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## Taxonomic Relationships of the Zuni Mountain Sucker, *Catostomus discobolus yarrowi*

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AND DAVID J. INNES

*Catostomus discobolus yarrowi* of the Little Colorado River drainage in New Mexico and Arizona is variable, with populations morphologically and biochemically intermediate between *C. discobolus* of the Colorado drainage and *C. plebeius* of the Rio Grande drainage. Specimens of *C. yarrowi* from the headwaters of the Little Colorado in the Zuni Mountains, New Mexico, are especially similar to populations of *C. plebeius* from just across the continental divide. Downstream populations are more like *C. discobolus*. Morphological and biochemical characters show slightly different trends among samples, but the patterns are consistent with the hypothesis that a late Pleistocene stream capture resulted in introgression of *C. plebeius* characters into *C. discobolus*.

IN 1874, E. D. Cope described "*Minomus jarrovi*" from the Zuni River headwaters of the Little Colorado River drainage in New Mexico, based on specimens with 9 dorsal fin rays and the lower jaw "with acute cartilaginous edge, regularly convex forwards." The types (USNM 15783) were collected by H. W. Henshaw in 1873. [Cope gave the type locality as Provo, Utah, but Cope and Yarrow (1875) corrected it to the Zuni River, New Mexico.] Fowler (1913) referred to specimens from the same drainage, at Fort Wingate and Nutria, New Mexico, as *Pantosteus plebeius*, a species with the above characters, living in the Rio Grande drainage. The populations were rediscovered in other Zuni tributaries by W. J. Koster: the Rio Pescado in 1948 and Nutria Creek in 1960.

Smith (1966) showed that the Zuni River suckers (Fig. 1a, d) were similar to *C. discobolus* Cope (1872) of the Colorado drainage (Fig. 1c) in the number of gill rakers, but were similar to *C. plebeius* Baird and Girard (1854) of the Rio Grande drainage (Fig. 1b) in numbers of vertebrae and dorsal rays, jaw size and shape, and pigment. The mosaic of *C. plebeius* and *C. discobolus* characters in the Zuni and other Little Colorado River populations were regarded to be the result of an ancient stream capture from the Rio Grande to the Zuni, and introgressive hybridization. Smith (1966) assigned the Zuni populations to *C. discobolus* because they possessed the diagnostic gill raker numbers of that species. Although the Zuni populations were interpreted as descendants of intergrades, the

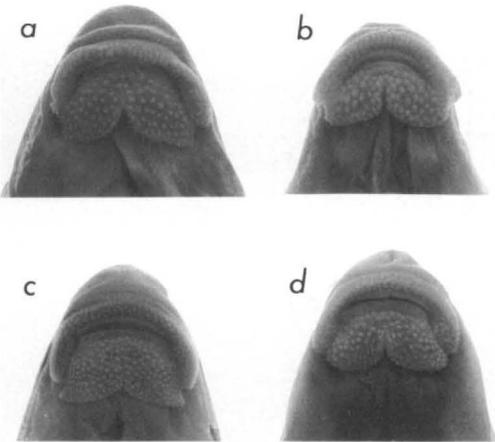


Fig. 1. Shapes of jaws and lips of a) *C. d. yarrowi* ( $\times 1.4$ ), Nutria Cr.; b) *C. plebeius* ( $\times 2$ ), Cottonwood Cr.; c) *C. d. discobolus* ( $\times 1.4$ ), Whiskey Cr.; d) *C. d. yarrowi* ( $\times 1.4$ ), Rio Pescado.

much reduced overlap in the number of gill rakers (see below) was used to justify failure to synonymize *C. plebeius* and *C. discobolus*. The contention that the Zuni Mountain sucker populations are natural, not introduced, is based on the presence of the phenotype in 1873, before extensive fish transplants were practiced in the West.

In 1978, specimens were collected in the Zuni River drainage in order to test the hypothesized stream capture and intergradation. Reference samples of *C. discobolus* and *C. plebeius* were also taken. Morphological and biochemical characters are used to estimate the nature of the similarity of the Zuni populations to *C. plebeius* and *C. discobolus*.

Several alternative hypotheses must be considered. They are not all mutually exclusive. It is possible that the Zuni populations are 1) intergrades resulting from a stream capture, 2) an intermediate part of a polytypic species including *C. plebeius* and *C. discobolus*, 3) the expression of ecophenotypic or locally selected character states with no historical interpretability or 4) a distinct species. Hypothesis (1) was suggested by Smith (1966) based on morphological data analyzed one character at a time. It predicts that the biochemical characters should also show a mosaic of *C. plebeius* and *C. discobolus* states, with *C. plebeius* states predominant nearest the site of the supposed capture and *C. discobolus* states predominant downstream. Lack

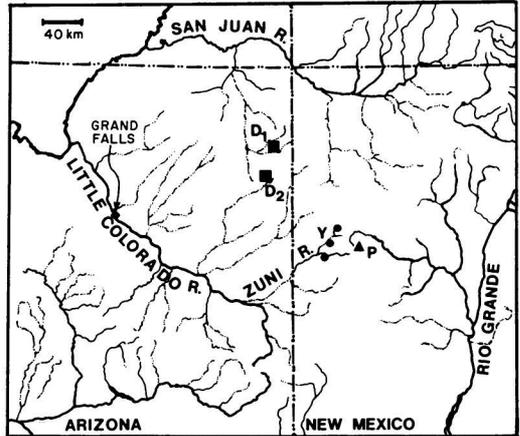


Fig. 2. Sample locations in the Little Colorado drainage and other drainages. D<sub>1</sub> = Whiskey Creek, *C. discobolus*; D<sub>2</sub> = Kin Li Chee, *C. d. yarrowi*; Y = Zuni drainage, *C. d. yarrowi*; P = Wells Spring, *C. plebeius*.

of *C. plebeius* character states, or a different pattern of state frequencies in the Zuni suckers would discredit this hypothesis. Possibility (2)—one polytypic species—is not inconsistent with (1) or (3), but involves a different taxonomic interpretation. It is favored if species-diagnostic distinctions between *C. plebeius* and *C. discobolus* cannot be demonstrated. Possibility (3), that the critical characters (jaws, lips, gill rakers, numbers of fin rays and scales) are expressions of ecophenotypic effects or results of local selection, can be examined in the context of observed variation of *C. plebeius* and *C. discobolus* in similar habitats elsewhere. (4) If the Zuni suckers were to display unique character states making them diagnostically separable from *C. plebeius* and *C. discobolus*, they would warrant specific recognition. Subspecies recognition will be supported by evidence of unique combinations of character states showing overlap with those of one of the species. This interpretation is not inconsistent with (1), (2) or (3).

#### METHODS

Tributaries in the Little Colorado River drainage were surveyed to determine the distribution and abundance of mountain suckers (Figs. 2, 3). Former habitats throughout the drainage (Smith, 1966:89) were sampled by electrofishing, including the Little Colorado in Navajo and Apache counties (three localities,

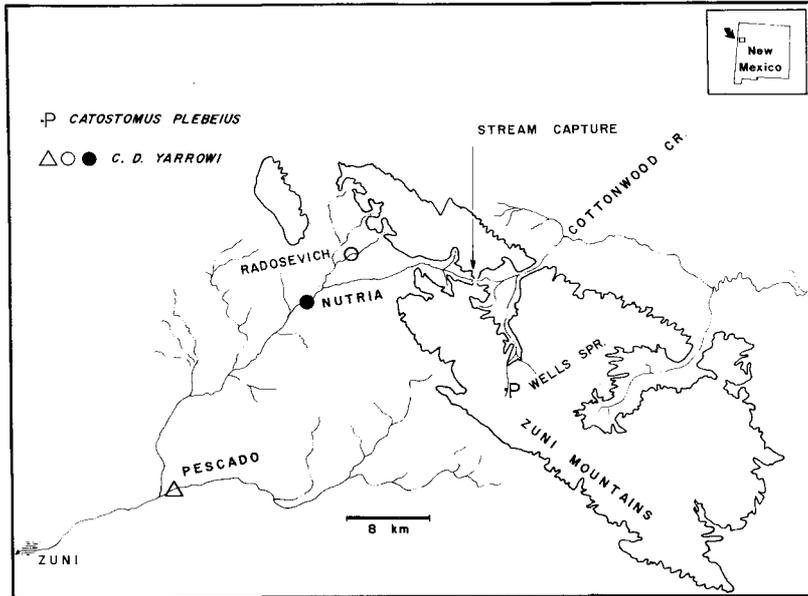


Fig. 3. Detail of upper Zuni drainage showing location of fish populations and the suspected stream capture across Continental Divide. Contour line at 2440 m.

no mountain suckers), East Clear Creek in Coconino County (two localities, one specimen), and Kin Li Chee Creek in Apache County, Arizona; and Nutria Creek, Rio Pescado and associated water in McKinley and Valencia Counties, New Mexico. Specimens from Nutria Cr. (UMMZ 209226–27; Fig. 1a), Rio Pescado (UMMZ 209229; Fig. 1d), and Kin Li Chee (UMMZ 209033–35) were suitable for morphological and biochemical analyses. The form is apparently extinct in the (seasonably dry) main stem of the Little Colorado drainage between St. Johns and Clear Creek. Samples of *C. plebeius* from Wells Spring in the San Jose drainage, Valencia County, New Mexico (UMMZ 209228; Fig. 1b), and *C. discobolus* from Whiskey Creek in the San Juan drainage, Apache County, Arizona (UMMZ 209234; Fig. 1c), were collected for comparison. Meristic counts (number of dorsal- and pelvic-fin rays, lateral-line and predorsal scale rows, gill rakers on the anterior and posterior rows of the first arch, and vertebrae) and morphometric measurements (width of lower jaw and isthmus, depth of caudal peduncle, standard length, and caudal length) were recorded for 247 specimens and analyzed with univariate and multivariate statistical methods to characterize each popula-

tion. Similarity among populations is examined by ordination techniques to determine the taxonomic levels of distinctness among the Zuni, *C. plebeius* and *C. discobolus* populations.

Principal component scores (Sneath and Sokal, 1973) are used to show patterns of similarities among individuals of the parental and putatively introgressed populations. Principal components were calculated on covariance matrices of counts and log-transformed measurements. The components are linear combinations of character values that summarize the major trends in variation of correlated characters among individuals. Meristic and morphometric characters were analyzed separately. Because some populations are represented by small individuals, the effect of size was removed using coefficients derived from regressions of general size (the principal axis of the within-group covariance matrix) on principal components centered by group (Humphries et al., 1981).

Electrophoresis of tissue and serum samples was employed to identify the products of 35 putative gene loci that could be used to characterize genetic differentiation among individuals, populations, and species (Table 1). Alleles that are not shared are evidence for genetic differentiation of the populations. Shared alleles

TABLE 1. TISSUE SOURCES AND ELECTROPHORETIC CONDITIONS FOR DETECTION OF VARIABLE AND/OR DIFFERENTIATED CATOSTOMID ENZYMES.

Enzyme	Locus	Tissue	Buffer systems (see text)
$\alpha$ -Glycerophosphate Dehydrogenase (1.1.1.8)	$\alpha$ GPDH-1; $\alpha$ GPDH-2	muscle	4.
Lactate Dehydrogenase (1.1.1.27)	LDH-1; LDH-2; LDH-3	muscle	4.
Malate Dehydrogenase (1.1.1.37)	MDH A1; MDH A2; MDH B1; MDH B2; MDH-M	muscle; liver	2.; 5.; 25 mg NAD/300 ml gel and cathode electrode buffer
Malic enzyme (1.1.1.40)	ME-1	liver	1.
NADP-Dehydrogenase Isocitrate (1.1.1.42)	IDH-1; IDH-2	liver	1.; 10 mg NADP/300 ml gel and cathode electrode buffer
6-Phosphogluconate Dehydrogenase (1.1.1.44)	6-PGDH-1; 6-PGDH-2	liver	4.
Glucose-6-phosphate Dehydrogenase (1.1.1.49)	G6PDH-1	muscle	1.; 10 mg NADP/300 ml gel and cathode electrode buffer
Superoxide dismutase (1.15.1.1)	SOD-1; SOD-2	liver	3.; 4.; 5.
Aspartate Aminotransferase (2.6.1.1)	AAT-1; AAT-2; AAT-3	liver	3.
Creatine Kinase (2.7.3.2)	CK-I	muscle	1.
Phosphoglucomutase (2.7.5.1)	PGM-1	muscle; liver	4.
Esterase (3.1.1.1)	Est-1; Est-2	liver	2.
$\beta$ -N-Acetylhexosaminidase (3.2.1.30)	HEX-1	liver	2.
Phosphoglucose Isomerase (5.3.1.9)	PGI-1; PGI-2; PGI-3	muscle; liver	1.

are evidence for genetic similarity between compared groups, though a single electrophoretic technique can underestimate the degree of differentiation (Coyne et al., 1979).

Individual tissues (muscle and liver) were dissected and homogenized by sonication for 10 s in approximately three volumes of 0.05 tris-HCl, pH 8.0 containing 20% glycerol. Homogenates were centrifuged at 14,500 g for 10 min at 4 C. Filter paper wicks were soaked in the supernatant and applied directly to starch gels and 10  $\mu$ l were applied directly to the sample pockets of acrylamide gels.

Polyacrylamide electrophoresis was performed in 7% acrylamide running gel overlaid with a 4% stacking gel. The running gel consisted of 6.65 gm acrylamide, .35 gm bis-acryl-

amide, 0.5 ml TMED and .005 ml Photo-flow (Kodak) per 100 ml of .38 M tris-HCl buffer, pH 8.9. The stacking gel was identical except the total acrylamide-bis-acrylamide concentration was 4%. Gels were polymerized at room temperature by the addition of 2.5 ml of a 10% solution of ammonium persulfate per 100 ml of gel solution. The electrode buffer was 4.9 mM tris-glycine, pH 8.3. Samples consisted of a mixture of 10  $\mu$ l muscle homogenate (or sera) and 2  $\mu$ l of tracking dye composed of 0.5% Bromophenol Blue and 30% sucrose in 4.0 mM, pH 8.9 tris-glycine buffer. Gels were run at 5 C at 400 V until the tracking dye had migrated at least 12 cm.

Proteins were visualized by fixing the gels for 1 h in 12% trichloroacetic acid and then stain-

TABLE 2. SUMMARY OF MERISTIC VALUES.

	N	Vertebrae			Gill Rakers (1st row)		
		Mean	Range	SD	Mean	Range	SD
<i>C. plebeius</i>	(47)	39.9	(39–42)	0.8	23.3	(20–27)	1.3
Nutria	(47)	41.1	(39–43)	1.1	26.0	(21–34)	2.8
Radosevich	(29)	40.4	(38–43)	1.2	30.2	(25–34)	2.7
Pescado	(50)	42.2	(39–45)	1.3	31.1	(27–36)	2.4
Kin Li Chee	(14)	41.0	(40–42)	0.7	35.8	(28–40)	3.1
<i>C. discobolus</i>	(52)	43.6	(42–45)	0.8	36.9	(30–41)	2.0
Scale Number							
		Lateral Line			Predorsal		
		Mean	Range	SD	Mean	Range	SD
<i>C. plebeius</i>		83.5	(76–97)	3.9	41.7	(37–46)	2.2
Nutria		86.3	(70–102)	6.6	45.3	(32–59)	5.0
Radosevich		92.4	(84–102)	4.5	49.8	(44–56)	3.0
Pescado		92.4	(80–110)	6.0	48.2	(41–59)	4.5
Kin Li Chee		99.3	(95–104)	2.4	50.7	(48–56)	2.5
<i>C. discobolus</i>		102.7	(85–122)	6.5	50.2	(42–58)	3.3
		Pelvic Fin Rays			Dorsal Fin Rays		
		Mean	Range	SD	Mean	Range	SD
<i>C. plebeius</i>		9.2	(8–10)	0.5	9.1	(8–10)	0.3
Nutria		9.2	(8–10)	0.4	8.9	(7–10)	0.7
Radosevich		9.2	(8–10)	0.6	9.6	(9–10)	0.5
Pescado		9.8	(9–11)	0.6	9.3	(8–10)	0.5
Kin Li Chee		8.8	(8–9)	0.4	9.9	(9–10)	0.3
<i>C. discobolus</i>		9.2	(8–10)	0.4	10.0	(9–11)	0.4

ing overnight in .05% Coomassie Brilliant Blue in 7% acetic acid. Gels were de-stained in 7% acetic acid.

Starch gel electrophoresis was performed on horizontal starch gels of 28 × 14 × 0.5 cm dimensions. Connaught starch was used throughout at 12%, unless otherwise noted. The following buffers were used for resolution of individual enzymes (Table 1) in starch gel electrophoresis.

1. *Tris-borate-EDTA*.—Stock: 0.9 M tris, 0.5 M boric acid, 0.2 M EDTA, pH 8.7. Anode electrode buffer: dilute stock 1:7; cathode electrode buffer: dilute stock 1:5; gel buffer: dilute stock 1:20. Gels were run at 160 V for 15–18 h.
2. *Tris-maleate*.—Stock: 0.1 M tris, 0.1 M maleic acid, 0.01 M EDTA, 0.01 M MgCl<sub>2</sub>, pH 7.4. Gel buffer: dilute stock 1:9; stock used for electrode chambers. Gels were run at 125–150 V for 15–18 h.
3. *Lithium hydroxide*.—Stock solution A: 0.03 M lithium hydroxide and 0.19 M boric acid,

pH 8.1. Stock solution B: 0.008 M citric acid and 0.05 M tris, pH 8.4. Gel buffer: 1:9 mixture of stock solutions A and B. Electrode buffer: stock solution A. Gels were run at 185 V for 15–18 h.

4. *Tris-citrate-I*.—Stock: 0.75 M tris, 0.25 M citric acid pH 6.9. Gel buffer: dilute stock 1:60; electrode buffers: dilute stock 1:20. Gels were run at 170 V for 15–18 h.
5. *Tris-citrate-II*.—Stock: 0.75 M tris adjusted to pH 7.0 with citric acid. Gel buffer: dilute stock 1:20; cathode buffer: dilute stock 1:4, anode electrode buffer: dilute stock 1:6. Gels were run at 200 V for 15–18 h in 15% starch.

Electrophoretic phenotypes were coded so that alleles at a locus differing in electrophoretic mobility received individual codes. For a pair of individuals compared at a polymorphic locus, a coefficient of similarity of 0, .5 or 1 was computed if the two individuals had 0, 1 or 2 alleles in common, respectively. Their similarity coefficient was then averaged over the number of loci compared. Principal coordinate analysis

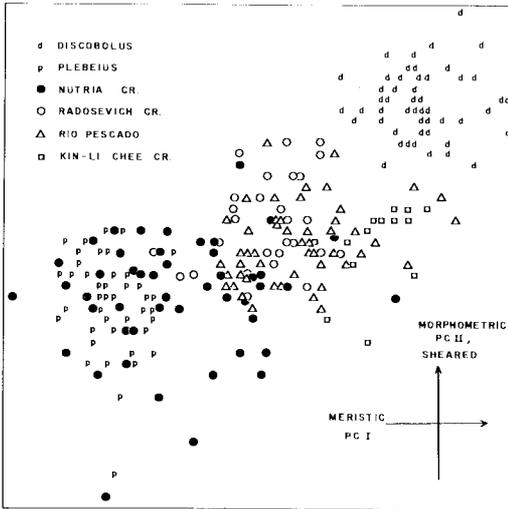


Fig. 4. Graphical display of specimen scores on principal components (morphological characters), showing degree of overlap and relative similarity of population samples.

(Sneath and Sokal, 1973) was used to summarize the dominant patterns of similarity and difference among the tested individuals. Due to computational limitations, this analysis could not include all individuals in all samples, simultaneously. Therefore, each population was subsampled and the set of subsamples treated by principal coordinate analysis. This analysis was replicated to ensure that there was no sample bias in selected individuals.

In the results from the analyses of both morphological and biochemical characters, overlap of population clusters on graphs is interpreted as evidence of phenotypic and genetic similarity, while non-overlap of clusters is taken as evidence of evolutionary differentiation.

## RESULTS

In all of the morphological characters except the number of pelvic fin rays, the values (Table 2) are consistent with the hypothesis that the Zuni suckers are intermediate between *C. plebeius* and *C. discobolus*, with the Nutria population being most like *C. plebeius* and Kin Li Chee being most like *C. discobolus*. Some values are different from those based on samples collected 15–30 years ago (Smith, 1965). (Scale counts in the study are about four fewer than in the previous study due to individual counter differences.) For example, the average number of lat-

eral-line scales in the Nutria population is 9.0 lower, the number of pelvic-fin rays in the Pescado population is 0.6 higher, and the number of vertebrae at Nutria is 0.4 higher. These results reflect instability over time. The character fluctuations may be due to seasonal reduction of population size and founder effects as well as small ecophenotypic effects.

The principal component analyses of new meristic and morphometric data discriminate the samples of *C. plebeius* and *C. discobolus*, and display the broad intermediacy of most Zuni suckers (Fig. 4). Component I accounts for 59% of the variance in the meristic data and reflects the correlated variation in all of the counts (coefficients = .34–.46) except those of pelvic rays (coefficient = .02). Component II accounts for an additional 14% of the variance and reflects variation in pelvic rays (coefficient = .97) by which the Rio Pescado sample differs (Table 2). The morphometric component of interest, sheared (size-free) PC II, reflects variation especially in caudal peduncle depth (.66), jaw width (.60) and tail length (.43). In both components the Zuni populations overlap broadly with *C. plebeius* and slightly with *C. discobolus*. The Nutria population is highly variable and overlaps *C. plebeius* most in both meristics and morphometrics. This is evidence consistent with hypothesized derivation of populations in the headwaters of Nutria Cr. from *C. plebeius* (Fig. 3). The Radosevich and Pescado populations broadly overlap the Nutria population, and are more intermediate between *C. discobolus* and *C. plebeius*. On other components (not figured, but much as in Fig. 5) the Pescado population stands somewhat apart, but overlaps other Zuni clusters. The population at Kin Li Chee is similar to *C. discobolus* meristically, but like some Zuni specimens morphometrically. It shows slight morphological evidence of introgression from the Zuni populations.

The analysis of biochemical phenotypes provides a test of the relationships among *C. discobolus*, *C. plebeius* and Zuni suckers that can be compared with the results based on morphological analyses. Of approximately 35 loci studied, the following 18 are monomorphic and identical among all population samples: isocitrate dehydrogenase-1, isocitrate dehydrogenase-2, aspartate aminotransferase-1, aspartate aminotransferase-2, glucose-6-phosphate dehydrogenase-1, -glycerol phosphate dehydrogenase-1, -glycerol phosphate dehydrogenase-2, lactate dehydrogenase-1, lactate dehydroge-

TABLE 3. A SUMMARY OF THE DISTRIBUTION OF ALLELES AMONG POPULATIONS. At each locus, the allele occurring exclusively or most commonly in *C. discobolus* is designated as A and the allele occurring exclusively or most commonly in *C. plebeius* is given as B. Additional alleles, when observed, are given designations C and D. The summary is intended to provide a simple visual illustration of how alleles at each locus are distributed among samples and thereby suggest certain taxonomic affinities. See text for explanation of Groups I–IV.

Locus N	<i>C. discobolus</i> 40–50	Kin Li Chee 11–37	Pescado 27–49	Radosevich 14–29	Nutria 27–52	<i>C. plebeius</i> 34–48
<i>Group I</i>						
Hex-1	A	A, C	A	A	A (N = 30)	B (N = 45)
Mdh-A1	A	A	A	A	A (N = 30)	B (N = 46)
Mdh-A2	A	A	A	A	A (N = 47)	B (N = 46)
<i>Group II</i>						
Mdh-M	A, C	A, C	A, C	A, C	A, B, C, D	B, D
Mp-4	A	A	A, B	A, B	A, B	B
Ldh-3	A	A, C	A	A	A, B	B
Sod-1	A, C (N = 48)	C (N = 11)	C (N = 27)	C (N = 10)	B, C (N = 27)	B (N = 45)
<i>Group III</i>						
Pgi-2	A, C (N = 50)	B, C (N = 37)	B, C (N = 49)	B, C (N = 29)	B, C (N = 51)	B (N = 47)
Aat-3	A, B	A	A	A	A, B	B
Pgi-1	A, B (N = 49)	B (N = 37)	B (N = 49)	B (N = 29)	B (N = 51)	B (N = 47)
<i>Group IV</i>						
Est-2	A, B	A, B	A, C	A, C	A, B	B
Pgi-3	A, B	B, C	B	B	B	B
6-Pgd-2	C	C	D	D	C	C
Pgm-1	C	C	C, D	C, D	C, D	C
Trf	A, C	A, C (N = 6)	B, D	—	B, D (N = 12)	B

nase-2, esterase-1, superoxide dismutase-2, malate dehydrogenase-B1, malate dehydrogenase-B2, muscle protein-1, muscle protein-2 and muscle protein-3.

Sixteen loci differ between at least two population samples and provide information on the degree of relationship between samples. Three loci, collectively described as Group I (Table 3) provide evidence for identity between Zuni suckers and *C. discobolus*. There were no allozyme loci which exhibited the reciprocal pattern. In contrast to the morphological analysis, the pattern of differences exhibited by these loci, in which Zuni suckers are distinct, especially from *C. plebeius* (Fig. 5), supports the formal designation, *C. discobolus yarrowi*.

Four loci (Group II, Table 3) provide strong evidence for an introgressive influence from *C. plebeius* to the Zuni suckers, originating in Nutria Cr. Mdh-M, Sod-1 and Ldh-3, all show restriction of a *C. plebeius* allele to the Nutria population of *C. yarrowi*. At the Mp-4 locus, the *C. plebeius* allele is present together with a *C. discobolus* allele in all samples from the upper Lit-

tle Colorado drainage, while at Pgi-2 the *C. plebeius* allele is present in all populations sampled in the Little Colorado drainage.

Four loci (Group III, Table 3) provide equivocal evidence for the hypothetical history of stream capture and introgression of *C. plebeius* alleles into the Zuni population of *C. discobolus*. The frequencies at these loci are consistent with ancient connection between *C. plebeius* and *C. discobolus*, but since the parental species share the alleles, evidence for hybridization is not compelling. Pgi-2 was placed in this group (rather than Group II) because we are not as confident of some of the genotypic determinations.

Group IV (Table 3) contains five loci that are more or less consistent with the hybridization hypothesis, but more significantly, display unique alleles in at least one of the samples from the Little Colorado River drainage. These loci provide evidence for some differentiation of Little Colorado River populations from both *C. plebeius* and *C. discobolus*.

Indices of genetic distance and similarity (Nei,

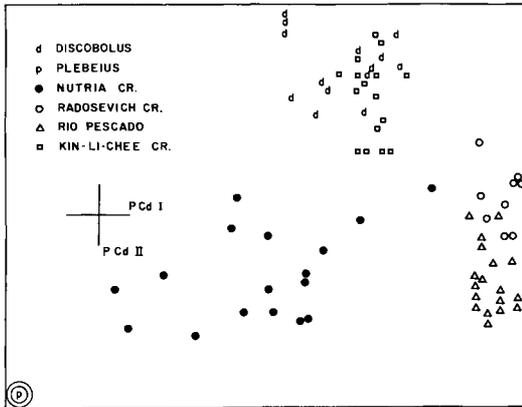


Fig. 5. Graphical display of specimen scores on principal coordinates (biochemical characters), showing degree of overlap and relative similarity of population samples. Since *C. plebeius* was monomorphic at all studied loci, a single individual can be used to represent this species.

1972) provide a summary of the locus-specific patterns of spatial variation described above (Table 4). All populations in the Little Colorado River drainage are similar to *C. discobolus*, while the average similarity between these populations and *C. plebeius* is only about .69. However, the Nutria Cr. population exhibits a higher degree of similarity with *C. plebeius*.

The principal coordinate analysis of biochemical phenotypes resulted in a pattern of clustering of individuals (Fig. 5) that differs somewhat from the pattern resulting from the principal component analysis of morphological characters (Fig. 4). Individuals from Kin Li Chee form a group that is virtually identical to *C. discobolus*. While the Pescado and Radosevich samples broadly overlap one another, both are distinct from other population samples. The Nutria sample forms an elongated cluster intermediate between *C. plebeius* and *discobolus* (Fig. 5), much as is observed in the morphological analysis (Fig. 4).

We draw the following conclusions from the results of our morphological and electrophoretic analyses: 1) populations of *yarrowi* are generally intermediate between *C. discobolus* and *C. plebeius*, though some individual characters are nonintermediate; 2) the Nutria population is geographically closest to a suspected stream capture and is most similar to *C. plebeius*; and 3) considerable variation exists within as well as among populations of *C. yarrowi*. Origin of

some, but possibly not all, of this variation may be a byproduct of hybridization. Fluctuation in some characters may result from founder effects due to local extinctions and repopulation.

## DISCUSSION

Four alternative hypotheses are under consideration: 1) stream capture and intergradation between *C. plebeius* and *C. discobolus*, 2) one clinal, polytypic species, 3) variation patterns due to ecophenotypic or locally selected character states, 4) a distinct species, *yarrowi*. The intermediate, mosaic pattern of morphological and biochemical variation among populations of the upper Nutria drainage and downstream through the Zuni (and formerly Little Colorado drainages) is consistent with (1), hypothesized introgressive hybridization of *C. plebeius* genes from across the continental divide in the Zuni Mountains. The Nutria population is closest to the continental divide (about 10 km) and about half the specimens are morphologically nearly identical to *C. plebeius* from the Rio Grande drainage, across the divide. Downstream populations in the little Colorado drainage are successively more like *C. discobolus* of the Colorado drainage. Biochemical characters include several loci indicative of *C. plebeius* influence, especially in Nutria Cr. (Table 3). Overall, however, more alleles are shared between the Zuni populations and *C. discobolus* (Table 4, Fig. 5).

Before discussing this hypothesis further and before evaluating the taxonomic possibilities, (2) and (4), it is necessary to examine the hypothesis that the observed patterns are selected or ecophenotypic responses to local conditions, and bear no historically relevant information. We think that interpretation untenable for the following reasons. The distinctive mouth shape (Fig. 1a, d) and the modal count of 9 dorsal fin rays, both characteristic of *C. plebeius*, occur nowhere else in the range of *C. discobolus* and in no other *Catostomus*. All headwater populations of *discobolus* outside the Little Colorado drainage have wide, rather square lower jaws, and large, finely-papillose lower lips, shallowly notched medially and deeply notched laterally, as in Fig. 1c. All other mountain headwater populations of *C. discobolus* have modally 10 or 11 dorsal rays. The Little Colorado headwater sample from East Clear Creek, Arizona, has dorsal fin-ray counts of 9(8), 10(107) and 11(21); those from headwaters of the San Juan in Colorado and New Mexico have 10(12), 11(21),

TABLE 4. MATRIX OF GENETIC DISTANCE (ABOVE) AND SIMILARITY (BELOW) AMONG SAMPLED POPULATIONS AND SPECIES.

	<i>C. plebeius</i>	<i>C. discobolus</i>	Kin Li Chee	Pescado	Radosevich	Nutria
<i>C. plebeius</i>	—	.37	.39	.46	.45	.20
<i>C. discobolus</i>	.69	—	.05	.11	.16	.14
Kin Li Chee	.68	.95	—	.15	.11	.16
Pescado	.63	.90	.86	—	.01	.13
Radosevich	.64	.85	.90	.99	—	.11
Nutria	.82	.87	.85	.88	.90	—

12(1) dorsal fin rays (Smith, 1965:304). The Little Colorado sample aside, there is no correlation between elevation and number of dorsal fin rays in the species. There is a slight correlation between number of dorsal fin rays and latitude in *C. discobolus* and in the subgenus, but the low number in Nutria Creek is much lower than would be predicted by that relationship. We conclude, therefore, that the cause of the *C. plebeius*-like characters in the Colorado drainage is unique to the upper Zuni drainage. High elevations, relatively southern climate, geological substrate, and known stream characteristics are not unique to that part of the Colorado drainage.

The *plebeius*-like characters are not peculiar to the environments of the Zuni Mountains in the Rio Grande drainage, either. They are characteristic of *C. plebeius* from southern Colorado south, through New Mexico and north-central Mexico.

The biochemical characters are not sufficiently known to be subject to broad geographic comparisons. The extent to which their pattern matches that of the morphological characters suggests that they are part of the same phenomenon—genetic exchange across the Zuni Mountains. The presence of these alleles on either side of the continental divide could date from a much older genetic continuity, but the data seem to require historical rather than environmental interpretation. We must turn to geological evidence to evaluate the timing of the connection across what is now the continental divide.

The continental divide between Nutria Cr. and Cottonwood Creek of the Rio Grande drainage is unusually low, offering a plausible site for a drainage connection. The area is mapped on the Page and Cottonwood Canyon quadrangles (U.S.G.S. 1:24,000) and has been examined by Smith and Koehn from a helicop-

ter and by R. R. Miller (14 Aug. 1962) on the ground. The divide is 15 m of gentle relief at  $2449 \pm 2$  m lying across the floor of a NW-SE valley 5 km long. The valley was probably cut by a southeast-flowing stream tributary to Cottonwood Creek (Fig. 2) at a time when the continental divide was about 6 km to the WNW. On the west side of Sec. 1 (T 12N, R 15W) is a small (1 km) northeast-flowing tributary that turns 90°NW and flows into the Nutria drainage. Its original northeast direction indicates that it was formerly tributary to Cottonwood Creek. Capture by Nutria Cr. would imply 15 m subsequent erosion, which would have taken perhaps 1,000–2,000 years. Other possible stream captures by Nutria Cr. are in Sec. 13–14 (T 12N, R 15W) and Sec. 35 (T 13N, R 15W) shown on the same maps. There have been three major cycles of Pleistocene erosion in the Little Colorado River drainage following reductions in base level of the drainage after major down-cutting in Grand Canyon. Several thousand m of Mesozoic sediments were removed from the lower basin, with subsequent canyon cutting headward (Childs, 1945). In view of the geological history it is surprising that the only evidence of exchange of mountain suckers between the Rio Grande and Colorado drainages is in the populations described here.

We conclude that at some time in the late Pleistocene, a tributary of Cottonwood Creek, inhabited by *C. plebeius*, was intercepted and captured by headward erosion of Nutria Cr. from the southwest. The population of *C. plebeius* was then in contact with *C. discobolus* from downstream, and at some time genetic exchange between the two forms occurred.

Morphometric, meristic and biochemical characters from *C. plebeius* show different expression downstream. *Plebeius*-like meristic characters predominate in Nutria Cr., but to a lesser extent elsewhere through the drainage

(Table 2). The meristic intermediacy of the Pescado and Radosevich samples (meristic PC1, Fig. 4) suggests some penetration of *C. plebeius* genes below Nutria Creek. There is also an indication of some independent differentiation (pelvic rays in Rio Pescado specimens, Table 2). Morphometrically, most Nutria specimens are almost indistinguishable from *C. plebeius*, and *C. plebeius* morphological influence is stronger than the meristic influence in the downstream populations (sheared morphometric PC II, Fig. 4; Smith, 1966: Fig. 18). On the other hand, biochemical characters (Table 4; Fig. 5) suggest modest influence of *C. plebeius* alleles in the Nutria population, and little influence elsewhere. The Pescado and Radosevich populations are nearly identical to each other and distinct from the other populations. The population at Kin Li Chee is not biochemically differentiated from Whiskey Creek *C. discobolus*.

The differentiation among samples (Fig. 5) suggests founder effects possibly due to fluctuations in population size. Much of the drainage, locally and downstream, has only intermittent flow, restricted to spring and early summer. Only short sections of Nutria and Pescado creeks have permanent flow. Local extinction of fishes is common and was, in fact, enhanced by frequent attempts to eradicate non-game fishes between 1960 and 1975. Eradication of each of the Zuni River populations studied here was once thought to have been complete, but populations were reestablished, probably by descendants of individuals that survived in isolated pools and spread during spring high water. Protective measures are now being carried out by several government agencies.

Seasonal desiccation now isolates the remaining populations in the Little Colorado drainage. Since approximately mid-Pleistocene these populations have been isolated from *C. discobolus* in the Colorado drainage by a lava dam at Grand Falls on the lower Little Colorado. The dam might have permitted some early differentiation in the drainage. The barrier probably had a slight effect on the equilibrium between upstream and downstream gene flow. The most *plebeius*-like population, in Nutria Creek, was once a small part of the populations in the Little Colorado drainage, but extinction downstream has eliminated many populations of *discobolus*-like intergrades reported by Smith (1966: Fig. 18). The pattern of relative similarity of the Zuni

populations to *C. plebeius* and *C. discobolus* is different as a result.

The taxonomic problem may be summarized in the following question: How many species are involved in this complex (one, two or three) and what is the correct designation of the Zuni mountain sucker? The multivariate analysis summarized in Fig. 4 suggests that one broad species is involved, especially since former downstream populations bridged the morphological gap between the Zuni suckers and *C. discobolus* (Smith, 1966:89). Biochemical analysis, on the other hand, suggests that the Zuni suckers are differentiated from *C. plebeius* and generally overlap *C. discobolus* (Fig. 5). We do not believe that recognition of the Zuni suckers as a distinct species, *C. yarrowi*, can be justified in view of the above overlap—the characteristics of *C. yarrowi* are interpreted here as lack of reproductive isolation, at some time in the past, between Zuni populations and *C. plebeius* and *C. discobolus*. Practical consideration supported by individual diagnostic characters and cladistic studies (Smith and Koehn, 1971), support recognition of Zuni suckers as a subspecies of *C. discobolus*, *C. discobolus yarrowi*.

Morphologically, *C. d. yarrowi* is diagnosed from *C. plebeius* by several characters (Table 2; Smith, 1966). While *C. d. yarrowi* usually has 25 or more gill rakers in the first row, *C. plebeius* usually has fewer than 25. Also, there are 35 or more gill rakers in the back row of the first arch in *C. d. yarrowi* whereas *C. plebeius* usually has fewer than 35. The edge of the lower jaw is straighter and the lips are smaller and less papillose (Fig. 1). The number of predorsal scales differs between the two taxa, being more than 50 in *C. d. yarrowi* but usually fewer than 50 in *C. plebeius*. Lastly, *C. d. yarrowi* generally exhibits more than 40 post-Weberian vertebrae while *C. plebeius* usually has 40 or fewer.

It is also possible to diagnose most *C. d. yarrowi* from other *C. discobolus*, especially by vertebral counts: *C. d. yarrowi* usually exhibits fewer than 42 while *C. discobolus* usually has more than 42. The depth of the caudal peduncle is usually more than .08 of the standard length in *C. d. yarrowi*, but usually less than this in *C. discobolus*. The Zuni drainage forms of *C. d. yarrowi* have a mean dorsal ray count of less than 10 while *C. discobolus* (and some downstream *C. d. yarrowi*) usually exhibit more than 10 dorsal rays. Also, the average number of lateral line scales is fewer than 100 in *C. d. yarrowi*, but

usually more than 100 in *C. discobolus*. The edge of the mandible is more convex anteriorly and its width is .05–.06 of standard length in *C. d. yarrowi*, but more than .06 in *C. discobolus* (Fig. 1).

Biochemically, *C. d. yarrowi* differs strongly from *C. plebeius* but modestly from *C. discobolus* (Table 4). Three loci enable complete discrimination of *C. discobolus* (including *C. d. yarrowi*) from *C. plebeius*: Hex-1, Mdh-A1 and Mdh-A2 (Table 3). Four loci have alleles that differentiate populations (but not all individuals) of *C. d. yarrowi* and *C. discobolus*: Sod-1, Pgi-1, Pgi-2 and Pgi-3 (Table 3).

Demonstration of a lack of reproductive isolation between *C. discobolus yarrowi* and *C. plebeius* at this time would lead most workers to synonymize *C. discobolus* Cope (1872) and *C. d. yarrowi* (Cope, 1874) with *C. plebeius* Baird and Girard (1854). Cladistically, however, *C. plebeius* and *C. discobolus* are at opposite ends of a five-species series, separated by more than a dozen apomorphic characters (Smith and Koehn, 1971), most of which are included in the present study. Hierarchical sister-group relationships between *C. discobolus* and *C. clarki* (lower Colorado), then *C. santaanae* (former lower Colorado connective in California), then *C. platyhynchus* (Great Basin), are defined by apomorphic characters. These four species (two of which are occasionally sympatric) are the sister group of *C. plebeius*, which is vicariantly separated from them by the dominant physiographic barrier in the west—the continental divide (a low point of which is, of course, the Zuni Mountains).

For the above cladistic reasons and on the basis of the diagnostic characters, *C. discobolus* (including *C. d. yarrowi*) and *C. plebeius* are treated as separate species. Alternatively, however, the complex character patterns seen in these populations could be used to justify recognition of one or three species, depending upon acceptance of different criteria applied to characters and the concept of reproductive isolation.

Biogeographically, the origin of *C. d. yarrowi* can be summarized as follows. Two vicariant cladistic entities, *C. plebeius* of the Rio Grande drainage, and *C. discobolus* and *C. clarki* of the (upper and lower) Colorado drainage, are separated by the dominant physiographic barrier in the region, the continental divide. The presence of a population of fishes west of the divide

(*C. d. yarrowi*), displaying characteristics of the species east of the divide (*C. plebeius*), indicates that a small, eastward shift of the divide occurred, probably during the late Pleistocene, owing to more rapid erosion on the west slope (Little Colorado drainage). The implied mechanism, a stream capture, evidently transferred upper Nutria Cr. and its fauna into contact with the Colorado drainage. The Nutria Cr. population is evidence for an ancient vicariance-generating barrier about 6 km NW of the present divide and predicts that other local organisms should show the same pattern.

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## *Anchoa argentivittata*, with Notes on other Eastern Pacific Anchovies and the Indo-Pacific Genus *Encrasicicholina*

GARETH NELSON

*Anchoa argentivittata* (Regan, 1904) is conspecific with *Anchoa arenicola* (Meek and Hildebrand, 1923) and is distinguishable from other Eastern Pacific species of *Anchoa* on the basis of vertebral counts. *Anchoviella miarcha* (Jordan and Gilbert) is a *nomen dubium*. *Anchoviella scitula* (Fowler) and *Anchoa duodecim* (Cope) are based respectively on single specimens of the Indo-Pacific species *Stolephorus indicus* (Van Hasselt) and *Thrissina encrasicholoides* (Bleeker), which are otherwise unreported from the New World. *Stolephorus mundeolus* Gilbert and Pierson is based on two species; selection of a lectotype leaves *S. mundeolus* provisionally in the synonymy of *Anchoa panamensis* (Steindachner). *Anchoa walkeri* is characterized by a certain pattern of the sensory-canal system, which has proven useful in identifying specimens of other engraulid species. Sensory-canal and other characters group the New World anchovies with *Engraulis* and *Encrasicicholina* (=Indo-Pacific species of *Stolephorus*, in part).

NEW World anchovies, numbering some 80 species in nine genera, were last reviewed by Hildebrand (1943, 1964). The taxonomic status of certain problematical species is reviewed here: *Anchoa argentivittata*, *Anchoviella miarcha*, *Anchoviella scitula*, *Anchoa duodecim* and *Anchoa mundeola*. Comparison with Indo-Pacific anchovies, numbering some 50 other species in six other genera, has revealed that the Indo-Pacific genus *Stolephorus* is complex, consisting of at least two groups of species. One group (*Stolephorus*) includes 13 species; the other group (*Encrasicicholina*, new usage) includes five species,

which are related more closely to the New World anchovies than to any or all of the 13 species of *Stolephorus*. The higher level systematics of anchovies is beyond the scope of this paper.

### *ANCHOA ARGENTIVITTATA* (REGAN)

Regan (1904) described *Engraulis (Stolephorus) argentivittatus* on the basis of three specimens from Las Peñas, Jalisco, Mexico (=Puerto Vallarta). The name was ignored by subsequent writers until Hildebrand (1943:67) considered it a possible synonym of *Anchoa lyolepis* (an At-