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Molecular Evidence for a Unique Evolutionary Lineage of Endangered Sonoran Desert Fish (Genus *Poeciliopsis*)

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Abstract: Efforts to restore an endangered species in its former range should be based on a sound understanding of evolutionary relationships among remaining natural populations. In this study mitochondrial (mt) DNA diversity within and among Gila River drainage populations of the endangered Sonoran topminnow (*Poeciliopsis occidentalis*) in Arizona was compared to that from neighboring populations in Sonora, Mexico, where the species remains locally abundant. No mtDNA diversity was detected within or among samples from the Gila River basin in Arizona. But considerable variation was found within and among populations from several river systems in Sonora. Examination of mtDNA from a population that inhabits the upper reaches of the Río Yaqui in southeastern Arizona revealed substantial divergence between it and all other populations examined. We comment on the implications of this divergent population for topminnow management in Arizona and argue for more-detailed genetic and morphological studies to determine the distributional limits and specific status of this highly divergent form.

Evidencia molecular de un linaje evolutivo único para peces en peligro de extinción (Genero *Poeciliopsis*) del Desierto de Sonora

Resumen: Los esfuerzos para restaurar una especie en peligro a su antigua área de distribución debe basarse en una comprensión apropiada de las relaciones evolutivas entre las poblaciones naturales remanentes. En este estudio, se comparó la diversidad de ADN mitocondrial dentro y entre poblaciones en peligro de *Poeciliopsis occidentalis*, que habita las corrientes del río Gila en Arizona, con la diversidad de poblaciones vecinas de Sonora (Mexico) donde la especie es todavía abundante. No se detectó diversidad alguna de ADN mitocondrial dentro o entre muestras de la cuenca del río Gila en Arizona. Sin embargo, se encontró una variación considerable dentro y entre poblaciones de varios sistemas de ríos en Sonora. El análisis de ADN mitocondrial de poblaciones que habitan los cauces superiores del río Yaqui en el sudeste de Arizona reveló una divergencia substancial entre esta población y todas las otras poblaciones examinadas. Discutimos las implicaciones de esta población divergente para el manejo del "topminnow" en Arizona y remarcamos la necesidad de estudios genéticos y morfológicos más detallados con la finalidad de determinar los límites del área de distribución y el estado específico de esta forma altamente divergente.

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Introduction

The Sonoran topminnow, *Poeciliopsis occidentalis*, was once the most abundant fish in the Gila River drainage of Arizona (Hubbs & Miller 1941). Currently, it persists there as a handful of fragmented populations representing a small portion of its former range (Minckley et al. 1977). The species remains abundant throughout most of its former range in Sonora, Mexico (Hendrickson & Juarez 1990). Population decline in Arizona has been dramatic, resulting in the addition of *P. occidentalis* to the federal endangered species list in 1973 (U.S. Department of the Interior 1980). The topminnow suffers from severe contractions of its former range due primarily to desiccation of habitat, stream canalization and impoundment, and the introduction of exotic species, particularly the western mosquitofish, *Gambusia affinis* (Minckley & Deacon 1968, 1991; Meffe et al. 1983; Hendrickson & Minckley 1984). Efforts to prevent the extinction of topminnows in Arizona have focused on restoring the Gila topminnow (subspecies *P. o. occidentalis*) throughout its former range (Simons et al. 1989). Elimination of mosquitofish from habitats harboring remnant topminnow populations and the reclamation of suitable habitats by regulating ground-water usage are also planned but have rarely been implemented (Simons et al. 1989). Preservation of a second subspecies in Arizona (*P. o. sonoriensis*, the Yaqui topminnow) has benefited from the establishment and management of the San Bernardino National Wildlife Refuge (NWR) in southeastern Arizona.

Knowledge of the genetic structure of remnant populations of an endangered species should play an integral role in any comprehensive recovery effort. But efforts to restore *P. occidentalis* in Arizona were undertaken before a genetic survey of the species was completed. Subsequently, a study of allozyme variation in natural populations from Arizona and the neighboring state of Sonora, Mexico, identified three genetically distinct lineages (Vrijenhoek et al. 1985). Group I comprised all populations from the Gila drainage in Arizona (Fig. 1) and the Ríos Sonora and de la Concepción in Sonora (Fig. 1a). Group II comprised topminnows from the Río Yaqui (including *P. o. sonoriensis* from the San Bernardino National Wildlife Reserve in Arizona), the Río Matape, and the lower Río Mayo. Group III comprised isolated populations of *P. occidentalis* from the upper stretches of the Río Mayo (Fig. 1a).

Compared to topminnows in Mexico, Arizona populations harbored little allozyme diversity (Vrijenhoek et al. 1985). In particular, the Monkey Spring topminnow population (site MS; Fig. 1b) had no detectable genetic diversity, although this population provided the stock for most of the re-introductions made to that time. Subsequently, it was learned that the Monkey Spring topminnows have lower fecundity, growth rate, and survival

than topminnows from populations that exhibit measurable genetic diversity (Meffe 1985; Quattro & Vrijenhoek 1989). Following recommendations outlined in Vrijenhoek et al. (1985), a new stock from a genetically variable and more phenotypically robust population, Sharp Spring (site SS; Fig. 1b), has replaced the Monkey Spring stock for future re-introductions within the Gila drainage (Simons et al. 1989).

Some differences in allozyme frequencies exist among Group I topminnow populations in Arizona, but differentiation among Group I populations is minor compared to the differences among the three major groups (Vrijenhoek et al. 1985). Several authors suggested that laboratory experiments should be conducted to test the vigor of offspring from crosses between different Group I populations from Arizona (Vrijenhoek et al. 1985; Meffe & Vrijenhoek 1988; Quattro & Vrijenhoek 1989). They argued that recent anthropogenic factors were most likely responsible for severing opportunities for gene flow among populations within the Gila drainage. Thus, it may be appropriate to mix Group I stocks if interpopulation hybrids and their descendants have a greater capacity for surviving in and adapting to reclaimed habitats. Simons et al. (1989) proposed an alternative strategy that would avoid genetic exchange among topminnow populations inhabiting four segments of the Gila River, thus preserving any significant but as yet undetected remnant genetic variation that may exist in these populations. The choice of these alternative plans rests on the nature of the genetic differences among local topminnow populations. If regional differentiation is due to recent isolation and population bottlenecks resulting from human activities, stock admixture might be an appropriate management strategy. But if regional differentiation is a result of natural selection and historical restrictions to gene flow, then mixing of stocks may lead to the loss of unique evolutionary lineages.

We conducted a restriction fragment analysis of mitochondrial DNA (mtDNA) to investigate patterns of genetic diversity within and divergence among populations of *P. occidentalis* from Arizona and Sonora. First, we used the mtDNA data to evaluate the hypothesis that the isolated populations of *P. o. occidentalis* in the Gila River represent unique evolutionary lineages. Second, we used this genetic data to compare the isolated population of *P. o. sonoriensis* from southeastern Arizona with other Group II populations from downstream portions of the Río Yaqui in Sonora. Finally, we comment on the management of these taxa in light of the present genetic results.

Materials and Methods

We analyzed mtDNA restriction site variation among 59 *P. occidentalis* representing all river systems within

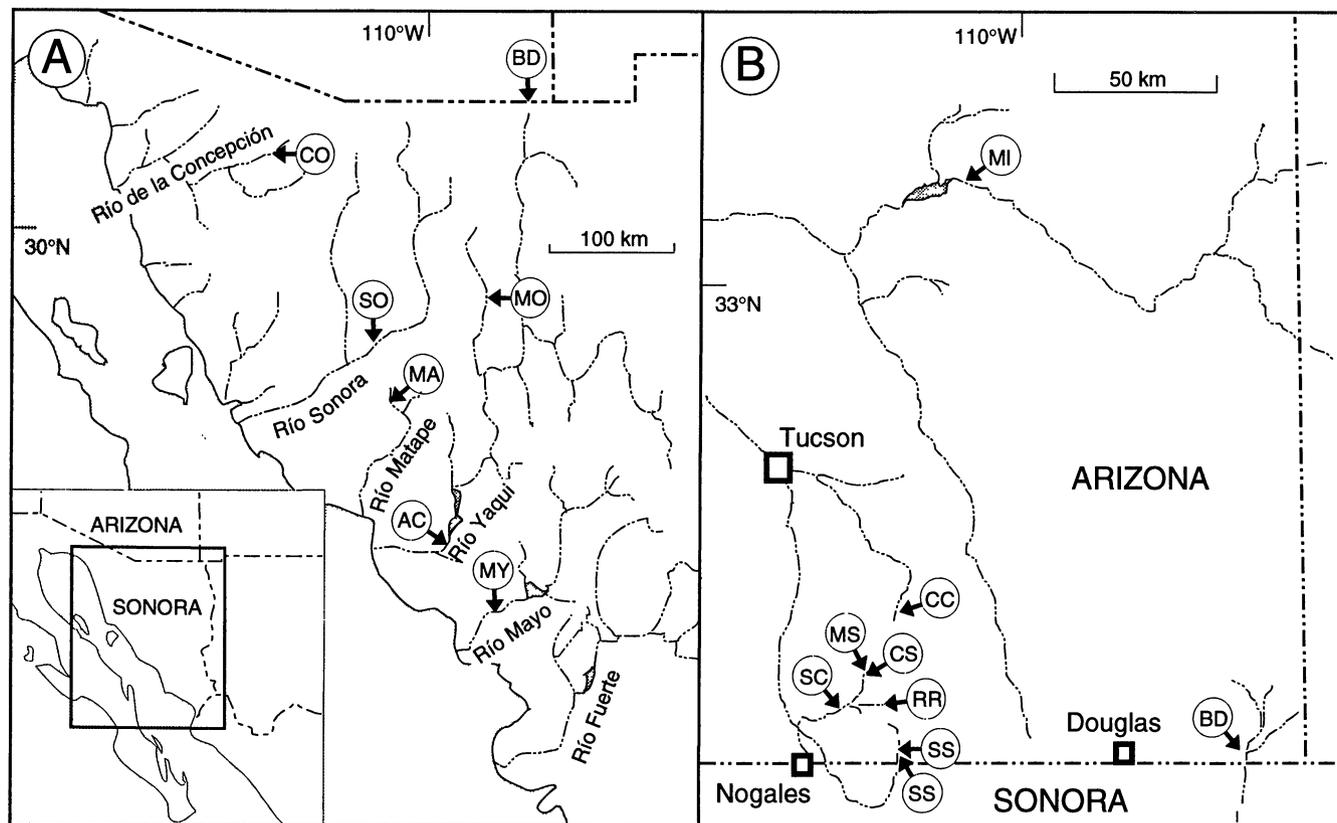


Figure 1. Sampling locations of *P. occidentalis* within Sonora, Mexico, and the Río Yaqui drainage, Arizona (A), and a detailed view of the southcentral Arizona area showing sampling locations within the Gila river drainage (B). Collection locale abbreviations are identified in Table 2.

their present range in Arizona and Sonora (Fig. 1). We include published mtDNA data from 15 specimens of *P. occidentalis* collected in Sonora (Quattro et al. 1992). Mitochondrial DNA was isolated from fresh tissues following the methods of Lansman et al. (1981). Purified mtDNAs were digested with 16 restriction endonucleases with five (*Ava*I, *Ava*II, *Hinc*II) and six (*Bam*HI, *Bcl*I, *Bgl*I, *Bgl*II, *Bst*EII, *Eco*RI, *Hind*III, *Nde*I, *Pst*I, *Pvu*II, *Spe*I, *Stu*I, *Xba*I) base-recognition sequences. Fragments were end-labeled with [³⁵S]dNTPs and separated in 0.8–1.2% agarose gels. After electrophoresis, gels were dried under vacuum onto filter paper backings and exposed to X-ray film for 24–72 hours.

We gave an arbitrary letter code to each restriction digest profile for a particular endonuclease. Composite scores, representing a letter code for each of 16 gel-fragment profiles, were assigned to each individual. Because we could interpret all gel-fragment profiles as specific site gains or losses, we constructed a matrix of the presence or absence of each polymorphic restriction site for each composite haplotype. We used PAUP (Version 3.0s; Swofford 1991) to construct a phylogenetic hypothesis from this matrix using the principle of maximum parsimony. We used heuristic searches with 10 random input orders of the data matrix, and we treated

characters as unordered in all analyses. Restriction-site data from a closely related species, *P. lucida* (Quattro et al. 1992), were used to root the phylogeny. The stability of the branching order of the shortest tree was evaluated by 100 bootstrap replications.

We estimated the average number of nucleotide substitutions per site among populations (d) using the maximum likelihood method described in Nei and Tajima (1983). Using MEGA (Kumar et al. 1993), an unrooted phylogeny based on this pairwise distance matrix was estimated by the neighbor-joining method (Saitou & Nei 1987). We calculated nucleon diversity (h), a measure of mtDNA haplotype variability, following Nei and Tajima (1981).

Results

A previous study revealed 8 mtDNA haplotypes (O.1–O.8; Table 1) among 15 specimens of *P. occidentalis* from the five Mexican river systems (Quattro et al. 1992). To be consistent with that study we retain the Roman letter *O* prefix (for *occidentalis*) and a numerical code following the decimal to designate each haplotype in the order of its discovery. Two new mtDNA haplo-

Table 1. Restriction-site polymorphism in *Poeciliopsis occidentalis*, expressed as binary characters (1 = present, 0 = absent).

Haplotype	Restriction site*									
	BamHI a	BclI b c	BstEII d	EcoRI e	PvuII f g	SpeI h	AvaII i j k	BglI l m	AvaI n	StuI o
O.1	1	1 0	1	1	1 1	0	0 0 0	0 0	0	1
O.2	1	1 0	1	1	1 1	0	0 0 1	0 0	0	1
O.3	1	0 0	1	1	1 1	0	0 0 0	0 0	0	1
O.4	1	1 0	0	1	1 1	1	0 0 0	0 0	0	0
O.5	1	1 0	0	1	1 1	1	1 1 0	1 0	0	1
O.6	1	1 0	0	1	1 1	1	0 0 0	0 1	0	1
O.7	1	1 0	0	1	1 1	1	0 0 0	0 0	0	1
O.8	1	1 0	0	1	0 1	1	0 0 0	0 0	0	1
O.9	1	1 0	0	1	1 1	1	0 0 0	0 0	1	1
O.10	0	1 1	0	0	1 0	1	1 1 0	0 0	0	1

*Although 71 potential restriction sites were assayed in each individual, only polymorphic sites are shown.

types (O.9 and O.10) were identified among the 59 specimens examined in the present study. Mutational divergence among the 10 haplotypes could be attributed to base substitutions within 15 polymorphic restriction sites (Table 1).

The 10 mtDNA haplotypes were not distributed randomly among the six river systems. Haplotypes O.1, O.2, and O.3 were found primarily in the Ríos Mayo, Yaqui (Moctezuma), and Matape, whereas haplotypes O.4, O.6, O.8, and O.9 were found exclusively in the Ríos de la Concepción and Sonora (Table 2). The most common haplotype surveyed, O.7, was fixed in all eight Gila River populations and was common in the Ríos de la Concepción and Sonora. Haplotype O.5 was found only in the Río Yaqui at Moctezuma. The most divergent haplotype sampled, O.10, was fixed in the 12 topminnows sampled from the Black Draw population.

Considering the phylogenetic relationship among the mtDNA haplotypes, there is a rough concordance between the present mtDNA data and the allozyme data of Vrijenhoek et al. (1985). Populations defined as either Group I (Gila River and Ríos Concepción and Sonora) or Group II (Ríos Matape and Mayo) based on protein electrophoresis are each defined by clades of closely related mtDNA haplotypes in the genic phylogeny (Fig. 2). However, a third distinct grouping of mtDNA haplotypes, undetected in the previous allozyme survey, is evident in the phylogeny. This "Yaqui" clade comprises mtDNA haplotypes surveyed from two of seven individuals sampled from the Río Yaqui at Moctezuma (haplotype O.5) and all 12 individuals sampled from Black Draw (haplotype O.10). These three distinct groups of haplotypes were found in greater than 80% of the bootstrap trees (Fig. 2). Overlap between these three major groups occurred at the Río Moctezuma locale (electrophoretically designated as Group II), which harbored mtDNA haplotypes associated with individuals representing Group I (O.7), Group II (O.1), and the Yaqui clade.

A neighbor-joining tree based on pairwise distances

among populations provides additional support for the distinctiveness of the three major groups of *P. occidentalis* suggested by the genic phylogeny (Fig. 3). As in the allozyme survey, Group I includes all populations of topminnows from the Gila River and the Ríos Concepción and Sonora, whereas Group II comprises populations sampled from the Ríos Matape and Mayo. Unlike the phylogeny constructed from allozyme data, the Black

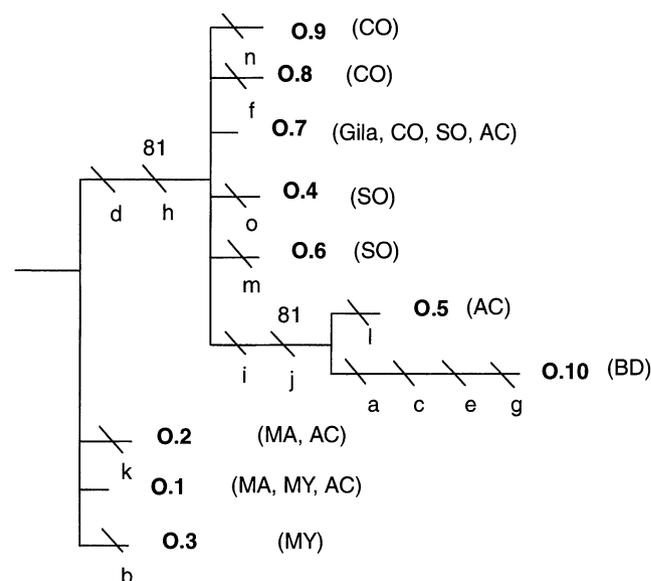


Figure 2. Phylogenetic tree summarizing relationships among observed mtDNA haplotypes in *Poeciliopsis occidentalis*. Slashes represent the number of mutations necessary to relate individual mtDNA haplotypes, and lower-case letters refer to specific restriction-site polymorphisms in Table 1. Codes in parentheses summarize the observed distribution of each haplotype. Numbers along the branches of the tree represent the percentage of 100 bootstrap replicates supporting the particular clade. The tree was rooted using restriction-site data from a closely related congener, *P. lucida* (Quattro et al. 1992; data not shown).

Table 2. Sources of fish specimens, locality codes, and observed mtDNA haplotypes.

<i>Drainage locality</i>	<i>Code</i>	<i>n</i>	<i>mtDNA haplotype</i>	<i>Nucleon diversity</i>
Upper Gila				
Middle Spring	MI	4	0.7	0.00
Cienega Creek				
Cienega Creek	CC	5	0.7	0.00
Sonoita Creek				
Cottonwood Spring	CS	3	0.7	0.00
Monkey Spring	MS	5	0.7	0.00
Redrock Canyon	RR	3	0.7	0.00
Sonoita Creek	SC	3	0.7	0.00
Upper Santa Cruz				
Sharp Spring	SS	6	0.7	0.00
Sheehy Spring	SH	2	0.7	0.00
Río de la Concepción				
La Providencia Cienega	CO	5	0.7	0.52
		1	0.8	
		1	0.9	
Río Sonora				
Ures	SO	1	0.4	0.46
		1	0.6	
		6	0.7	
Río Yaqui				
Moctezuma	AC	2	0.1	0.76
		2	0.5	
		3	0.7	
San Bernardino Ranch	BD	12	0.10	0.00
Río Matape				
San Jose de Pimas	MA	3	0.1	0.60
		2	0.2	
Río Mayo				
Navajoa	MY	3	0.1	0.50
		1	0.3	
Across all populations	—	8	0.1	0.59
		2	0.2	
		1	0.3	
		1	0.4	
		2	0.5	
		1	0.6	
		45	0.7	
		1	0.8	
		1	0.9	
		12	0.10	

Draw population is highly divergent and does not fall within the confines of the Group II clade. The Yaqui (Moctezuma) population is intermediate in its affinity to any Group I population and the second Yaqui population (Black Draw) because its composition of haplotypes comprises all three major groups.

We estimated nucleon diversity (b) as a measure of mtDNA haplotype variability (Table 2). Over all populations surveyed, nucleon diversity was quite high ($b = 0.59$), reflecting the mixture of mtDNA haplotypes representative of three major topminnow groups. In con-

trast, however, no detectable mtDNA diversity was found within any of the Arizona populations examined ($b = 0.0$), although considerable mtDNA variability was found within all Sonoran sites. Nucleon diversity was highest at the Río Yaqui (Moctezuma) locality ($b = 0.76$), where mtDNA haplotypes indicative of topminnows of Groups I and II and the Yaqui clade overlap.

Discussion

We find no support for the hypothesis of long-term genetic isolation among *P. o. occidentalis* populations in Arizona because no mtDNA diversity was found within or among populations of topminnow inhabiting different stream segments of the Gila River drainage. This result parallels the previous allozyme study, which found low levels of genetic diversity in populations of *P. o. occidentalis* from Arizona, where the species is endangered, compared with populations from Sonora, where the species remains abundant (Vrijenhoek et al. 1985). Although we might explain the lack of mtDNA diversity within Arizona populations as an artifact of small sample sizes ($n = 2-6$ for most populations), all sampled Sonoran populations ($n = 4-8$) contained considerable mtDNA variability.

The patterns of allozyme and mtDNA diversity are broadly congruent in that topminnows from the Gila drainage and the Ríos Sonora and de la Concepción (Group I) represent a distinct evolutionary lineage from populations inhabiting the Río Matape and lower Río Mayo (Group II). But there are exceptions to the general concordance between the two types of genetic data. First, topminnows from the Moctezuma branch of the Río Yaqui were assigned to Group II based on allozymes, but they harbored mtDNA haplotypes indicative of Groups I and II (Vrijenhoek et al. 1985). Reexamination of the Distance-Wagner dendrogram summarizing genetic relationships among these populations indicates that topminnows from the Río Moctezuma were placed near the node that separates the branches defining Groups I and II. The evolutionary relationships among at least some of these conspecific groups are most likely reticulate as a result of genetic exchange occurring between the Ríos Moctezuma and Sonora via some historical vicariant event. Admixture between Groups I and II through stream capture was hypothesized previously by Vrijenhoek et al. (1985) to explain high genetic diversity and intermediate allelic frequencies of sites in the Río Matape (at San José de Pima) and Río Sonora (at Ures). The present geographic distributions of other fish species also suggest historical connections between the Ríos Sonora, Matape, and Yaqui (Hendrickson et al. 1980; DeMarias 1991).

A more significant exception to the general congruence between the allozyme and mtDNA data occurs in

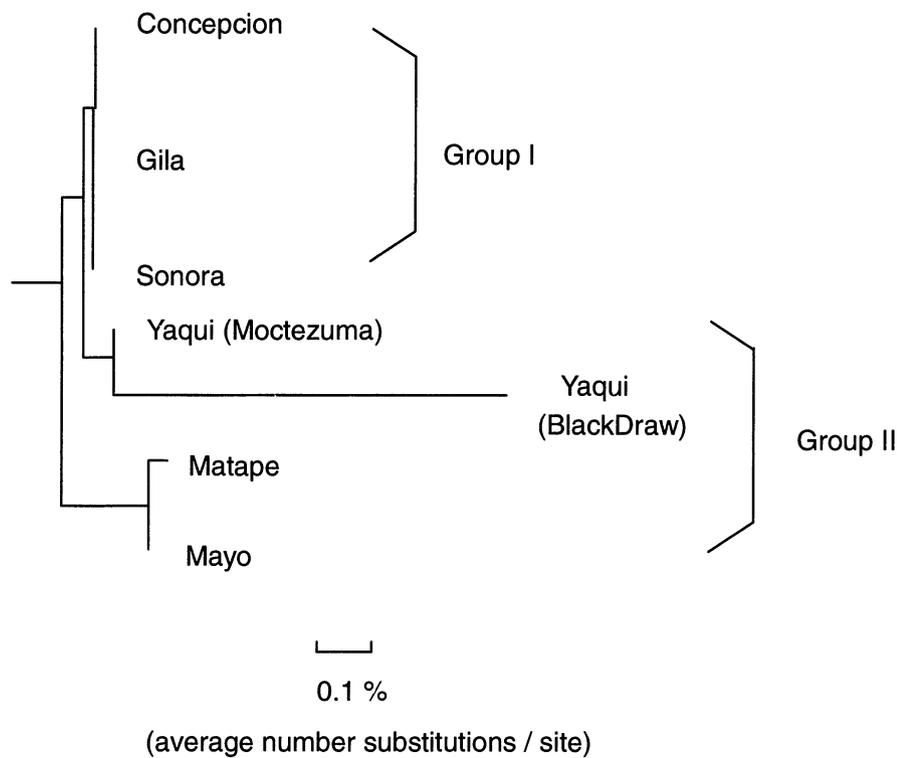


Figure 3. Neighbor-joining phylogeny based on pairwise distances among populations. Although constructed as an unrooted phylogeny the tree is drawn with the root placed as suggested in Fig. 2. Group designations are as described by allozyme data (see text and Vrijenhoek et al. 1985).

comparisons of *P. o. sonoriensis* from Black Draw to other *P. occidentalis* populations in Arizona and Sonora. Although allozymes distinguished Black Draw *P. o. sonoriensis* from Gila River *P. o. occidentalis* populations, no unique allozymes differentiated the Black Draw population from downstream Río Yaqui topminnows in Sonora (Vrijenhoek et al. 1985). In contrast, the present mtDNA data show that the Black Draw topminnows differ substantially from all other topminnows sampled in Arizona and Sonora. Indeed, this difference far exceeds that observed in pairwise comparisons between populations comprising Group I and Group II. Historical isolation of the Black Draw locality from other Río Yaqui sites is supported by parallel studies of a morphologically unique species, *Gila purpurea* (related to the broadly distributed *G. eremica*), that is endemic to the northernmost reaches of the Río Yaqui (DeMarias 1991).

Topminnows from San Bernardino Creek, Mexico (contiguous with Black Draw), were described originally as a distinct species, *Girardinus sonoriensis* (Girard 1859). Jordan and Gilbert (1883) considered *sonoriensis* synonymous to *occidentalis*. They provide no justification for this action; but it may have been based on a comment by Gunther (1866) that the two taxa were identical. Although Cope and Yarrow (1875) listed *G. sonoriensis* as a distinct species, most recent taxonomic treatments do not recognize the specific designation (Rosen & Bailey 1963), with the exception of Miller and Lowe (1964). Subtle morphological differences between Gila River and San Bernardino Creek topminnows prompted Minckley (1969, 1971) to relegate the latter to a separate subspe-

cies, *P. occidentalis sonoriensis*. Given the striking mtDNA differences between the Black Draw topminnows and all other *P. occidentalis* populations sampled, topminnows in the San Bernardino area represent a highly unique evolutionary lineage. Little is known about the genetic composition or abundance of *P. occidentalis* in the upper Yaqui drainage from San Bernardino to Río Moctezuma. We suggest that genetic and morphological studies be undertaken immediately to determine the distributional limits and specific status of the highly divergent topminnows at Black Draw.

To protect any remnant genetic variation harbored within the Gila drainage populations of *P. o. occidentalis*, Simons et al. (1989) suggested that introductions not be made between four proposed management areas. Although the Endangered Species Act recognizes genetically unique populations of vertebrates as evolutionary units worthy of protection (Waples 1992), the lack of mtDNA diversity among Gila River populations provides no evidence for historical isolation among these areas. This lack of mtDNA variability among Gila River populations must be interpreted with caution when used as a measure of differentiation, but the existence of a single haplotype within all Gila River populations and the sharing of this haplotype in high frequency with Sonoran Group I populations suggests that all Group I populations share a common ancestor in recent evolutionary time. We point out that differences in life-history traits (Constanz 1979; Meffe 1985) and allozyme frequencies (Vrijenhoek et al. 1985) have been reported among extant populations of the Gila topminnow. Conflicting in-

formation from the ecological and genetic studies and the present mtDNA data makes it difficult to determine if these populations should be preserved in isolation or if gene flow among them should be reestablished.

Given the recent history of population reduction and isolation during the past 100 years, it seems likely that allozyme and life-history differences among Gila drainage populations stem from severed opportunities for gene flow and concomitant population bottlenecks, not from long-term isolation. Evidence for this bottleneck hypothesis is provided by the higher mtDNA and allozyme diversity with Sonoran Group I populations, which have not experienced the massive range contractions encountered by topminnow populations in Arizona. This hypothesis notwithstanding, the lack of mtDNA differentiation among Gila drainage populations argues for high levels of gene flow through interconnections in place over recent evolutionary time-scales.

If historical corridors for gene-flow have been only recently severed by anthropogenic factors, then the adverse effects of a loss of genetic diversity in small, subdivided topminnow populations could potentially be reversed by small-scale introductions among previously contiguous populations (Meffe & Vrijenhoek 1988). Indeed, the recency of historical interconnection among Group I topminnow populations reflected in the lack of significant among-population mtDNA differentiation, supports the concept that such transplantations would not prompt an unnatural union of highly divergent evolutionary lineages. It has been shown that inbreeding can have large effects on processes related to population viability, such as population growth rate (Leberg 1990). However, the restoration of genetic variability in a homozygous, founder population of a related species, *Poeciliopsis monacha*, had manifold effects on fitness, increasing competitive abilities (Vrijenhoek 1989) and resistance to parasites (Lively et al. 1990). In a recent experiment with *Drosophila melanogaster*, introduction of a single migrant individual into inbred lines had the dramatic effect of doubling the fitness of the descendent cultures (Speilman & Franklin 1992). If isolated populations of fish are not inbred, however, it is unlikely that the introduction of genetic material from other sites will have large effects on their viability (Leberg 1993), but matings of individuals from different evolutionary lineages could even result in outbreeding depression (Allendorf & Leary 1986). Thus, the management strategy of supplemental gene flow must be practiced with caution, particularly in light of the unexpected yet dramatic level of mtDNA divergence characterizing the Black Draw locality from other sites within the Río Yaqui.

Our studies with endangered topminnows emphasize the need to use many types of biological data when formulating management decisions involving endangered populations. Life histories, morphology, allozymes, and mtDNA each provide unique but seemingly incomplete

perspectives concerning the evolutionary relationships among remnant populations. Furthermore, our understanding of the genetic relationships among topminnow populations is far from complete. As additional analytical tools become available, systematic relationships of these and other threatened species should be reassessed so that conservation biologists can make sound decisions regarding potential management strategies.

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