Reports

Late Pleistocene Vegetation and Degree of Pluvial Climatic Change in the Chihuahuan Desert

Abstract. *Eight Pleistocene wood rat middens at elevations of 1200, 880, and 600 meters in the Chihuahuan Desert contain abundant macrofossils of pinyon pine, juniper, shrubby liveoak, and* Opuntia, *together with smaller quantities of* Agave lecheguilla *and other xerophytes of existing desert vegetation, which indicate a xerophilous woodland vegetation in the lowlands, as much as 800 meters below existing woodland, during the Wisconsin pluvial. Ten radiocarbon dates show ages that range from 11,560 to 14,800 and 16,250 to 20,000 years, and to more than 40,000 years. Absence of most mesophytic montane species in deposits as high as 1200 meters indicates a lack of equivalent downward displacement for the ponderosa pine zone or other zones of montane vegetation. Uneven stocking of isolated peaks in the Chihuahuan Desert province with montane species suggests that long-distance transport of propagules, rather than former continuity, may account for the disjunct distributions of many species.*

Midden deposits of Pleistocene age, accumulated by wood rats (*Neotoma*) in dry caves and rock shelters, provide a chronological record of former vegetation in arid regions of North America. A large number of these peculiar deposits, which contain rich collections of well-preserved plant macrofossils, were found in the Mohave Desert of Nevada and California, and their radiocarbon ages have been determined (*1*). Eight Pleistocene wood rat middens have recently been uncovered in the Chihuahuan Desert of western Texas (*2*). The Chihuahuan Desert province is a fruitful area for inquiry into the history of vegetation because it is adjacent to the Sierra Madre Oriental of Mexico and the Edwards Plateau of Texas, which harbor on their bold escarpments many Arctotertiary plant genera common to the deciduous forests of eastern North America and eastern Asia (*3*). A number of mesophytic, broad-leaf deciduous species, often more or less conspecific with species of the eastern deciduous forest, have isolated occurrences further west on high mountain ranges surrounded by the desert lowlands of Chihuahua, Coahuila, and western Texas (*4*). Also, the highest peaks of the Chihuahuan Desert region support widely disjunct coniferous forests similar in composition to those of the southern Rocky Mountains or northern Sierra Madre (*5*). One possibility which has been considered is that the now disjunct Arctotertiary floristic elements common to Mexico and the United States attained their present distribution, or renewed an older continuity, during pluvial phases of the Pleistocene (*6*). A corollary to this notion would be that the pluvial climate at low elevations in the Chihuahuan Desert province was sufficiently moist to permit the presently disjunct montane species to migrate across the vast lowlands from one isolated mountain range to the next.

Evidence from late Pleistocene wood rat middens found at a wide range of desert elevations in the Big Bend area of western Texas (Fig. 1) makes the latter hypothesis untenable for all but the more xerophytic woodland species during the Wisconsin pluvial. The species constituting the bulk of the plant remains of the *Neotoma* deposits are pinyon pine (*Pinus cembroides remota*), juniper (chiefly *Juniperus pinchotii*), algerita (*Berberis trifoliolata*), shrubby live-oak (*Quercus pungens* and *Q. grisea*), and prickly pear (*Opuntia macrocentra*), and a more xerophytic character is imparted to this woodland assemblage by the presence of *Agave lecheguilla*, *Acacia roemeriana*, *Dasylirion leiophyllum*, and a few other important elements of the present Chihuahuan Desert vegetation (Table 1). It is clear that the area of existing desert shrubland at about 29°N in the Chihuahuan Desert was occupied by decidedly xerophilous woodlands during the Wisconsin pluvial.

The Pleistocene middens are located in rock shelters or small caves in Tertiary volcanics on Burro Mesa and in Cretaceous limestones near Dagger Mountain and Maravillas Canyon, at elevations of 1200, 880, and 600 m, respectively (Fig. 1). This range of elevation is arid to very arid at present and does not support woodland vegetation or even relict individuals of woodland trees. Existing vegetation at the midden sites is a sparse desert shrub community typical of a wide range of elevations in the Chihuahuan Desert region. Existing pinyon-juniper-oak woodlands are confined to higher elevations, chiefly above the 1500-m contour, and are 50 km distant from the Maravillas Canyon midden sites. Pinyon pine, which is a principal tree in the existing woodlands of the Chisos Mountains and is also abundant in the Pleistocene middens, provides the basis for an estimate of downward displacement of the woodland zone during the Wisconsin pluvial. Since the lower limit of pinyon pine in the Chisos Mountains is approximately 1400 m (on north-facing walls of deep canyons) and since the lowest Pleistocene midden containing abundant leaves, cone-scales, and seeds of pinyon pine is at 600 m in Maravillas Canyon (also on a north-facing wall), a pluvial lowering of the woodland zone by 800 m is established during a time spanned by five radiocarbon dates ranging in age from 11,560 to 14,800 years (Table 1). This compares with a maximum figure of 600 m (with radiocarbon ages of 10,100 and 17,450 years) recorded in middens from the Mohave Desert (*1*). However, there is an important difference between the Pleistocene pinyon pine at what are now desert elevations in Texas and the existing pinyon pine in the Chisos Mountains. Whereas the existing pinyon pine has predominantly three (but sometimes two) needles per fascicle (*Pinus cembroides* Zucc.), the abundant Pleistocene midden material (several thousand intact leaf fascicles have been examined) shows consistently two needles per fascicle (Fig. 2). In fact, the fossil specimens share many characters with a recently named two-needled race of pinyon pine (*Pinus cembroides remota* E. L. Little) which persists today as small relict populations along the Balcones Escarpment in the southwestern sector of the Edwards Plateau of central Texas, more than 200 km east of the Pleistocene fossil localities in the Big Bend area. It may be inferred that the existing disjunct distribution of pinyon pines in Texas was preceded by a pluvial continuity. A recent study of the ecological significance of the number of needles per cluster in *Pinus* suggests that two needles per fascicle is a more xerophytic condition than three needles (*7*). Hence, the presence of pinyon pines with consistently two-needled fascicles over a wide range of lower elevations in the Chihuahuan Desert province during the Wisconsin pluvial seems to be additional evidence for a relatively dry, though possibly cool, pluvial woodland climate in the lowlands. Limits on coolness are placed by the fossil occurrence of *Agave lecheguilla, Berberis trifoliolata, Dasylirion, Juglans microcarpa,* and other species of relatively warm habitats (Table 1).

The degree of postpluvial climatic change indicated for the lowlands of the Chihuahuan Desert province may be expressed in another way by contrasting available meteorological records for the lower woodland zone and the desert shrub zone in Trans-Pecos Texas. The mean annual precipitation at five stations in or near the lower woodland zone ranges from 42 to 50 cm, averaging 45 cm, while comparable figures for five stations in the desert shrub zone range from 23 to 31 cm, averaging 27 cm. These differences are enhanced by differences in temperatures corresponding to the existing lapse rates. Temperatures, and hence rates of potential evapotranspiration, are lower in the woodland zone (*8*).

The pluvial expansion of the woodland zone revealed by the wood rat midden record documents a former continuity across the intervening lowlands for existing disjunct stands of pinyon-juniper-oak woodland on the numerous isolated high mountains of the Chihuahuan Desert region; but the indicated downward displacement of 800 m leaves little or no room for the existing, treeless, desert shrub community and implies the absence of desert climate throughout the extensive Chihuahuan Desert province during the pluvial correlated with the Wisconsin glaciation. Much of the present Chihuahuan Desert lowland lies above 1000 m, and the desert floors of many arid bolsones in the Mexican plateau sector are considerably higher in elevation. The lowest, warmest, and most arid sector of the desert is along the trough of the Rio Grande Valley, and the Pleistocene midden sites in the broad, open Maravillas Canyon at 600 m are in the lowest elevation range of the existing Chihuahuan Desert. To the east, elevation decreases downstream along the Rio Grande, but rainfall gradually increases in the direction of the Gulf, and there is a transition to the semiarid Tamaulipan thorn shrubland province east of the Pecos River. Hence, it appears that lower, more arid areas than the Maravillas Canyon locality, which might have harbored an extensive, regional, treeless, desert shrub community, were not available here during the Wisconsin pluvial. On the other hand, presence of the entire Chihuahuan Desert flora as a subordinate element of the pluvial woodland vegetation in xeric habitats is not precluded. An analysis of the existing pinyon-juniper-oak woodland vegetation in the Chisos Mountains shows an astonishing number of Chihuahuan Desert species coexisting with open stands of xerophytic conifers and oaks at the lower limit of woodland (1500 m). Furthermore, some of the most characteristic desert species which define the existing Chihuahuan Desert vegetation zone by their dominance extend to remarkably high elevations within the woodland zone of dominance, chiefly on the summits of rocky ridges and scarps with southerly exposure. For example, the creosote bush (*Larrea divaricata*) attains 1740 m; the ocotillo (*Fouquieria splendens*), sotol (*Dasylirion leiophyllum*), and whitethorn (*Acacia constricta*) ascend to nearly 2100 m; and the ubiquitous lechuguilla (*Agave lecheguilla*) and prickly pear (*Opuntia engelmannii*) attain nearly 2200 m. The breadth of overlap with woodland is indicated by the fact that open stands of pinyon pine (*Pinus cembroides*) descend to 1500 m on xeric upland sites and to 1400 m on shaded canyon walls; and even the yellow pine (*Pinus ponderosa*) descends to 1600 m in Pine Canyon. Projecting back to pluvial times, the desert flora of the Chihuahuan region may have coexisted with the woodland flora in much the same manner, but at lower elevations. Direct fossil evidence of a former coexistence is provided by the presence in several of the Pleistocene *Neotoma* middens of spiny leaf tips of *Agave lecheguilla*, leaf fragments of *Dasylirion*, legumes and armed twigs of *Acacia roemeriana*, and numerous spiny areoles of *Opuntia*, closely associated with the much more

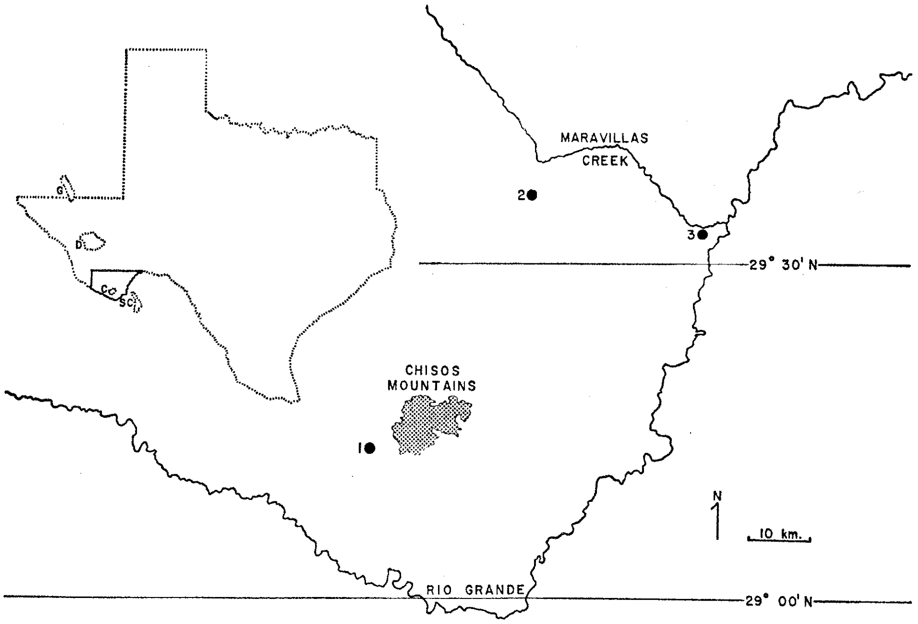

Fig. 1. Big Bend area of western Texas, showing approximate extent of existing woodland and forest vegetation zones (shaded area) in the Chisos Mountains, chiefly above the 1500 m contour. Pleistocene wood rat midden localities and elevations are: 1, Burro Mesa, 1200 m; 2, Dagger Mountain, 880 m; and 3, Maravillas Canyon, 600 m. Outline of Texas (inset) shows location of Guadalupe (*G*), Davis (*D*), and Chisos (*C*) mountains of Trans-Pecos Texas, and the Sierra del Carmen (*SC*) of Coahuila, with maximum elevations of 2670, 2550, 2370, and about 3000 m, respectively.

abundant remains of woodland conifers and oaks (Table 1).

Hence, the pluvial xerophilous woodland vegetation, which then occupied the lowlands of the Chihuahuan Desert province, seems to have reconstituted the hypothetical undifferentiated Madro-Tertiary local flora, as it may have existed before a treeless desert shrub community had gradually segregated in response to increasing aridity during the Pliocene and major interglacials of the Pleistocene, essentially as postulated by Axelrod (*9*) for the North American deserts in general. The greater part of the evolutionary history of many of the xerophytes peculiar to the Chihuahuan Desert flora (for example, *Agave lecheguilla*, one of the more dominant species of the existing desert vegetation) probably took place in a woodland setting.

The dated macrofossil record of woodland vegetation at elevations now desert suggests that pluvial climatic conditions were sustained in the Chihuahuan Desert over long periods of time, ranging from at least 11,560 to 20,000 years ago, and again at more than 36,600 years ago. The wood rat

Table 1. Fossil plants and radiocarbon ages of wood rat middens from three localities in the Chihuahuan Desert of western Texas. B, Burro Mesa; D, Dagger Mountain; and M, Maravillas Canyon. Symbols: +, present in midden but not abundant; ++, abundant or principal constituent of midden. The radiocarbon ages are from the UCLA series of radiocarbon dates, numbers 758, 934, 1039–1046, 1063, and 1064; determined at Institute of Geophysics, University of California; based on organic residue (chiefly cell-wall material) after treatment of fossiliferous strata from middens with HCl. M-1, a, b, and c, upper middle, and lower strata of the largest Pleistocene wood rat deposit yet uncovered, measuring a few thousand liters in volume.

Species and structures in midden	Abundance in midden sites *									
	B-1	B-2	D-1	D-2	D-3	M-1a	M-1b	M-1c	M-2	M-3
					Trees					
Pinus cembroides, leaves, cones, seeds	++	++	++	++	++	+	+	++	++	++
Juniperus pinchotii, leafy twigs, seeds	++	++	++	++	++	++	++	++	++	++
J. deppeana, leafy twigs, seeds	++									
Quercus grisea, leaves, acorns	+	+								
Q. arizonica × *Q. grisea*, leaves	+									
Q. pungens, leaves, acorns			+	+	+	++	++	+	++	++
Celtis reticulata, endocarps	+	++	+	+	+	+		+	+	+
Juglans microcarpa, endocarps			+	+				+		
					Shrubs					
Acacia roemeriana, twigs, legumes						+	+			
Artemisia cf. *ludoviciana*, leaves		+								
Atriplex canescens, fruits		+								
Berberis trifoliolata, leaves	++		+					+	+	+
Ephedra aspera, seeds		+	+				+			
Eysenhardtia texana, leaflet, legume							+		+	
Forestiera sp., endocarps			+	+	+	+				+
Gymnosperma glutinosum, heads						+				
Leucaena retusa, seeds			+			+	+	+		
Prunus cf. *havardii*, endocarps	+	+	+			+	+	+		+
Ptelea trifoliata, samaras	+									
Zanthoxylum sp., twigs		+								
					Agavaceae					
Agave lecheguilla, leaves	+	+	+	+	+	+	+	+		
Dasylirion sp., leaves			+			+	+	+		
Nolina sp., leaves						+	+	+		
Yucca rostrata, leaves						+	+			
Y. torreyi, leaves						+	+			
					Cactaceae					
Echinocereus sp., areoles			+	+		+	+			
Opuntia cf. *macrocentra*, areoles, seeds	++	++	++	++	++	++	++	++	+	+
					Grasses and forbs					
Bouteloua ramosa, inflorescence							+			
Buchloe dactyloides, fruit		+								
Heteropogon contortus, fruits		+	+			+		+		
Tridens muticus, spikelets			+	+		+	+	++		
Lithospermum sp., nutlets	+		+	+				+	+	+
Machaeranthera sp., heads			+			+	+	+	+	+

* Elevation and age of sites: B-1, 1200 m, 18,750 ± 360 years; B-2, 1210 m, > 36,600 years; D-1, 880 m, 20,000 ± 390 years; D-2, 880 m, > 40,000 years; D-3, 850 m, 16,250 ± 240 years; M-1a, 600 m, 11,560 ± 140 years; M-1b, 600 m, 12,000 ± 150 years; M-1c, 600 m, 12,550 ± 130 years; M-2, 600 m, 13,350 ± 170 years; M-3, 600 m, 14,800 ± 180 years.

midden of "full-glacial" age (18,750 years) and greatest elevation (1200 m) yielded remains of a few relatively mesophytic woodland species, such as alligator juniper (*Juniperus deppeana*) and hop tree (*Ptelea trifoliata*), which have not been detected at lower elevations. However, woodland vegetation of comparable age (20,000 years), recorded in a midden at an elevation of 880 m, is scarcely less xerophytic than assemblages of much younger age (to 11,560 years) at the site of lowest elevation (600 m). A late persistence of pluvial climate equivalent to that of the classical Wisconsin glacial maximum (from about 18,000 to 20,000 years ago) is apparent. Fluctuations in climate sufficient to cause major shifts in vegetation zones during the time interval from 11,500 to 20,000 years ago have not been observed in the wood rat midden record. A conspicuous, light-colored deposit at an elevation of 600 m, which does contain abundant remains of a typical assemblage of Chihuahuan Desert shrubs, including ocotillo (*Fouquieria splendens*), lechuguilla (*Agave lecheguilla), Opuntia macrocentra, Acacia roemeriana, Yucca torreyi, Dasylirion*, and others, but not a trace of woodland species, has a radiocarbon age of 4200 ± 80 years (U.C.L.A. No. 1062). More material is needed to establish the time of onset of desert conditions at lower elevations in this region.

Significant in a negative way are the plant contents of the *Neotoma* deposits of greatest elevation at 1200 m on Burro Mesa near the west flank of the Chisos Mountains, only 200 m below existing woodlands. Absence of Douglas fir–aspen forest, deciduous oak-maple-cypress forest, or even ponderosa pine "parkland" at this relatively high elevation during the Wisconsin pluvial is implied by absence of fossil remains of *Pseudotsuga, Populus tremuloides, Quercus gravesii, Q. muehlenbergii, Q. gambelii, Acer grandidentatum, Cupressus arizonica, Pinus ponderosa*, and many others from a full-glacial midden with a radiocarbon age of 18,750 ± 150 years and from another midden with an age greater than 36,600 years. Presence of a rather xerophytic pinyon-juniper-oak woodland assemblage in the Burro Mesa middens at 1200 m indicates that relatively xerophilous woodlands probably extended to still higher elevations. Even without this extrapolation, it may be inferred from existing lower limits of 1600 m for *Pinus ponderosa* and associated species that the relatively mesophytic species of the existing montane forest zone of the Chisos Mountains descended less than 400 m during the pluvial correlated with the Wisconsin glacial maximum, whereas the xerophilous woodland zone enjoyed at least a twofold greater downward expansion, 800 m below its present lower limits, as evidenced by abundant remains of woodland species in the Maravillas Canyon deposits. There has been a facile assumption by biogeographers of the Pleistocene that vegetation zones have moved up and down in elevation by quantum intervals of displacement, with an approximately equal interval for each zone *(10)*. The fact that existing montane vegetation zones are often very unequal in vertical and areal extent provides little support for this view. The extensive pinyon-juniper-oak woodland zone of the Chisos Mountains prevails from the summit of Emory Peak at 2370 m down to approximately 1400 m on the lower slopes, a vertical span of 970 m, but the relictual forest zone of relatively mesophytic conifers (Douglas fir, yellow pine, Arizona cypress) and broadleaf deciduous trees (for example, maple, redbud, hop hornbeam, and Gambel's, Grave's, and chinquapin oaks) is largely restricted to small areas of mesic canyon environment over a vertical range of about 500 m. Evidence from the wood rat middens clearly indicates that the pluvial climate of Wisconsin time permitted a very extensive growth of the now chiefly montane but relatively xerophilous pinyon-juniper-oak woodland zone over much of the available span of elevation in the vast regional lowlands of the Chihuahuan Desert, but apparently did not allow the strictly montane forest zone of more mesophytic conifers and broadleaf deciduous trees to expand much beyond the narrow confines of the central mass of the Chisos Mountains.

Studies of oceanic temperature fluctuations during the Pleistocene by means of oxygen-isotope ratios of carbonates, or species composition, of foraminiferal microfossils preserved in deep-sea sedi-

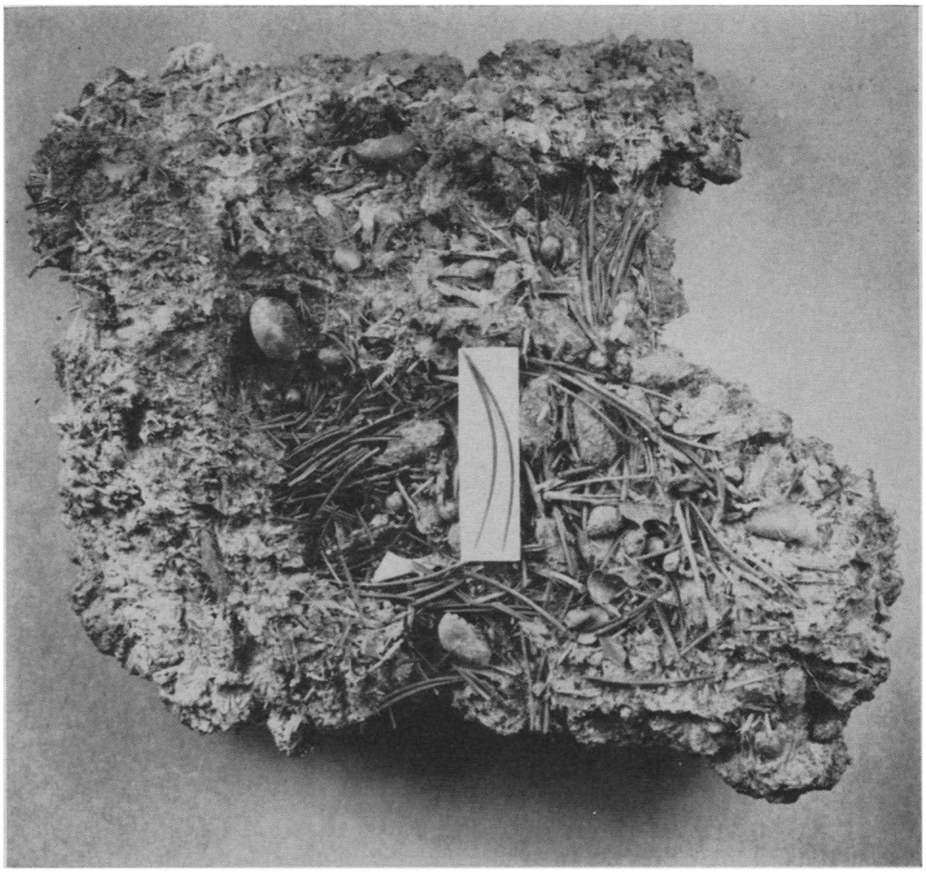

Fig. 2. Fragment of wood rat midden from Maravillas Canyon, Texas; radiocarbon age 14,800 ± 180 years. Two-needled leaf fascicles of pinyon pine (*Pinus cembroides remota* E. L. Little) predominate; several seeds of pinyon and juniper, leaf fragments of oak and algerita, and a small portion of a bone (white triangle) are visible. Actual size (longest dimension of fragment), 15 cm. [Photograph by Hollings T. Andrews, University of Kansas]

ments suggest that minimal temperatures at the plankton level were similar during a number of Pleistocene glacial stages (*11*). Also, the areas covered by continental ice sheets in North America during four principal glacial stages were rather similar in scope (*12*). By analogy, the maximum pluvial depression of vegetation zones on mountains in lower latitudes of the now arid Southwest was probably not greatly different during the several glacial maxima of the Pleistocene. It is noteworthy, however, that the Pleistocene pollen record in the very long core of sediments from pluvial Lake San Augustin, near the continental divide (elevation about 2000 m) in New Mexico, shows only one major maximum (about 35 percent) of spruce (*Picea*) pollen against a high background level of pine pollen (about 65 percent), and this was during the Wisconsin glacial maximum, as indicated by two radiocarbon dates. However, only minor maxima (about 10 percent or less) of spruce pollen were recorded during a long time span which probably includes earlier glacial maxima of the Pleistocene and possibly extends to the Pliocene (*13*). "Nonglacials" were indicated by maxima (as high as 50 percent) of pollen of anemophilous semidesert shrubs and grasses, also against a high background level of pine pollen (about 50 to 80 percent) with virtual absence of spruce pollen. The most recent level of pine pollen at the top of the core is nearly 80 percent, but the existing vegetation of the lowermost slopes and floor of the basin near the drilling site is treeless blue-grama grassland with halophytic semidesert shrubs on the alkaline playa deposits, and pinyon and ponderosa pines are restricted to successively higher elevations on the slopes. Although spruce is now absent in this drainage basin, it occurs within 25 km of the drainage divide at an elevation of only 2700 m (*14*). However, it is possible that the high level of spruce pollen unique to the Wisconsin pluvial at Lake San Augustin was the result of chance dispersal of spruce at that time across intervening lowlands into some of the many isolated islands of high elevation on mountains rising above 2700 m immediately adjacent to the floor of the San Augustin basin, providing a much closer and more abundant source of *Picea* pollen than had hitherto been available.

Since the pluvial climate during the glacial maximum of Wisconsin time evidently permitted only the xerophilous woodland zone to attain continuity across the extensive lowlands of the Chihuahuan Desert province, there is a suggestion that the presently disjunct, relatively mesophytic, montane vegetation zones on isolated peaks have been discontinuous since Tertiary time (*15*). Indeed, it is quite likely that many mesophytic montane species have never had a continuous distribution across the intervening lowlands. For example, the Douglas fir (*Pseudotsuga*) now occurs in the Sierra del Carmen, the Guadalupe Mountains, and even the relatively small Chisos Mountains, but not in the Davis Mountains, which are higher, more massive, and 200 km further north than the Chisos Mountains (Fig. 1, inset). The Davis Mountains have much more extensive forests of *Pinus ponderosa* than the Chisos, and the tall southern race of *Pinus flexilis* is present, as are *Quercus hypoleucoides, Styrax youngae, Viburnum affine*, and numerous other relatively mesophytic species absent in the Chisos Mountains; but many of these species are present in the Sierra del Carmen, southeast of the Chisos Mountains.

On the other hand, the Chisos Mountains have the hop hornbeam, *Ostrya chisoensis*, an endemic, mesophytic, deciduous tree which is closely related to *O. baileyi* of the Guadalupe Mountains and also shares some characters with *O. virginiana* of eastern Texas, but *Ostrya* is unknown from the Davis Mountains (*16*). Although there are many other mesophytic species of the Chisos Mountains which do not occur in the Davis Mountains, there are also numerous species of this type common to both ranges, for example, a relative of the sugar maple (*Acer grandidentatum*), aspen (*Populus tremuloides*), Gambel's oak (*Quercus gambelii*), and chinquapin oak (*Q. muehlenbergii*). The fact that the Chisos and Davis mountains are unevenly stocked with mesophytic plant species, including several endemics in each range, somewhat in the manner of oceanic islands, suggests a history of isolation from each other and from the main bodies of relatively mesophytic forests of the Rocky Mountains, Sierra Madre, and Edwards Plateau. Since long distance transport of propagules must account for many anomalous features of geographic distribution on oceanic islands throughout the world (*17*), it seems appropriate to consider that this mechanism has been operative in the stocking of islands of mesic environment on isolated high mountain peaks of the Chihuahuan Desert province, with mesophytic plants unable to grow in the surrounding lowlands, even during pluvial climatic phases of the Pleistocene (*18*).

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References and Notes

1. P. V. Wells and C. D. Jorgensen, *Science* **143**, 1171 (1964); P. V. Wells, *Bull. Ecol. Soc. Amer.* **45**, 76 (1964); G. J. Fergusson and W. F. Libby, *Radiocarbon* **4**, 109 (1962); ———, *ibid.* **5**, 1 (1963); ———, *ibid.* **6**, 318 (1964); R. Berger, G. J. Fergusson, W. F. Libby, *ibid.* **7**, 336 (1965). Dated middens from the Mohave Desert total 17.
2. P. V. Wells, *Bull. Ecol. Soc. Amer.* **43**, 197 (1965); R. Berger, G. J. Fergusson, W. F. Libby, *Radiocarbon* **7**, 336 (1965), and unpublished data.
3. A. J. Sharp, *Evolution* **5**, 1 (1951).
4. The following species of this type have been collected in one or more of the higher mountain ranges of the Chihuahuan Desert province of Trans-Pecos Texas: *Acer grandidentatum* (bigtooth sugar maple), *Andrachne phyllanthoides* (∼ *Savia arida,* maidenbush), *Celastrus scandens* (bittersweet), *Celtis reticulata* (hackberry), *Cercis canadensis* (redbud), *Crataegus tracyi* (hawthorn), *Cocculus diversifolius* (snailseed), *Fraxinus texensis* (ash), *Juglans microcarpa* (walnut), *Lonicera albiflora* (honeysuckle), *Morus microphylla* (mulberry), *Ostrya baileyi* and *O. chisoensis* (hop hornbeam), *Parthenocissus vitacea* (Virginia creeper), *Prunus murrayana* (plum), *P. serotina* (black cherry), *P. virginiana* (chokecherry), *Ptelea trifoliata* (hop tree), *Quercus gravesii* (Shumard oak complex), *Q. muehlenbergii* (chinquapin oak), *Rhus copallina* (winged sumac), *R. toxicodendron* (poison oak), *Styrax youngae* (snowbell), *Viburnum affine* (arrow-wood), *Zanthoxylum parvum* (prickly ash).
5. Species of western Texas are: *Cupressus arizonica, Pinus flexilis, P. ponderosa, Pseudotsuga menziesii, Populus tremuloides.* A true fir (*Abies,* probably *A. coahuilensis,* endemic to Mexico) has been reported from the high Sierra del Carmen, Coahuila, by the late Alden H. Miller [*Condor* **57**, 154 (1955)].
6. E. S. Deevey, *Bull. Geol. Soc. Amer.* **60**, 1374 (1949). However, other reviewers of biogeographic evidence held that the widely disjunct condition in the distributions of most species of this type is a product of late Tertiary aridity in the lowlands of southern Texas and Tamaulipas, interrupting a former (pre-Pliocene?) continuity which was not renewed during the Pleistocene. For discussion, see E. L. Braun, *Botan. Rev.* **21**, 297 (1955); and especially P. S. Martin and B. E. Harrell, *Ecology* **38**, 468 (1957).
7. J. R. Haller, *Brittonia* **17**, 354 (1965).
8. U.S. Weather Bureau, *Climatic Summary of the United States, Section 31-Southwestern Texas, and Supplement 1931-through 1952* (Government Printing Office, Washington, D.C., 1932, 1958).
9. D. I. Axelrod, *Carnegie Inst. Wash. Publ. 590* (1950), p. 215.
10. For example, a recently produced map of full-glacial vegetation in the southwestern United States shows a broad arm of yellow pine (*Pinus ponderosa*) "parkland" projecting southward deep into the heart of the Big Bend area of western Texas [P. S. Martin and P. J. Mehringer, in *The Quaternary of the United States*, H. E. Wright and D. G. Frey, Eds. (Princeton Univ. Press, Princeton, N.J., 1965), p. 439]. The peninsular shape of the salient is congruent with alleged areas of pinyon-juniper woodland and desert grassland as mapped by Shantz and Zon [H. L. Shantz and R. Zon, in *Atlas of American Agriculture* (Government Printing Office, Washington, D.C., 1924)]. A drastic downward shift of the ponderosa pine zone is envisioned, neatly displacing

the pinyon-juniper woodland and desert grassland zones of Shantz and Zon, with spruce and fir occupying the existing ponderosa pine zone. There is a serious error in the Shantz and Zon map from which the "full-glacial" map was traced: pinyon-juniper woodland is lacking throughout much of the peninsular salient so mapped in the Big Bend area. Even the Santiago and Dead Horse mountains, which form the axis of the salient, are sparsely vegetated with desert shrubs and grasses, and the very few relict populations of woodland species are narrowly restricted to the highest elevations of the mountains. [For a description of the vegetation of the Dead Horse Mountains, see P. V. Wells, *Southwestern Nat.* **10**, 256 (1965).] Furthermore, the pluvial presence of xerophilous woodland vegetation dominated by two-needled pinyon pine at a relatively high elevation (as evidenced by abundant macrofossils in the full-glacial wood rat midden deposit at Burro Mesa, only 400 m below existing stands of *Pinus ponderosa*) suggests that the magnitude of downward displacement of ponderosa pine "parkland" in the Southwest (as much as 1200 m, as evidenced by high relative percentages of pine pollen, species undetermined, in pluvial sediments) has been overestimated.

11. C. Emiliani, *J. Geol.* **63**, 538 (1955); D. B. Ericson, M. Ewing, G. Wollin, *Science* **146**, 723 (1964).
12. R. F. Flint, chairman, *Glacial Map of North America* (Geological Society of America, New York, 1945.)
13. K. H. Clibsy and P. B. Sears, *Science* **124**, 537 (1956).
14. L. D. Potter, *Ecol. Monogr.* **27**, 113 (1957).
15. The Chisos and Davis mountains of Trans-Pecos Texas are disjunct bodies of intrusive volcanic or extrusive rocks of early to mid-Tertiary age. They lie between the Sierra del Carmen (a lofty northwestern outpost of the Sierra Madre Oriental in Coahuila) and the Guadalupe Mountains (a southeastern outpost of the Sacramento Mountains of New Mexico), two massive Tertiary uplifts of pre-Tertiary rocks, chiefly limestones. Regardless of the age of the rocks, the existing montane landforms of high elevation in Trans-Pecos Texas are relatively recent, dating from mid-Tertiary (or later) block-faulting and emplacement of intrusive bodies, with uplift, especially during the Pliocene and Pleistocene [P. B. King, *Bull. Amer. Assoc. Petrol. Geol.* **19**, 221 (1935); ———, in *The Quaternary of the United States*, H. E. Wright and D. G. Frey, Eds. (Princeton Univ. Press, Princeton, N. J., 1965), p. 845]. Hence, limits are placed on the age of high-elevation habitat in the Chisos and Davis mountains, and therefore the time available for its colonization by existing vegetation.
16. D. S. Correll, *Wrightia* **3**, 128 (1965).
17. C. Darwin, *The Origin of Species* (Murray, ed. 6, London, 1889), p. 347; A. R. Wallace, *Island Life* (Macmillan, London, 1892), p. 257; H. N. Ridley, *The Dispersal of Plants Throughout the World* (L. Reeve, Ashford, England, 1930), p. 675; S. Carlquist, *Island Life* (Natural History Press, Garden City, New York, 1965), p. 9.
18. Although long distance transport of seeds, followed by successful establishment, must be regarded as a highly infrequent event, a significant number of such incidents probably occurs during time periods of more than 10^6 years. Nearly half of the 70 ligneous species which make up the bulk of montane vegetation in the Chisos and Davis mountains have small baccate fruits apt to be dispersed by a variety of frugivorous birds which pass the stony seeds or pits unharmed. A possible agent of dispersal for the heavier propagules of other mesophytic montane plant species of these isolated ranges is the band-tailed pigeon (*Columba fasciata* Say). A large, seed-eating bird with strong powers of flight, it possessses a capacious crop, or esophagal pouch, in which fruits and seeds are temporarily stored. Darwin long ago observed: "But the following fact is more important: the crops of birds do not secrete gastric juice, and do not, as I know by trial, injure in the least the germination of seeds; now after a bird has found and devoured a large supply of food, it is positively asserted that all the grains do not pass into the gizzard for twelve or even eighteen hours. A bird in this interval might easily be blown to the distance of 500 miles, and hawks are known to look out for tired birds, and the contents of their torn crops might be thus readily scattered" [C. Darwin, *The Origin of Species* (Murray, ed. 6, London, 1889), p. 308]. The band-tailed pigeon habitually fills its crop with the largest seeds and fruits, such as acorns (one of its principal foods) and greater numbers of smaller propagules, as of *Arbutus, Pinus, Prunus, Rhamnus, and Sambucus* [A. C. Bent, *U.S. Nat. Mus. Bull.* **16**, 353 (1932)]. It breeds in the montane forests of the Sierra del Carmen, Chisos, Davis, and Guadalupe mountains even at the present time and migrates or wanders extensively throughout the region, chiefly at higher elevations. The distance from the Sierra del Carmen in Coahuila to the Chisos Mountains across the Rio Grande is scarcely 50 km (as the pigeon flies, an hour's journey), and the extensive stands of *Pseudotsuga* (Douglas fir) in the Sierra del Carmen seem to be the most probable source of seed for colonization of the isolated Chisos Mountains. On the other hand, the lofty Davis Mountains, which display an anomalous lack of Douglas fir, are formidably remote from the *Pseudotsuga* seed sources in the Sierra del Carmen and the Guadalupe Mountains (distances of 200 and 150 km, respectively). For many of the Arctotertiary species in the Davis or Chisos mountains, such as the mesophytic deciduous trees *Acer grandidentatum, Quercus gravesii, Q. muehlenbergii*, and *Ostrya chisoensis*, the time period available for migration extends back into the Tertiary, perhaps for some millions of years (*15*), but seed sources and target areas on isolated mountain peaks were undoubtedly most extensive during pluvial phases of the Pleistocene, particularly for conifers of boreal character, such as *Pseudotsuga*.
19. Supported by NSF grant GB-1821. Radiocarbon ages were determined by Drs. Rainer Berger and W. F. Libby of the University of California, Los Angeles. I thank Dr. Barton H. Warnock of Sul Ross State College, Alpine, Texas, who discovered the principal midden site in Maravillas Canyon, and made available his collections of existing flora.

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3 June 1966 ■

Butler, Missouri: An Unusual Iron Meteorite

Abstract. *The Butler iron meteorite has been found to have, with respect to other iron meteorites, an unusually high cobalt content (1.4 percent by weight), unusually high germanium contents in the kamacite and the taenite phases, and an unusually low cooling rate (0.5°C/10^6 years). It is suggested that Butler formed in a different environment from that of the rest of the iron meteorites.*

Analyses of approximately 160 iron meteorites to date have revealed a very wide range of Ge concentrations extending from 400 parts per million (ppm) down to 0.03 ppm. As shown by Wasson (*1*), the Butler iron meteorite has an unusually high Ge content, 2000 ppm. This high Ge content, as well as the high Ge/Ni ratio, makes Butler an exception to two geochemical generalizations regarding iron meteorites (*1*). This exception implies that Butler may be unusual in other ways. Below I report the measurements of major element distributions and of the cooling rate of Butler, further showing its unusual characteristics.

The structure of the Butler meteorite, which has 16 percent (*2*) Ni (*1*), is transitional between a fine octahedrite and an ataxite. A photomicrograph of the meteorite is shown in the cover photograph. The large kamacite plates make up the well-defined Widmanstätten pattern typical of the octahedrites. The interior areas between the kamacite plates of the major pattern are regions of transformed taenite (plessite) which contain a micro-Widmanstätten pattern sometimes found in the ataxites. As shown by Goldstein and Ogilvie (*3*), this micro-pattern formed late in the meteorite's cooling history.

Analysis of the metallic phases of the meteorite with the electron microprobe showed that only Fe, Ni, Co, and Ge

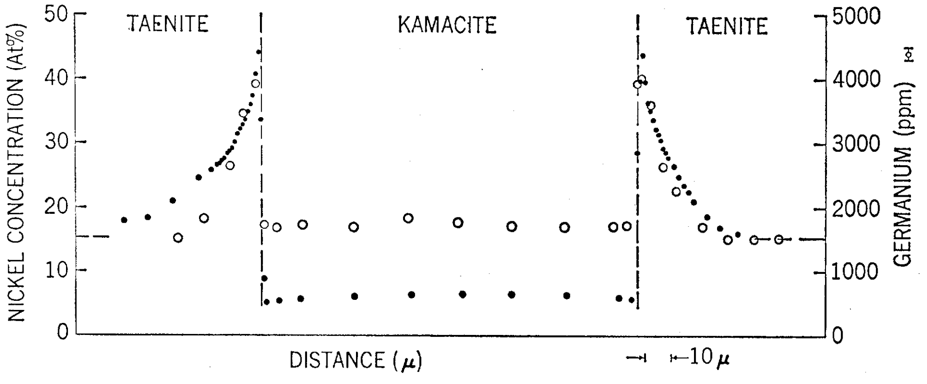

Fig. 1. Distribution of nickel (small filled circles) and germanium (open circles) in the Butler iron meteorite, which has 16 percent nickel by weight and 2000 ppm germanium. *At%*, atomic percent. The small vertical mark above the right-hand label represents the 95-percent confidence limits for germanium (± about 100 ppm).