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ORIGIN OF THE CREOSOTE BUSH (*LARREA*) DESERTS OF SOUTHWESTERN NORTH AMERICA¹

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ABSTRACT

The North American creosote bush (*Larrea tridentata*) has undergone a simple cytogeographic differentiation, with the ancestral diploid population in the Chihuahuan Desert, and with tetraploid and hexaploid derivatives in the Sonoran and Mohave Deserts, respectively. The chromosomal races have annectant but largely allopatric distributions, which coincide remarkably well with the boundaries of their respective desert provinces. However, during the glacials of the Pleistocene, the lowlands of these provinces were extensively invaded by evergreen woodlands dominated by various species of *Juniperus*, *Pinus*, and *Quercus*; and the generality of the phenomenon during the Wisconsin glacial has been abundantly documented by some of the most detailed macrofossil evidence of relatively xerophytic plants ever obtained. The ¹⁴C-dated macrofossil assemblages, preserved in rock-sheltered *Neotoma* deposits, demonstrate a persistence of woodland conifers and consistent absence of *Larrea* throughout most of its present range in the Southwest during the last major glacial episode of the Pleistocene from > 40,000 BP to about 11,000 BP. The oldest reliable record of *Larrea* in North America is dated on macrofossils of *Larrea* itself at 10,580 BP, and the site, near Wellton, Yuma County, Arizona, is one of the lowest (162 m) and most arid in the present Sonoran Desert. Hence, the major features of the modern geographic pattern of *Larrea tridentata* in North America must have originated during the climatic transition from the late Wisconsin to the Holocene, when a desiccating climate gripped the immense lowlands of the Southwest, opening a vast and varied desert niche into which a burgeoning population of *Larrea* could have expanded and differentiated explosively.

The biogeography of *Larrea* during the Pleistocene is a particularly interesting enigma because there is an intriguing possibility of a late, intercontinental dispersal from South America, where the genus exhibits markedly greater ecomorphological and chemical diversity than it does in North America. Also, the genera most closely allied to *Larrea* are endemic to South America. While several "r"-selected, herbaceous genera of Zygophyllaceae have much wider world-distributions, *Larrea* is unique among woody Zygophyllaceae in having an amphitropical, intercontinental disjunction in its range. The specialization of *Larrea* on intensely arid deserts with relatively open plant communities would facilitate establishment after dispersal to a new desert area. However, the migration of *Larrea* to North America must have lacked continuity. If the extremely xerophytic species, *Larrea divaricata*, had been able to follow a hypothetically continuous route across the wet tropics during a period of drier climate, then a much greater amphitropical disjunction of American zygophyllaceous genera should be expected. Long distance transport of seeds across the wet tropics is the only feasible alternative for *Larrea*.

The creosote bush [*Larrea tridentata* (Sessé & Moc. ex DC.) Cov.] is the most abundant and widely distributed woody plant in the warm or subtropical deserts of North America. It forms a massively continuous population throughout the Mohave Desert and the Colorado River sector of the Sonoran Desert, and extends eastward on the more arid plains to the "desert grasslands" of southeastern

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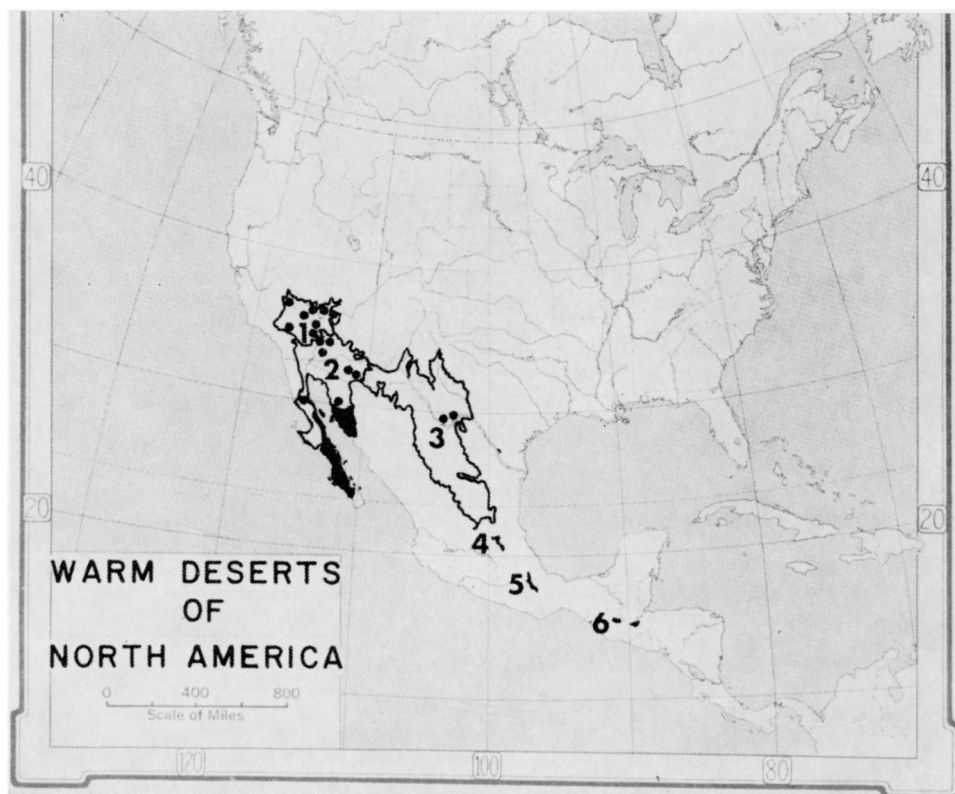


FIGURE 1. Distribution of the warm, subtropical, and tropical deserts of North and Middle America: (1) *Mohavean*. (2) *Sonoran* (including the shaded areas in southern Baja California and southern Sonora). (3) *Chihuahuan*. (4) *Hidalgan* (Río Extorax, Querétaro, to northwest; Valle del Mezquital, Hidalgo, to southeast). (5) *Pueblan* (Valle de Tehuacán, Puebla, to northwest; Valle de Tomellín, Oaxaca, to southeast). (6) *Guatemalan* (Valle de Chixoy to west, Valle de Motagua to east). Shaded areas in the southern Sonoran Desert and the tropical, rain-shadowed, pockets of aridity (desert "islands," numbered 4, 5 and 6) were probably full-glacial, Pleistocene refugia for thermophilous desert xerophytes, but possibly not for *Larrea*. *Larrea* is lacking in areas 5 and 6, which are dominated by dense, thorn woodland or shrubland with gigantic cacti. Cytogeographically, *Larrea tridentata* is hexaploid in desert area (1); tetraploid in area (2); diploid in areas (3) and (4) and also throughout the range of its counterpart in South America. Localities for Pleistocene *Neotoma* records of pluvial woodland within the present range of *Larrea* are marked by large dots (map compiled and annotated by P. V. Wells).

Arizona and southern New Mexico, and again dominantly and continuously throughout the Chihuahuan Desert to its southern extremity south of the Tropic of Cancer (Fig. 1). Thus, the creosote bush extends from southern California and southwestern Utah, south through Baja California and Sonora, and southeastward through western Texas, Chihuahua, Coahuila and San Luis Potosí (Shreve, 1942; Rzedowski & Medellín Leal, 1958; Wells, 1977). There is a major disjunction for more than 100 km to the southeast of San Luis Potosí, which isolates a substantial population of *L. tridentata* on the Extorax-Tula drainage of eastern Querétaro from the main body of *Larrea* to the north; and a small colony or two occurs in

the Valle del Mezquital (Rzedowski & Medellín Leal, 1958) on another branch of the same drainage system in Hidalgo, just north of Mexico City (Fig. 1). Aside from these disjunct populations in the south, and a patchy distribution in the desert grasslands, the North American creosote bush is very nearly one continuous population, extending over many millions of square kilometers in more or less pure stands. Nevertheless, there has been a remarkable cytological differentiation, and some parallel morphological variations within this wide geographic range; *Larrea* exists as distinct, diploid ($n = 13$), tetraploid ($n = 26$), and hexaploid ($n = 39$) cytogeographic races in the Chihuahuan, Sonoran, and Mohave deserts, respectively (Yang, 1967, 1968, 1970; Barbour, 1969).

The strikingly annectant, though largely allopatric, distributional areas of the three chromosomal races are nearly congruent with the boundaries of their respective deserts, but all of these existing areas of desert vegetation are now known to have undergone extensive geographical changes during the Pleistocene. Most of the present areas of the warm deserts in North America were occupied by pluvial woodlands dominated by low, xerophytic evergreen trees, with various species of junipers (*Juniperus*), and to some extent pinyon pines (*Pinus*) and oaks (*Quercus*), segregating geographically among the Mohave-Sonoran and Chihuahuan desert provinces (Wells, 1966, 1969, 1977; Wells & Berger, 1967; Van Devender, 1973). The woodlands persisted in what are now desert lowlands until the waning phases of the Wisconsin glacial, beginning to decline perhaps as early as about 12,000 years ago at low elevations (< 600 m) in the subtropical latitudes of the Chihuahuan and Sonoran deserts, but lingering until about 9,000 BP or less at the higher elevations generally (> 1000 m) of the northerly and winter-cold Mohave Desert (Wells, 1977). Hence, the present distributional range of *Larrea* in North America appears to be recent.

Indeed, the sharply delineated spatial pattern of its polyploid races (Yang, 1970) strongly suggests that the cytogeographic differentiation of *Larrea* in the North American deserts has developed *pari passu* with a northwestward migration from southern Mexico, the most likely Ice Age refugium for the ancestral diploid, or perhaps its original point of immigration from South America (see below). Since there is no evidence for more than one species of *Larrea* in North America, the doubling and tripling of its chromosome number amounts to autopolyploidy. Investigations of protein spectra, acid-soluble phenolics, and cuticle resins of *Larrea* all indicate a rather uniform chemistry for the three cytological races that are segregated among the major deserts of the Southwest (Hunziker et al., 1972; Mabry et al., 1977). The data suggest interracial autopolyploidy. The Mohavean hexaploid could have been derived from a combination of reduced and unreduced gametes due to meiotic irregularity in the Sonoran tetraploid at the cooler and drier northwestern limits of its range. Although the possibility of an earlier cycle of expansion of the creosote bush deserts (followed by contraction to one or more refugia during the last glacial, and by reexpansion during the Holocene) cannot be ruled out on the present evidence, it seems unlikely that the remarkably simple existing cytogeography and chemistry of *Larrea* in North America could stem from so complicated a history.

OLDEST RECORDS OF *LARREA* IN NORTH AMERICA

The major features of the modern geographic pattern of *Larrea* on this continent probably originated during the climatic transition from the late Wisconsin glacial to the Holocene, when a desiccating climate gripped the immense lowlands of the Southwest, opening a vast and varied desert niche into which a burgeoning population of *Larrea* could have expanded and differentiated explosively. The oldest, well-documented record of *Larrea* in North America is dated at $10,580 \pm 550$ BP. The radiocarbon age was determined on macrofossils of *Larrea tridentata* itself, preserved in an ancient, rock-sheltered *Neotoma* (wood rat) midden from the Wellton Hills, east of Yuma in southwestern Arizona, at the very low elevation of 162 m (Van Devender, 1973). The deposit contains a desert assemblage similar to the xerophilous Sonoran Desert scrub presently growing at the site, except for the abundant macrofossils of an *Ephedra* which is now absent from the immediate area. An early occurrence of desert conditions slightly different from today seems to be established. However, other deposits obtained by Van Devender (1973) at the same locality have a similar content of *Larrea* and *Ephedra*, but have yielded much younger dates, ranging from $6,600 \pm 370$ to $7,950 \pm 370$ BP on *Larrea* macrofossils, and from $8,150 \pm 260$ to $8,750 \pm 320$ BP on *Ephedra* macrofossils. The predominance of younger dates suggests that the entire series of deposits from the Wellton Hills is early Holocene in age. If the 10,580 BP date (A-1407) is indeed accurate, it indicates an early onset of modern desert conditions at a very low elevation in one of the most arid sectors of the Sonoran Desert.

On the other hand, there are 26 dated *Neotoma* records from the lowlands of the Sonoran Desert that document the prevalence of pluvial woodlands dominated by *Juniperus*, but with no trace of *Larrea*, during the Wisconsin glacial from about 10,000 to $> 38,000$ BP (Wells, 1977). The pluvial, juniper *sans* creosote-bush woodland is recorded throughout the Sonoran Desert, even in the southern sector, and at elevations ranging from about 600 m down to about 260 m, less than 100 m above the Wellton Hills site (at 162 m). Although the latter site has been regarded as a refugium for the *Larrea* desert during the Wisconsin glacial (Van Devender, 1973), the *Neotoma* deposits are too young to prove the point. The strong positive evidence for a widespread occurrence of pluvial woodlands in the Sonoran Desert complements the negative evidence on *Larrea* (Table 1). It should be pointed out that negative *Neotoma* evidence on a potentially dominant element of the vegetation, like *Larrea*, is a fairly robust indication, so assiduous are the wood rats at collecting detailed inventories of the local flora (Wells, 1976). An authenticated contemporaneity of *Larrea* and *Juniperus* has proven to be elusive in Ice Age middens of *Neotoma*, despite the fact that modern examples of this combination are not uncommon within the narrow elevational overlap of these outstanding zonal dominants. Furthermore, *Larrea* has contributed abundantly to the ubiquitous Holocene *Neotoma* middens at desert elevations in the Southwest, amply demonstrating a lack of bias against *Larrea*. The few instances of commingling of *Larrea* and *Juniperus* macrofossils in Pleistocene wood rat deposits are apparently due to redeposition. For example, one

TABLE 1. Oldest *Neotoma* records of *Larrea* in North America are compared to records of *Juniperus*, with the sites arranged in 3 increments of elevation. *Larrea* replaced *Juniperus* as early as 10,500 BP, but only at the lowest elevation range of the subtropical Sonoran Desert. *Juniperus* persisted as late as 8,400 BP at higher elevations, especially in the winter-cold Mohave Desert. Thus, the early Holocene, cliseral transition from *Juniperus* (or pinyon-juniper) woodland to *Larrea* desert in the lowlands of the Southwest was time transgressive. References are: (1) Mehrlinger & Hooke (1969). (2) Van Devender (1973). (3) Wells & Berger (unpublished). (4) Wells & Berger (1967). (5) Van Devender & King (1971). (6) Wells & Jorgensen (1964).

Site	Desert	Elevation (m)	¹⁴ C Date, BP	Macrofossils		Reference
				<i>Larrea</i>	<i>Juniperus</i>	
Death Valley, Calif. Wellton Hills, Ariz. Wellton Hills, Ariz. Wellton Hills, Ariz. Chemehuevi Mt., Calif. Central Sonora	Mohave	Low-Elevation Range (0-500 m)	990 ± 110	abundant	nil	(1)
	Sonoran		6,600 ± 370	abundant	nil	(2)
	Sonoran		7,950 ± 370	abundant	nil	(2)
	Sonoran		10,580 ± 550	abundant	nil	(2)
	Sonoran		16,900 ± 190	nil	abundant	(3)
	Sonoran		> 38,000	nil	abundant	(3)
New Water Mt., Ariz. Newberry Cave, Calif. N. Muddy Mt., Nev. Artillery Mt., Ariz. New Water Mt., Ariz. Shift House Mt., Ariz. N. Muddy Mt., Nev. Turtle Mt., Calif.	Sonoran	Mid-Elevation Range (500-1,000 m)	603	abundant	nil	(2)
			2,710 ± 280	abundant	nil	(4)
	Mohave		7,400 ± 100	abundant	nil	(3)
	Mohave		9,900 ± 100	nil	abundant	(5)
	Sonoran		10,250 ± 200	nil	abundant	(2)
	Sonoran		603	nil	abundant	(2)
	Sonoran		551	nil	abundant	(2)
	Mohave		533	nil	abundant	(4)
	Sonoran		850	nil	abundant	(4)
			19,500 ± 380	nil		
Spotted Range, Nev. Mercury Ridge, Nev. Lucerne Valley, Calif. Aysees Peak, Nev. Spotted Range, Nev. Ranger Mt., Nev. Ranger Mt., Nev.	Mohave	High-Elevation Range (1,000-2,000 m)	1830	nil	abundant	(4)
			8,420 ± 100	nil	abundant	(6)
			9,000 ± 250	nil	abundant	(4)
			9,140 ± 140	nil	abundant	(6)
			1325	nil	abundant	(4)
			9,320 ± 300	nil	abundant	(6)
			1550	nil	abundant	(4)
			1100	nil	abundant	(6)

Neotoma deposit from an arid sector of the Sonoran Desert in Yuma County, Arizona, contained *Larrea* together with juniper and oak. However, mono-specific dating of separated macrofossils of the different species gave a radiocarbon age of only $2,710 \pm 280$ BP (late Holocene) for the *Larrea*, in contrast to $11,000 \pm 505$ BP (late Wisconsin) for the *Juniperus* (Van Devender, 1973).

The exact time of onset of desert conditions in the lowlands of the Southwest is not known, but a shift to drier climate may be inferred from compositional changes in the youngest series of *Neotoma* deposits in Maravillas Canyon, Texas, which at 600 m is close to the minimal elevation for the entire Chihuahuan Desert province, and lies 800 m below existing woodland. One thick sequence has a basal layer with a radiocarbon age of $12,550 \pm 130$ BP. The layer contains a rich assemblage of woodland species, with relatively more pinyon pine and juniper than scrub oak, and it has comparatively few "desert" species. Moreover, the composition of this deposit is essentially the same as nearby deposits of more or less full-glacial age ($14,800 \pm 180$, $16,250 \pm 240$, and $20,000 \pm 390$ years BP) at the same elevation (600 m) or even higher (880 m). Hence, climatic conditions equivalent to the maximal pluvial effects of the Wisconsin glacial in the Chihuahuan Desert region were still in force there at the lowest elevations about 12,500 years ago (Wells, 1966).

In contrast, the two younger deposits in normal superposition in the series, with radiocarbon ages of $12,000 \pm 150$ and $11,560 \pm 140$ years BP, have much more scrub oak and juniper than pinyon pine, and contain several "desert" or semidesert species lacking in older deposits (but no *Larrea*): *Acacia roemeriana* Scheele (armed shrub); *Yucca rostrata* Engelm. and *Y. torreyi* Shafer (semi-succulent rosette shrubs); *Echinocereus* cf. *dasyacanthus* Engelm. (stem succulent). These changes clearly indicate that the climate already had begun to warm or to desiccate about 12,000 years ago, and this trend was still continuing about 11,500 years ago. It is as yet uncertain whether the apparent lack of further deposition by wood rats, immediately after 11,500 years ago, signifies the termination of pluvial woodland climate in the lowlands of the Chihuahuan Desert at about that time. Since *Larrea* now grows abundantly near this and other ancient *Neotoma* sites in the deserts of the Southwest, its consistent absence in deposits older than 8,000–10,000 BP is compelling, even though negative, evidence (Table 1).

FULL-GLACIAL DISPLACEMENT OF WOODLANDS INTO THE WARM DESERTS OF NORTH AMERICA

The pluvial woodlands that occupied what is now the *Larrea* zone left an abundant macrofossil record in numerous Pleistocene *Neotoma* middens sheltered in dry caves throughout the Southwest. The greatly expanded Pleistocene woodlands varied geographically in species composition, as do the drastically shrunk modern remnants that have retreated upward 600–800 m or more to the relatively restricted areas of higher elevation (Wells, 1969). In the more arid, orographic rain shadows of the Mohave Desert region, a well-marked, late-Pleistocene zonation was developed within the woodland zone, as follows: (1) Higher elevations: *Pinus monophylla* Torr. & Frém. (single leaf pinyon), *Juni-*

perus osteosperma (Torr.) Little (Utah juniper), *Acer glabrum* Torr. (a xerophytic maple), *Ceanothus greggii* A. Gray (an evergreen sclerophyll of chaparral), *Chamaebatiaria millefolium* Maxim. (fern bush). (2) Lower elevations: *Juniperus osteosperma*, *Yucca brevifolia* Engelm. (Joshua tree), *Y. whipplei* Torr. (Our Lord's candle, now extinct in the Mohave Desert), *Atriplex confertifolia* S. Wats. (shadscale), and other desert shrubs, but never *Larrea* (Wells & Jorgensen, 1964; Wells & Berger, 1967, unpublished; Wells, 1977).

The lower part of the juniper-Joshua tree zone extended from the eastern Mohave Desert south along the trough of the lower Colorado River valley into what is now the northwestern Sonoran Desert, descending to an elevation of 260 m, and possibly lower (Wells & Berger, 1967; Wells, 1972, 1977; Van Devender, 1973; Phillips & Van Devender, 1974). A *Neotoma* midden with the xerophilous juniper-Joshua tree woodland assemblage of macrofossils, but without a trace of *Larrea*, was found at the latter elevation between Needles and Parker in the midst of the extremely arid *Larrea* zone of the Colorado sector of the Sonoran Desert. The deposit has a radiocarbon age of $16,900 \pm 190$ BP (UCLA-1666), which is equivalent to full-glacial age. Presence of *Juniperus* and absence of *Larrea* is also recorded in *Neotoma* deposits (one dated at $> 38,000$ BP) from the low plains (450 m) of the southern Sonoran Desert in the latitude of Hermosillo, Sonora (29° N), an area now dominated by saguaro-paloverde/creosote-bush desert, and lacking mountains high enough to support *Juniperus* at present (Wells & Berger, unpublished).

The higher elevation zone of the pluvial woodlands of the Mohave region also occurred in the mountains along the northwestern fringe of the Sonoran Desert province in southeastern California and western Arizona. Thus, *Pinus monophylla* and *Juniperus osteosperma* dominated the long-vanished, pluvial pinyon-juniper zone of the now arid Turtle Mountains, being recorded at about 14,000 BP in *Neotoma* middens as low as 730 m, in what is now paloverde-ironwood/creosote-bush desert (Wells & Berger, 1967). From the lower Colorado River valley eastward across the Sonoran Desert, shrubby live oaks (*Quercus turbinella* Greene, *Q. palmeri* Engelm.) were important associates of the pluvial woodland conifers at elevations above 600 m (Leskinen, 1970; Van Devender & King, 1971; Van Devender, 1973), just as they are today at much higher elevations along the Mogollon Rim and in the mountains of northwestern Arizona and southern Nevada. The Pleistocene *Neotoma* records of live oaks from southwestern Arizona, dated as recent as about 11,000 BP, are supplemented by relictual colonies of a shrubby, xerophytic oak (*Q. turbinella* with some characters of *Q. ajoensis* C. H. Muller), surviving to the present day in deep, mesic canyons of the low and isolated Shit House and Castle Dome mountains (Tucker & Muller, 1956). The latter ranges are remarkable in still harboring a live-oak, while becoming too arid to support the xerophilous conifers of the pinyon-juniper woodland, which formerly associated with it in this sector of the Sonoran Desert (e.g., in the Shit House Mountains at 862 m, about 13,000–14,000 BP). Presence of evergreen oaks in the pluvial woodlands at higher elevations of what is now the Sonoran Desert suggests a mild climate there during the glacials of the Pleistocene.

Far to the southeast, this trend was developed to a greater degree in the Big Bend area of the Chihuahuan Desert, with a different set of evergreen oaks (*Quercus pungens* Liebm., *Q. grisea* Liebm., *Q. arizonica* Sarg.) sorting out in Wisconsin-age *Neotoma* middens throughout the range of elevation of the existing desert, together with the different pinyon pine (*Pinus cembroides* Gord.) and junipers (*Juniperus pinchotii* Sudworth, *J. deppeana* Steud.) of the region (Wells, 1966). Hence, the pluvial woodlands of the Chihuahuan Desert province differed significantly from those of the Sonoran and Mohave desert provinces in having a much lesser degree of zonation with elevation (that is, no evidence of downward segregation of a pineless, oakless, juniper zone). In fact, the full-glacial *Neotoma* record shows a uniform dominance of pinyon, juniper, and scrub live-oak over the entire span of elevation available in the Chihuahuan Desert (Wells, 1977). Again, as in the other deserts now dominated by the creosote bush, no trace of *Larrea* was detected in the pluvial-age *Neotoma* deposits (Wells, 1966). Absence during the Wisconsin glacial of segregated *Juniperus*, *Juniperus-Yucca*, or *Yucca* zones at lower elevations in the northern Chihuahuan Desert stands in striking contrast with the very characteristic zone of arborescent yuccas and other Agavaceae within and just below the montane woodlands in the province today (Wells, 1965). The lack of zonation, and the consistent presence of evergreen oaks, indicate that the Chihuahuan Desert province enjoyed an even more mesic, pluvial woodland climate in its vast, now arid lowlands than the Sonoran Desert, which, in turn, was probably more equable (mild, even climate) than the cool-arid, oakless, Mohavean province to the northwest. The apparent east-west, paleoclimatic gradient of increasing aridity in the lowlands during the Wisconsin glacial may have been caused by decreasing summer rainfall in the westward direction, as a function of decreasing penetration of moist air masses with increasing distance from the Gulf of Mexico, essentially as in the modern pattern.

FULL-GLACIAL REFUGIA FOR WARM-DESERT SPECIES

The decidedly high elevation (1,500–2,300 m) of the *Larrea* plains in the southern sector of the Chihuahuan Desert in Zacatecas and San Luis Potosí would seem to render them even less suitable as warm-desert refugia under the full-glacial climate than the low elevation (600–1,400 m) trough along the Río Grande. The strongly meridional atmospheric circulation during the glacials would have greatly augmented the present wintry visitations of rainy or snowy cold fronts caused by outbreaks of polar air from the north (the *norte*, or norther), which would have had a telling effect on thermophilous desert vegetation at such high elevations. Moreover, the 800 m pluvial downward displacement of the pinyon-juniper-oak woodland zone, firmly established by abundant macrofossil evidence in the much lower and presently hotter and more arid Big Bend area of the Río Grande valley (Wells, 1966), would have been more than enough to shift the main body of the woodland zone down onto the high intermountain plateau of the southern Chihuahuan Desert province (Wells, 1977).

Where then did the floristically rich, warm deserts survive the glacials of the Pleistocene? Suitable full-glacial refugia for the extremely xerophytic, thermo-

philous desert vegetation of North America might be sought where there is a combination of low elevation, tropical latitude, orographic rain shadow (also providing protection from outbreaks of polar air), and therefore local or regional aridity, well buffered against pluvial invasion by more competitive, mesophytic trees and shrubs. One example might be the arid, rain-shadow pocket on the Extorax-Tula drainage in eastern Querétaro at 21° N, which now harbors a remarkably isolated area of *Larrea*-dominated landscape at elevations ranging from 1,000 m or less to about 1,500 m (northwestern sector of desert "island," numbered 4 in Fig. 1). A significantly large number of Chihuahuan Desert species are known to share this distribution. For example, Quintero (1968) lists 47 species in 34 genera that are important elements of the Chihuahuan Desert vegetation, and which occur in the Valle del Mezquital, Hidalgo (southeastern part of desert "island," Fig. 1, number 4). These include *Larrea*, *Flourensia cernua* DC., *Euphorbia antisiphilitica* Zucc., and *Agave lecheguilla* Torr. Hence, the flora of the Chihuahuan Desert has extended into this southeasterly pocket in full force.

The mild but arid climate in Querétaro and Hidalgo is reflected in the rich diversity of succulents, including about 18 genera and 77 species of cacti (Bravo, 1936; 1937; Britton & Rose, 1920). The fact that many of the cacti are narrowly endemic within this limited area strongly suggests a considerable antiquity for the desert plants confined there. The endemics almost certainly antedate the later glacials of the Pleistocene, but did they evolve *in situ*? In this connection, there are several species of large, temperature-sensitive cacti in the same area, namely the columnar *Cephalocereus senilis* Pfeiff. (endemic) and *Pachycereus marginatus* Britton & Rose (endemic); the gigantic, candelabriform *Lemaireocereus dumortieri* Britton & Rose and *Myrtillocactus geometrizans* Cons.; and enormous barrel cacti of the genus *Echinocactus*. Large, succulent cacti are known to be extremely sensitive to frost (Shreve, 1951). The relatively hardy saguaro (*Carnegiea gigantea* Britton & Rose), which has the most northerly distribution of any of the columnar giants of México, is nevertheless subject to damage from frost in Arizona if temperatures drop below -5° C for a brief period, and death may result from exposure to frost (0° C) for 29 consecutive hours (Shreve, 1911). It may be inferred that the giant succulents of southern Mexico are at least as good indicators of mild winter climate as the saguaro, and that the narrowly endemic columnar or candelabriform giants are located in areas that have not been subjected to severe frost during their long tenure. Hence, it seems very likely that the lower elevation range of the Querétaro-Hidalgo rain-shadow pocket had a relatively mild, frost-free climate during the glacials of the Pleistocene. At the same time, the climate must have been arid enough to harbor the rich and partly endemic assemblage of xerophytes presently sequestered there, inasmuch as the rain-shadow is an isolated cul-de-sac, and there is no lower or drier area available which could have served as a better refugium for the desert flora. At lower elevations, the Río Tula drainage cuts through the Sierra Madre Oriental and enters a much wetter climate with dense, nondesert vegetation.

There are a few other rain-shadow deserts in southern Mexico and Guatemala (see Fig. 1), and no other desert in North America is richer in bizarre xerophytes

than the Valle de Tehuacán, Puebla, with about 9 genera and 24 species of gigantic cacti. However, each of these islandlike pockets of aridity has its own unique assemblage of desert plants, and all of the deserts south of Hidalgo lack *Larrea* (Wells, 1977). Thus, there is no phytogeographic indication of any massive connection of the isolated deserts of Puebla-Oaxaca and Guatemala with the main body of the North American deserts about 500 km or more to the north, even if such a connection were physiographically possible. In fact, the Neovolcanic Axis is studded with lofty volcanos from Volcán Orizaba near the Gulf of Mexico to Volcán Colima near the Pacific coast, and the interconnecting high divides interpose a formidable east-west barrier to the north-south migration of thermophilous desert plants, even now. Of course, vegetation zones were much lowered during the glacials, when the high peaks were glaciated (Flint, 1971), thus enhancing the montane barrier.

The Sonoran Desert was undoubtedly a major desert refugium during the Pleistocene. With 141 families, 731 genera and 2,581 species of vascular plants (Shreve & Wiggins, 1964), the Sonoran Desert has the richest flora of all the deserts in North America, although it is not the most areally extensive of the warm deserts, being exceeded in this respect by the Chihuahuan Desert. The high rate of endemism in the subtropical flora of the Sonoran Desert (about 30% of the 2,581 species are unknown outside its boundaries), and the rich assemblage of cacti (20 genera, 173 species), constitute the best evidence that some areas in the vicinity of the existing desert served as an Ice Age refugium for desert plants. Since the known macrofossil record from southeastern California, southwestern Arizona, central Sonora and northern Baja California documents an extensive incursion of pluvial woodlands throughout the greater part of the northern Sonoran Desert, the refugium was most likely in the southernmost sector, including the southern half of Baja California, the southern extremity of Sonora, and perhaps northern Sinaloa (Fig. 1, shaded area). The desert flora of Baja California, with 1,450 species, comprises more than half (56%) of the flora of the Sonoran Desert, and with 461 endemic species accounts for nearly 60% of the endemism, despite the relatively small area of the peninsula compared to the mainland. Thus, southern Baja California has almost certainly been a major refugium for desert xerophytes during at least the Wisconsin glacial. Whether it was a refugium for *Larrea* remains unknown.

ORIGIN OF THE NORTH AMERICAN POPULATION OF *LARREA*

The biogeography of *Larrea* during the Pleistocene is a particularly interesting enigma because there is an intriguing possibility of a late, intercontinental dispersal from South America, where the widely disjunct genus exhibits markedly greater morphological and ecological diversity than it does in North America (Hunziker et al., 1972). There are four very different species of *Larrea* in South America, but only one species is present in North America, namely, *L. tridentata* (Sessé & Moc. ex DC.) Cov., which is evidently a derivative of the South American *L. divaricata* Cav. The two very similar taxa have been regarded as conspecific, the North American one being *L. divaricata* subsp. *tridentata* (Sessé & Moc. ex DC.) Felger & Lowe.

Among the several lines of evidence supporting a South American origin for the North American population of *Larrea*, the most important phylogenetic point is that two of the endemic South American species occurring in less xeric (and therefore less specialized) habitats in Argentina and Chile, namely *L. ameghinoi* Speg. and *L. nitida* Cav., have multifoliolate, pinnately compound leaves, which are ancestral traits within their family, the Zygophyllaceae. However, the peculiar bifoliolate leaf of the North and South American populations of the more xerophilous *L. tridentata* and *L. divaricata* is reduced to only the basal (?) pair of leaflets of a pinnate leaf. Also, the virtually unifoliolate leaf of the even more xerophilous Argentinian endemic, *L. cuneifolia* Cav., presents a further simplification by partial fusion of the two leaflets. The leaves of *L. cuneifolia* are uniquely specialized in their vertical orientation with respect to the noonday sun, thus reducing insolation in the manner of the well known "compass" plants (e.g. *Silphium laciniatum* L. of the North American prairie). *Larrea divaricata* (s. lat.) and *L. cuneifolia*, with their specialized, reduced leaves, are by far the most xerophytic species in the genus, occurring in some of the most arid deserts in the world, and the latter species occurs in even drier habitats than the former (Hunziker et al., 1972). Thus, *L. cuneifolia* is the xerophytic culmination of an evolutionary reduction series from the relatively mesophytic, multifoliolate, pinnate leaf, with some steps in the pattern surviving today only in South America. Another uniquely South American vegetative character in this genus of erect shrubs is seen in *L. ameghinoi*, which has a prostrate, creeping growth habit, no doubt conferring fitness in its native habitat on the windy plains of Patagonia. It is unlikely that the strikingly ecomorphological phyletic pattern of *Larrea* in South America has evolved as a result of a hypothetical introduction from North America of the evolutionarily advanced taxon, *L. tridentata*, although this is a possibility that has been considered by a respected minority of botanists.

On the other hand, the North American *L. tridentata* has differentiated into a series of polyploid races, diploid ($n = 13$) toward the southeast, and hexaploid about 1,000 km to the northwest (see above), whereas the South American vicariant, *L. divaricata*, is consistently diploid throughout a 2,500 km transect of *Larrea* desert (Hunziker et al., 1972). But the latter taxon has putatively contributed a complement of chromosomes to the genome of the allotetraploid ($n = 26$) South American endemic, *L. cuneifolia*. The natural triploid hybrid between *L. cuneifolia* and the diploid, South American *L. divaricata* formed 13 bivalents + 13 univalents in nearly 50% of the pollen mother cells examined (Hunziker et al., 1972). Hence, *L. divaricata*, despite its apparent lack of *infraspecific* cytological differentiation, must be a more ancient resident of South America than its allopolyploid offshoot, *L. cuneifolia*, the most xerophytic, and perhaps the most evolutionarily advanced, member of the genus *Larrea*. The striking cytogeographic differentiation within the North American *L. tridentata*, together with the complete distinctness of the insect faunas on *Larrea* in North and South America (C. D. Michener, personal communication), suggest that *Larrea* is also of some antiquity on the North American continent (Turner, 1972; Porter, 1974). However, electrophoretic analyses of proteins (seed albumins),

paper chromatography of acid-soluble phenolic compounds, and chemical analyses of phenolic, cuticle resins establish a uniform chemistry throughout the geographically extensive, cytologically differentiated populations of *L. tridentata* in North America (Hunziker et al., 1972; Mabry et al., 1977). These data suggest an autopoloid, and probably recent, origin for the cytogeographic races of *L. tridentata* in North America. The South American species of *Larrea*, including *L. divaricata*, show considerable interspecific and geographic diversity in their chemistry, again indicating a greater antiquity for the genus in South America (Mabry et al., 1977).

REPRODUCTIVE STRATEGY AND MIGRATION

The biogeography of the other genera in the family Zygophyllaceae offers some perspective on the origin of the enormous disjunction in the distribution of *Larrea*; it should be pointed out that the northernmost outlier population of *L. divaricata* near Ica, Peru (Morello, 1958) is separated by more than 5,000 km of unsuitably humid tropical vegetation from the southernmost outlier population of *L. tridentata* near Ixmiquilpan, Hidalgo, México (Rzedowski & Medellín Leal, 1958), while the main populations are about 7,000 km apart. However, other genera of Zygophyllaceae show even wider disjunctions (Table 2). *Kallstroemia* has 17 species segregated in North and South America, and the related *Tribulopsis* has 7 species in Australia. Both genera relate to the now subcosmopolitan, weedy genus *Tribulus*. *Fagonia* has 9 species in North America, 3 in South America, and 38 in Africa-Eurasia. *Peganum* has 1 species in the Chihuahuan Desert of México and another 2 species in the aridlands of North Africa-Eurasia (Porter, 1974). But *Kallstroemia*, *Tribulus*, *Tribulopsis*, *Fagonia*, and *Peganum* are herbaceous annuals or perennials (or subligneous in many *Fagonia*) of relatively dry, open habitats that have opted for an "r" strategy with a high ratio of reproductive to vegetative effort (Gadgil & Solbrig, 1972). Indeed, *Tribulus terrestris* L. and *Peganum harmala* L. are very weedy herbs, aggressively spreading through the warmer or drier regions of the world. In general, "r"-selected, herbaceous or subligneous species have a well-developed dispersal capacity, which confers fitness by enabling them to invade open habitats that are distant from the parent population and relatively free of intense competition, which favors successful ecesis. The invasive, colonizing way of life, associated with a large reproductive effort and brief longevity, predisposes "r"-strategists to the vagaries of long-distance, even intercontinental, dispersal, as in the weedy, light-seeded, wild tobaccos, which have reached North America, and even Australia (cf. *Tribulopsis*) and the South Pacific islands, from their ancestral seat in northern South America (Wells, 1959; Goodspeed, 1954).

In contrast, woody shrubs and trees have a relatively "K" strategy of allocation of photosynthate, assigning a large proportion to vegetative growth (as wood), and producing fewer, relatively heavy seeds with reduced potential for dispersal, but with a greater chance for success at carrying capacity ("K") population-densities. Salisbury (1942) has thoroughly documented the relative seed weights and dispersal capacities of herbs and woody plants (cf. Baker, 1972). The general principle of greater intercontinental dispersal capacity of herbs

TABLE 2. Intercontinental distributions of the American genera of Zygophyllaceae, and some allied genera of South Africa and Australia, with the number of species per continent. Basic chromosome number (x) from literature (largely from Porter, 1972, 1974). Compare the wide, intercontinental disjunctions within herbaceous, "r"-selected genera, and the narrow, continental endemism of woody, relatively "K"-selected genera, with the notable exception of *Larrea*.

Genera	x	N. America	S. America	S. Africa	N. Africa- Eurasia	Australia
Woody:						
<i>Bulnesia</i>	13	0	8	0	0	0
<i>Larrea</i>	13	1	4	0	0	0
<i>Porlieria</i>	13	0	3	0	0	0
<i>Plectrocarpa</i>	13	0	2	0	0	0
<i>Metharme</i>	—	0	1	0	0	0
<i>Pintoa</i>	10	0	1	0	0	0
<i>Guaiacum</i>	13	5	1	0	0	0
<i>Morkillia</i>	—	2	0	0	0	0
<i>Sericodes</i>	15	1	0	0	0	0
<i>Viscainoa</i>	13	1	0	0	0	0
<i>Neoluederitzia</i>	—	0	0	1	0	0
<i>Sisyndite</i>	10	0	0	1	0	0
Herbaceous or subligneous:						
<i>Kallstroemia</i>	16	7	10	0	0	0
<i>Tribulopsis</i>	—	0	0	0	0	7
<i>Fagonia</i>	9-12	9	3	2	36	0
<i>Peganum</i>	11-12	1	0	0	2	0

(more so for annuals than perennials) relative to woody plants is beautifully exemplified by the amphitropical, disjunct distributions in the floras of North and South America. More than 200 species, or vicarious species-pairs, show the amphitropical disjunction, but woody plants and K-selected herbs of closed communities are scarcely represented (Raven, 1963). Significantly, the few woody genera with more or less conspecific, amphitropical disjuncts are desert shrubs of open, readily colonized habitat: *Atamisquea emarginata* Miers and *Koeberlinia spinosa* Zucc., both of the Capparidaceae, and the vicariant pair *Larrea divaricata*-*L. tridentata*.

On the other hand, *Larrea* is unique among the many woody genera of the xerophytic family Zygophyllaceae in having a major, *intercontinental* disjunction in its range, and doubly so, because the disjunction is due to very closely related, vicariant species. The North American population of *Larrea* is classified as a separate species, *L. tridentata*, but it differs mainly in having acute stipules and somewhat falcate leaflets (Porter, 1963). In the great majority of characters, including a diversity of other vegetative and floral traits, protein spectra, and acid-soluble phenolics, the North American population of *Larrea* parallels the South American species *L. divaricata* (Hunziker et al., 1972). If current studies show that genetic barriers to reproduction exist (experimental hybrids are semi-sterile), then perhaps *L. tridentata* is properly accorded the rank of semispecies or sibling species with *L. divaricata* (Yang, Hunziker, et al., unpublished). The greater morphological and ecological differentiation of *Larrea* in South America suggests a greater antiquity for the genus in that segment of the disjunction.

The distribution of woody genera even remotely related to *Larrea* is predominantly confined to the two large continents of the southern hemisphere (Table 2). Thus, there are 7 genera and 20 species of woody Zygophyllaceae in South America and 3 monotypic genera in southern Africa; this compares with 5 genera and 10 species in North America. Moreover, the genera closest to *Larrea* are the South American endemics *Metharme* (monotypic) and *Plectrocarpa* (ditypic), according to Engler (1896), who made a comprehensive study of the distribution and systematics of the Zygophyllaceae. The genus *Larrea* has no close relatives in North America, although it shares a few characteristics with the monotypic genus *Sericodes*, an endemic shrub of the Chihuahuan Desert with a deviant karyotype ($n = 15$). *Sericodes* has similar, densely pubescent fruits, dividing into tiny, light, hairy mericarps with a potential for long-distance, ectozoic dispersal, and it may have had a migrational history similar to that of *Larrea*.

MODE OF INTERCONTINENTAL MIGRATION

The weight of biogeographic evidence supports a South American origin for the genus *Larrea*, but the migration to North America must have lacked continuity. If the extremely xerophytic species *Larrea divaricata* had been able to follow the hypothetically continuous route across the now wet tropics (from northern South America through the Central American isthmus to southern Mexico) during a period of drier climate (Johnston, 1940), then a much greater amphitropical disjunction of zygophyllaceous genera should be expected to exist between the deserts of North and South America. As it is, the only real disjunctions are in *Larrea* and *Fagonia* (Porter, 1974). The single species of *Guaia-cum* (*G. officinale* L.) reaching South America is a relatively mesophytic, island-hopping tree of the West Indies, and *Kallstroemia* has some species in Central America (Standley, 1937). Thus, there are 10 genera of xerophytic Zygophyllaceae which do not share the amphitropical distribution attained by *Larrea* (Table 2), including the widely dispersed herbaceous genus, *Peganum*, which has attained an even greater disjunction between the deserts of northern Mexico and northern Africa!

Absence of the genus *Bulnesia* in North and Central America is a particularly difficult anomaly for the continuity theory, because *Bulnesia* has a much wider ecological amplitude than *Larrea*, having two relatively mesophytic species of trees (*B. arborea* Engelm., *B. carrapo* Killip & Dugand.) in humid tropical woodlands north of the equator in Venezuela and Colombia (Porter, 1974). *Bulnesia* parallels *Larrea* in its xeromorphic evolutionary trend with a reduction series from multifoliolate, pinnately compound leaves (as in *B. arborea*) to the bifoliolate leaves of *B. sarmientoi* Lorentz ex Griseb. However, *Bulnesia* also exceeds *Larrea* in the xerophytic direction, inasmuch as *B. retama* occurs in sectors of the South American deserts much too arid for *Larrea divaricata*, or even *L. cuneifolia*. Any continuous route across the tropics, hypothetically traversed by *Larrea*, should have been more readily negotiated by the ecologically more versatile genus *Bulnesia*, with its 8 extant species all endemic to South America. The argument could be extended with the plethora of examples proving a lack

of free exchange between the xerophytic floras of North and South America (Raven, 1963). Also, the insect faunas more or less indigenous to *Larrea* are distinctly different on either side of the amphitropical disjunction (Michener, personal communication; Raven, 1963), a fact strongly suggesting rapid passage through a bottleneck or filter. On the one hand, these biogeographic data defeat the idea of trans-tropic continuity for *Larrea* or most other desert plants in the Americas, but they also point to a South American origin and differentiation for *Larrea*, followed by a relatively recent colonization of the corresponding desert niche in North America by the evolutionarily advanced species, *L. divaricata*.

There remains the major question as to how *Larrea* reached North America. Long-distance transport across the wet tropics seems to be the only feasible possibility (cf. Raven, 1963). Among the available carriers would have been the golden plover (*Pluvialis dominica*), remarkable for its long-distance, nonstop flights during its annual intercontinental migrations between North and South America. Less well known is the similar migration of the upland plover (*Bartramia longicauda*). Unlike most shorebirds (order: Charadriiformes), these two species frequent dry, upland habitats, and winter on the shrub-steppes and grasslands of Argentina. *Pluvialis* winters on the pampas and *Larrea* steppes as far south as Bahía Blanca and inland to the very arid, desert province of Mendoza, while *Bartramia* has similar wintering grounds, but also extends south into the Patagonian *Larrea* country of the Río Negro province (Olrog, 1959; Wetmore et al., 1957: 173). Both species were enormously abundant prior to the onslaught of the market gunners and sportsmen of the late nineteenth century (Hudson, 1918: chap. 21; 1920).

In the northern spring season, when the birds departed from Argentina for their breeding grounds in the Arctic tundra (*Pluvialis*) or the prairies (*Bartramia*) of North America, it was autumn in the southern hemisphere, and the hairy mericarps of *Larrea* were available for dispersal. It has been established by experimental feeding of caged birds that a related charadriid plover, the killdeer (*Charadrius vociferus*), retains some viable seeds in its gizzard for periods as long as 77 to 160 hours, and sometimes up to 340 hours, or about 2 weeks (Proctor, 1968). Since plovers cruise at speeds of about 70 km/hr, with top speed of about 90 km/hr (McLean, 1930), intercontinental transport of ingested seed is indeed possible; a distance of 7,000 km could be traversed in 100 hours of flying time. The very light, densely hairy mericarps of *Larrea* suggest an alternate, ectozoic mode of carriage, possibly cemented to the undertail coverts by the birds' own excrement (the "slovenly plover" mechanism, suggested informally by G. Ledyard Stebbins). On its spring migration the golden plover flies northwestward from Argentina across Bolivia and the Peruvian Andes, and more or less nonstop across Central America, whence it proceeds northward through México, including the arid interior plateau (Wetmore et al., 1957). With millions of birds flying this route for thousands of years, even a seemingly highly improbable event would have been feasible. Thus, diploid South American *Larrea divaricata*, which is at least in part self-compatible (Hunziker et al., 1972; cf. Baker, 1955), could have reached the Chihuahuan Desert of North America by a single, direct dispersal from Argentina. Note, however, the existing

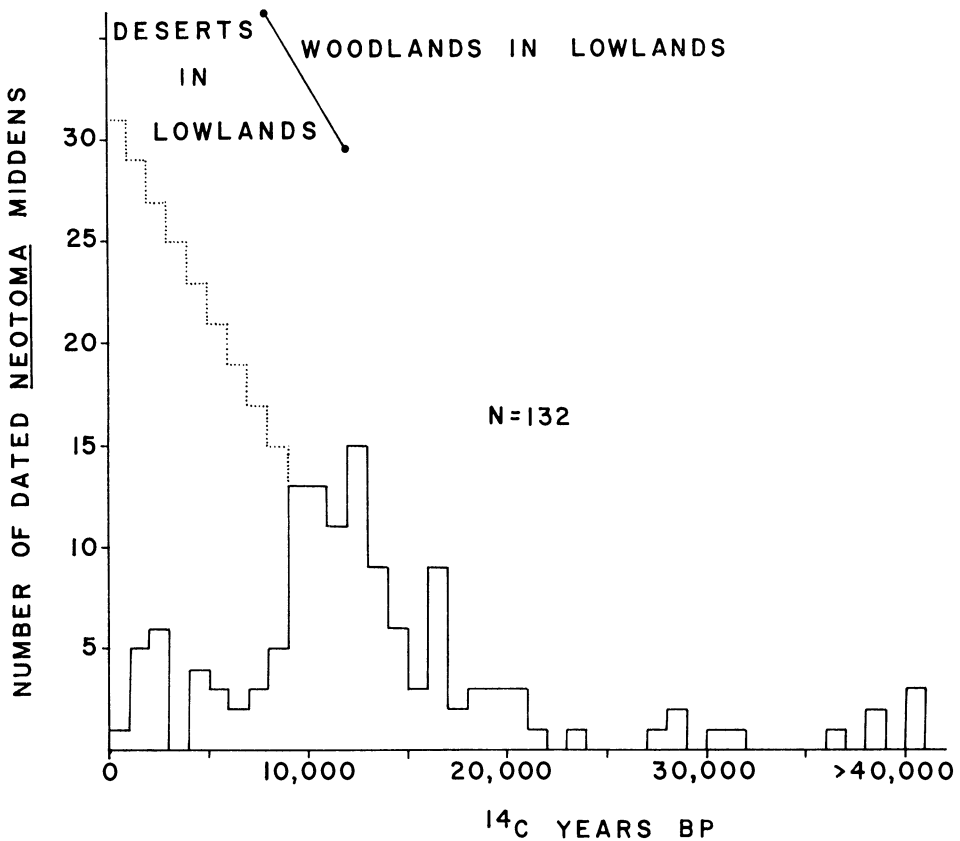


FIGURE 2. Frequency distribution plot of 132 radiocarbon dates obtained on subfossil *Neotoma* middens that have been preserved in dry rock shelters in western North America. The dates are grouped by time intervals of one millenium. The apparent modal peak at 9,000 to 12,000 BP is an artifact of under-representation of the ubiquitously abundant Holocene deposits. An extrapolated projection, based on the late-glacial trend, is added as a dotted line to give a more realistic plot for the Holocene. The vegetational change from pluvial woodland to desert scrub in the lowlands of the Southwest is time transgressive, depending on latitude and elevation of site; cf. Table 1.

way-stations for *Larrea* in northern South America and southern Mexico, mentioned above.

The "way-station" or stepping-stone hypothesis of long-distance migration for amphitropical disjuncts was advocated by Raven (1963), and it appears plausible for some taxa. However, recently obtained data on the chemistry of *Larrea* (Mabry et al., unpublished) argue against the way-station idea for creosote bush. *Larrea tridentata* (North America) shares 85% of 20 flavonoid aglycones with *L. divaricata* from Argentina, but has only 45% of them in common with the northernmost putative "way-station" for *Larrea* in Peru. Unexpectedly, the less distant Peruvian population of *L. divaricata* differs markedly from the Argentinian population, having only 40% of the same set of flavonoids in common. These data support the inference that the Peruvian population of *Larrea* is an older segregate

than the North American vicariad, despite the more dramatic disjunction of the latter. Thus, an *independent* history of isolation is suggested for North American and Peruvian populations of *Larrea*. We infer that *Larrea* colonized North America directly from Argentina, and *not* via Peru, even though the latter station may have been established earlier.

As to the timing of the North American colonization, the paleobotanical evidence is as yet incomplete. Whether *Larrea* arrived in southern Mexico before or during the transition from Pleistocene to Holocene, there is conclusive evidence that the present wide dominance of the *Larrea* zone throughout southwestern North America was not attained before the Holocene (Fig. 2). As discussed above, *Larrea* has not been detected in the full-glacial *Neotoma* record from any part of the Mohave Desert, nor from the Sonoran Desert in southeastern California, northern Baja California, and central Sonora, nor from the Chihuahuan Desert in Texas. During the height of the Wisconsin-age pluvials, any extensive creosote bush deserts must have been displaced far to the south by the great expansion of the woodland zone throughout most of the vast lowlands presently dominated by *Larrea* in southwestern North America. Of course, the current inadequate state of knowledge does not preclude the existence of *Larrea* in one or more North American refugia during the glacials of the Pleistocene, but the available evidence is in agreement with a relatively recent, perhaps late-Wisconsin or early Holocene, age for *Larrea* in North America.

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SEIWA-EN, A NEW JAPANESE GARDEN AT THE MISSOURI BOTANICAL GARDEN

Displayed on the banner of this issue is a very early spring view of a portion of the new Japanese Garden that has been under development since 1974. It has been named *Seiwa-En*, meaning “garden of pure, clear harmony and peace.” Designed by Prof. Koichi Kawana, professor of Environmental Design at the University of California, Los Angeles, this beautiful new addition to the Missouri Botanical Garden was formally dedicated 5 May 1977. With a four-acre lake as the focal point, the new garden features, among other things, three islands, two waterfalls, a traditional Japanese teahouse, four bridges of different traditional styles, dry rock gardens, and extensive plantings of trees and shrubs with an emphasis on pines, *Cryptomeria*, *Euonymus*, quince, azaleas, and cherries. Totalling twelve acres, this garden is the largest of its kind in the United States.—*Editor*