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HISTORICAL VICARIANCE AND POSTGLACIAL COLONIZATION EFFECTS ON THE EVOLUTION OF GENETIC STRUCTURE IN *LOPHOCEREUS*, A SONORAN DESERT COLUMNAR CACTUS

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Abstract.—Distinguishing the historical effects of gene migration and vicariance on contemporary genetic structure is problematic without testable biogeographic hypotheses based on preexisting geological and environmental evidence. The availability of such hypotheses for North America's Sonoran Desert has contributed to our understanding of the effect of historical vicariance and dispersal events on the diversification of this region's vertebrate biota but have not yet been applied to its flora. In this paper we describe a detailed allozyme analysis of the population genetic structure and phylogeography of the Sonoran Desert columnar cactus, *Lophocereus schottii* (senita). Inferred phylogroup distributions reflect two historical vicariance events: (1) a middle Pliocene northward transgression of the Sea of Cortéz that is reflected in well-supported Baja California peninsular and continental phylogroups but not in current taxonomic treatments of the species; and (2) a late Pliocene transpeninsular seaway across southern Baja that is reflected in tentative support for peninsular and southern Cape Region phylogroups corresponding to taxonomic varieties *L. schottii* var. *schottii* and *L. schottii* var. *australis*, respectively. A middle Pleistocene midpeninsular seaway hypothesized to explain congruent phylogroup distributions in several vertebrate taxa is not reflected in *L. s.* var. *schottii*, nor is the distinction of a third variety, *L. s.* var. *tenuis*, from continental populations of *L. s.* var. *schottii*. Linear regression of pairwise estimates of interpopulation differentiation ($\hat{M}$ and $F_{ST}/[1 - F_{ST}]$) on interpopulation geographic distance revealed significant evidence of isolation by distance within peninsular and continental phylogroups but not between them, consistent with historical vicariance between but not within these regions. We also found significant evidence of isolation by distance between putative *L. s.* var. *schottii* and *L. s.* var. *australis* phylogroups, suggesting that reproductive isolation between peninsular and Cape Region forms is incomplete. Within peninsular, but not continental, phylogroups, northward range expansion from southern Pleistocene refugia is reflected in significant declines in genetic variation with increasing latitude and in an area phenogram in which populations are progressively nested from south (ancestral) to north (descendant) along the Baja peninsula. Although the geographic concordance of phylogenetic topologies suggests that ancient vicariance events, and not dispersal, have primarily influenced the biogeographic distributions of Baja's vertebrate biota, the phylogeographic structure of *L. schottii* suggests that Sonoran Desert plant species may exhibit genetic signatures of postglacial range expansion and gene flow as well as vicariance.

Key words.—Cactaceae, genetic structure, *Lophocereus*, phylogeography, range expansion, Sonoran Desert, vicariance.

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Contemporary biogeographic patterns of genetic variation are determined by historical patterns of gene flow and vicariance among populations (Hewitt 1996; Soltis et al. 1997; Avise 2000). This history should be reflected in the genetic structure and phylogeography of extant populations, providing information to infer evolutionary processes and to test biogeographical scenarios underlying patterns of genetic differentiation. Models of gene flow and vicariance predict that each process should generate a distinct genetic signature and phylogeography. If gene flow is spatially restricted among populations, as occurs in most organisms (stepping-stone and isolation-by-distance models), then genetic structure is generated in which relatedness among populations declines monotonically as a function of the length of the path of migration between them (Wright 1943; Kimura and Weiss 1964; Slatkin 1993). If net dispersal is anisotropic, as with range expansion from refugial populations, this pattern of isolation by distance will be accompanied by intraspecific phylogenies with recently derived populations serially nested within successively ancestral ones along the axis of expansion (i.e., the ''progression rule'' sensu Funk and Wagner 1995). Vicariance events, in contrast, should generate discontinuities in these biogeographic patterns due to the formation of reciprocally monophyletic lineages on opposite sides of a presumptive barrier to gene flow (Brooks and McLennan 1991; Avise 2000).

Distinguishing the effects of dispersal, vicariance, and other processes (e.g., selection) on the genetic structure of a species requires the unambiguous interpretation of population genetic and phylogeographic patterns. Although the effects of these different processes can be difficult to discriminate (Bossart and Prowell 1998), interpretation of genetic data is stronger when testing existing hypotheses concerning dispersal and vicariance as opposed to generating hypotheses from the genetic data post hoc (Cruzan and Templeton 2000). Based on plate tectonics, geological evidence, and taxonomy, several biogeographic and phylogenetic hypotheses have been proposed for the biota of the Sonoran Desert (Riddle et al. 2000c). In particular, three major vicariance events have been predicted for Baja California and Sonora, Mexico (Gastil et al. 1983; Lonsdale 1989; Fig. 1). One is the formation of the Sea of Cortéz, resulting from a northern extension of

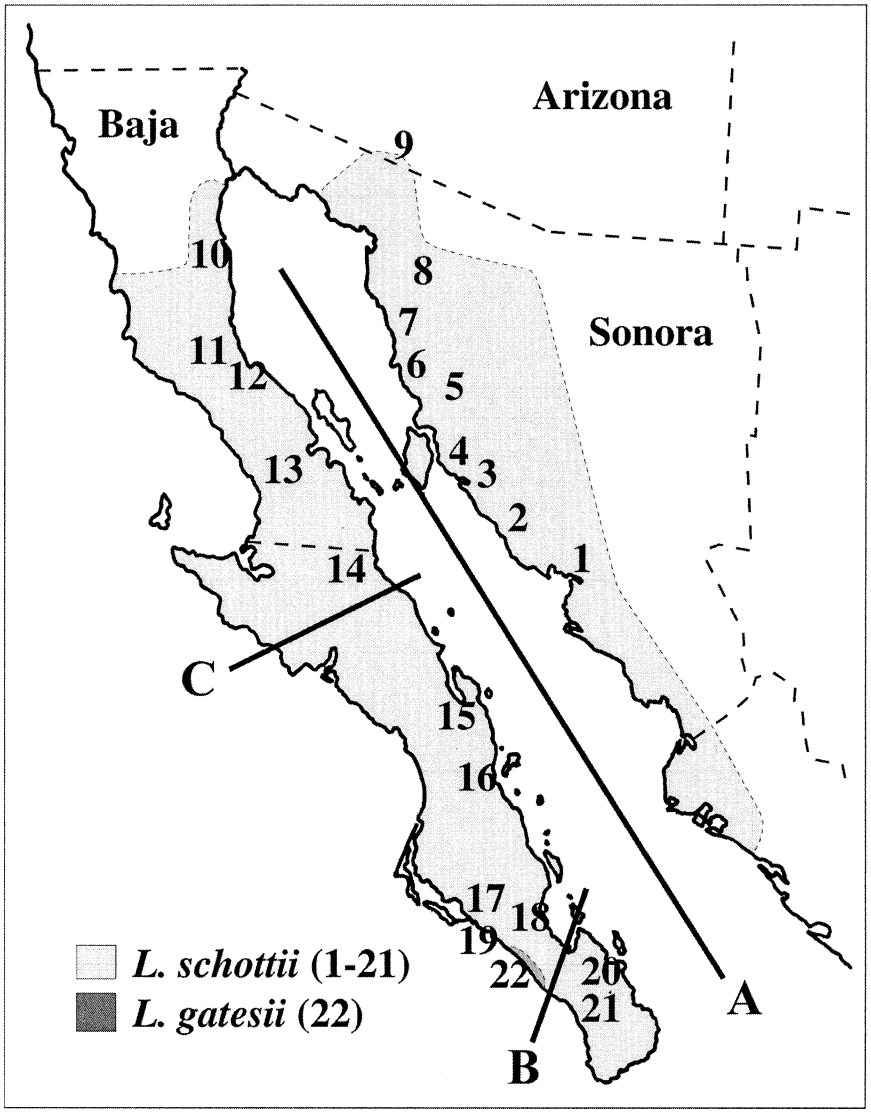

FIG. 1. Hypothetical sources of vicariance for Sonoran Desert fauna and flora: (A) the formation of the Sea of Cortéz 3–5 million years ago; (B) formation of the Isthmus of La Paz 3 million years ago; and (C) the formation of a midpeninsular seaway 1 million years ago. The current geographic distribution of *Lophocereus* is indicated by the shaded areas. The 22 populations sampled in this study represent *L. schottii* var. *tenuis* (population 1), *L. schottii* var. *schottii* (2–19), *L. schottii* var. *australis* (20, 21), and *L. gatesii* (22).

the Gulf of California during the late Pliocene (~3–5 million years ago), separating peninsular Baja from mainland Sonora. Originating at about 3 million years ago, a second area of vicariance was the Isthmus of La Paz, separating the Cape Region from south-central Baja and resulting from the formation of a transpeninsular seaway connecting the Sea of Cortéz and the Pacific Ocean. These hypothesized events are supported by recent mitochondrial DNA and allozyme studies of several vertebrate species revealing distinct continental, peninsular Baja, and Cape Region phylogroups (Upton and Murphy 1997; Riddle et al. 2000a,b,c). These studies also reveal concordant northern and southern Baja phylogroup distributions across several species leading to the hypothesis, not previously suggested by morphological and geological analyses, of a third, cryptic vicariance event in central Baja resulting from the formation of a transpeninsular seaway during the mid Pleistocene (~1 million years ago; Upton and Murphy 1997; Riddle et al. 2000c). These findings, and in particular the geographic concordance of contemporary phylogenetic topologies with ancient vicariance events, suggest that Pleistocene climatic fluctuations have had relatively little impact on the biogeographic distributions of Baja California's vertebrate biota (Riddle et al. 2000c).

In contrast to the strong effects of vicariance revealed in vertebrate phylogenies, the life-history characteristics of Sonoran Desert plant species lead us to predict historical distributions and genetic architectures profoundly influenced by climatic environmental change as well as geological vicariance. Species with adaptations to similar environmental conditions may share similar geographic ranges. A common history of climatic change, then, may cause correlated temporal and spatial patterns of range contraction and expansion promoting concordant but evolutionarily independent patterns of genetic structure across taxa (Hewitt 1996; Comes and

Kadereit 1998). Many plant species characteristic of the Sonoran Desert are of tropical origin and require mild, virtually frost-free winters and monsoonal summer rainfall (Shreve 1964; Van Devender 1990). Periods of Pleistocene cooling should have increased the frequency of winter freezes and decreased summer precipitation relative to warmer periods, driving predictable changes in plant species composition and range distributions. Consistent with these predictions, paleoecological analyses of plant material in packrat middens show Sonoran Desert floristic elements expanding their ranges into northern Baja and Sonora only within the last 4000–8000 years of the current interglacial period, with particularly frost tolerant species (e.g., *Carnegiea gigantea*) appearing first and a diverse flora assembled later (Van Devender 1990; Van Devender et al. 1994).

The shared history of geological vicariance and climatic change has important, yet unresolved, implications for understanding the evolutionary forces underlying the biogeographic congruence or incongruence of genetic structure in different plant species (as well as their coevolved associates, such as herbivores and pathogens). Animals possess physiological and behavioral means of thermoregulation (e.g., mobility, endothermy, and hibernation or estivation) that may stabilize their geographic distributions relative to historical environmental fluctuations. As a result, in animals distinct phylogroups may be less prone to extinction and more likely to persist on opposite sides of historical sources of vicariance (Riddle et al. 2000c). In plants, however, it is likely that many northern lineages went extinct due to climate change causing repeated range contraction-and-expansion events, a process resulting in contemporary phylogroups with interglacial distributions that span historical barriers to gene flow. In this case, we would predict range expansion proceeding via dispersal and isolation from refugial populations in southern Baja and Sonora to generate isolation by distance among populations nested within distinct phylogroups formed by previous, long-lasting isolation events (Brooks and McLennan 1991; Funk and Wagner 1995; Hewitt 1996; Soltis et al. 1997; Cruzan and Templeton 2000). Furthermore, if the recolonization process is associated with bottlenecks in population size, then range expansion from a single refugial source may also be expected to generate a geographical pattern of genetic structure in which genetic diversity declines with increasing latitude (i.e., from older to younger populations; Hewitt 1996). This shared history of range contraction and expansion is expected to generate population genetic and phylogeographic structures that are significantly correlated across evolutionarily independent plant lineages.

Despite testable hypotheses concerning historical vicariance and dispersal events and a rapidly developing understanding of the effect of these processes on the diversification of Baja California's vertebrates, previous studies of the population genetic structure and phylogeography of the region's flora have not been framed with respect to the geological and environmental history of the region. In this paper we report on the phylogeography of the Sonoran Desert columnar cactus, *Lophocereus schottii*. Pollination exclusion experiments conducted on *L. schottii* in Sonora and Arizona indicate an obligate pollination mutualism with the pyralid moth, *Upiga virescens* (Fleming and Holland 1998; Holland and Fleming 1999a,b). Much like the highly coevolved fig-wasp and yucca-moth mutualisms, *L. schottii* is dependent upon *U. virescens* for the pollination of its flowers and *U. virescens* is dependent upon developing seeds of *L. schottii* for the nourishment of its larvae. Chloroplast DNA (cpDNA) investigations of the phylogenetic origins of this unusual pollination system (Hartmann et al. 2002) confirm predictions based on stem chemistry (Gibson and Horak 1978) and morphology (Gibson and Horak 1978; Cornejo and Simpson 1997), placing *Lophocereus* within the genus *Pachycereus* (making *Pachycereus* paraphyletic) and sister group to the hummingbird-pollinated *P. marginatus*, the only other nonbat pollinated taxon within the *Pachycereus* clade. Low levels of cpDNA variation within *Lophocereus* (no substitutions within 1959 bp of sequenced intergenic spacers; Hartmann et al. 2002) as well as extensive paralogy of internal transcribed spacers (ITS) of ribosomal DNA (Hartmann et al. 2001) suggest a recent diversification of the genus and indicate the limited utility of the chloroplast genome and nuclear rDNA for intraspecific genetic analysis. A battery of allozyme marker loci, in contrast, enables us to test the predicted relationships between genetic structure and historical geological and climatic events and establish the basis for future work interpreting the phylogeography of *U. virescens* with respect to its host.

To investigate the phylogeographic and spatial population genetic structure of *Lophocereus*, we assayed multilocus allozyme genotypes of individuals sampled from 21 populations of *L. schottii* and one population of *L. gatesii*, representing the only two species in the genus. Using these data we addressed the following questions. Is the genetic signature of historical vicariance events, predicted by geology and the analysis of vertebrate taxa, evident in the intraspecific phylogeny of *L. schottii* and does it support current taxonomic treatments? Are geographic patterns of genetic variation within and between *L. schottii* phylogroups indicative of post-Pleistocene range expansion and/or reproductive isolation between phylogroups? To what extent do the population genetic and phylogeographic structures of *L. schottii* conform to patterns observed to date for vertebrate species? Are they largely congruent, or does genetic variation in *L. schottii* exhibit greater evidence of range contraction and expansion, a working hypothesis that we predict may be more characteristic of the historical biogeography of Sonoran Desert flora than fauna?

Materials and Methods

Study Species

Members of the genus *Lophocereus* grow throughout much of the Sonoran Desert of south-central Arizona and northwestern Mexico, including the Baja peninsula and mainland Sonora and Sinaloa (Lindsay 1963). As currently circumscribed, *Lophocereus* consists of only two species, the highly localized Baja endemic, *L. gatesii*, and the widespread *L. schottii*, which grows in Sonoran and peninsular desert habitats throughout much of Baja California and the adjacent continental desert (Fig. 1). *Lophocereus schottii* currently consists of three taxonomic varieties delimited on the basis of morphological variation (Lindsay 1963). *L. s.* var. *australis* is restricted to the Cape Region of southernmost Baja and *L.*

s. var. *tenuis* is restricted to the coastal plains of southern Sonora and northern Sinaloa, whereas *L. s.* var. *schottii* is more widespread, growing throughout much of the intervening desert habitats with a disjunct peninsular and continental distribution. This classification is consistent with the prediction of a distinct Cape Region phylogroup but does not support the other predicted relationships between the diversification of lineages and geological history.

Lophocereus schottii var. *schottii* is multistemmed, 2–5 m in height, with *L. s.* var. *australis* being generally taller and having a more distinct trunk and *L. s.* var. *tenuis* having more ribs per stem. The funnelform flowers of *L. schottii* are about 4 cm long and 3 cm wide and cream to pinkish in color. Flowering is nocturnal, with *U. virescens* as the primary pollinator, although during cool mornings flowers may remain open and be visited by halictid bees (Fleming and Holland 1998). Mature fruits contain approximately 180 small black seeds imbedded in a red pulp with the seeds presumably being largely bird dispersed. Flowering occurs from April through August, with the fruits maturing within 30 days (Holland and Fleming 1999a; Fleming et al. 2001). In addition to pollen and seed dispersal, vegetative reproduction occurs by rooting from stem fragments in some populations (Parker and Hamrick 1992), perhaps more so toward the northern limits of the geographic range. Unlike pollen or seed movement, however, it is unlikely that vegetative reproduction represents significant potential for long-distance gene dispersal.

Lophocereus gatesii, the putative sister species to *L. schottii*, is restricted to a small coastal area of the Magdalena plain west of La Paz in southern Baja California. Fog from the Pacific Ocean accounts for a significant proportion of precipitation in this area and is responsible for epiphytic plants growing on much of the terrestrial vegetation. In contrast to *L. schottii*, *L. gatesii* reaches 1–2 m with the burnt-salmon colored flowers opening in July and August (Lindsay 1963). The two species are also morphologically quite distinct, with *L. gatesii* having more ribs per stem and more closely spaced areoles than *L. schottii*.

Sample Populations

Populations of *L. schottii* and *L. gatesii* were assayed for allozyme variation in May 1996 and May 1997. In *L. schottii* 21 populations were sampled, spanning hypothetical sources of vicariance and taxonomic varieties from throughout the species range (Table 1, Fig. 1). These samples include one population of *L. s.* var. *tenuis* (population 1), 18 populations of *L. s.* var. *schottii* (populations 2–8 in Sonora, 9 in southern Arizona, and 10–19 in Baja), and two populations of *L. s.* var. *australis* (populations 20 and 21). Within each population, genetic material was obtained from flower buds sampled haphazardly over 1–4 ha from each of 48 spatially discrete plants assumed to represent different genets. All populations contained more than 48 reproductive-sized individuals, although in some populations fewer than 48 individuals were in flower at the time of sampling. Due to difficulty of access, only a single population of *L. gatesii* was assayed for genetic analysis. This population was sampled in a manner comparable to that of *L. schottii*; however, due to the absence of flower bud and fruit material, a small piece of stem material ($\sim$1 cm^3) was taken from each plant. Isozyme expression from stem tissue was confirmed to be consistent with that from flower buds.

TABLE 1. Geographic locations of 21 *Lophocereus schottii* and one *L. gatesii* population. Populations are numbered according to their relative locations along a transect beginning in southern Sonora, extending north to southern Arizona, and then south to southern Baja (see Figure 1). Population 1 is *L. s.* var. *tenuis*, populations 2–19 are *L. s.* var. *schottii*, and 20 and 21 are *L. s.* var. *australis*.

Population number	Population code	Latitude (N)	Longitude (W)	Elevation (m)
L. schottii				
1	CP	27°56′46.1″	110°39′34.6″	15
2	TS	28°24′17.7″	111°21′56.6″	15
3	SN	28°49′16.4″	111°47′56.8″	30
4	Seri	28°52′34.0″	111°57′18.4″	30
5	SG	29°23′42.0″	112°03′13″	248
6	SI	29°45′13.6″	112°30′18″	297
7	PL	30°23′26.6″	112°35′29″	106
8	LF	30°40′59.8″	112°16′15.2″	616
9	SnB	31°56′57″	112°52′13″	503
10	SnF	30°45′47.6″	114°43′38.6″	79
11	Ctv	29°43′41.9″	114°43′7.6″	515
12	SLG	29°35′25.3″	114°24′10.4″	419
13	PtP	29°04′53.2″	114°02′6.1″	432
14	SnI	27°17′38″	113°01′8.2″	448
15	BaC	26°35′12.2″	111°47′13.9″	6
16	Lig	25°43′38.4″	111°15′58″	9
17	StR	24°54′37.6″	111°37′53″	15
18	SnE	24°27′08.4″	110°41′43″	15
19	PtC	24°11′20.2″	111°09′9.3″	34
20	LaV	24°02′30.2″	109°59′13.6″	15
21	TsS	23°34′34″	110°20′25″	9
L. gatesii				
22	LaG	23°58′25.2″	110°52′56.0″	5

Electrophoretic Methods

Material collected from all 22 *Lophocereus* populations was immediately frozen in liquid nitrogen and then returned to the University of Georgia for horizontal starch gel electrophoresis. Individual samples were ground to a powder in liquid nitrogen and combined with the extraction buffer of Mitton et al. (1979). The resulting extract was absorbed through Miracloth (Calbiochem, La Jolla, CA) onto filter paper wicks and stored at −70°C until electrophoretic analysis.

For each population 15 enzyme systems were assayed for banding patterns consistent with Mendelian patterns of inheritance and known subunit structures: aspartate aminotransforase (*Aat*, EC 2.6.1.1), aconitase (*Acn*, EC 4.2.1.3), diaphorase (*Dia*, EC 1.8.1.4), fluorescent esterase (*Fe*, EC 3.1.1.-), glutamate dehydrogenase (*Gdh*, EC 1.4.1.2), isocitrate dehydrogenase (*Idh*, EC 1.1.1.42), malate dehydrogenase (*Mdh*, EC 1.1.1.37), malic enzyme (*Me*, EC 1.1.1.40), menadione reductase (*Mnr*, EC 1.6.99.2), phosphoglucomutase (*Pgm*, EC 5.4.2.2), glucose-6-phosphate isomerase (*Gpi*, EC 5.3.1.9), 6-phosphogluconate dehydrogenase (*Pgd*, EC 1.1.1.44), shikimate dehydrogenase (*Skdh*, EC 1.1.1.25), triose-phosphate isomerase (*Tpi*, EC 5.3.1.1), and UDPglucose pyrophosphorylase (*Ugpp*, EC 2.7.7.9). These enzymes were resolved in the following gel-electrode buffer systems: *Dia*, *Gpi*, and *Pgm* in system 6, *Aat*, *Me*, and *Mnr* in system 7,

Fe, Gdh, and *Tpi* in system 8, and *Acn, Idh, Mdh, Pgd, Skdh,* and *Ugpp* in system 11. Gel-electrode buffer system designations and enzyme stain recipes are from Soltis et al. (1983) except for *Dia* and *Ugpp,* which are from Manchenko (1994). These 15 enzyme systems resulted in the detection of 32 putative Mendelian loci, of which 29 were polymorphic in at least one *L. schottii* population.

Phylogeographic Analysis of Population Genetic Structure

Phylogenetic relationships among populations within *L. schottii* were examined using Nei's genetic distance (Nei 1972) calculated from allozyme frequencies. Population phenograms were constructed from the genetic distance matrix using neighbor-joining (Saitou and Nei 1987) and *L. gatesii* to root the tree. In addition to its distinct morphology, the sample population of *L. gatesii* was found to exhibit diagnostic differences at two allozyme loci, supporting its use as an outgroup in our phylogenetic analyses of *L. schottii*. Bootstrap support for individual nodes within each tree was obtained from a consensus tree generated from 1000 bootstrap resamplings of the original allozyme frequency data. Computer programs for genetic distance estimation, neighbor-joining, and bootstrapping were obtained from J. Felsenstein's package PHYLIP (available via http://evolution.genetics.washington.edu/phylip.html).

Population phenograms were tested for concordance with area cladograms constructed based on independent historical climatic and paleoecological data. These cladograms reflect the hypothesis of unidirectional range expansion via dispersal from glacial refugia and predict a tree topology in which descendent populations are serially nested within successively older ones along the axis of range expansion (Fig. 2A). To assess concordance we used the program GeneTree (Page 1998) to determine the number additional extinct and unsampled lineages (i.e., duplications and losses) that must be postulated to reconcile a population phenogram with the associated area cladogram. The null distribution of this statistic was estimated by calculating its value for 1000 random area cladograms generated using a Yule (Markovian) model. The concordance of the observed phenogram to the hypothetical area cladogram was considered significant at the 0.05 level if less than the 50th lowest ranked value of the null distribution.

Estimation of Hierarchical F-Statistics

We calculated Wright's *F*-statistics (Wright 1951) for a three-level population hierarchy in which populations (subscripts S) of *L. schottii* were nested within phylogroups (sub-

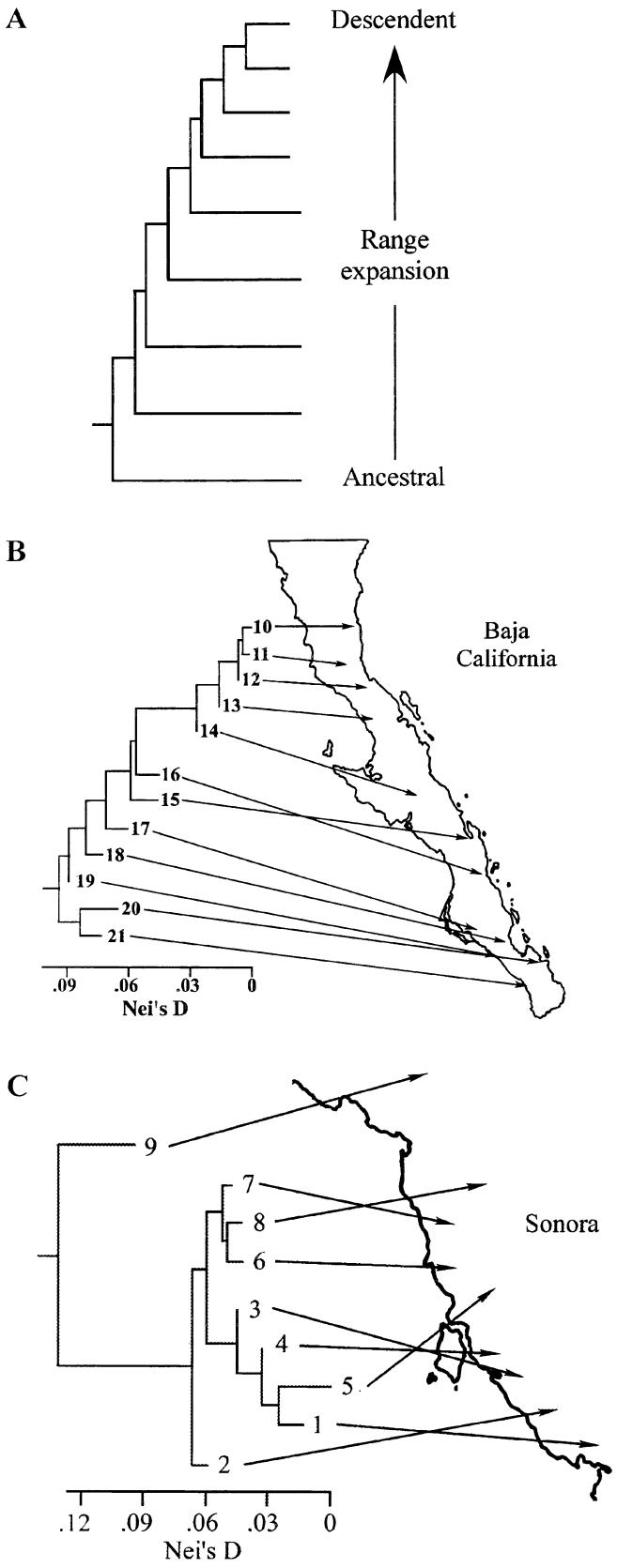

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FIG. 2. (A) The shape of a hypothetical area cladogram showing the progressive nesting of populations, from ancestral to descendent, expected under a unidirectional model of range expansion. (B) The population phenogram for *Lophocereus schottii* in Baja California reflects a progressive nesting of populations along the peninsula extending from Pleistocene refugia in the south to recently derived populations (< 3000 years ago) in the north. (C) The phenogram for continental populations of *L. schottii* indicates no such geographic structure.

script P) inferred via phylogeographic analysis, which in turn were nested within the total population (subscript T). This hierarchical structure provides estimates of the correlation of genes within individuals relative to populations (F_{IS}) and of individuals, populations, and phylogroups relative to the total population (F_{IT}, F_{ST}, and F_{PT}, respectively). Of particular biological interest are F_{IS}, which measures deviations from Hardy-Weinberg equilibrium within populations (as may result from inbreeding), and F_{PT}, which is a measure of allele frequency variation among phylogroups. To obtain phylogroup specific measures of genetic structure, we estimated F_{IS}, F_{IT}, and F_{ST} separately for each phylogroup, treating the phylogroup as the total population. Estimates of these parameters (Weir and Cockerham 1984) as well as their 95% bootstrap confidence limits were obtained using P. Lewis and D. Zaykin's program GDA (available via http://lewis.eeb.uconn.edu/lewishome/software.html).

Models of Historical Gene Migration

Recent theoretical work by Slatkin (Slatkin and Maddison 1990; Slatkin 1991, 1993) and Rousset (1997) has shown that the relationship between F_{ST} and geographic distance can be used to identify spatial patterns of gene migration and isolation by distance between populations. In our analyses of *Lophocereus*, Slatkin's and Rousset's methods provide very similar pictures of genetic structure, so we describe our methods and results only with respect to the former approach.

Using Slatkin's method, F_{ST} was estimated between all possible pairs of populations within phylogroups and used to calculate the pairwise effective migration rate as $\hat{M} = [(1/F_{ST}) - 1]/4$. $\hat{M}$ is similar to the more familiar measure *Nm* except that it is calculated for pairs of populations as opposed to summarizing in a single measure the mean effective gene flow over a set of populations (Slatkin 1993). In a system of populations at migration-drift equilibrium, the effective migration rate between pairs of populations, $\hat{M}$, should be negatively correlated with interpopulation distance (d) when dispersal is restricted. The slope of the regression of $\log_{10}(\hat{M})$ against $\log_{10}(d)$ is also indicative of the spatial dimension of gene flow and, at equilibrium, is expected to be approximately -1.0 under a one-diamensional stepping stone model, -0.5 under a symmetric two-diamensional model, and 0.0 under the island model (Slatkin and Maddison 1990; Slatkin 1991). A significant negative relationship is thus evidence of isolation by distance among populations, whereas the absence of this relationship between regional sets of populations, varieties, or phylogroups is consistent with historical vicariance and reproductive isolation. The observation of significant isolation by distance between putatively independent evolutionary lineages (i.e., regions, varieties, or phylogroups), however, is evidence of gene flow between them. Patterns indicative of these processes, as well as their absence, have been found in several recent empirical studies (e.g., Slatkin 1993; Hellberg 1996; Kudoh and Whigham 1997; Petterson and Denno 1997; Baer 1998; Williams and Benzie 1998).

Geographic distance in this context summarizes the historical path of gene movement between pairs of populations, the length of which may be determined by factors such as the spatial distribution of populations, habitat suitable for pollen and seed dispersers, or potential barriers to dispersal. In this study we used simple linear regression of the relationship between $\log_{10}(\hat{M})$ and $\log_{10}(d)$ to examine models of gene migration within and between phylogroups of *L. schottii*. Within and between phylogroups nested within continental and peninsular regions, geographic distance was calculated simply as the straight-line, Euclidean distance between all possible pairs of populations.

Under the hypothesis that the inferred phylogroups constitute monophyletic lineages, comparisons between their populations should not reveal a significant relationship between $\log(\hat{M})$ and $\log(d)$. The finding of a significant negative relationship, therefore, is evidence that reproductive isolation between these units is weak or absent. Such a finding also has taxonomic implications because evidence of significant isolation by distance between *L. s.* var. *schottii* and *L. s.* var. *australis*, for example, would suggest subsuming variety *australis* within the widespread variety *schottii*. In this case, the unique morphological characteristics of *L. s.* var. *australis* populations would likely represent regional adaptation to the biotic and abiotic environments of Baja's Cape Region as opposed to phylogenetic independence from *L. s.* var. *schottii*.

Isolation by distance between continental and peninsular phylogroups was assessed by evaluating three alternative models of gene migration reflecting different hypotheses concerning spatial patterns of genetic connectivity between populations. In the first, gene migration is two-dimensional with geographic distance calculated as the Euclidian distance between pairs of populations. In the second, gene migration between populations in Baja and Sonora is constrained to pass through a point (29°00′51″N, 112°26′34″W) on Isla Tiburon in the Midriff Islands. Islands in this chain across the Sea or Cortéz are separated by no more than 20 km and may serve as stepping-stones for historical gene flow between Baja and Sonora. In the third, gene migration between populations in Baja and Sonora is constrained to pass through a point (32°08′34″N, 114°56′00″W) in the Colorado River delta at the extreme northern limit of the Sea of Cortéz. Although this represents a purely terrestrial model of gene flow, populations of *L. schottii* do not currently occur in this area.

The slope (β) and coefficient of determination (R^2) of the relationship between the logarithms of $\hat{M}$ and distance for each migration model were obtained using least squares regression. Because pairwise estimates of $\hat{M}$ are not independent, confidence limits for β and the significance of the regression for each migration model were determined via randomization procedures (Mantel test) as implemented by the freeware program Permute! (available via http://www.fas.umontreal.ca/BIOL/Casgrain/en/labo/permute/index.html). In the case of interpopulation comparisons between continental and peninsular phylogroups, the coefficient of determination was used as the criterion for identifying the migration model providing the best fit to the data.

Biogeographic Patterns of Genetic Variation

Genetic variation was measured over monomorphic and polymorphic loci for each *Lophocereus* population using the proportion of polymorphic loci (P), number of alleles per locus (A), number of alleles per polymorphic locus (AP), and

expected heterozygosity (H_e). Estimates of within-population genetic variation were obtained by averaging over populations within the phylogroups inferred from the phylogeographic analyses described above. Total-population-level estimates of diversity, in contrast, were obtained by pooling population allele frequencies within phylogroups to create a single, larger population. Variances for all of the above estimates were calculated over loci.

Under a process of northward range expansion proceeding via dispersal and isolation from Pleistocene refugia in southern Baja and Sonora, genetic variation is expected to decline with increasing latitude. We tested this hypothesis for populations in each inferred phylogroup by simple linear regression of *P, A, AP,* and H_e on latitude conducted using the software package JMP (SAS Institute, Inc., Cary, NC). We also tested for the occurrence of genetic bottlenecks associated with range expansion. For selectively neutral loci in populations in mutation-drift balance, bottlenecks generate departures from equilibrium such that the observed gene diversity (H_e) should be higher than the equilibrium diversity (H_{eq}) computed from the observed number of alleles (Cornuet and Luikart 1996). This disequilibrium is strongest initially but may be detectable for up to $4N_e$ generations in postbottleneck populations of constant effective size (Luikart and Cornuet 1998). *Lophocereus schottii* is long-lived (~75 years; Shreve 1935) so that, for postbottleneck populations of effective size $N_e > 10$, bottlenecks during postglacial range expansion are theoretically detectable. To determine whether a population exhibits a significant number of loci with $H_e > H_{eq}$ we used the program Bottleneck (available via http://www.ensam.inra.fr/URLB/bottleneck/bottleneck.html) to conduct a Wilcoxon sign-rank test over polymorphic loci assuming an infinite alleles model of evolution (Luikart and Cornuet 1998). To control for multiple tests we adjusted our significance criterion by the Dunn-Sidák method (Sokal and Rohlf 1995): for experimentwise error rate $\alpha = 0.05$, we use testwise $\alpha' = 1 - (1 - \alpha)^{1/n} = 0.002$ where $n = 21$ is the number of independent tests (i.e., populations). Because we predict bottlenecks to occur more frequently in recently founded than in refugial populations, we expect the detection of bottlenecks to be positively correlated with increasing latitude. To test for this geographic pattern, we regressed the fraction of loci with $H_e > H_{eq}$ on latitude for peninsular and continental populations of *L. schottii* using the program JMP (SAS Institute, Inc.).

Results

Phylogeographic Analysis of Population Genetic Structure

The population phenogram constructed using *L. gatesii* as outgroup indicates regional and varietal differences within *L. schottii*. Within *L. s.* var. *schottii* there is a distinct clustering of continental and peninsular populations. Bootstrap analyses provide strong (98%) support for the monophyly of Sonoran populations (nos. 1–8) and the position of the Arizona population (no. 9) is basal to this group. The relative position of this continental phylogroup within the tree is equivocal, however, with placement ranging from within a Baja phylogroup to basal to peninsular populations of *L. s.* var. *schottii* as well as *L. s.* var. *australis* in different bootstrap datasets. This result coupled with the absence of isolation by distance between continental and peninsular populations (see below) suggests that Sonora and Baja represent distinct phylogroups. Within Baja the topology of the phenogram is highly congruent ($P < 0.001$) with a hypothetical area cladogram positing postglacial range expansion northward along the peninsula from refugial population(s) located in southern Baja (Figs. 2A, B). In Sonora, in contrast, the correspondence of tree topology with the associated area cladogram is not significant ($P = 0.72$, Fig. 2C). The lone Arizona population clusters basal to the Sonoran phylogroup; however, bootstrap support for this position is weak (47%) and the population does not exhibit significant isolation by distance with either Sonoran or Baja populations of *L. schottii* (see below).

At the varietal level, there is strong (74%) bootstrap support for *L. s.* var. *australis* (populations 20 and 21) being basal to *L. s.* var. *schottii* populations within Baja. There is no support, in contrast, for the evolutionary independence of *L. s.* var. *tenuis* (population 1) as the single sample population is nested within Sonoran populations of *L. s.* var. *schottii*.

In summary, and for the purpose of further analysis, we recognize Sonoran populations of *L. s.* var. *schottii* and *L. s.* var. *tenuis* as forming a single phylogroup distinct from a peninsular phylogroup consisting of Baja populations of *L. s.* var. *schottii*. In this case, the inferred phylogroups are consistent with biogeographic groupings, indicating the Sea of Cortéz as the source of vicariance between these regions. Also, we tentatively recognize *L. s.* var. *australis* as evolutionarily independent of Baja populations of *L. s.* var. *schottii* (the peninsular phylogroup), supporting the distinct nature of the Cape flora. This conclusion is called into question, however, by significant evidence of gene migration between peninsular and Cape Region populations (see below).

Hierarchical F-Statistics

For the three-level hierarchy (S, populations; P, phylogroups; and T, total population), estimates of Wright's *F*-statistics and their 95% confidence limits were $F_{IS} = 0.014$ (−0.031–0.057), $F_{IT} = 0.440$ (0.331–0.551), $F_{ST} = 0.431$ (0.330–0.536), and $F_{PT} = 0.302$ (0.177–0.435). F_{IS} was not significantly greater than zero, suggesting little evidence of inbreeding or other systematic forces generating significant deviations from Hardy-Weinberg expected genotypic frequencies within *L. schottii* populations. F_{ST}, in contrast, was highly significant, indicating substantial allele frequency variation among populations. F_{PT} was also highly significant, indicating that 30% of the total genetic variation is attributable to differences among phylogroups (continental, peninsular, and Cape Region). The high value of F_{PT} suggests that much of the variation among populations may be attributable to differences among phylogroups.

Differences among phylogroups in the degree of population variation were assessed by examination of two-level hierarchies. Consistent with the three-level model, F_{IS} estimates were not significantly greater than zero whereas F_{ST} estimates were significant for each of the three phylogroups (Table 2). Based on nonoverlapping 95% confidence intervals, the degree of genetic differentiation among populations differed significantly between continental ($F_{ST} = 0.111$) and

TABLE 2. Multilocus estimates of hierarchical *F*-statistics and their bootstrapped 95% confidence intervals (in parentheses) for inferred phylogroups and all populations of *Lophocerus schottii*. Estimates significantly different from zero are indicated by asterisks.

Phylogroup	*F*-statistic			
	F_{IS}	F_{IT}	F_{ST}	F_{PT}
Continental	0.027 (−0.038–0.099)	0.135* (0.067–0.199)	0.111* (0.071–0.149)	
Peninsular	0.007 (−0.038–0.046)	0.237* (0.161–0.320)	0.232* (0.158–0.308)	
Cape Region	0.007 (−0.060–0.074)	0.211* (0.104–0.326)	0.205* (0.057–0.350)	
All *L. schottii* populations	0.014 (−0.031–0.057)	0.440* (0.331–0.551)	0.431* (0.330–0.536)	0.302* (0.177–0.435)

peninsular phylogroups ($F_{ST} = 0.232$) but not between these and the Cape Region phylogroup ($F_{ST} = 0.205$). These results indicate that variation among populations, and not inbreeding within populations, is responsible for the significant F_{IT} estimates at the phylogroup level (Table 2).

Models of Historical Gene Migration

Randomization tests revealed a significant negative relationship between $\log(\hat{M})$ and $\log(d)$ for *L. s.* var. *schottii* populations within peninsular ($P < 0.001$) and continental ($P < 0.01$) phylogroups (Fig. 3). In Baja, the Euclidean distance between populations (d) explains 61% of the total variation in $\hat{M}$. Although the relationship is less strong in Sonora ($R^2 = 0.18$), these data are consistent with restricted gene flow and a pattern of isolation by distance within both of these regions. Regression coefficients for Baja and Sonora are −0.62 and −0.30, respectively, and more consistent with a two-dimensional than a one-dimensional pattern of gene migration within these regions. Pairwise comparisons between the lone Arizona population (no. 9) and Sonoran populations were singled out in Figure 3B because this population was unique in exhibiting no evidence of isolation by distance with other populations in the continental phylogroup (it similarly shows no evidence of isolation by distance with peninsular populations).

Each of the three models constructed to test historical pathways of gene migration between Baja and Sonora indicate little correlation between $\hat{M}$ and distance. Although model three, constraining gene migration between Baja and Sonora to pass north of the Sea of Cortéz, was marginally significant ($P = 0.03$), the slope of this line was positive and the regression model accounted for only a small proportion of the total variance in $\hat{M}$ ($R^2 = 0.04$). Given the significant isolation by distance found within these regions, these data support the conclusion that the Sea of Cortéz has been a barrier to gene flow over evolutionary time.

In contrast to the lack of isolation by distance between peninsular and continental phylogroups, randomization tests revealed a significant negative relationship ($P < 0.001$) between $\log(\hat{M})$ and $\log(d)$ for pairwise comparisons between populations within peninsular (*L. s.* var. *schottii*) and Cape Region (*L. s.* var. *australis*) phylogroups within Baja (Fig. 4). In this case, the Euclidean distance between populations explained 73% of the total variation in migration rate ($R^2 = 0.73$). These results indicate that the rate of gene migration between populations of these two groups is a function of the distance between them, calling into question both their varietal taxonomic distinction and their recognition as distinct phylogroups.

Genetic Variation

Of the 32 loci assayed, 29 were polymorphic in *L. schottii* and *L. gatesii*. Of these an average of 50% and 66% were polymorphic within populations of *L. schottii* and the single population of *L. gatesii*, respectively. When examined with respect to phylogroup, continental and peninsular groups of *L. s.* var. *schottii*, as well as *L. s.* var. *australis* and *L. gatesii* from the Cape Region, maintain similar levels of within-population genetic diversity (Table 3). Within the peninsular phylogroup, however, linear regression analyses indicate significant declines in polymorphic loci, alleles per locus, and expected heterozygosity with increasing latitude (Fig. 5), a geographic pattern that is not significant for continental populations. Patterns of total-population-level genetic variation in *L. s.* var. *schottii* are similar to those found at the within-population level (Table 3) with genetic diversity higher in southern Baja than in northern Baja or Sonora.

When populations were assessed individually for genetic bottlenecks using a Type I error rate of 0.05, seven of 21 tests (for populations 2, 6, 7, 9, 16, 19, and 21) were significant and indicative bottlenecks in effective population size. When a testwise error rate ($\alpha' = 0.002$) was employed to achieve an experimentwise error rate of $\alpha = 0.05$, however, none of the bottleneck tests of individual populations were significant. Regressions of the fraction of loci with $H_e > H_{eq}$ on latitude for peninsular and continental populations also were not significant.

DISCUSSION

The geographic distributions of plant and animal species and communities have been profoundly influenced by long-term patterns of global climate change. Despite differences in life histories, various North American and European taxa indicate southward range contraction during the last glacial period followed by northward range expansion during the Holocene. Because of this shared history, extant species should exhibit correlated geographic patterns of genetic structure. The strength of this correlation will be influenced both by the number of refugia, differential rates of extinction within refugia, and species-specific rates of mixing of refugial lineages during range expansion (Comes and Kadereit 1998).

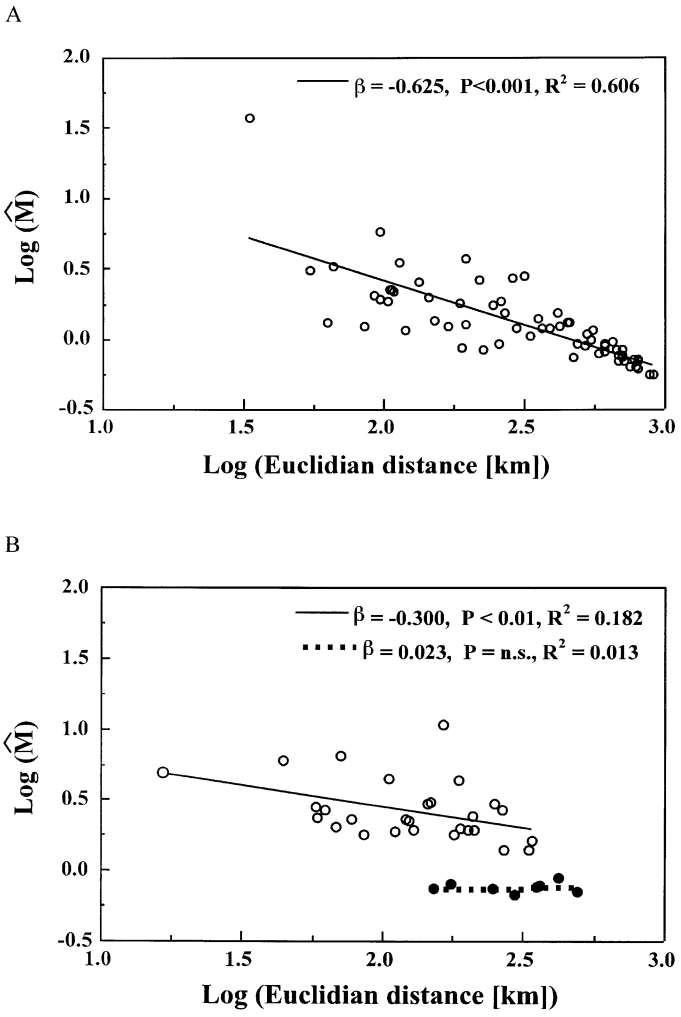

FIG. 3. Relationship between the effective migration rate ($\hat{M}$) and geographic distance for (A) peninsular and (B) continental populations of *Lophocereus schottii* var. *schottii*. Filled circles and dashed regression line in B denote pairwise comparisons Sonoran populations (populations 1–8) with population 9 from southern Arizona.

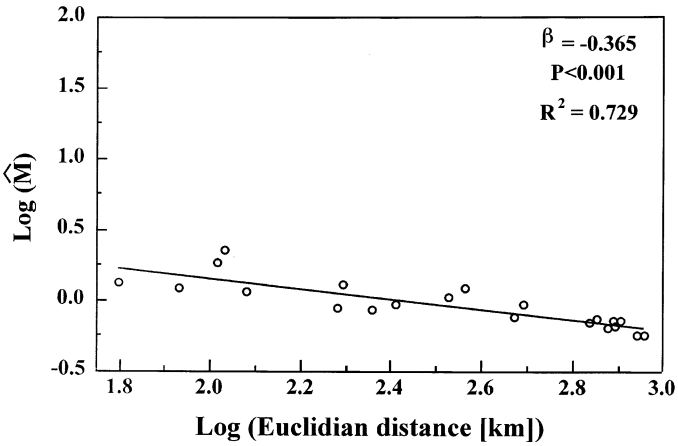

FIG. 4. Relationship between the effective migration rate ($\hat{M}$) and geographic distance between two putative phylogroups; peninsular populations of *Lophocereus schottii* var. *schottii* and Cape Region populations of *L. s.* var. *australis.*

The simplest scenario involves simple diffusion from a single southern refuge with colonists arising from the leading edge of a relatively compact wave range expansion. Assuming population and genetic bottlenecks associated with colonization, this hypothesis predicts a pattern of isolation by distance among populations as well as reductions in genetic diversity resulting from bottlenecks along the axis of range expansion (Hewitt 1996). Alternative scenarios resulting in more complex patterns of genetic structure involve rare, long-distance dispersal and founding events (Ibrahim et al. 1996) and range expansion from multiple isolated refugia resulting in a continuous geographic distribution overlying major genetic discontinuities (Soltis et al. 1997; Taberlet et al. 1998).

The peninsular and continental regions of the Sonoran Desert have been subject to historical geological and environmental processes expected to strongly influence the genetic architectures and hence the systematic classifications of its plant and animal species. Genetic and biogeographic analyses of *L. schottii* indicate that it comprises distinct phylogroups that are not reflected in the current taxonomic classification of the species. In particular, *L. s.* var. *schottii* populations in Baja California and Sonora constitute geographically isolated peninsular and continental phylogroups, variety *L. s.* var. *tenuis* (population 1) nests within Sonoran populations of *L. s.* var. *schottii*, and there is evidence of significant gene flow and isolation by distance between Cape Region populations of *L. s.* var. *australis* and peninsular populations of *L. s.* var. *schottii*. These results for *L. schottii* are consistent with phylogeographic analyses of Sonoran and peninsular desert vertebrate biota in providing strong evidence of vicariance resulting from the northward transgression of the Sea of Cortéz during the Pliocene. In contrast, however, *L. schottii* exhibits only weak evidence of historical vicariance resulting from a transpeninsular seaway across southern Baja at the isthmus

TABLE 3. Estimates of genetic diversity for inferred phylogroups of *Lophocerus schottii*. Within-population-level estimates are weighted averages over populations, whereas total-population-level and species-level estimates are calculated from allele frequencies pooled over populations within groupings. Because *L. gatesii* is represented by a single sample population, only within-population estimates are presented for this species. *N* is the number of populations per region, and *P*, *A*, *AP*, and H_e are described in the text.

Level of analysis	*N*	*P*	*A*	*AP*	H_e
Within-population-level estimates					
Continental phylogroup	8	0.512	1.605	2.188	0.151
Peninsular phylogroup	11	0.497	1.699	2.385	0.154
Northern region	6	0.427	1.568	2.318	0.126
Southern region	5	0.581	1.856	2.466	0.188
Cape Region phylogroup	2	0.469	1.609	2.313	0.138
L. gatesii	1	0.656	1.655	2.000	0.153
Total-population-level estimates					
Continental phylogroup	8	0.563	2.094	2.611	0.167
Peninsular phylogroup	11	0.687	2.469	3.045	0.192
Northern region	6	0.469	2.094	2.800	0.142
Southern region	5	0.688	2.375	2.955	0.212
Cape Region phylogroup	2	0.594	1.906	2.421	0.148
Species level estimate					
L. schottii	21	0.906	2.781	3.038	0.226

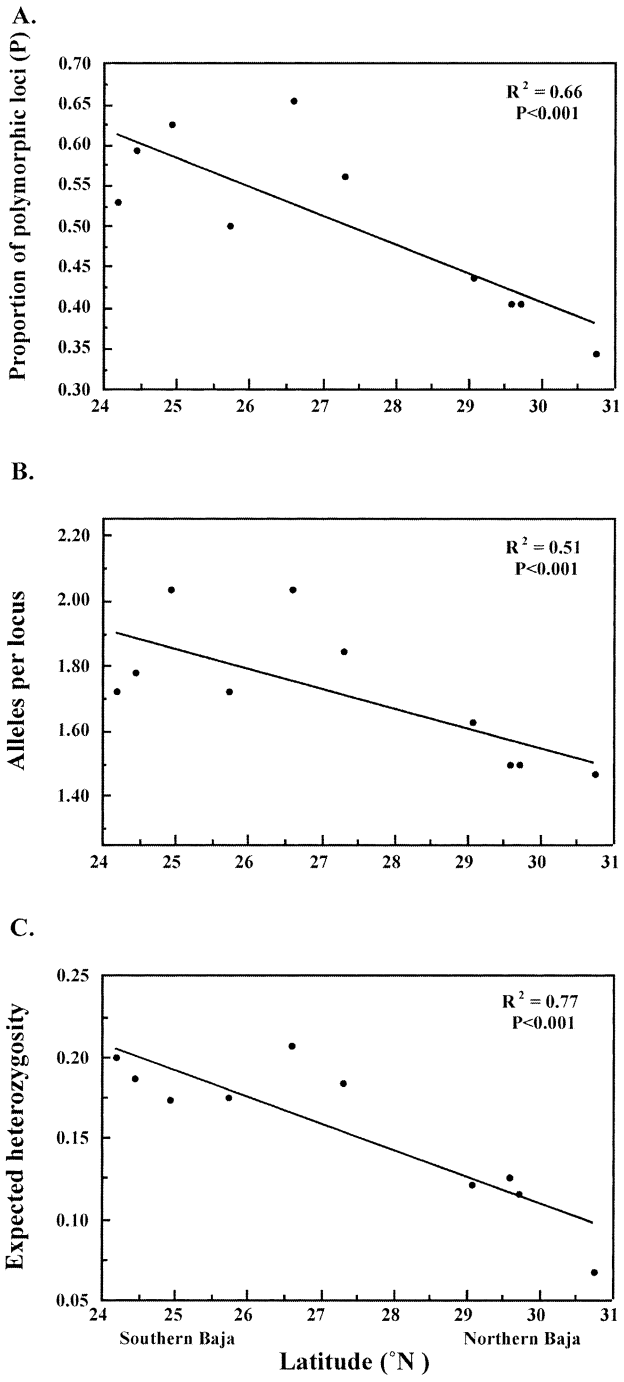

FIG. 5. Significant negative linear regressions of genetic diversity on latitude for Baja California populations of *Lophocereus schottii*. (A) Proportion of polymorphic loci. (B) The number of alleles per locus. (C) Hardy-Weinberg expected heterozygosity.

of La Paz in the late Pliocene and no evidence of the geologically cryptic, midpeninsular seaway that Riddle et al. (2000c) hypothesized from the congruence of phylogeographic structure across several vertebrate taxa.

Although *L. schottii* exhibits little evidence of vicariance resulting from an isthmus of La Paz seaway, it could still be true that *L. gatesii* represents a remnant signature of this event. If *L. gatesii* is truly basal to peninsular and continental phylogroups of *L. schottii*, its divergence would have to predate vicariance ultimately resulting from the Sea of Cortéz. There are also two reasonable explanations why detectable evidence of the midpeninsular seaway was not found in the genetic structure of *L. schottii*. One is that, because the event was presumed to have occurred relatively recently (≈ 1 million years ago; Upton and Murphy 1997), lineages on either side of the geological barrier to gene flow have yet to pass from polyphyly to reciprocal monophyly. The alternative explanation is that populations north of this barrier derived from post-Pleistocene range expansion from southern refugia. This hypothesis postulates that if an ancient vicariance event did arise, it has since been lost due to extinctions north of the barrier during periods of glacial maxima and subsequent range expansion from the south during interglacial periods, such as the present. Based on several lines of evidence, we believe this latter explanation to be the more likely scenario. First, we found significant evidence of isolation by distance (Fig. 3A) across the presumptive historical barrier to gene flow. Second, we also found apparently continuous declines in genetic diversity with increasing latitude along the Baja peninsula (Fig. 5). Further support for this scenario comes from the topology of the phenogram for peninsular populations of *L. s.* var. *schottii*. In general, refugial populations are expected to be ancestral to more recently founded populations within an intraspecific phylogeny. Thus, under a model of unidirectional range expansion, we would predict tree shape to show a progressively deeper nesting of populations from south (ancestral) to north (descendent) along the Baja peninsula. The concordance of the phenogram for peninsular populations of *L. s.* var. *schottii* to this predicted area cladogram (Figs. 2A, B) is highly significant, supporting the range expansion hypothesis.

Continental populations, in contrast, show a weaker pattern of isolation by distance (Fig. 3B) and do not exhibit significant reductions in genetic diversity with latitude or a tree topology consistent with range expansion. The weaker geographic pattern of genetic structure in Sonora than in Baja suggests two possible explanations. First, this difference may be due to differences in rates of gene flow within continental and peninsular phylogroups. Consistent with this hypothesis, interpopulation differentiation within the continental phylogroup (F_{ST} = 0.111) is significantly lower than within the peninsular phylogroup (F_{ST} = 0.232; Table 2). Despite this difference, differentiation within the continental phylogroup is still significantly greater than zero (Table 2) and comparable to the mean for other long-lived woody plants (F_{ST} = 0.124; Hamrick et al. 1992), including columnar cacti (F_{ST} = 0.145 for n = 7 taxa; Hamrick et al. 2002). As a result, we cannot conclude that gene flow has been sufficient to homogenize geographic patterns of genetic variation within either continental or peninsular phylogroups of *L. schottii*.

A more likely alternative is that the number of Pleistocene refugia surviving to contribute to postglacial range expansion was greater in the continental than the peninsular desert. In mainland Mexico, Pleistocene refugia for Sonoran Desert flora are hypothesized to have been located inland in the Plains of Sonora and along the coastal plain of southern Sonora and northern Sinaloa (T. Van Devender, pers. comm.). The possibility of an additional refugial location is suggested by the

relatively weak clustering of the genetically diverse Arizona (population 9) population with the Sonoran populations (1–8, Fig. 2C), as well as the absence of isolation by distance between these two groups (Fig. 3B). Thus, in contrast to Baja California, range expansion from multiple refugia (and perhaps weaker barriers to gene flow) may have generated historically complex patterns of genetic structure not easily inferred from general geographic trends in the distribution of nuclear marker data. Taberlet et al. (1998) reached a similar conclusion, suggesting that the general lack of concordance in geographic patterns of allozyme variation for four tree species in Europe (*Abies alba*, *Fagus sylvatica*, *Picea abies*, and *Quercus* spp.) is the result of differences in the number of surviving glacial refugia.

Implications for Codistributed Taxa

The growing number of molecular phylogeographic studies has provided the opportunity to compare the intraspecific genetic structure of unrelated taxa across the same areas to identify concordant patterns of geological vicariance, glacial refugia, and postglacial colonization routes, especially in vertebrates (Avise 2000). The phylogeographies of the peninsular desert's vertebrate biota strongly reflect ancient vicariance events due to a geologically cryptic midpeninsular seaway (nine of 10 taxa) and, in a few cases, a transpeninsular seaway at the Isthmus of La Paz (two of three taxa; reviewed in Riddle et al. 2000c). Notable exceptions to these trends include the red-spotted toad, *Bufo punctatus*, which exhibits peninsular versus continental divergence but no signature at midpeninsula (Riddle et al. 2000c), and the California gnatcatcher, *Polioptila californica*, which in addition to lack of genetic structure consistent with transpeninsular seaways, shows convincing evidence of recent range expansion from southern Baja northward into southern California (Zink et al. 2000). As with these two species, the genetic signatures of transpeninsular vicariance events are weak or absent in *L. schottii*. Comparative studies of genealogical concordance across codistributed, tropically derived plant species in Baja have yet to be conducted. However, if the genetic structure of *L. schottii* is indicative of these taxa, then the historical biogeographic distributions and intraspecific genetic architectures of plants and vertebrates in Baja California may exhibit some fundamental differences. The peninsular vicariance events occurred over geological timescales that were likely of sufficient duration for populations on opposite sides of the seaways to evolve reproductive isolation and reciprocal monophyly. That lineages of many vertebrates today exist adjacent to these ancient geological barriers argues for the local persistence of their populations throughout periods of extreme global climate change from the late Pliocene to the present. Modern Baja California populations of *L. schottii* do not exhibit evidence of reproductive isolation but rather isolation by distance spanning these ancient barriers to gene flow. This genetic structure, together with climatic and paleoecological data, argues for climatic fluctuations driving waves of extinction and recolonization in this species. Like *L. schottii*, most Sonoran Desert flora are frost intolerant and would have experienced southward contractions and northward expansions of their ranges in response to periods of global cooling and warming, respectively, a prediction supported by the analysis of fossil data obtained from packrat middens. As a result, the genetic architecture of *L. schottii* may serve as a useful, general model for the phylogeographic structures of the many woody, insect-pollinated species comprising the continental and peninsular desert floras.

To date, there are relatively few comparative phylogeographic studies of codistributed plant species (e.g., Soltis et al. 1997; Taberlet et al. 1998) and fewer yet involving plants and their associated insect herbivores and seed parasites. Compared to vertebrates, the interaction of phytophagous insects with their plant hosts is likely to be relatively species-specific. This may promote the concordance of genetic structures if insects closely track the biogeographic distributions of their hosts and so experience a shared history of geological sources of vicariance and climatic change. As a test of this hypothesis, we are currently studying the genetic structure of the pollinator and seed parasite moth *U. virescens* for comparison to data now available for *Lophocereus* (its host) and codistributed vertebrate taxa. More generally, it is important is to ask whether the tremendous species diversity of phytophagous insects is driven, at least in part, by the effect on these insects and their hosts of a shared biogeographic history. If a shared history generates concordant patterns of genetic structure, then host and insect would be expected to codifferentiate, driven largely by factors affecting host distribution. For geological and climatic events to generate higher rates of differentiation in insects than their hosts, they must form barriers to gene flow to which the insect is more sensitive, permitting it to evolve multiple independent lineages (phylogroups) within the range of a single host phylogroup. Comparative studies of codistributed plant and insect species pairs will help elucidate the concordance of their genealogies, providing deeper insight into the processes of differentiation in phytophagous insects and how they differ from those operating in other animal groups.

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