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Morphology and Foods of Arizona Catostomid Fishes: *Catostomus insignis*, *Pantosteus clarki*, and Their Putative Hybrids

ROBERT W. CLARKSON AND W. L. MINCKLEY

Morphology and food habits of putative hybrids between two widespread western American catostomid fishes, *Catostomus insignis* (Sonora sucker) and *Pantosteus clarki* (desert sucker), were compared with their parental forms. Hybrid intermediacy was demonstrable in morphological characters that differed between parental fishes, although tendencies were toward *C. insignis*. Coefficients of variation were similar in hybrid and parental samples, which, along with relatively low variation in canonical variables of discriminant function analysis, implied a lack of backcrossing. Foods of hybrids averaged intermediate to parental forms, but variation was high. Hybrids utilized a broad food base, with feeding habits that collectively spanned those of each parent. Additive inheritance of morphological and behavioral traits seems influenced by dominance and/or interallelic suppression that tend to produce deviations from often-assumed intermediacy in hybrid fishes.

ONE basic premise in identification of hybrid fishes has been an assumed intermediacy of presumed F_1 individuals in morphological features that distinguish their parental forms (Hubbs, 1955). However, phenotypic expression of characters may not be intermediate if dominance and/or interallelic suppression exists. Beliefs that most morphological traits in fishes are products of additive inheritance may therefore be questionable (Hubbs, 1956; Greenfield and Greenfield, 1972; Ross and Cavender, 1981). Some studies further indicate that behavior of hybrid fishes may be expressed in an intermediate manner (Hagan, 1967; Nelson, 1968; Greenfield and Deckert, 1973), while others imply such expression may be extreme to that of either parent (Hubbs and Hubbs, 1931, 1933; Bailey and Lagler, 1938).

Natural intermediates between two broadly sympatric catostomid fishes, *Pantosteus clarki* (Baird and Girard) (desert sucker) and *Catostomus insignis* Baird and Girard (Sonora sucker), provide one of the most clear-cut and commonly reported examples of apparent hybridization in North American freshwater fishes (Hubbs et al., 1943; Barber and Minckley, 1966; Minckley, 1973). Miscegenation is geographically widespread and not associated with any fixed zone.

The desert sucker is one of the most specialized products of the evolution of *Pantosteus* (Smith, 1966; Koehn, 1967; Smith and Koehn, 1971), with the development of cartilaginous

sheaths on the jaws as an adaptation for scraping diatoms and other materials from solid substrates (Fisher et al., 1981; Schreiber and Minckley, 1982). Other specializations associated with herbivory are a black peritoneum and an elongate digestive tract (Smith, 1966). The Sonora sucker is a generalized carnivore, foraging in pools and slower runs on aquatic invertebrates (Schreiber and Minckley, 1982). Its feeding preferences are often facultative, however, since Minckley (1973) noted ingestion of algae, mud, seeds, and other plant material at some times of year. The species nonetheless lacks specialized jaws, a darkened peritoneum, and a markedly lengthened gut. The availability of a number of specimens of presumed F_1 hybrids between these divergent fishes provided an opportunity to assess hypotheses concerning intermediacy of hybrids in both morphology and behavior.

MATERIALS AND METHODS

Specimens of *C. insignis*, *P. clarki*, and presumed hybrids from Bonita and Aravaipa creeks, southeastern Arizona, were collected between 1964 and 1982 and housed in Arizona State University Collection of Fishes (ASU). Both streams are relatively small, gravel-bottomed tributaries of the Gila River system. Drainage and habitat descriptions have appeared elsewhere (Barber and Minckley, 1966; Clarkson, 1982).

Hybrids were identified by 10 morphometric and seven meristic features: standard (SL), head (HL), snout (SN), and mouth (ML) lengths; length of union of lower lips (LU); width of cartilaginous ridge of lower jaw (RW), isthmus (IW), and mouth (MW); head (HD) and caudal peduncle (CP) depths; numbers of scales along lateral line (LL), below lateral line (BL), around caudal peduncle (AP), and above lateral line (AL); number of rows of papillae crossing midline of lower lip (LP); and numbers of dorsal-fin (DR) and pelvic-fin (PR) rays. Data collection followed Hubbs and Lagler (1958), with exception of excluding the opercular flap from measurement of HL. Sizes and sexes of parental specimens were matched with those of putative hybrids to minimize allometric and sexually dimorphic differences.

Three methods were used in analysis, each having inherent limitations. First was the hybrid index (HI) of Hubbs and Kuronoma (1942), expressed as:

$$HI = 1/m \sum_{i=1}^m (X_{hi} - U_{1i}/U_{2i} - U_{1i})$$

where m is number of characters measured, X_{hi} is the value of character i for suspected hybrid h , and U_{1i} and U_{2i} are character means in parental populations 1 and 2. Averages of characters 1 through n in the first parental population become 0.0 and those of the second 1.0; hybrids theoretically fall near 0.5. A major criticism is that the required selection of distinguishing characters may "verify" subjective decisions of a priori identifications (Smith, 1973; Schueller and Rising, 1976; Neff and Smith, 1979).

A second method was discriminant function analysis (DFA), a multivariate technique maximizing distances between a priori assigned groups relative to variance within those groups. Typical output consists of graphs of the first one or two canonical variates (a linear combination of variables, maximizing differences among group means) for each individual of each group. DFA does not require use of distinguishing characters, but its application in hybrid identification has been questioned because of inherent circularity shared with HI (e.g., assignment to a priori groups) (Neff and Smith, 1979).

A third technique was sheared principal components analysis (PCA), which quantifies shape differences independent of size (Humphries et al., 1981). Like DFA, components are formed

in directions of greatest variance within the data matrix. However, PCA does not require a priori identification of groups, and therefore does not weight between-group differences. A graph of scores of each individual on axes of the first unsheared principal component (PC-I; largely size related) and the second sheared component (H2) visually displays position of and variation among individuals in both data sets (Smith, 1973; Neff and Smith, 1979; Bookstein et al., 1985).

Food habits were examined according to a modified point system of relative volumes (Hynes, 1950). The foregut anterior to the first post-esophageal loop was arbitrarily considered as a "stomach." Volume of contents was estimated relative to potential total volume and assigned a value from 0 (empty) to 100% (full). Due to limited numbers of specimens, the food of fishes with empty stomachs was determined by examination of intestines; empty guts were excluded from computations. Invertebrates were identified to family, and taxa were later combined to produce a total animal volume. Occurrence and relative volumes of parasites also were estimated. Diatoms and vascular plant fragments were recorded separately. Filamentous algae included mostly *Cladophora glomerata*, plus infrequent unidentified forms. Inorganic materials were mostly sand and caddisfly cases.

Percentage volume of each category was estimated on an ocular grid. Relative volumes (arcsine transformed) were compared through DFA. Whenever possible, comparisons were with parental specimens from the same collections that contained hybrids. When unavailable, comparative specimens were from samples temporally and spatially as near as possible to hybrid samples.

RESULTS

Hybrid identification.—Measurements and counts were relatively uniform for parental forms (Table 1), with exception of those for five *P. clarki* from a collection in Bonita Creek that appeared distinctive, and were therefore separated for multivariate analyses. Hybrid means were intermediate in all characters that broadly discriminated the presumed parental species. SN, DR, PR, and AL differed little among parentals and hybrids. The five atypical specimens from Bonita Creek aligned with *P. clarki*, although trending toward hybrids in a few characters (e.g., ML, RW, MW, LL, and BL). Coef-

ficients of variation were similar among groups for all characters.

HI for separate characters of individual specimens were in a majority of cases within limits of parental means (0.0 = *Catostomus insignis*, 1.0 = *P. clarki*) from both streams (Table 2). However, SN and meristic features that differed little between species (DR, PR, and AL) exceeded means for parental species in 50% or more cases from Aravaipa Creek, and DR and SN behaved similarly in the Bonita Creek sample. Mean indices per character were within parental means for Aravaipa Creek, with a single exception of SN. All fell between parental means in Bonita Creek fish. Six of 16 fish from Aravaipa Creek had individual means of all characters varying outside parental means, typically toward *C. insignis* (Table 2), to produce a grand mean HI of 0.23. When the four characters of limited parental discrimination are excluded, HI places presumed hybrids at a level of 0.36. All presumed hybrids from Bonita Creek were clearly intermediate without selective exclusion of characters (HI grand mean 0.33; Table 2).

DFA character loadings for canonical variables (CV) I and II are in Table 3. LP, LU, RW, and IW were weighted highest in formation of CV-I in both samples, although not in identical order. Formation of CV-II involved removal of the most discriminating characters (LP for Aravaipa, LU for Bonita Creek). Aravaipa loadings for CV-II included those weighted heavily in CV-I, while CV-II loadings for Bonita Creek fish were mostly highest for different characters.

Hybrids segregate from and are intermediate between parental samples in plots of CV-I and CV-II (Fig. 1). Hybrids are slightly nearer *C. insignis*, as similarly indicated by HI. The five atypical specimens from Bonita Creek separate from typical *P. clarki* along CV-II, and four of the five along CV-I as well. The fifth aligns with *P. clarki* through formation of six variables, the maximum performed by the program. Dispersion of combined Bonita Creek *P. clarki* was not markedly greater than that of the Aravaipa Creek sample.

Morphometric character loadings in PCA were similar to those from DFA (Table 3). Unsheared PC-I loadings were highest for RW, LU, and IW in both streams; sheared H2 loaded highest for LU and CP. Plots of components place putative hybrids intermediate to parental forms, with only one presumed hybrid from Aravaipa Creek overlapping the range of scores

of a parental form (*C. insignis*) along H2 (Fig. 2). The five atypical *P. clarki* yielded low H2 scores, aligning near the lower boundary of their group and relatively near the hybrid cluster.

Foods.—Averages of estimated stomach fullness (excluding parasites) were between 29 and 53% among fishes that contained foods. Five *C. insignis* from Aravaipa, and one *C. insignis*, one hybrid, and a *P. clarki* from Bonita Creek, were excluded due to empty guts.

Catostomus insignis ate the greatest number of food categories in both streams, consuming the most invertebrates (primarily ephemeropteran nymphs) both by relative volume and frequency of occurrence (Table 4). Invertebrates were far less important by volume than vegetative material in *P. clarki* (10.2 and 18.2% for Aravaipa and Bonita creeks, respectively), despite being frequent in occurrence (51.6 and 88.9%). Hybrids ate the same foods as *P. clarki*, and consumed volumes intermediate to those of *C. insignis* and *P. clarki*.

Plant detritus was a conspicuous part of the diets of all suckers in Aravaipa Creek (18.8, 6.8, and 13.2% estimated volumes in *C. insignis*, hybrids, and *P. clarki*, respectively), but occurred only as traces (<2.0%) in Bonita Creek fish. Diatoms and filamentous algae were significant by volume in hybrids and *P. clarki* in both streams, but for the most part were not used by *C. insignis*. Unidentified organic matter averaged between 10 and 32% of relative volumes in all groups.

Sand in digestive tracts differed qualitatively and quantitatively among fishes. *Pantosteus clarki* ingested large amounts of fine sand (<0.2 mm diameter; 53.0 and 19.8% relative volumes for Aravaipa and Bonita creeks, respectively), while *C. insignis* contained smaller amounts (5.0 and 9.4%) of larger diameter (>0.5 mm) grains. Hybrids ingested fine particles typical of *P. clarki*, at intermediate (Aravaipa) or lesser (Bonita) volumes than that species (Table 4).

Relative volumes of major categories of stomach contents were entered into DFA to ascertain variability among groups and individuals. Inorganic and animal categories contributed most to CV-I in Aravaipa Creek fishes, while animal material and diatoms were best discriminators among groups in Bonita Creek (Table 5). Variation was insufficient among groups to obtain robust formation of CV-II. Comparisons of relative volumes of gut contents of Aravaipa Creek samples indicate variation in CV-I of

TABLE 2. HYBRID INDICES FOR PUTATIVE *Catostomus insignis* × *Pantosteus clarki* SPECIMENS FROM ARAVAIPA AND BONITA CREEKS, ARIZONA. See text for character descriptions and abbreviations.

Standard lengths	HL	SN	ML	LU	RW	MW	HD	IW	CP
Aravaipa Creek									
58.0	.185	−1.000	.048	.607	.148	.410	.238	.525	.789
60.9	.074	1.000	.762	.536	.185	1.000	−.238	.625	.158
68.9	.370	−1.000	.143	.464	.296	.282	.048	.200	.263
76.0	.444	−6.000	−.238	.429	.074	.077	.619	.400	.684
78.0	.296	1.000	.381	.394	.074	.615	−.143	.625	.737
104.3	.815	−4.000	−.381	.357	−.074	−.103	.286	.325	.579
107.6	.926	−7.000	−.190	.143	.222	.179	.762	.225	.316
108.8	1.000	−11.000	.095	.393	.222	.308	.238	.350	.211
117.0	1.333	−19.000	−.190	.357	.037	−.051	.857	.150	.579
119.2	1.519	−7.000	.048	.321	.037	0.000	.286	.350	.842
132.5	.889	−4.000	.048	.250	.185	.410	.429	.175	.105
133.4	.407	10.000	.095	.214	.333	.538	.143	.500	.105
151.1	1.037	2.000	−.190	.179	.370	.077	.143	.250	.579
153.2	.889	4.000	.190	.143	.185	.333	.762	.300	.211
156.0	.519	13.000	.268	.143	.333	.615	.095	.450	.526
164.0	1.185	−9.000	0.000	.286	.296	−.026	.143	.525	.737
Means	.743	−2.375	.056	.326	.183	.292	.292	.373	.464
Bonita Creek									
70.9	0.000	3.000	.792	.360	.625	.342	0.000	.561	.714
80.1	.355	−2.333	.458	.360	.292	.421	−.636	.463	.286
103.1	.742	.667	.042	.120	.250	.026	0.000	.610	−.143
107.7	.516	−2.333	−.333	.400	.167	−.079	.545	.537	.929
115.2	.194	.667	.292	.120	.292	.421	−.091	.463	.429
116.8	.613	−.333	.458	.120	.458	.132	.364	.146	.143
117.5	.742	1.667	−.500	.640	.333	.263	.364	.439	.714
126.2	.355	1.000	.083	.320	.542	.342	.409	.293	.500
138.7	.871	1.000	−.250	.200	.458	−.053	.409	.463	.857
149.0	.419	1.000	.042	.200	.208	−.026	.227	.244	.643
156.6	.387	−1.000	0.000	.120	.625	.237	.045	.756	−.071
Means	.472	.273	.099	.269	.386	.184	.149	.452	.455

* HI excluding SN, DR, and PR; see text for explanation.

hybrids exceeding or attaining that of parental species, with an intermediate mean. One individual hybrid showed the lowest CV-I value (Fig. 3a). The pattern in Bonita Creek was similar, *P. clarki* having low and *C. insignis* relatively high CV-I scores (Fig. 3b). Two hybrid specimens were near *P. clarki*, but most had values nearer *C. insignis*. The hybrid mean was intermediate to those for parental forms, but near that for *C. insignis*.

An intestinal cestode tentatively identified by Mpoame (1982; Mpoame and Rinne, 1983) as *Isoglaridacris bulbocirrus*, was abundant in *C. insignis* and hybrids from Aravaipa Creek (Table 4). Incidence was 26.3% in the former (10 of 38 fish), averaging 20.9% of estimated total volume in fish which contained the worm. Infes-

tation in the 16 hybrids was 37.5% (six fish); however, volumes occupied by cestodes averaged only 10.7%. No *P. clarki* from Aravaipa supported parasites in the anterior digestive tract. In contrast, infestation of Bonita Creek *P. clarki* was occasionally extreme; mean volume occupied by tapeworms was 69.7%, and occurrence was 53.8%. Many foreguts were essentially filled (>90.0%) by the parasite. Cestodes accounted for about 23.4% of gut volume in *C. insignis* at a 38.5% infestation. Only one of 11 Bonita Creek hybrids contained parasites.

DISCUSSION AND CONCLUSIONS

Circumstantial evidence developed by three analytical techniques support hybrid origin for

TABLE 2. EXTENDED.

LL	BL	AP	AL	LP	DR	PR	\bar{X} HI	\bar{X} HI*
Aravaipa Creek								
.602	.381	.310	-.071	.313	0.000	-.500	.187	.345
.505	-.095	-.167	1.357	.521	1.250	4.500	.748	.402
.602	-.095	-.405	1.357	.104	0.000	9.500	.758	.279
.699	.381	.071	.643	.313	0.000	4.500	.194	.354
.117	-.095	.071	-.071	.313	0.000	-.500	.238	.255
.796	-.095	-.167	.643	.521	1.250	-.500	.016	.269
.893	.381	.310	.643	.104	1.250	-5.500	-.396	.378
.990	.381	.598	.643	.313	1.250	-.500	-.282	.442
.117	.381	.071	-.017	.313	0.000	-.500	-.973	.303
.893	.381	.548	.643	.521	0.000	-5.500	-.382	.491
.408	.381	.548	.643	.313	0.000	9.500	.643	.368
.602	-.095	.548	.643	.313	0.000	-.500	.865	.334
.505	.381	.786	.643	.313	1.250	-.500	.489	.390
.699	-.095	-.167	1.357	.313	1.250	-.500	.617	.394
.699	.381	.786	-.071	.313	0.000	-.500	1.097	.389
.990	.381	.548	-.071	.104	1.250	-.500	-.197	.392
.632	.202	.268	.554	.313	.547	.750	.226	.362
Bonita Creek								
.339	.100	.302	1.067	.395	-.167	.273	.544	.431
.339	1.100	.302	.400	.395	1.500	.273	.248	.349
.339	.433	.113	.400	.628	-.167	-.636	.214	.274
.102	.100	.302	.400	.395	-.167	.273	.110	.306
.339	.433	.679	1.067	.163	-.167	-.636	.292	.369
-.055	.100	.113	1.067	.163	-.167	.273	.225	.294
.496	.100	.679	-.267	.395	1.500	.273	.490	.338
.732	.100	.679	.400	.395	1.500	.273	.495	.396
.575	.100	.113	1.067	.395	1.500	.273	.499	.400
.102	.100	.491	.400	.395	-.167	.273	.284	.265
.890	.433	.113	.400	.163	1.500	-.636	.248	.315
.382	.282	.353	.582	.353	.591	.025	.332	.340

specimens from Aravaipa and Bonita creeks, Arizona, which are morphologically intermediate between *C. insignis* and *P. clarki*. These fishes are the only catostomids in these streams (Barber and Minckley, 1966; Minckley and Clarkson, unpubl.; Minckley, unpubl.). Hybridization most likely occurred by chance (Hubbs, 1955) due to common times (winter, spring) and places (gravelly riffles) of reproduction (Constantz, 1981).

Although morphological analyses may not be sensitive enough to distinguish among parents, F_1 s, and F_2 s when backcrossing is extensive (Smith, 1973; Neff and Smith, 1979; Rakocinski, 1980), the present hybrids are considered to represent the F_1 generation. Introgressive hybridization between *C. insignis* and *P. clarki*

in evolutionary time has been suggested, however, by analyses of blood proteins (Koehn, 1967, 1969). Among species of *Pantosteus*, serum enzyme patterns of *P. clarki* exhibit unique affinities with *C. insignis* and other *Catostomus* (sensu stricto; Minckley, 1973). *Catostomus insignis* was the only species of its genus examined that had a cathodally-migrating electrophoretic hemoglobin element typical of *P. clarki*, which may document hybridization as a contributor of genetic variability in the long-term history of a genome. Hubbs et al. (1943) further obtained a near perfect HI (0.48) for putative *P. clarki* \times *C. insignis* from the Gila River basin. Even by excluding characters of minimal parental discrimination, our specimens produced average HI near 0.35 (Table 2).

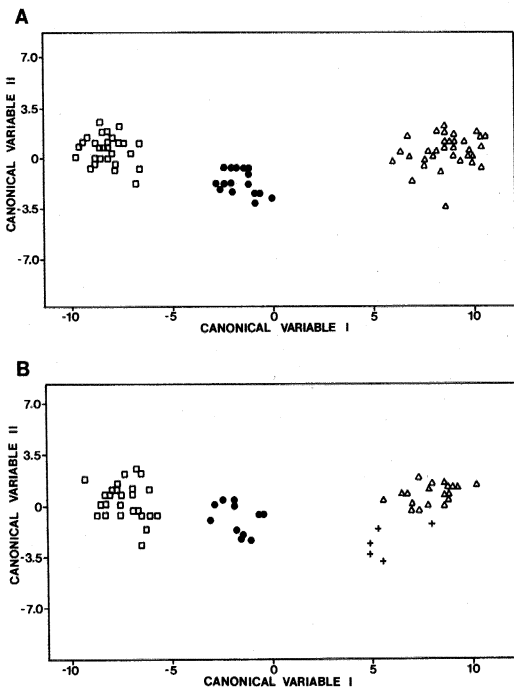


Fig. 1. Plots of scores for *Catostomus insignis* (squares), *Pantosteus clarki* (triangles), their putative hybrids (circles), and "atypical" *P. clarki* (+) on the first canonical variates from DFA of nine morphometric and seven meristic characters: A) Aravaipa Creek, Arizona, based on three, a priori groupings; B) Bonita Creek, Arizona, based on four, a priori groupings.

We cannot predict morphology of F_1 hybrid \times parental backcrosses, but consider equivalent coefficients of variation among parental forms and hybrids (Table 1) and compact clustering along CV-I in DFA (Fig. 1) to provide independent indications of a lack of introgression. Overlapping DFA scores, which scarcely occur among our specimens, would have provided a strong indication of ongoing backcrossing (Rowher, 1972; Butcher, 1980). Trends toward *C. insignis* in some characters (ML, RW, MW, HD, BL, and AP [Aravaipa Creek] and ML, LU, MW, HD, and BL [Bonita Creek]) may be due to our greater sample size compared with that of Hubbs et al. (1943), or alternatively explained by sampling error or influences of different combinations of characters. Such tendencies support the conclusion of Ross and Cavender (1981) that genic dominance and/or interallelic suppression alters intermediate expressions of phenotypes that may exist in fish hybrids.

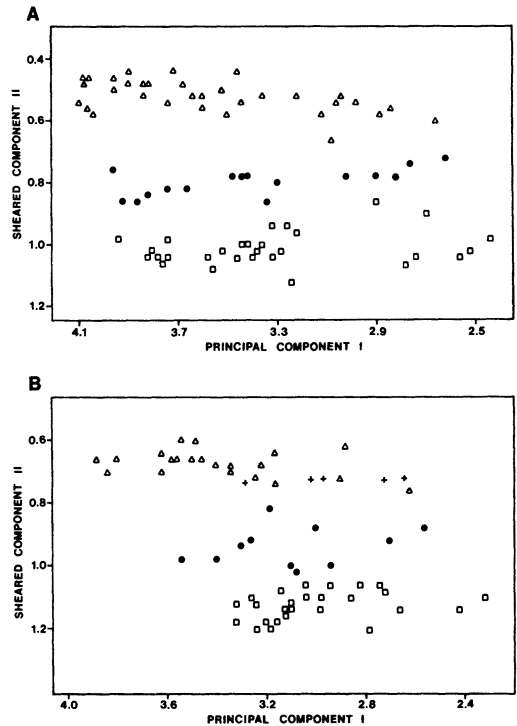


Fig. 2. Plots of scores for *Catostomus insignis* (squares), *Pantosteus clarki* (triangles), their putative hybrids (circles), and "atypical" *P. clarki* (+) on PC-I and sheared PC-II from PCA of 10 morphometric characters: A) Aravaipa Creek, Arizona; B) Bonita Creek, Arizona.

Five unique specimens from Bonita Creek, with obvious affinity to *P. clarki* but atypical in mouth morphology, failed to segregate from that species or align with either hybrids or *C. insignis* (Table 1, Figs. 1–2). Smith (1966) considered Gila River basin *P. clarki* the most uniform sub-population of an otherwise remarkably variable taxon. We are uncertain if the specimens represent expressions of that variation, some form of polymorphism, or are aberrant.

Although not demonstrable in all food categories in all specimens, hybrid feeding behavior indicated by stomach contents was intermediate in Aravaipa Creek, where parental foods were qualitatively and quantitatively distinctive (Table 4). Results of DFA support the hypothesis of hybrid intermediacy, or at least an ability of hybrids to use both parental food bases (Fig. 3a). Differences between parental feeding habits were less pronounced in Bonita Creek, where hybrids ingested quantities and kinds of foods

TABLE 3. CHARACTER LOADINGS FOR DFA AND PCA OF CATOSTOMID FISHES FROM ARAVAIPA AND BONITA CREEKS, ARIZONA. DFA loadings are based on three, a priori groups from Aravaipa and four from Bonita Creek; see text for character descriptions and abbreviations.

Character	Aravaipa Creek ^a				Bonita Creek ^b			
	CV-I	CV-II	PC-I	H2	CV-I	CV-II	PC-I	H2
SL	—	—	0.29	−0.18	—	—	0.24	−0.19
HL	58.0	10.5	0.26	−0.25	52.1	10.0	0.20	−0.30
SN	1.7	2.0	0.31	−0.17	1.6	1.0	0.26	−0.18
ML	66.0	6.8	0.33	−0.01	44.9	8.2	0.32	0.02
LU	362.5	26.8	0.36	0.75	203.2	—	0.49	0.73
RW	287.4	23.7	0.37	0.20	103.2	8.8	0.40	0.17
MW	142.1	7.3	0.33	0.09	86.5	14.1	0.35	0.07
HD	94.6	5.3	0.28	−0.28	33.0	11.9	0.20	−0.31
IW	208.2	22.9	0.35	0.25	156.9	12.1	0.37	0.28
CP	155.5	8.5	0.27	−0.34	46.4	1.5	0.19	−0.33
LL	105.1	19.8	—	—	56.1	5.3	—	—
BL	90.4	8.7	—	—	37.1	7.3	—	—
AP	76.3	4.6	—	—	52.6	2.8	—	—
AL	21.3	4.6	—	—	17.6	5.3	—	—
LP	408.7	—	—	—	129.0	4.5	—	—
DR	19.7	2.0	—	—	5.6	1.2	—	—
PR	0.6	0.1	—	—	4.8	0.9	—	—

^a $\alpha = -0.12$, $\beta_1 = 0.99$, $\beta_2 = 0.12$.
^b $\alpha = 0.28$, $\beta_1 = 0.96$, $\beta_2 = 0.27$.

more typical of *C. insignis*. An exception was the algal component of foods of hybrids, which resembled that of *P. clarki* (Table 4). DFA placed average hybrid feeding as intermediate, but its distance from the average for *C. insignis* is probably not significant (Fig. 3b). Hybrids from Bo-

nita Creek also were capable of using foods typical for each parent.

Discrepancies between food data from Aravaipa and Bonita creeks are not surprising when one considers the temporal nature of sampling (specimens from Aravaipa were caught over a

TABLE 4. AVERAGE PERCENTAGE RELATIVE VOLUMES AND FREQUENCIES OF OCCURRENCE IN PARENTHESES OF MAJOR CATEGORIES OF ITEMS (EXCLUDING CESTODE PARASITES) IN STOMACHS OF *Catostomus insignis*, *Pantosteus clarki*, AND THEIR PUTATIVE HYBRIDS FROM ARAVAIPA AND BONITA CREEKS, ARIZONA. Tr = trace (<2.0%). Detailed data on animal foods are in Clarkson (1982).

Items	Aravaipa Creek			Bonita Creek		
	<i>C. insignis</i> (N = 33)	Hybrids (N = 16)	<i>P. clarki</i> (N = 31)	<i>C. insignis</i> (N = 24)	Hybrids (N = 10)	<i>P. clarki</i> (N = 25)
Identified animal material ^a	60.5 (93.9)	28.1 (75.0)	10.2 (51.6)	54.8 (100.0)	52.6 (100.0)	18.2 (88.9)
Unidentified organic material	15.2 (90.0)	10.9 (62.5)	10.2 (87.1)	29.4 (100.0)	24.2 (100.0)	31.9 (100.0)
Diatoms	Tr (21.1)	10.4 (56.3)	6.1 (83.9)	Tr (66.7)	2.1 (60.0)	17.4 (92.0)
Filamentous algae	Tr (33.3)	6.7 (50.0)	7.1 (48.4)	5.7 (37.5)	10.2 (60.0)	10.9 (64.0)
Detritus	18.8 (90.9)	6.8 (62.5)	13.2 (64.5)	Tr (37.5)	Tr (40.0)	Tr (24.0)
Inorganic material	5.0 (97.0)	37.0 (78.5)	53.0 (100.0)	9.4 (100.0)	9.0 (90.0)	19.8 (96.0)

^a All invertebrates, and trace amounts of fish and insect ova, combined.

TABLE 5. LOADINGS ON RELATIVE VOLUMES OF MAJOR CATEGORIES OF FOODS FOR CV-I AND CV-II FROM DISCRIMINANT FUNCTION ANALYSIS OF THREE, A PRIORI GROUPS OF CATOSTOMID FISHES FROM ARAVAIPA AND BONITA CREEKS, ARIZONA.

Categories	Aravaipa Creek		Bonita Creek	
	CV-I	CV-II	CV-I	CV-II
Identified animal material ^a	29.8	4.3	16.5	—
Unidentified organic material	1.1	0.9	0.7	<0.1
Diatoms	8.5	3.8	13.6	3.2
Filamentous algae	3.7	6.1	0.8	1.8
Detritus	2.9	1.4	<0.1	<0.1
Inorganic material	33.4	—	3.3	0.1

^a All invertebrates, and trace amounts of fish and insect ova, combined.

period of 14 yr as compared to 2 yr in Bonita Creek) and physical and biological differences between the streams. *Catostomus insignis* and *P. clarki* in Aravaipa Creek have been shown (Schreiber and Minckley, 1982) respectively more carnivorous and herbivorous than indicated by our data. However, earlier information

was from a period of relatively stable hydrology, while this study in part spanned hydrologic conditions ranging from drought, through "normal," to flood (Meffe and Minckley, 1987). Such variations in desert streams influence habitat diversity (Harrell, 1978; Minckley and Meffe, 1987) and abundance and availability of foods

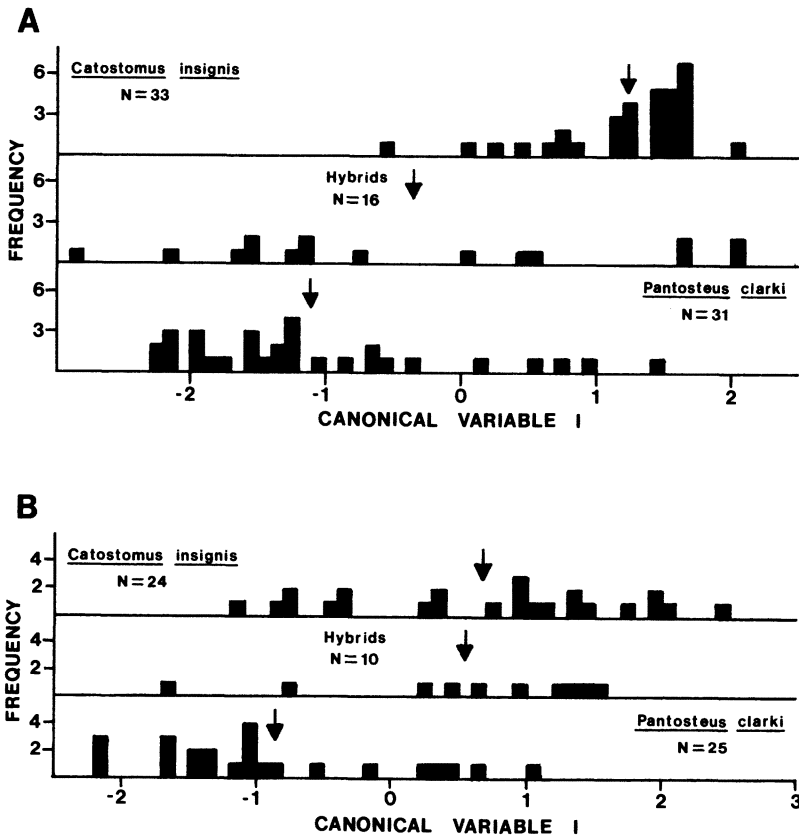


Fig. 3. Histogram of scores for *Catostomus insignis*, *Pantosteus clarki*, and their putative hybrids on the first canonical variate from DFA of relative volumes of six categories of items in foreguts: A) Aravaipa Creek, Arizona; B) Bonita Creek, Arizona. Arrows denote means.

(Bruns and Minckley, 1980; Gray, 1981; Gray and Fisher, 1981; Fisher et al., 1982), which must in turn be reflected in foods and feeding of fishes.

Fewer associated native fishes in Bonita Creek as compared with Aravaipa Creek (four species vs six) also could account for differences in feeding patterns, as could presence of a considerable introduced fish fauna in lower reaches of the former (Minckley and Clarkson, unpubl.). Few introduced fishes have been recorded from Aravaipa Creek (Minckley and Meffe, 1987).

Five of seven Aravaipa species (Schreiber and Minckley, 1982) and two of five in Bonita Creek (unpubl.) rely on ephemeropteran nymphs as a major food base, although one (*Agosia chrysogaster*, which occurs in both streams) is a facultative omnivore. Perhaps relative absence of heavy predation on ephemeropterans in Bonita Creek allowed hybrids to concentrate on that resource, which might be preferred over vegetative material due to their short intestine compared to that of *P. clarki* (Hubbs et al., 1943). A disparity in relative abundance of the parental forms in Bonita Creek also may have allowed foods of hybrids to resemble those of *C. insignis*. *Pantosteus clarki* comprised 35.5% and *C. insignis* only 2.7% of the total number of fishes in samples from Bonita Creek in the late 1970s. Comparable estimates for Aravaipa Creek were respectively 27.3% and 23.8% (Minckley, unpubl.).

Grain size of sand in guts further supported an hypothesis of greater potential for hybrid feeding interactions with *P. clarki* than *C. insignis*, despite some apparent contradictions. Small particles typically accumulate in pools (where *C. insignis* is most common) and coarser materials should occur in riffles (where *P. clarki* feeds). Particle sizes in guts were opposite this trend, which may be explained by plants on riffles that sieve fine sand and other debris from the water column (e.g., Nelson and Scott, 1962). Fine sand must have been ingested by *P. clarki* during scraping of epilithic and epiphytic foods. Hybrids ingested the same sized particles, while *C. insignis* ate coarser sand, presumably while foraging near stones or within interstices of rubble adjacent to riffles.

In instances where hybridization occurs in distinct zones, hybrids are typically restricted to an intermediate or unique part of the environment, which may be reflected in feeding (Hagan, 1967; Greenfield and Deckert, 1973). Hybrids reported here, although not known to occur in special zones of either stream, may thus

feed in areas physically or biologically intermediate between those of the parental species. Spatial partitioning of fishes in Aravaipa Creek is pronounced (Barber and Minckley, 1966; Schreiber and Minckley, 1982), and we have no reason to believe that hybrids do not participate in this pattern. On the other hand, wide individual variation in foods (Table 4, Fig. 4) indicate feeding behaviors are facultative even within the same stream, and that hybrids should be capable of exploiting the same or similar physical space as their parents.

Finally, reasons for differences and similarities in foods of hybrids and their parental species are not necessarily ecological. If there are real phenotypic expressions of dominance or interallelic suppression, as suggested by morphology, such may pervade the entire genetic structure of a hybrid (i.e., in behavior as well as morphology). Thus, a tendency for *C. insignis* × *P. clarki* hybrids to morphologically resemble *C. insignis* appears in feeding behavior as well.

MATERIAL EXAMINED

Catostomus insignis.—MORPHOLOGY: Aravaipa Creek, Graham Co.—ASU 1607 (XI-21-64); 6750 (XI-9-74); 7201 (II-19-77); 7569 (XI-11-76). Pinal Co.—7193 (II-15-77); 7439, 7444, 7445 (IX-23-77); 7575 (XI-11-76). Bonita Creek—7598, 7605 (XI-16-77); 7670 (XII-18-77); 7696, 7710 (II-4-78); 7897 (V-14-78); 7966 (I-22-77). FOODS: Aravaipa Creek, Graham Co.—1607 (XI-21-64); 3316 (II-12-67); 3370 (II-11-67); 3421 (VIII-28-66); 3525, 3532 (VIII-21-67); 7569 (XI-11-76); 7660 (XII-3-77). Pinal Co.—666 (IV-17-64); 1600 (XI-6-64); 4693 (VI-26-66). Bonita Creek—7232 (VI-24-77); 7237, 7966 (I-22-77); 7598, 7605 (XI-16-77); 7696, 7701 (II-4-78).

Pantosteus clarki.—MORPHOLOGY: Aravaipa Creek, Pinal Co.—ASU 3455 (VIII-14-66); 3465 (X-15-66); 7214 (II-15-77); 7306 (VIII-19-77); 7308 (VII-19-77); 7403 (IX-17-77). Bonita Creek—7135 (V-26-77); 7615, 7622 (XI-16-77); 7695, 7700 (II-4-78); 7891 (V-14-78); 7923 (VI-24-77). FOODS: Aravaipa Creek, Graham Co.—1608 (XI-21-64); 3338, 3371 (II-11-67); 3388 (VIII-29-67); 7571 (XI-11-76); 7661 (XII-3-77). Pinal Co.—665 (IV-17-64); 1599 (XI-6-64); 3300 (VI-25-66); 7443 (IX-23-77). Bonita Creek—7234 (VI-24-77); 7254 (I-22-77); 7604, 7615, 7622 (XI-16-77); 7695, 7700, 7705, 7708 (II-4-78).

Catostomus insignis × *P. clarki*.—Aravaipa Creek, Graham Co.—ASU 1609 (XI-21-64); 3337, 3372 (II-11-67); 3389 (VII-29-67); 7570 (XI-11-76); 7656 (XII-3-77). Pinal Co.—667 (IV-17-64); 1601 (XI-6-64); 3299 (VI-25-66); 7442 (IX-23-77). Bonita Creek—7231 (VI-24-77); 7253 (I-22-77); 7606, 7620 (XI-16-77); 7697, 7702, 7706 (II-4-78).

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A New Species of *Allodontichthys* (Cyprinodontiformes: Goodeidae), with Comparative Morphometrics for the Genus

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Allodontichthys polylepis, new species, is described from two localities in the upper reaches of the Rio Ameca basin, Jalisco, Mexico. Its distribution is disjunct from that of the rest of the genus, which is restricted to the Rio Armeria and Rio Coahuayana systems. The new species differs from the other three species of *Allodontichthys* primarily in a higher lateral-line scale count. Shape differences between the four species and between the sexes are examined using multivariate morphometrics, and growth patterns for each sex (as shown by allometric coefficients) are compared. These analyses distinguish *A. hubbsi* from its congeners, but do not resolve the remaining three species.

Se describe *Allodontichthys polylepis*, una nueva especie de la familia Goodeidae, de la cuenca del Rio Ameca, cerca de las villas de Ameca y Guachinango, Jalisco, México. Su distribución es descoyuntado de la distribución de los otros de este género, que se limita a las cuencas de los ríos Armeria y Coahuayana. *Allodontichthys polylepis* se distingue de los tres otros especies de *Allodontichthys* basicamente por el grande número de escamas de la línea lateral. Las diferencias de la forma del cuerpo entre las cuatro especies de este género y entre los dos sexos de *A. polylepis* se examenan con la metodología de morfométrico, y los crecimientos alométricos por cada sexo de las cuatro especies que son presentados. *Allodontichthys hubbsi* se distingue de sus congeneres en estos analisis, pero los tres otros especies no se resuelven.

THE upper reaches of the Rio Ameca system, in Jalisco, Mexico, hold a rich and endemic fish fauna (Miller and Smith, 1986). In this paper, I describe a new species of goodeid

from this locality. The new form is allopatric with respect to the rest of the genus, which is confined to the Rio Armeria and Rio Coahuayana systems, in Jalisco and Colima, Mexico. Fol-