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Phylogeographic histories of representative herpetofauna of the southwestern U.S.: mitochondrial DNA variation in the desert iguana (*Dipsosaurus dorsalis*) and the chuckwalla (*Sauromalus obesus*)

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Abstract

To determine whether genetic variation in representative reptiles of the southwestern U.S. may have been similarly molded by the geologic history of the lower Colorado River, we examined restriction site polymorphisms in the mitochondrial DNA (mtDNA) of desert iguanas (*Dipsosaurus dorsalis*) and chuckwallas (*Sauromalus obesus*). Observed phylogeographic structure in these lizards was compared to that reported for the desert tortoise (*Xerobates agassizi*), whose mtDNA phylogeny demonstrates a striking genetic break at the Colorado River.

Both the desert iguana and chuckwalla exhibit extensive mtDNA polymorphism, with respective genotypic diversities $G = 0.963$ and 0.983, close to the maximum possible value of 1.0. Individual mtDNA clones, as well as clonal assemblages defined by specific levels of genetic divergence, showed pronounced geographic localization. Nonetheless, for each species the distributions of certain clones and most major clonal groupings encompass both sides of the Colorado River valley, and hence are clearly incongruent with the phylogeographic pattern of the desert tortoise. Overall, available molecular evidence provides no indication that the intraspecific phylogenies of the southwestern U.S. herpetofauna have been concordantly shaped by a singular vicariant factor of overriding significance.

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Introduction

Vicariant biogeographic analyses commonly focus on congruent patterns among monophyletic assemblages of species or higher taxa, and hence address the role of ancient geologic events in shaping biological distributions on a broad (e.g., continental) spatial scale. More recent vicariant events may have shaped patterns of intraspecific variation in ways appropriate for resolving questions of biogeography on a local or regional scale. Rosen (1978) endorsed the use of information on population fragmentation and differentiation to test biogeographic hypotheses, noting that differentiated conspecific populations "are potentially informative with respect to the relationships of their area to other areas." Conversely, other authors (e.g., Chernoff, 1982) have urged caution in interpreting intraspecific patterns, because certain characters (especially meristic and morphometric traits) may be environmentally responsive or temporally unstable.

The growing literature on intraspecific mitochondrial DNA (mtDNA) polymorphism contains numerous examples of geographic population genetic structure (Wilson et al., 1985; Avise et al., 1987; Moritz et al., 1987; Avise, 1989; Bernatchez and Dodson, 1991). Because mtDNA in higher animals is rapidly evolving and uniparentally (maternally) transmitted, patterns of differentiation among non-recombining mtDNA haplotypes can be used to estimate matriarchal phylogeny within species (Avise, 1989). A commonly encountered situation is one in which discontinuities in mtDNA phylogeny are associated with extrinsic barriers to dispersal. Such outcomes offer promise for fine scale biogeographic reconstruction. Namely, if certain physiographic features confer a phylogeographic structure among mitochondrial genotypes in one species, then they may be similarly operative on other species. Concordant patterns detected among intraspecific mtDNA phylogenies could help elucidate those historical features that figure prominently in recent regional biogeography.

Can multi-species comparisons of mtDNA phylogenies be used to gauge the biogeographic influence of regional events? Preliminary surveys suggest that they can. Bermingham and Avise (1986) assayed mtDNA variation in five species of freshwater fishes across 14 river drainages in the southeastern United States. Geographic structuring of mtDNA phylogenies was evident for all assayed species. Furthermore, the respective phylogenies demonstrated concordant geographic breaks that were coincident with drainages previously recognized as important zoogeographic boundaries. A similar biogeographic association has been identified for coastal marine species in the southeastern U.S. Phylogenetic discontinuites distinguishing Atlantic versus Gulf of Mexico populations were observed for a diverse array of taxa, including the horseshoe crab (Saunders et al., 1986), American oyster (Reeb and Avise, 1990), seaside sparrow (Avise and Nelson, 1989), and diamondback terrapin (Lamb and Avise, 1992). Restrictions to gene flow in these species may be proximately maintained by marine current patterns and ecological transitions along the east coast of Florida, while the origin of these genetic differences appears to trace to historical climatic and geologic events in the South Atlantic and Gulf region (detailed in Avise, 1991).

The preceding examples suggest that regional events can indeed shape independent mtDNA phylogenies in a concordant manner. Whether such outcomes are common remains to be determined. The efficacy of comparative surveys of mtDNA variation in testing biogeographic hypotheses, either by identifying or confirming regional tracks or barriers, will require additional examples from a variety of geographic realms.

One such favorable setting is the lower Colorado River, extending through the Mojave and Sonoran deserts of Arizona, California, and Nevada. Recent comparisons of mtDNA variation in the desert tortoise (*Xerobates* (=*Gopherus*) *agassizi*) revealed three major phylogenetic subdivisions, two of which are partitioned along the length of the lower Colorado drainage (Lamb et al., 1989). Estimates of mtDNA sequence divergence between the eastern and western tortoise assemblages were provisionally related to the geology of the lower Colorado River valley. In Pliocene times (ca. 3–5 mya), marine transgressions inundated this region, extending the Sea of Cortez as far north as southern Nevada (Smith, 1970; Lucchitta, 1979). The resulting embayment, a shallow, 40–50 km wide incursion known as the Bouse sea (Metzger, 1968), may have functioned as a dispersal barrier to ancestral tortoise populations. In addition, allozymic surveys of other vertebrate species point to the zoogeographic influence exerted by the lower Colorado River valley (Avise et al., 1974; Patton and Yang, 1977).

In this study we evaluate population-genetic structure in two species of iguanine lizards to determine whether their mtDNA phylogenies have been influenced by the same historical events that presumably shaped the phylogeographic subdivisions of the desert tortoise. The desert iguana (*Dipsosaurus dorsalis*) and the chuckwalla (*Sauromalus obesus*) were selected for this comparative survey for the following reasons: 1) they share nearly identical distributions with the desert tortoise, with the northern range bisected by the Colorado River; 2) both species are relatively common; and 3) both species exhibit pronounced habitat specificity and show reduced dispersal tendencies, two features that might accentuate mtDNA differentiation.

Materials and methods

During spring and summer of 1988, 37 *D. dorsalis* and 51 *S. obesus*, from 13 and 25 localities, respectively, were captured and transported live to the laboratory. Where habitat permitted, both species were collected at or near the same locales (Fig. 1; Appendix). Overall, sample sites corresponded rather closely with the U.S. locales previously surveyed in the desert tortoise study (Lamb et al., 1989).

Preparation of purified mtDNA from fresh liver was conducted according to Lansman et al. (1981), with the minor modifications described by Lamb et al. (1989). Restriction digests of mtDNA samples were generated with the following 20 endonucleases: *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*I, *Bgl*II, *Bst*EII, *Cla*I, *Eco*RI, *Hin*cII, *Hin*dIII, *Kpn*I, *Msp*I, *Nde*I, *Pst*I, *Pvu*II, *Sac*I, *Spe*I, *Stu*I, and *Xba*I. Digestion fragments were end-labeled with 35-S-radionuclides, separated through

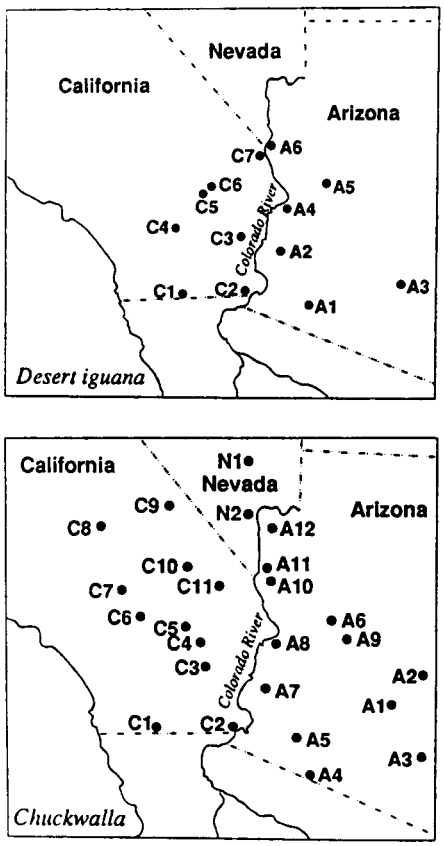

Fig. 1. Maps of the lower Colorado River region showing collection sites for the desert iguana and chuckwalla. Site codes are keyed to locality data and per-site sample sizes in Appendix.

1.0–1.6% agarose gels, and revealed by autoradiography. Fragment lengths were estimated by comparison to the 1-kb ladder available from Bethesda Research Laboratories.

Each distinct restriction profile produced by a given endonuclease was assigned an uppercase letter code, with "C" designating the most common profile. (Those enzymes considered uninformative, i.e., producing zero or one cut for all mtDNA samples, were excluded from consideration.) Composite codes, compiled from the array of informative endonucleases, identified unique mtDNA genotypes (clones).

Using the "site" approach of Nei and Li (1979), estimates of nucleotide sequence divergence (p) were calculated from cleavage site changes inferred from the fragment profiles (procedures in Avise et al., 1989). The resulting distance estimates were employed to cluster mtDNA genotypes using the average linkage algorithm

(which is the same as UPGMA [Sneath and Sokal, 1973]). MtDNA clonal diversity was estimated by the approach of Nei and Tajima (1981):

$$G = n(1 - \Sigma f_i^2)/(n - 1)$$

where f_i, is the frequency of the ith genotype and n is the number of individuals surveyed. Genotypic diversity values can range from 0, when all individuals exhibit the same genotype, to 1.0, when each individual displays a unique genotype.

In addition, parsimony analysis of the mtDNA variation observed in each species was conducted using PAUP (phylogenetic analysis using parsimony) program (Swofford, 1985). A data matrix encoding presence-absence status of each restriction site in each mtDNA genotype was used to generate networks with PAUP's branch and bound algorithm. In the absence of appropriate outgroups, the trees were rooted at the midpoint of the longest path.

Results

Identification and diversity of clones

A total of 78 restriction sites (produced by fourteen informative endonucleases) were scored in the desert iguana assays, revealing 18 composite genotypes (clones) among the 36 animals surveyed (Table 1). For the 51 chuckwallas assayed, the

Table 1. The mtDNA clones observed in desert iguanas. Letters of the composite genotypes refer to restriction fragment patterns for the following endonucleases (in order, from left to right): *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*I, *Cla*I, *Hin*cII, *Hin*dIII, *Kpn*I, *Msp*I, *Pst*I, *Pvu*II, *Spe*I, and *Stu*I. Collection locales are illustrated in Fig. 1.

Clonal designation	Composite genotype	No. of lizards	Locale(s)
1	CCCCCCCCCCCCCC	3	C2, C3, C4
2	CCCCCCCCCACCCC	1	C1
3	CCCCCCCCCBCCCC	2	C1
4	CCCACCCCCCCCCC	5	A2, A4, C3
5	CCCACCCCCDCCCC	1	C3
6	CCCCCCCCCCCCBC	1	C4
7	CCCBCCCCCCCCBC	2	C4
8	CCCBCCCCCCCCBB	1	C4
9	CCDCCDCCBCCCCC	5	A6, C6, C7
10	CCDCCDBBBCCCCC	1	C3
11	CCDCCDCCBFCCCC	1	C6
12	CCDCCDCCBCCCCD	1	C7
13	CCDCCDCCBCCCCA	1	A6
14	CCDCCDACBCCCCC	1	C5
15	CCDBCCCECACCCC	3	A1, A3
16	CCCACCCCCACCCC	1	A4
17	CCCACCCACCCCCC	5	A5
18	CCCBCCCDCCCCCC	1	A4

Table 2. The mtDNA clones observed in chuckwallas. Letters of the composite genotypes refer to restriction fragment patterns for the following endonucleases (in order, from left to right): *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*I, *Bgl*II, *Bst*EII, *Eco*RI, *Hin*cII, *Hin*dIII, *Spe*I, and *Stu*I. Collection locales are illustrated in Fig. 1.

Clonal designation	Composite genotype	No. of lizards	Locale(s)
1	CJFBBDCCCEI	2	A1
2	CJFBBDCCCEJ	1	A3
3	CCCDCCCCCGC	3	A2
4	CECCCCCCCGH	1	A4
5	CCCCCCCCCGH	3	A5
6	DACCCCCCCHH	1	A4
7	CJEBCECCDED	3	A10, A11
8	CKEBCECCDED	3	A6, A9, C11
9	CKEBCECCDEN	2	C5, C6
10	CJEBCECCDEN	1	C5
11	COCBCECCDEN	1	C5
12	CDEBCECCDED	2	C11
13	CHCCBBCDCCG	1	C3
14	CHKCBBCCCCG	3	C3, C4
15	CHCCBBCCCCG	3	A7, C2
16	CJFBBDDCCEI	1	C2
17	CHCBBBCCCCG	1	C1
18	CHBBBCCCCCH	1	C1
19	BMICBCCCDEL	3	C8
20	CQGBBDCCCEI	1	A5
21	GMCCBCCACEP	1	A12
22	CQFBBDDCCEI	1	A7
23	ESEBBECCDED	1	A8
24	CKEBCECCDFD	1	A8
25	CKEECECCDEN	4	C6, C7, C10
26	BMICBCCCCEO	1	C9
27	BMICBCCCCEP	1	C9
28	BMICBCCBCEO	1	C9
29	FMCCBCCACEP	1	N1
30	GMCCBCCACEP	2	A12, N2

number of mtDNA genotypes observed was substantially higher: based on 11 informative endonucleases and 51 restriction sites, 30 clones were distinguished (Table 2). Given the large number of clones identified for each species relative to the number of individuals sampled, all clones were rare. Among the desert iguanas, the most common clone was represented by five individuals, and 61% of the genotypes were restricted to single individuals. Similarly, no chuckwalla clone was distributed among more than four individuals, and 60% were restricted to single specimens.

As a result of the above findings, mtDNA genotypic diversities were remarkably high for both species: $G = 0.950$ and 0.976, respectively. The desert iguana and the

chuckwalla exhibit some of the highest levels of mtDNA variability yet reported for vertebrates (Avise et al., 1989). Moreover, when genotypes distinguished by unequivocal size variation are coupled with those identified by restriction-site differences, the estimates of G become higher still. Two additional genotypes were clearly resolved for the desert iguana when size variants (< 500 base pairs) were considered. Notable size variation in chuckwalla mtDNA (16.5–17.5 kb) allowed the identification of five additional genotypes for this species. Estimates of genotypic diversity increased accordingly, with $G = 0.963$ for the desert iguana and $G = 0.983$ for the chuckwalla (very near the maximum assumable value of 1.0).

Geographic variation

Desert iguanas

The extensive polymorphism detected among the desert iguana mtDNAs was characterized by many localized genotypes (Fig. 2A). Fourteen of the 18 site-variant clones were observed only at single locales (Table 1), and no clone encompassed more than three sample sites (Fig. 2A; Table 1).

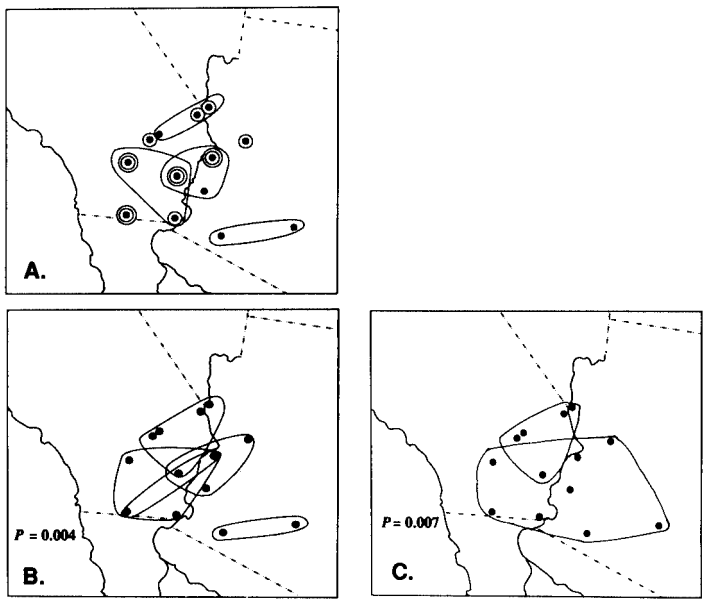

Fig. 2. Geographic distributions of mtDNA clones and clonal assemblages in the desert iguana. Each dot represents a collection site, and lines encompass all individuals belonging to: A) each distinguishable mtDNA clone (double concentric lines indicate two or more genotypes occurred at a locale); B) sets of clones clustering within genetic distance level $p = 0.004$ (see Fig. 3); and C) sets of clones clustering within genetic distance level $p = 0.007$ (Fig. 3).

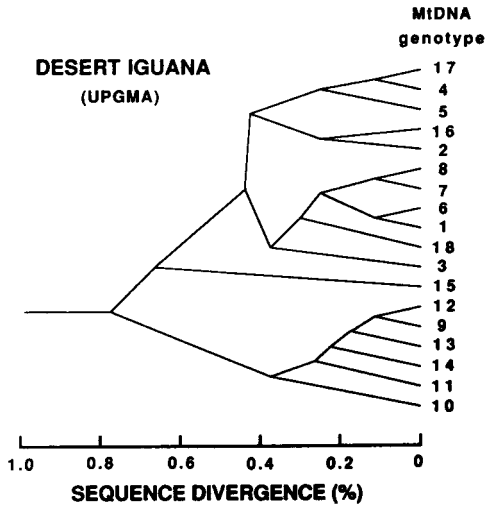

Fig. 3. UPGMA phenogram of mtDNA genetic distances observed in desert iguanas. Genotypes are numbered as in Table 1.

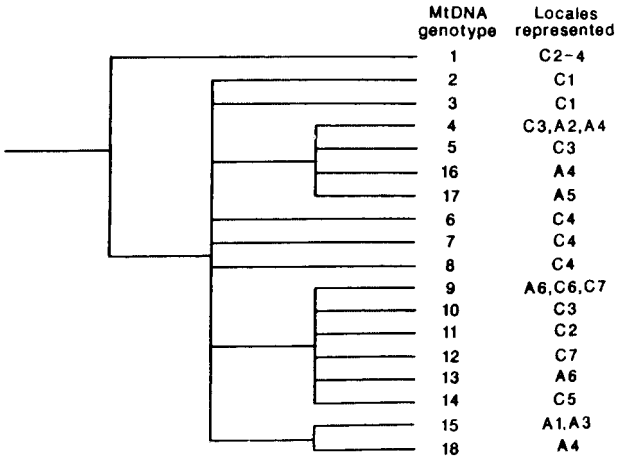

Fig. 4. Consensus tree of the desert iguana mtDNA clones produced by the CONTREE program of PAUP.

The mtDNA phenogram generated from the genetic distance matrix for the desert iguana genotypes is shown in Fig. 3. Using arbitrarily chosen genetic distances in the UPGMA clustering hierarchy, the geographic distributions of extended clonal assemblages can also be plotted (Figs. 2B and 2C). For example, five clonal groupings are evident at the $p = 0.004$ clustering level, and two groupings are present at the level bounded by $p = 0.007$. As might be expected for a

species with limited dispersal characteristics, increasingly wide geographic distributions are associated with increasing depths in the desert iguana phenogram.

Nonetheless, there is no evidence, either from the distributions of individual clones (Fig. 2A) or from the extended clonal assemblages (Fig. 2B and 2C), that the lower Colorado River valley has functioned as a particularly significant historical barrier to dispersal in this species. For example, two of the four clones that were distributed across locales had representatives on both sides of the river. Increasingly large clonal groupings clearly demonstrate east–west distributions that extend well across the Colorado River valley (Fig. 2B and 2C). Furthermore, the shallow

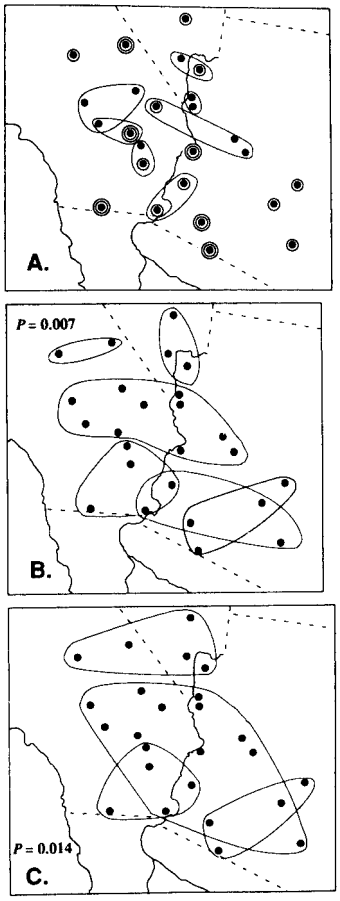

Fig. 5. Geographic distributions of mtDNA clones and clonal assemblages in the chuckwallas. Each dot represents a collection site, and lines encompass all individuals belonging to: A) each distinguishable mtDNA clone (double concentric lines indicate two or more genotypes occurred at a locale); B) sets of clones clustering within genetic distance level $p = 0.007$ (see Fig. 6); and C) sets of clones clustering within genetic distance level $p = 0.014$ (Fig. 6).

branching patterns in the phenogram (compared to those in the chuckwalla or desert tortoise mtDNA phenograms, see Fig. 8) indicate relatively low levels of genetic differentiation, even among the more divergent clusters.

Parsimony analysis of the restriction site matrix for the desert iguana clones generated a series of equally parsimonious networks. This outcome was not particularly surprising. Many of the clones differ only by single site changes, and as a result, the majority of the restriction sites are simply uninformative (i.e., pleisiomorphic or autapomorphic characters) with respect to network construction. Although informative restriction sites consistently identified certain clonal assemblages, the fine-scale branching patterns within these assemblages proved highly ambiguous. Therefore, a consensus tree, was created using the CONTREE program of PAUP. The consensus tree, with its apparent polychotomies, reflects the equivocal resolution within clonal assemblages (Fig. 4). It should be emphasized that this tree is not intended as a true phylogeny; rather, it provides a different, qualitative perspective to illustrate general relationships among the mtDNA clones. Nonetheless, major clonal groupings within the consensus network, like the clonal clusters of the phenogram, provide no evidence for a major genetic break at the Colorado River.

Chuckwallas

The chuckwallas also exhibited geographic localization of mtDNA genotypes. Twenty-three of the 30 site variant clones (77%) were represented by single locales

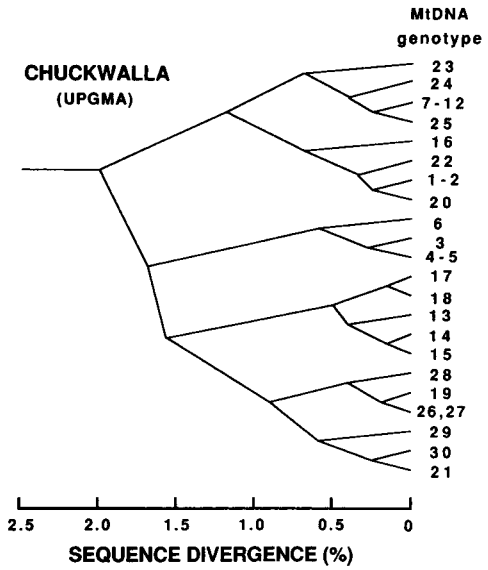

Fig. 6. UPGMA phenogram of mtDNA genetic distances observed in the chuckwallas. Note that certain terminal branches of the phenogram are represented by two or more of the genotypes listed in Table 2. This results from the exclusion of two enzymes (*Ava*II, *Stu*I) whose profiles proved too heterogeneous (and therefore ambiguous) for site inference.

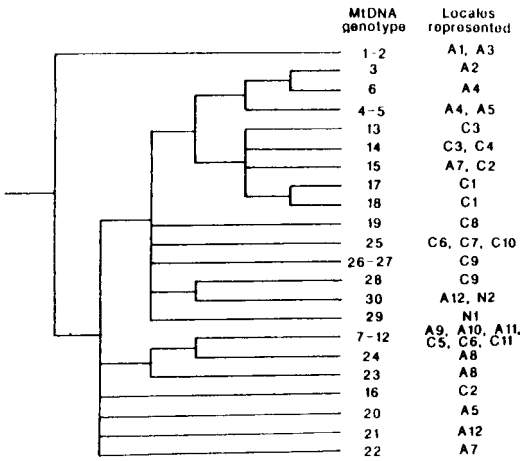

Fig. 7. Consensus tree of the chuckwalla mtDNA clones produced by the CONTREE program of PAUP.

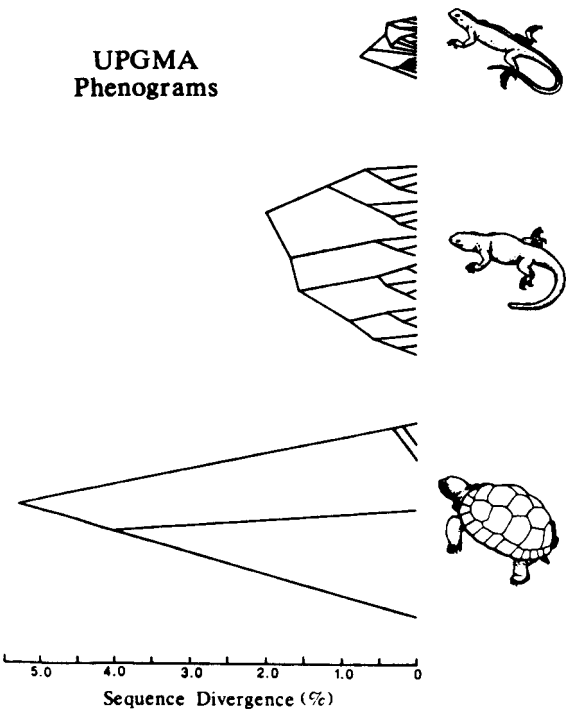

Fig. 8. UPGMA phenograms of (from top to bottom) the desert iguana, chuckwalla, and desert tortoise. The nucleotide sequence divergence scale applies to all three trees, permitting comparisons of their relative depths.

(Fig. 5A), and of the seven remaining genotypes, six were restricted to two locales. Three of the clones were observed on both sides of the Colorado River.

Relatively high divergence levels among some mtDNA genotypes are evident in the UPGMA phenogram for chuckwallas (Fig. 6). Many genetic distances appear considerably greater than those observed in the desert iguana (Fig. 8). However, the geographic structure of extended clonal groupings was somewhat similar to those of the desert iguana, with several mtDNA clusters exhibiting broad east–west distribution patterns that encompass both sides of the Colorado River basin (Figs. 5B and 5C). A similar pattern was observed for the geographic distributions of the clonal assemblages in the consensus tree generated by PAUP (Fig. 7).

Discussion

MtDNA variability and spatial structure

The sampling regime and mtDNA assays of this survey were designed to examine further the possible zoogeographic influences of the lower Colorado River area on the region's herpetofauna. An interesting though unanticipated finding of our investigation was the exceptional levels of mtDNA clonal diversity in these lizards. Among 14 species of higher animals for which genotypic diversity values have been calculated (all based on comparable methods of assay involving a nearly identical battery of restriction endonucleases), the chuckwalla and desert iguana rank second ($G = 0.983$) and fourth ($G = 0.963$), respectively (Avise et al., 1989).

Many clones and even certain clonal assemblages appeared geographically highly localized. Due to small sample sizes per locale, we hesitate to draw conclusions about intra- or inter-population variability with respect to mtDNA clones, or to attempt an interpretation of the microgeographic spatial patterns. A more extensive sampling regime will be necessary to determine whether the distributions of observed clones are truly localized or merely an artifact of limited sampling from extremely diverse populations.

It is worth noting that certain ecological and life history attributes of these lizards might account, in part, for both the genotypic diversity and the degree of fine scale differentiation in mtDNA phylogeny. Chuckwallas, for example, are exclusively saxicolous, confined largely to the scattered outcroppings that characterize much of the topography of the southwestern U.S. As such, suitable habitat for this species is patchy and often isolated. Life history traits that include delayed maturity, high adult survivorship (annual survivorship near 75% for individuals one yr or older), low annual reproductive frequency, and limited migration confined mostly to males (Abts, 1987) all may be conducive to mtDNA differentiation in chuckwallas. Desert iguanas are also relatively habitat specific, occurring most frequently in sandy desert flatlands supporting creosote communities (Stebbins, 1985). Dispersal is apparently very limited in these lizards as well (Parker, 1972; Krekorian, 1984).

Phylogeographic patterns

Although broad-scale geographic structure is also evident for the chuckwalla and desert iguana mtDNAs (Figs. 2 and 5), two major points argue against a primary role for the Bouse embayment in shaping observed phylogeographic patterns. First, various genetic units of both species, ranging from clones to major phenetic assemblages, are well represented on both sides of the Colorado River (although dispersal subsequent to the embayment's recession could explain these present distribution patterns). Second, the levels of nucleotide sequence divergence calculated for the major subdivisions within these two species suggest that the differences are too recent to have been determined by population isolation dating to the Pliocene events that formed the Bouse Sea (ca. 3–5 mya).

If we assume a "conventional" estimate for the rate of vertebrate mtDNA evolution, about 2% sequence divergence per million years between lineages (Brown et al., 1979; Wilson et al., 1985; Shields and Wilson, 1987), then divergence between the most genetically distinct chuckwalla assemblages ($p = 0.019$) dates to approximately 975 000 yr B.P., and divergence between the two most divergent desert iguana assemblages ($p = 0.008$) dates to about 390 000 yr B.P. It should be noted that recent evidence has been compiled that suggests a deceleration in mean microevolutionary rate of turtle mtDNA, emphasizing caution in the acceptance of a universal mtDNA clock for the vertebrates (Avise et al., 1992). Thus, while the above estimates for lizard divergence times are provisional, substantially higher divergence levels (e.g., $p > 0.04$) would be expected for a probable association to Pliocene events (Fig. 8).

Fossil and geologic evidence lead some support to our molecular findings. Although an extensive fossil record indicates that chuckwallas were distributed widely throughout the southwestern U.S. (Arizona, California, Nevada) during the late Pleistocene some 15–16 000 yr B.P. (Van Devender and Mead, 1978; Estes 1983), no fossil material predating the Lower Pleistocene has been reported for this region (Estes, 1983). Furthermore, there are no Pliocene or Pleistocene records for desert iguanas in the southwestern U.S. (Estes, 1983). However, Miocene/Pliocene histories have been inferred for both genera on the Baja peninsula and various islands in the Sea of Cortez (Murphy, 1983). Based on geologic and paleobiogeographic data, Murphy (1983) postulates that through Miocene vicariance events, the islands that created the Cape region of Baja California Sur may have been possible centers of origin for the lizard genera *Dipsosaurus* and *Sauromalus*. If *Dipsosaurus* and *Sauromalus* did originate on the Cape area, then they would not have been in position, spatially or temporally, to be influenced by the Bouse marine incursion of the Colorado River valley.

Comparative mtDNA surveys and regional zoogeography

The fundamental purpose of this investigation was to extend the search for concordant phylogeographies among conspecific populations to another regional fauna conceivably shaped by a common biogeographic history. Chuckwallas and desert iguanas were selected as appropriate candidates for comparison to the previously-studied desert tortoise because of similar geographic ranges and habitat

usage. However, common phylogeographic patterns require shared histories, and we have found no molecular evidence that intraspecific phylogenies of the assayed herpetofauna of the southwestern U.S. have been concordantly shaped by any singular vicariant factor of overriding significance. Nonetheless, the mtDNA data do indicate extensive geographic population structure in both chuckwallas and desert iguanas, a finding which appears compatible with their limited dispersal tendencies and fragmented habitats. Thus even in settings where concordant phylogeographic partitions are lacking, molecular genetic data may contribute to an understanding of the idiosyncratic evolutionary histories of particular species.

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Appendix

Locality data for the lizards collected for this survey are listed in tabular form below.

Dipsosaurus dorsalis		
Collection locality	N	Site code
Near Jacumba, Imperial Co., CA	3	C1
Algondones Dunes, Imperial Co., CA	2	C2
Ford Dry Lake Basin, Riverside Co., CA	5	C3
Indio City, Riverside Co., CA	5	C4
Sheep Hole Mts, San Bernardino Co., CA	1	C5
Bristol Lake, San Bernardino Co., CA	1	C6
Needles, San Bernardino Co., CA	3	C7
Mohawk Dunes, Yuma Co., AZ	2	A1
Stone Cabin, Yuma Co., AZ	2	A2
Rainbow Valley, Maricopa Co., AZ	1	A3
Near Parker, La Paz Co., AZ	5	A4
Burro Ck., Mohave Co., AZ	5	A5
Bullhead City, Mohave Co., AZ	2	A6
Sauromalus obesus		
Jacumba Mts., Imperial Co., CA	2	C1
Near Winterhaven, Imperial Co., CA	2	C2
Desert Center, Riverside Co., CA	3	C3
Coxcomb Mts., San Bernardino Co., CA	1	C4
Sheep Hole Mts., San Bernardino Co., CA	3	C5
Near Yucca Valley, San Bernardino Co., CA	2	C6
Near Barstow, San Bernardino Co., CA	1	C7
Near Ridgecrest, Kern Co., CA	3	C8
Ibex Pass, San Bernardino Co., CA	3	C9
Near Kelso, San Bernardino Co., CA	2	C10
Near Essex, San Bernardino Co., CA	3	C11
South Mt., Maricopa Co., AZ	2	A1
Four Peaks, Maricopa Co., AZ	3	A2
Near Redrock, Pinal Co., AZ	1	A3
Tule Desert, Yuma Co., AZ	2	A4
Mohawk Mts., Yuma Co., AZ	4	A5
Near Bagdad, Yavapai Co., AZ	1	A6
Stone Cabin, Yuma Co., AZ	3	A7
Near Parker, La Paz Co., AZ	2	A8
Date Creek Mts., Yavapai Co., AZ	1	A9
Black Mts., Mohave Co., AZ	2	A10
Bullhead City, Mohave Co., AZ	1	A11
Detrital Valley, Mohave Co., AZ	2	A12
Sheep Range, Clark Co., NV	1	N1
Near Henderson, Clark Co., NV	1	N2