most of the foregoing types (Martin and Sharrock, 1964), and may on occasion be dominated by single species used for food only seasonally, such as *Populus*, short-spine Compositae (cf. *Dicoria*), and a large-sized grass pollen.

The pollen content of the sediments of certain archaeological sites may show an increase in pine in the 11th and 13-14th centuries that Schoenwetter (1962) and Hevly (1964a) believe can be associated with climatic changes. If it can be established that these changes are independent of cultural disturbance, or of changes in the non-pine pollen sum (Leopold *et al.*, 1963), it will be possible to interpret cultural history more directly in terms of climate than has been possible previously. Perhaps the best evidence of late prehistoric climatic fluctuation is still that found in the tree-ring record, plus the very fact of Pueblo abandonment.

In summary, the Southwestern pollen record of the Pleistocene indicates (1) difficulties in correlating with continental glaciation of the Early and Middle Pleistocene; (2) direct correlation with Wisconsin glaciation, starting perhaps 70,000 years ago, with biotic zones descending 900-1,200 m; (3) a rapid rather than gradual recovery of postglacial vegetation about 12,000 B.P., and (4) intriguing but relatively minor changes in pollen proportions, suggesting 150-400 m of vertical displacement in vegetation zones over the last 12,000 years. These minor changes in postglacial pollen profiles can be associated with arroyo cutting, Pueblo abandonment, and other significant climatic and cultural events.

PLEISTOCENE BIOGEOGRAPHY

The biogeographic storm long raging in eastern United States regarding the degree to which biotic communities were affected by glaciation can be traced into the Southwest, where the nature of Pleistocene climates has also been a matter of perennial interest, considerable difference in opinion, and some contention (compare Merriam, 1890, p. 20-21; Epling, 1944; Deevey, 1949, p. 1394-1400; McVaugh, 1951; Antevs, 1951; Dillon, 1956; Croizat, 1958, p. 42; Norris, 1958, p. 305; Darrow, 1961, p. 37-41; and Howden, 1963). Among the first to consider the effect of the Pleistocene on plant distribution in the west was John Muir (1877), who observed that groves of the giant sequoias occupy unglaciated areas in California between glaciated valleys such as King's River, Tuolumne, and the Merced. Muir concluded that sequoias were not distributed more extensively in the Sierra Nevada in postglacial time.

Recent summaries of Tertiary paleobotany (Axelrod, 1950, 1958; Darrow, 1961; MacGinitie, 1958) present evidence for arid climates from the Miocene to the Late Pliocene, the time when Axelrod assumes the desert vegetation had achieved approximately its present composition. Doubts about such a recent evolution of the desert have arisen in the minds of those biogeographers studying the strikingly diverse, endemic Mexican xerophytes (Rzedowski, 1962), but no serious challenge to Axelrod's thesis of deserts in the Pliocene has appeared. Pollen types associated with arid-land plant communities can be traced to the late Miocene (Martin and Gray, 1962).

Regarding the migrations that led to the development of the present biotic communities in the Southwest it is clear that the late-Tertiary record shows a contraction of humid forest (the "Arcto-Tertiary Geoflora") and the expansion of more xeric communities ("Madro-Tertiary Geoflora") moving north from Mexico. But in historical reconstruction it is logically necessary to place *last* things first, i.e. to see if present patterns of distribution can be satisfactorily explained in terms of the most recent climatic events before turning to the effect of older changes. Belief that the present biota of the Southwest attained, and has retained, its present geographic distribution since the end of the Pliocene was based on certain biogeographic inference now largely invalidated by the Pleistocene fossil record.

To be more specific, the fossil pollen record of Wisconsin-age pine parkland with spruce south of the Colorado Plateau means sufficient downward displacement of plant communities to allow several invasions of "Arcto-Tertiary Geofloras" into the desert mountains during the Pleistocene. For example, the extraordinary occurrence of lungless salamanders (*Aneides hardyi*) in the Sacramento Mountains, New Mexico, has been interpreted as the result of late-Tertiary expansion of their favored habitat—mixed conifer forest with Douglas fir (*Pseudotsuga*)—spreading southward through the Rockies from the Pacific Northwest where relatives of these salamanders live now (Lowe, 1950). On paleobotanical grounds Lowe severed the connection in the Pliocene. The Pleistocene fossil record by no means disproves Lowe's interpretation, but, as Murray (1957) pointed out, dispersal of *Aneides* through the Rocky Mountains likely occurred several times since the Tertiary, and it is certainly conceivable that final isolation of *Aneides* in the Sacramento Mountains did not occur until the beginning of the postglacial.

OAKS, WHIP-TAILED LIZARDS, AND CREOSOTE BUSH

Some uncertainty lingers regarding Tertiary versus Pleistocene contacts in widely separated species pairs not closely related, such as the frogs *Rana boylei* and *R. tarahumare* (Zweifel, 1955) and the fringe-toed lizards *Uma exul* and *U. scoparia* (Norris, 1958). But in the case of closely related species most taxonomists have come to view the last stage of interconnection between disjunct populations as probably Late Pleistocene, or even postglacial. In the case of the evening primrose *Clarkia rhomboidea*, Mosquin (1964) postulates a more or less continuous Wisconsin-age distribution through the Great Basin, a region it encircles but largely avoids at present. Double Pleistocene invasions ending in

sympathy in southern California is the case in paired species within the salamander genera *Ensatina* and *Batrachoseps*, frogs of the genus *Rana*, and lizards of the genus *Eumeces* (see Peabody and Savage, 1958, p. 182). The lizard *Uma* most likely found that the Mohave and Great Basin Deserts were uninhabitable during glacial time. Its present range is thought to represent the outcome of a postglacial invasion (Norris, 1958). Findley and Jones (1962) believe that during the Wisconsin pluvial the long-tailed and montane voles (*Microtus longicaudus* and *M. montanus*) were widespread. During postglacial times they found their preferred habitats—cool, mesic grass-sedge meadows and woods' edges near coniferous forest—in the highest and wettest mountains of Arizona and New Mexico. Invasion from the north at a time when the climate was cool and dry can be documented by the fossil record of the sage vole (*Lagurus*) and other mammals in Isleta caves of New Mexico (Harris and Findley, 1964). As a final case among many, hybridization between the whip-tailed lizards, *Cnemidophorus tigris gracilis* and *C. t. marmoratus*, almost surely represents postglacial contact along the Arizona–New Mexico boundary. The two populations were widely separated during the full-glacial. It is possible that the hybrids developed only since the arroyo cutting, overgrazing, and climatic change of the last 70 to 80 years (Zweifel, 1962).

A group recently receiving careful biogeographic and ecologic attention is the western oaks (*Quercus*), represented by 14 species in Arizona and 16 in California. In a determined effort at resolving some of the taxonomic chaos Tucker (1961, 1963) has been studying various populations included within the *undulata* complex. The main contributor is *Quercus gambelii*, the most mesic of the Arizona–New Mexico oaks and one of relatively few deciduous species in the Southwest. It hybridizes occasionally with *Quercus arizonica*. Because of the dependence of *Quercus arizonica* on summer rains, it is likely that it and *gambelii* were not in contact in the Southwest during the Late Pleistocene and that the small number of hybrids known at present are strictly a postglacial development. In the case of the more numerous hybrids between *Quercus turbinella* (scrub oak) and *Q. gambelii* there is a remarkable extension of hybrid populations north to the Wasatch Range of Utah, where *turbinella* itself is absent (Cottam et al., 1959; Tucker et al., 1961).

A similar pattern among shrubs of the Rosaceae is reported by Stutz and Thomas (1964). Intergeneric hybrids of *Cowania* (cliff rose) and *Purshia* occur north of the region where the parent populations are sympatric. *Cowania*-like characters can be found in *Purshia* 300 km north of its present limit. In the case of both the scrub oak and the cliff rose it is possible that the missing parent recently ranged much farther north, perhaps in the Altithermal. On the other hand, Stutz and Thomas suggest that natural selection alone might allow *Cowania* genes to move northward by stepwise backcrossing. Whatever the explanation for the origin of the hybrids, it appears that their pattern of distribution is no older than the postglacial.

Admittedly, in the absence of direct fossil evidence the conclusion that Southwestern plants and animals were on the move during the Wisconsin and earlier in the Pleistocene

tells us nothing about species age. Leaves of both *Quercus gambelii* and its near relative *Q. margaretta* contributed to the rich Early Pleistocene fossil record of Rita Blanca Lake in west Texas, presently an oakless region (Kirkland and Anderson, 1963). In the case of *Quercus ajohensis*, a species almost surely left as a postglacial relict after Wisconsin pluvial invasion of chaparral into the Sonoran Desert, fossil leaves show that its ancestors lived at much higher latitudes in central Washington in the Lower Pliocene (Tucker and Muller, 1956).

Finally, although it seems to us that the Pleistocene and in particular the full-glacial and postglacial climates of the last 20,000 years will account for a great deal of what one sees in the present distribution patterns of plants and animals throughout the Southwest, certain paradoxes in distribution as yet defy satisfactory explanation. An inescapable example is the fact that the most abundant of Southwestern desert shrubs, the creosote bush (*Larrea tridentata*), as well as *Koeberlinia spinosa*, *Celtis tala*, and other distinctive aridland plants of the Southwest, also occurs in the deserts of South America (see Johnston, 1940; Axelrod, 1950; Garcia *et al.*, 1960). The zoologist may find some comfort and a valuable clue in the fact that only xeric plants display this challenging gap in their ranges. "Of the hundreds of species of insects associated with *Larrea* in the two hemispheres, not one is shown to have a range similar to that of *Larrea*" (Raven, 1963, p. 165). It is unlikely that the amphitropical relationships in American desert floras entail Late Pleistocene dispersal.

PLANTS AND ANIMALS IN PREHISTORIC REFUSE

We have emphasized that there is little evidence of major climatic change in the postglacial pollen record of the Southwest. Regarding the non-cultivated-plant record from the oldest occupied prehistoric caves of the Southwest, 70 species identified from Danger Cave, Utah (Jennings, 1957, p. 228), 15 species from Ventana Cave, Arizona (Haury, 1950, p. 163-169), and 44 species from Bat Cave, New Mexico (Smith, 1950), all are to be found today within a day's walking distance of the ancient middens. In the case of vertebrates the pattern is similar. From beds lying above the 11,000-year-old volcanic debris in Ventana Cave, Allen (in Haury, 1950, p. 151) examined over 300 pounds of selected mammal bones. Of the species present, only the prairie dog (*Cynomys*) might not have lived near the cave in prehistoric times. Among 13 species of birds, Howard (in Haury, 1950, p. 152) found nothing more extraordinary than brown pelican, possibly brought from the Gulf of California. Beyond some suggestion of a size increase in *Neotoma albigula* and *Peromyscus maniculatus*, 7,300 identified bones from Wupatki, Arizona, revealed little change between the fauna of 800 years ago and that of the present, (Lincoln, 1962). Over 3,000 identified bones from prehistoric sites at Point of Pines, Arizona, were mainly deer and antelope (Stein, 1963), as were bones from the Awatovi site, Arizona (Lawrence, 1951). In each case, all the ecologically sensitive small mammals could have come from the immediate vicinity, and no range changes were noted. Minor exceptions are the Pueblo-age middens in northern New Mexico

that Harris (1963) believes show range changes of less than 20 km among the cottontails and long-tailed vole.

In reviewing the results of analysis of bird bones from a number of Indian middens, mainly of postglacial age, Miller (1963) reported only one extinct species, the vulture *Coragyps occidentalis*, and one major range extension, that of the California condor. The ichthyologist may fare better with archaeofaunal material. Miller (1955) reported the recently described hump-backed chub *Gila cypha* from Catclaw Cave along the Colorado River, and Gehlbach and Miller (1961) found *Lepisosteus* and *Cycleptus* in northern New Mexico, in each case from stream reaches where these species are unrecorded within historic times.

A record of biological conservatism appears the main conclusion to be drawn from the postglacial middens examined. Altithermal drought, if it occurred, left no obvious macrofossil evidence. Somewhat drier conditions after the Los Pinos–Sambrito phases of the Pueblo Period (A.D. 1-700) are suggested in northern New Mexico (Harris, 1963). But if the middens are generally undistinguished for the vertebrates they contain, they are intriguing for what they do not. No trace of the large extinct Pleistocene mammals and tortoises has been reliably reported from Southwestern prehistoric sites of the last 6,000 years and none was found in Danger Cave, carbon-dated at over 10,000 B.P. (Jennings, 1957, p. 93).

THE ECOLOGY OF LATE PLEISTOCENE EXTINCTION

The use of radiocarbon dating has established that the distinctive large mammals of the Pleistocene in North America, such as native horses, camels, sloths, elephants, glyptodonts, certain species of peccary, antelope, and bison, disappeared together over 8,000 years ago. In dry caves of the arid Southwest, soft parts such as hair and hide of extinct sloths (*Nothrotherium*) may endure at least 10,000 years (Simons and Alexander, 1964), while sloth dung of similar vintage from Rampart Cave, Arizona, still smells like barnyard manure. In New Mexico unusual polished rocks, evidently opalized by silica from the backs of large mammals that rubbed against them in prehistoric time, are found at the foot of desert mountains (Lang, 1947).

The effect on desert shrubs of large herds of mammals with highly varied forage adaptations is a subject seldom explored in the paleobotanical literature. Although he overlooked the Pleistocene fauna, Ellison (1960, p. 65) felt that ". . . the fact that, under the apparent handicap of millennia of grazing, most of the dominant species of the world's herblands are palatable plants, not only to buffalo and elk but to domestic livestock, is very impressive indeed." Ellison suggested an ecosystem in which plants would benefit by grazing, the implication being that through simple chemical adaptations all native range plants could readily evolve poisonous properties like the famous locoweed (*Astragalus nothoxys* and related species) and theoretically might achieve a high degree of protection against large herbivores.

In the Southwestern deserts the large number of either thorny or resinous shrubs rich in terpenes and other aromatic oils suggests a long history of plant-animal adaptation in which effective defenses against unlimited over-browsing

were evolved. While only about 5.5% of the browse plants in national forest ranges possess very considerable forage value to existing animals (Dayton, 1931, p. 3), it is also noteworthy that only about 3.2% are known to be poisonous. The fact that range shrubs typically evolved repellant rather than lethal mechanisms to prevent over-browsing would seem to support Ellison's inference that some benefit was derived by being consumed. Whatever the nature of the equilibrium evolved during the Late Cenozoic between plants and large herbivores, it was suddenly upset early in postglacial time with the extinction of a majority of the native large mammals of the Southwest, and upset again after about 8,000 years by the introduction of range cattle, horses and burros, and sheep and goats. Why the large native mammals disappeared when they did remains one of the major unsolved problems in the study of the Pleistocene.

In a review of Pleistocene biography, Martin (1958) concluded that the Late Pleistocene environment must have had some unique attributes to account for the unique ecological pattern of Late Pleistocene extinction. Only large or relatively large herbivores plus their associated predators, scavengers, and parasites are involved. In the Southwest, extinction of a dozen native genera occurred within about 2,000 years, soon after man arrived in the New World, at a time when the climate and ecology of the region was much like it is at present. Native plants, invertebrates, aquatic vertebrates, small terrestrial vertebrates (except associated species such as cowbirds and vampire bats), were unaffected (Martin, 1958). None of these observations is new, and the suggestion that man's arrival in the New World triggered big-game extinction has been previously made by certain paleontologists without capturing the endorsement of very many archaeologists. One reason is that some rather large problems remain to be solved, or at least explained away, such as the minimum number of hunters and the rate of predation necessary to lead to the extinction of any single species, the fact that rather few associations of man with certain mammals such as mastodon are known, and the fact that big game endured in Africa largely intact despite man's long history of evolution on that continent.

Current studies on the Pleistocene of the Southwest have added to but not basically changed our knowledge of the extinction pattern. Holman (1962) notes that herpetological evidence consistently indicates that fewer amphibians and reptiles became extinct during the Pleistocene than birds and mammals. The relatively large extinct element among birds can be attributed partly to a reduction of scavengers such as *Teratornis* and to extinction of flightless species such as *Chendytes* of the California coast. Hester (1960) thoroughly reviewed the carbon-dated records of all species of extinct mammals, detailing the evidence that most of them disappeared suddenly between about 11,000 and 8,000 years ago.

Confining his analysis to carefully excavated, carbon-dated archaeological sites, Haynes (1964) shows that mammoth extinction evidently occurred in the Rocky Mountains and High Plains about 11,000 years ago, somewhat earlier than Martin (1958) and Hester (1960) in-

dicated and soon after the deglaciation of a mid-Canadian corridor, which Haynes believes was the entry route of Early Man. Folsom bison hunters, who replaced Clovis mammoth hunters 10,500 years ago, were limited to the western plains, while pre-Folsom big-game hunters enjoyed a relatively homogeneous culture and ranged from coast to coast (Mason, 1962). Other cultural attributes are less easy to infer from the record of the artifacts, but Wendorf and Hester (1962, p. 168) note that the butchering techniques of the Paleo-hunters were cruder than those of historic and prehistoric hunters in the Plains, who utilized *Bison bison* more thoroughly. Woodbury (1963, p. 57) infers a considerable degree of cooperative effort among the hunters, with hunting concentrated at waterholes and streams.

Crucial to the claim that climate had little to do with extinction is evidence that Pleistocene herbivores occupied major plant communities such as are found in the Southwest today. The pollen record associated with extinct mammals at Tule Springs (Mehringer, in press) and at the Lehner site, Naco, and Ventana Cave (Fig. 6) points to such a conclusion. In the case of the Shasta ground sloth *Nothrotherium*, the paleobotanical evidence is decisive. Both pollen and macroscopic plant material found in its dung show that 10,000 to 11,000 years ago at Rampart Cave, Arizona, in Gypsum Cave, Nevada, and at Aden Crater, New Mexico, sloths were browsing on many of the desert shrubs dominant in the Southwest at present (Martin *et al.*, 1961; Aden Crater sloth date in Simons and Alexander, 1964).

A more ambiguous case is that of the large tortoises (*Geochelone* and large extinct species of *Gopherus*); extinction apparently occurred before disappearance of the elephants, horses, and sloths. In reviews of tortoise paleoecology, Hibbard (1960) and Brattstrom (1961) conclude that intolerance of freezing temperatures and inability to burrow led to tortoise extinction at the end of the Sangamon, a time when Hibbard (1960) believes the climate became especially severe. *Geochelone* (formerly included with the Old World genus *Testudo*) survived only in South America, including the Galapagos Islands. If the full-glacial is considered, Hibbard's unconventional paleoclimatic interpretation that the Wisconsin was more extreme than earlier glacials is entirely in accord with the Southwestern Pleistocene pollen record. His suggestion that large tortoises can be used as indicators of frostless climates has been widely adopted, for example by Slaughter *et al.* (1962), Wood (1962), and Holman (1962).

Yet the case of the large tortoises provokes some unsettling questions. If freezing temperatures are crucial in large-tortoise extinction, must we assume that no frost-free habitats were available in Mexico, Central America, and the West Indies to harbor tortoises during the height of Wisconsin glaciation? And is *Geochelone* unknown in the Southwest in the Wisconsin? The Clear Creek local fauna contains *Geochelone* of moderate size (Holman, 1963). While Slaughter and Ritchie (1963) correlate the Clear Creek faunas with the Sangamon, they report a radiocarbon date of $28,840 \pm 4,740$ B.P. on shells in the Clear Creek deposits, much too young to be Sangamon as

commonly understood by most Pleistocene geologists. Auffenberg (1962) alludes to other Wisconsin records of *Geochelone*, and Hibbard and Taylor (1960) mention small *Geochelone* from Friesenheim Cave, Texas, a Late Pleistocene (Wisconsin) fauna. Slaughter (manuscript) lists this species (*Geochelone wilsoni*) from late-glacial faunas at Blackwater Draw and Domebo, Oklahoma. While there seems little doubt that *G. wilsoni* disappeared along with the large mammals at the end of the Wisconsin, the extinction of the larger tortoises may have occurred earlier.

Finally, is the claim of *Geochelone* and large *Terrapene* in association with prehistoric hearths at the Lewisville site (Crook and Harris, 1957, 1962) without substance? Admittedly, the radiocarbon dates at Lewisville of over 37,000 years are hard to square with lack of sturdy documentation for man in the New World elsewhere at this time. And most students of prehistory find the report of a Clovis point associated with the Lewisville artifacts too much of a good thing. Perhaps the controversy raging over the Lewisville site will spur efforts to establish—or discount—the provocative interpretations of Crook and Harris.

In brief, the stratigraphic evidence from both caves and alluvial deposits in Texas establishes large-tortoise extinction *after* the end of the Sangamon 70,000 years ago. Whether the event is related to the first arrival of man in the New World, to unusual thermal stress during the Wisconsin full-glacial, or to other yet unidentified causes will require refined geochronological and paleoecological evidence. Hopefully, paleontologists excavating Pleistocene tortoises will not overlook the possibility that dirt adhering to the bones may contain crucial pollen evidence regarding vegetation and climate of the time.

Similar evidence obtained from pollen in matrix containing mammoth, tapir, and sloth bones shows that some highly unwarranted assumptions have been made regarding their paleoclimatic meaning. Despite claims to the contrary, their extinction cannot be laid to drought (Martin, 1963a, p. 64-65). Some conservative ecological assumptions may be reasonable—a shift from browsing mastodon to grazing mammoth appears to accompany desiccation of the Monahans Dunes area (Green, 1961, p. 44), and the fossil record at the foot of the Rocky Mountains suggests the presence of camels on upland ranges while mammoth were grazing the floodplains (Hunt, 1954, p. 119). Different species of large herbivores undoubtedly occupied different ecological niches on the prehistoric range. But in view of the failure to explain satisfactorily large-mammal extinction as a function of climatic change, similar theories applied to the extinction of large tortoises must be viewed with suspicion. Archaeological sites show that extinction closely followed man's arrival in the New World. While the case is by no means closed, this circumstance, in our view, best accounts for the Late Pleistocene "age of overkill."

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Summary

Pleistocene pollen analysis in the American Southwest was first attempted in the 1930's. Rapid growth of the field in the present decade has exposed important and occasionally provocative evidence regarding climates of the Pleistocene in arid America. While much remains to be learned about the limitations of pollen analysis, the presence of abundant fossil pollen and spores in a variety of sediments, including playa lake mud, alluvium, cave earth, archaeological trash, and prehistoric coprolite, ensures increasing use of the method in future paleoecological investigation.

From the pollen content of drill cores it appears that prior to Wisconsin glaciation climatic changes corresponding to the advance and retreat of continental glaciers are not easily recognized. Present difficulties may be overcome as our knowledge grows, but the pollen-stratigraphic record of the longest and most thoroughly studied drill core examined to date, that of Clisby and Sears from the San Augustin Plains, is not easily correlated climatically with multiple glaciation.

The difficulties with climatic correlation do not extend into the Wisconsin, where there is a carbon-dated maximum in biotic-zone depression of 900-1,200 m about 20,000 years ago that corresponds to the maximum in Wisconsin ice advance recognized in the eastern United States. Furthermore, the Rich Lake Interpluvial in the Llano Estacado of Texas appears to correspond with the Plum Point Interstadial of the eastern United States. Earlier stadial-interstadial climatic fluctuations can be recognized in the pollen record of Wisconsin-age drill cores. The carbon-dated full-glacial pollen records suggest a vegetation pattern considerably altered from that of the present and one that must have imposed many changes in plant and animal distributions.

A change to warm-dry postglacial climates appears to have occurred rather rapidly around 12,000 B.P. Except perhaps in the High Plains of Texas, the shift from full-glacial to postglacial climates is not clearly marked by late-glacial fluctuations, and no Valders or Younger-Dryas-age return of pluvial climates is evident. Postglacial alluvium of the desert grassland shows sharp changes in composite and cheno-am proportions, changes likely to be related to episodes of arroyo cutting and filling. In juniper-piñon areas of northern Arizona and New Mexico fluctuations in the tree-pollen record include a major rise in tree pollen coincident with or following abandonment of many Southwestern villages 700-500 years ago.

Evidence for an Altithermal drought, which is supported by reduction in tree-pollen counts in profiles from the Great Basin, the Central Rockies, and the Pacific Northwest, is not evident in southern Arizona and New Mexico, where mid-postglacial spectra may contain more rather than less tree pollen. The widely held concept of Altithermal drought in the Southwest is theoretically questionable, and some of the Altithermal phenomena, such as intense arroyo cutting and calichification, may reflect an intensified summer monsoon.

While pre-Pleistocene climatic change is widely recognized as responsible for the origin of arid-land plants, some of which can be traced to the Late Miocene, it now seems likely that many, perhaps all, Southwestern plants and animals were on the move in the Pleistocene. Certainly climatic change in the Wisconsin glacial period must have transformed the range of many species. Broken distributions in the range of boreal or Cordilleran plant and animal populations can be attributed to full-glacial invasion from the north ending 14,000 years ago. The postglacial return of desert, grassland, and Mexican woodland communities took place within the last 12,000 years, some species apparently "overshooting" to leave relict outposts or hybrid populations considerably to the north of the main range of the species.

In the Southwest, as elsewhere in the New World, the extinction of elephants, native horses, camels, sloths, and other large vertebrates is a major event of the Late Pleistocene. Evidently it occurred at least 1,000 years after the change to warm, dry postglacial climates. Generic extinction is not seen in the Late Pleistocene record of plants, invertebrates, or small vertebrates; these endured intact. While doubt remains regarding the association of Early Man and certain of the extinct vertebrates, it appears that most of the large herbivores were hunted by Early Man, whose culture was drastically altered by their disappearance and who may be held responsible for the Late Pleistocene "age of overkill."