MORPHOLOGICAL VARIATION IN CATOSTOMID FISHES OF THE GRAND CANYON REGION, MIDDLE COLORADO RIVER BASIN

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Collections of fishes from within Grand and Glen canyons on the Colorado River were made specifically for this study by C. 0. Minckley, Flagstaff, Arizona. Support for the project was through Grand Canyon National Park, Grand Canyon, Arizona, through the offices of R. Roy Johnson. Measurements and counts were made by student assistants under my supervision at Arizona State University. G. Dan Overmann and P. L. Minckley assisted with computerization of data.

Conclusions herein are tentative, subject to further interpretation and checking of data. Citation of this report is discouraged other than in light of the last statement and with permission of the author.

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INTRODUCTION

Catostomid fishes of the American Southwest exhibit remarkable intra- and interpopulation morphological variation. In addition to geographic isolation in periodically disrupted drainage basins, which predictably led to local differentiation, they also are thought by some workers to respond to local environmental conditions. Elongated,Big-finned, "swift-water forms" occur in torrential, canyon-bound rivers, while their thick-bodied counterparts occupy quieter waters of tributaries. In addition, catostomid fishes are long-lived and reach large sizes, and demonstrate considerable change in body shape and form with increased age and size. Lastly, they have pronounced sexual dimorphisms.

These variations resulted in early description of numerous species, many of which have now been re-interpreted, synonymized, and put forth as wide-ranging, polytypic taxa. Smith (1966) so dealt with the mountain-suckers, genus Pantosteus, which he considered a subgenus of Catostomus. Smith and Koehn (1971) studied broader relationships among western Catostomus (including Pantosteus) from the standpoints of both biochemical and morphological features. Smith (1978) reviewed the zoogeography of fossil and recent catostomid species. Otherwise, little has recently been published on the systematics of these fishes, and especially on the genus Catostomus. I consider Catostomus and Pantosteus as distinct genera (Minckley 1973; see also, Miller 1976).

The flannelmouth sucker, Catostomus latipinnis Baird and Girard, occupies much of the Colorado River basin (Minckley and Holden 1980). Its nomenclature has been remarkably stable because of: "its slim body, enlarged fins and very prominent lips.... it would be difficult to mistake

this species for any other sucker (LaRivers 1962)." In the course of examination of large numbers of suckers for preparation of the "Fishes of Arizona," I detected far more variation in the latter species than was anticipated. Populations of the Little Colorado River basin had thick bodies, small fins, and small lips, and were referred to "Catostomus sp." (Minckley 1973). A similar fish was recognized in the Virgin River basin, and was presumed to be an introduced species that hybridized with C. latipinnis in the Santa Clara River, Utah (Minckley loc. cit.). Later, large adults from the mainstream Colorado River in Grand Canyon also were found to be heavy bodied, with small fins and tiny mouths, quite unlike C. latipinnis.

The present report examines morphological variation in suckers of the genus Catostomus (sensu stricto) from the middle Colorado River region. As defined by Miller and Hubbs (1960), this includes the Virgin River drainage, Colorado River in Grand Canyon, and the Little Colorado River basin. Additional specimens from lowermost Glen Canyon of the Colorado River and from the upper Colorado River basin are included for comparative purposes.

MATERIALS AND METHODS

All specimens examined are housed in the Arizona State University Collection of Fishes. Counts and measurements were made following Hubbs and Lagler (1970), with exceptions noted in text. Data were compiled and analysed on Univac 1110/42 computer hardware using analysis of variance for unequal sample sizes (Zar 1974). All morphological features are reported as per mille standard length; no transformations or other

data manipuations were attempted. Assessment of allometric changes with growth (size) was made by the method of least squares using standard lengths versus proportional ( ) measurements.

Horizontal lines in figures represent means, with rectangles denoting 95% confidence limits. Means in tabular material are presented + two standard errors. Qualitative information, e.g., life colors, shapes of fins, etc., are reported from living specimens as observed in the field.

RESULTS

Reliability of Characters

Of morphological features examined, eight showed pronounced allometric changes with growth (size) (Table 1). Larger fish had relatively smaller heads (by 7.0 to 9.9%), orbits (41.0 to 48.1%), lengths of depressed dorsal fins (3.5 to 13.6%), and length of lips (7.0 to 34.3%). This pattern changed in the other four characters in one or more populations. Predorsal length was proportionately greater in smaller fish (2.3 to 7.7%) in all but those from tributaries of the Colorado River above Grand Canyon. That feature remained essentially the same over the available size range for the last group. Length of the caudal peduncle was relatively greater in large fish from the Virgin River mainstream (-6.5%), tended to become shorter with increased length in those from the Little Colorado River (16.1%), and remained isometric in other samples. Width of lips remained relatively isometric, or became longer or shorter depending upon the population.

There was little evidence of allometric effects on meristic counts such as fin rays and scales in the lateral line. Counts of papillae on

TABLE 1. Relative changes in selected body proportions in catostomid fishes from the Grand Canyon region of the Colorado River basin. Limits of standard lengths in millimeters were compared with proportional values (per **mille** standard length) by the method of least squares. Values given for body proportions correspond to limits of standard lengths.

Characters	Virgin River mainstream	Little Colorado River	Colorado River in Grand Canyon	Tributaries above Grand Canyon
Number of specimens	65	62	36	44
Standard lengths	69 - 270	92 - 340	98 - 402	95 - 283
Head length	256 - 231	259 - 237	243 - 226	253 - 228
Predorsal length	471 - 460	488 - 471	493 - 455	486 - 485
Orbit length	54 - 28	45 - 25	39 - 23	46 - 25
Drpressed dorsal fin length	317 - 274	276 - 239	256 - 247	290 - 253
Pectoral fin length	226 - 211	214 - 202	165 - 165	222 - 193
Caudal peduncle length	169 - 180	161 - 135	163 - 164	161 - 162
Length of lips	69 - 46	57 - 44	67 - 44	57 - 53
Width of lips	87 - 85	71 - 64	45 - 49	85 - 77

the lips of small fish were generally low, so only adult specimens were used to assess those features.

Sexual dimorphism, although evident in some characters (Table 2), did not produce differences significant enough to influence taxonomic decisions. Males generally have larger fins than females, as demonstrated by data on lengths of depressed dorsal fin and dorsal fin-base, but other features were generally similar.

Patterns of Morphology

The original description of Catostomus latipinnis follows (Baird and Girard 1854: 388):

> General shape subfusiform; head proportionally small, contained five times and a half in the total length. Eyes small, situated near the upper surface of the head; the mouth is small, the lips large and fleshy. All the fins are very much developed and constitute a very prominent feature. The upper margin of the dorsal is slightly concave; the posterior margin of the caudal, crescent shaped; the anal, ventrals and pectoral are posteriorly rounded or subconical.
>
> D. 1. 14. A 11. 8. C 5. 1. **i. i.** 1. 6. V 10. P 18.
>
> The scales are of medium size, considerably smaller on the back than on the sides and belly. The lateral line runs through the middle of the sides from head to tail.
>
> The upper part of the body is reddish brown; the upper part of tail and sides, greenish brown; the belly, yellowish orange; the caudal is olive; the anal, ventrals and pectorals, show traces of deep orange, especially on their outer margin.

A streamlined body with thin caudal peduncle, short head and bulbous snout, small mouth with fleshy lips, expansive fins (especially the dorsal and caudal fins), and fine scales all are used to characterize this fish in numerous published works (Simon 1951, Beckman 1953, LaRivers 1962, Sigler and Miller 1973, Minckley 1973). Characters were therefore selected to demonstrate variations in these features.

TABLE 2. Sexual dimorphism in selected body proportions in comparable-sized catostomid fishes of the Grand Canyon region of the Colorado River basin. Values are per mille standard length + two standard errors of the mean.

Characters	Virgin River mainstream		Little Colorado River	
	Males	Females	Males	Females
Number of specimens	3	17	15	13
Head length	240 ± 8.6	247 ± 8.6	242 ± 3.0	247 ± 4.9
Orbit length	38 ± 4.6	44 ± 5.4	31 ± 1.4	33 ± 1.8
Snout length	122 ± 16.6	116 ± 7.8	99 ± 3.6	106 ± 3.4
Post-orbital length	90 ± 5.6	101 ± 3.0	115 ± 3.0	118 ± 3.8
Interorbital width	103 ± 4.6	112 ± 4.4	107 ± 3.6	108 ± 2.2
Nape to snouth	202 ± 9.0	210 ± 9.6	187 ± 3.2	194 ± 2.4
Depressed dorsal fin fin length	322 ± 23.2	303 ± 11.6		
Dorsal fin base	221 ± 11.6	204 ± 8.2	173 ± 5.8	165 ± 5.4
Caudal fin length	257 ± 13.6	278 ± 12.0	207 ± 4.4	200 ± 6.6
Caudal peduncle length	178 ± 13.2	184 ± 6.2	138 ± 4.4	145 ± 5.6

Body shape.--Predorsal length was least in the sample of fish from the mainstream Virgin River and greatest in those from above Grand Canyon and from East Clear Creek in the Little Colorado River basin (Fig. 1A). Postdorsal length was least in the Santa Clara River (Virgin River basin) and in East Clear and Chevalon creeks (Little Colorado River basin), and was generally comparable in other samples (Fig. 1B). Caudal peduncle depth was least in fish from the Virgin River basin, and was greatest in those from the Little Colorado River basin (Fig. 1C). The last fish have short caudal peduncles, spectacularly so in those from Chevalon Creek (Fig. 1D), while those from the Virgin River have long caudal peduncles; other samples have that structure variably thickened and elongated.

Features of the Head.--Length of head varied little among samples analysed, comprising ca. 23 to 26% of standard length, with no apparent geographic patterns (Fig. 2A). Those differences that exist are cranial rather than a function of opercular variation as indicated by measurement from nape to snout (Fig. 2B). Snout length (Fig. 2C) tends to be greater in fish from the Virgin River, and this was accompanied by a larger orbit and shorter postorbit (Fig. 2D-E). Fish from within Grand Canyon and lowermost Glen Canyon have narrower heads and isthmus than others (Fig. 2F-G).

Lip Morphology.--Specimens from the Virgin River basin and those from above Grand Canyon have by far the longest lip measurements, while fish from the Santa Clara River, Silver and Chevalon creeks in the Little Colorado River basin, and from Grand and Glen canyons are much shorter. Width of the mouth demonstrates a similar trend (Fig. 3A-C). Numbers

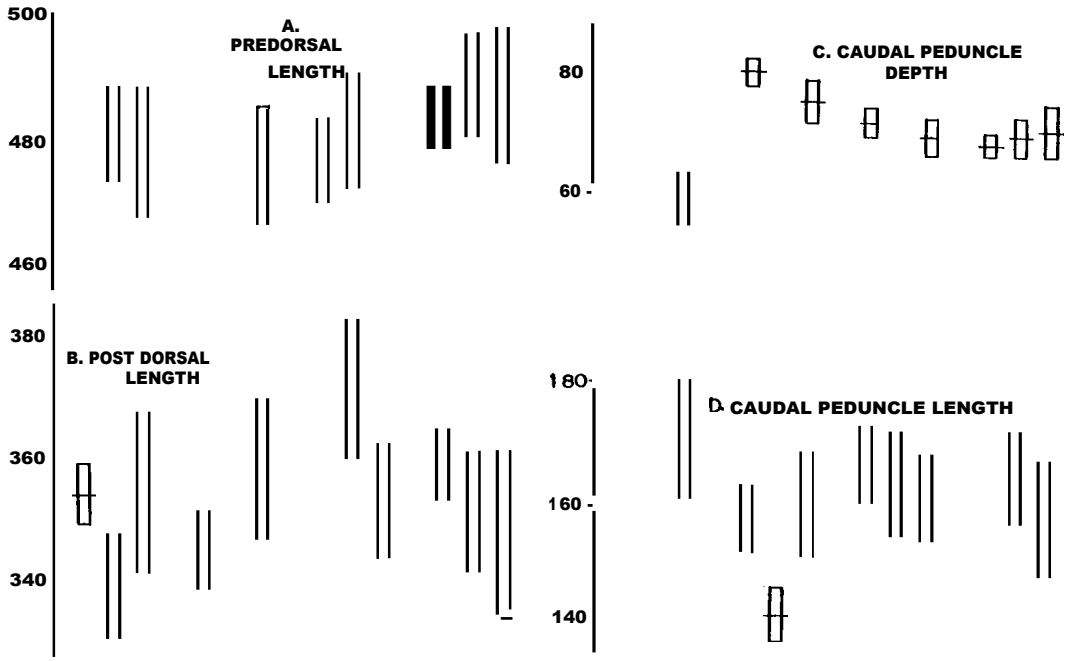

FIGURE 1. Features of body shape in catostomid fishes of the Grand Canyon region of the Colorado River basin. Left to right: Virgin R. basin - mainstream, UT, AZ, NV, Santa Clara R., UT, Meadow Valley Wash, **NV**; Little Colorado R. basin, **AZ -** East Clear Cr., Chevalon Cr., Silver Cr.; Grand and Glen canyons, AZ - Kanab Cr. mouth, Shinumo Cr. mouth, Paria R. mouth; upper Colorado R. - San Juan R., NM, La Plata R., NM, Strawberry R., **UT.**

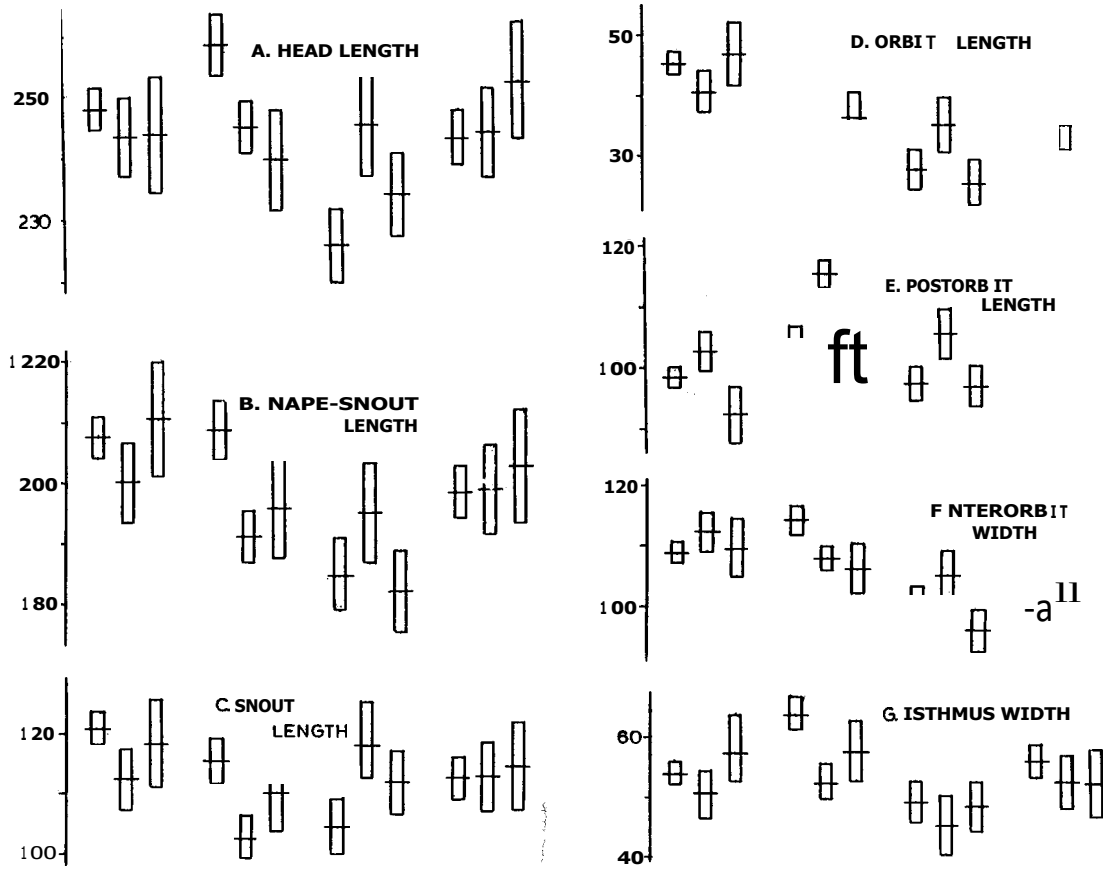

FIGURE 2. Features of the head of catostomid fishes of the Grand Canyon region of the Colorado River basin. Arrangement of samples given in Figure 1.

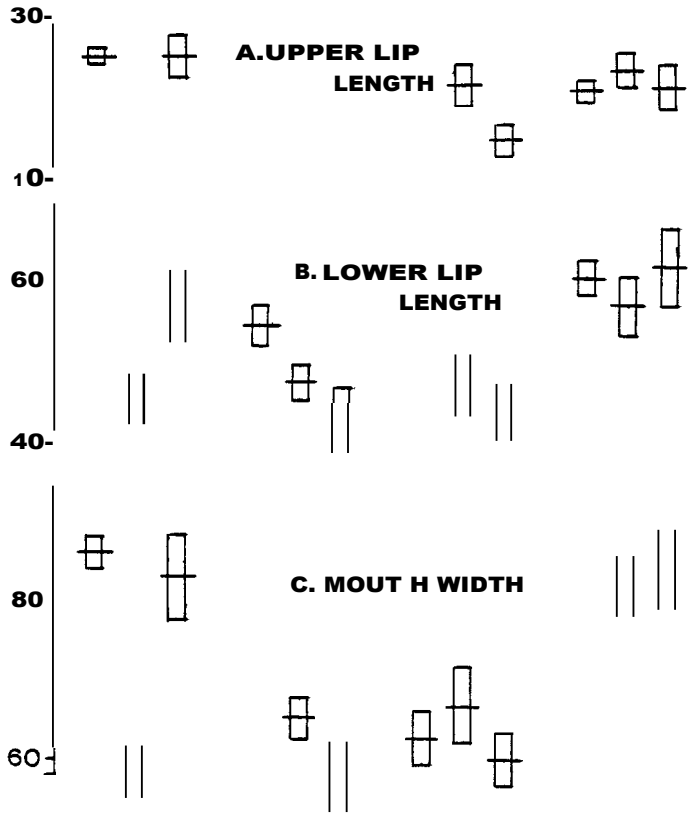

FIGURE 3. Features of the lips of catostomid fishes of the Grand Canyon region of the Colorado River basin. Arrangement of samples given in Figure 1.

of papillae crossing by an imaginary midline on the upper lip, and numbers crossed by a similar line on the center of the left lobe of the lower lip do not differ significantly among populations (Table 3).

Fin dimension.--Pectoral and pelvic fin lengths are least in fish from the Santa Clara River, uppermost Little Colorado River (Silver Creek), and in those from Grand and Glen canyons (Fig. 4A-B). This same pattern holds for vertical fins (Fig. 5A-C), but only the Virgin River populations are distinctive in measurements of fin bases, an index of expansiveness of the structures (Fig. 6A-B).

Only dorsal fin-rays were enumerated. All but the Virgin River populations fall within the limits of variation ascribed to Catostomus latipinnis in the literature (11 to 13). Fish in the Virgin River are extreme, with means near 13 rays and a range from 12 to 15 (Table 4).

Scales in the Lateral Line.--Scales in the lateral line are lowest in number in specimens from the Virgin River basin, tend toward intermediacy in the Little ColoradoRivermaterial and in Grand and Glen canyons, and are highest in fish from streams of the upper Colorado River basin (Table 5).

Qualitative Observations.--Suckers of the genus Catostomus from the Little Colorado River and from the Santa Clara River are sharply bicolored, dark above and silvery to white or yellow-white on the venter. Those from the mainstream Virgin River and juveniles from Grand and Glen canyons and the upper Colorado River are almost unicolored, sandy-brown or yellowish overall and only slightly lighter to white below. Adults from Grand Canyon and upstream become darker above and light below,

TABLE 3. Numbers of papillae crossed by an imaginary midline on the upper lip and crossed by a similar line on the left lobe of the lower lip in catostomid fishes from the Grand Canyon region of the lower Colorado River basin; number of specimens is in parentheses.

Populations	Upper Lip	Lower Lip
VIRGIN RIVER BASIN		
Mainstream	5.2 ± 1.1 (4)	9.6 ± 2.0 (3)
Santa Clara River	5.6 ± 1.8 (19)	9.3 ± 3.2 (19)
Meadow Valley Wash	5.2 ± 0.8 (6)	10.0 ± 2.6 (6)
LITTLE COLORADO RIVER BASIN		
East Clear Creek	5.6 ± 1.0 (23)	10.4 ± 1.4 (23)
Chevalon Creek	4.7 ± 0.8 (31)	9.4 ± 1.4 (33)
Silver Creek	4.8 ± 0.8 (1)	9.5 ± 2.2 (1)
MAINSTREAM COLORADO RIVER		
Kanab Creek mouth	4.9 ± 0.7 (8)	8.5 ± 2.4 (8)
Shinumo Creek mouth	5.1 ± 0.5 (16)	9.8 ± 1.1 (16)
Paria River mouth	5.5 ± 1.0 (12)	10.5 ± 0.1 (12)
UPPER COLORADO RIVER		
San Juan River	5.1 ± 0.6 (28)	10.6 ± 1.2 (28)
La Plata River	5.3 ± 1.0 (16)	10.3 ± 1.2 (16)
Strawberry River	5.0 ± 0.0 (7)	10.1 ± 1.4 (7)

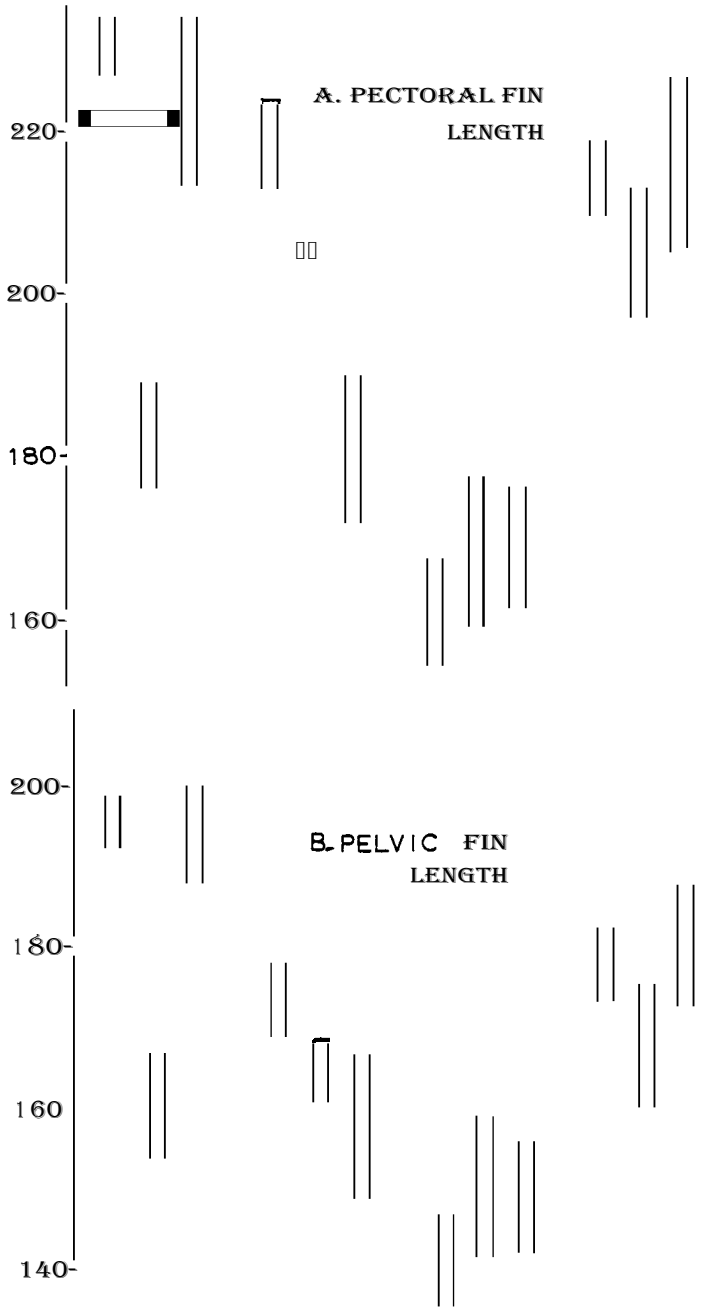

FIGURE 4. Features of the paired fins in catostomid fishes from the Grand Canyon region of the Colorado River basin. Arrangement of samples given in Figure 1.

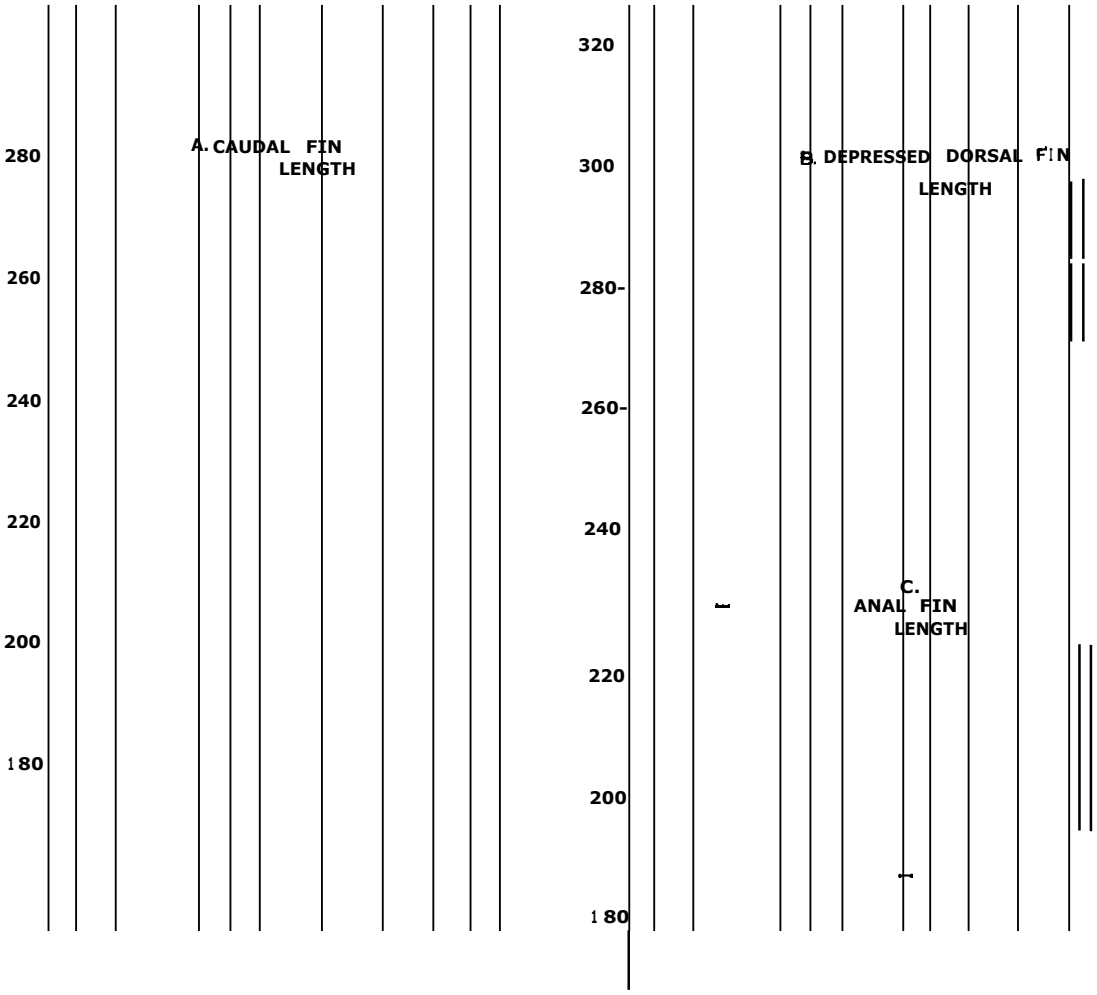

FIGURE 5. Features of the vertical fins in catostomid fishes from the Grand Canyon region of the Colorado River basin. Arrangement of samples given in Figure 1.

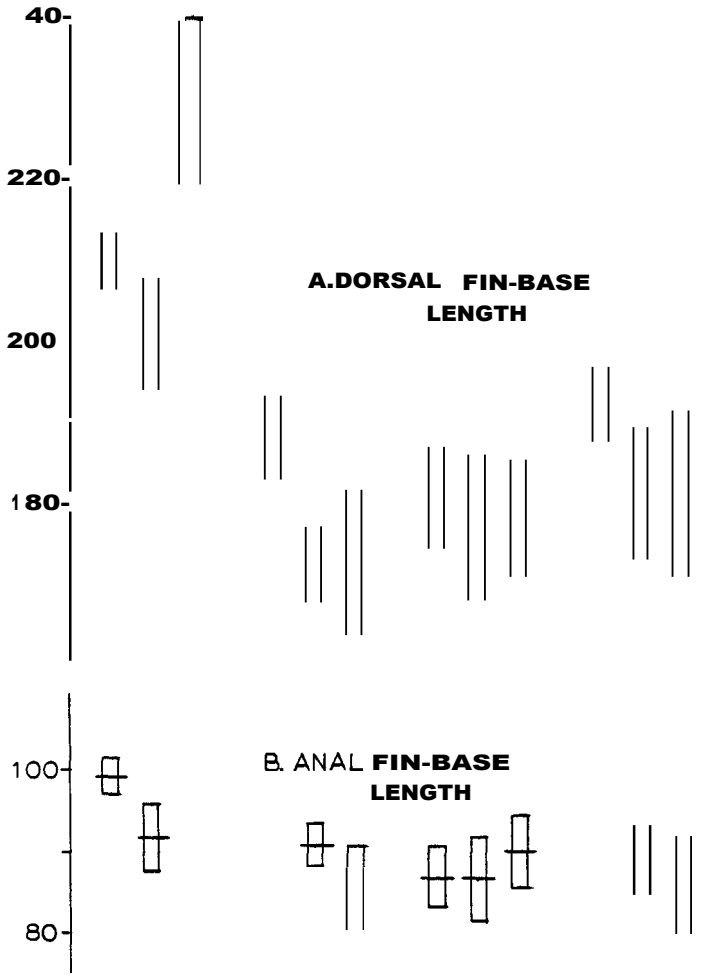

FIGURE 6. Features of some fin bases of catostomid fishes of the Grand Canyon region of the Colorado River basin. Arrangement of samples given in Figure 1.

TABLE 4. Dorsal fin-rays in catostomid fishes of the Grand Canyon region of the Colorado River basin; number of specimens followed by limits of counts in parentheses.

Populations	Dorsal fin-rays
VIRGIN RIVER BASIN	
Mainstream	13.1 + 0.9 (57, 12-15)
Santa Clara River	12.9 + 1.4 (15, 12-14)
Meadow Valley Wash	13.0 + 0.0 (6, 13)
LITTLE COLORADO RIVER	
East Clear Creek	12.2 + 1.6 (45, 10-13)
Chevalon Creek	10.9 + 0.5 (31, 10-11)
Silver Creek	11.5 + 1.0 (11, 11-12)
MAINSTREAM COLORADO RIVER	
Kanab Creek mouth	11.3 + 0.9 (8, 11-12)
Shinumo Creek mouth	12.3 + 1.0 (12, 12-13)
Paria River mouth	12.2 + 1.1 (16, 11-13)
UPPER COLORADO RIVER	
San Juan River	12.0 + 1.0 (28, 11-13)
La Plata River	11.9 + 1.2 (16, 11-13)
Strawberry River	11.7 + 1.0 (7, 11-12)

TABLE 5. Scales in the lateral line in catostomid fishes from the Grand Canyon region of the Colorado River basin; number of specimens followed by limits of counts in parentheses.

Populations	Scales in Lateral Line
VIRGIN RIVER BASIN	
Mainstream	97.7 ± 11.6 (59, 90–111)
Santa Clara River	100.8 ± 11.6 (18, 90–111)
Meadow Valley Wash	95.5 ± 10.3 (6, 86–100)
LITTLE COLORADO RIVER	
East Clear Creek	102.7 ± 8.8 (22, 9–110)
Chevalon Creek	105.6 ± 14.5 (30, 9–123)
Silver Creek	98.0 ± 9.8 (7, 90–103)
MAINSTREAM COLORADO RIVER	
Kanab Creek mouth	105.1 ± 19.2 (8, 9–118)
Shinumo Creek mouth	113.4 ± 11.3 (16, 9–121)
Paria River mouth	103.4 ± 7.8 (12, 9–112)
UPPER COLORADO RIVER	
San Juan River	112.0 ± 10.0 (28, 100–120)
La Plata River	111.4 ± 8.7 (16, 105–119)
Strawberry River	106.7 ± 9.1 (7, 7–110)

especially in breeding season, but do not become as intensely bicolored as those fromthe Little Colorado and Santa Clara rivers. I have not seen living specimens from Meadow Valley Wash, Nevada.

Only the fish from the Virgin River mainstream have expanded, falcate dorsal fins, and visibly enlarged caudal fins with pronounced procurrent rays. Fins of fish from the other streams tend toward emarginate or straight on their distal margins.

Specimens from Grand and Glen canyons, and from the upper Colorado River basin, are leathery in external appearance. Scales on the nape and dorsum appear deeply embedded when compared withotherpopulations. Skin on the head and on leading margins of paired and vertical fins also seems thickened on mainstream and upper Colorado River fish. Perhaps embedding of scales and thickening of skin are responses to the (formerly or at present) abrasive nature of the habitat in these canyon-bound rivers.

DISCUSSION AND CONCLUSIONS

Only the population of Catostomus from the mainstream Virgin River has features which, in composite, closely fit the conceptualized Catostomus latipinnis as represented in recent literature. Other populations present a mosaic of characteristics. Each is distinctive.

Fish from the Santa Clara River resemble those from the Little Colorado River basin in a number of quantitative features, especially in some head characteristics (Fig. 2), lip characters (Fig. 3), and in sizes of fins (Figs. 4-6). However, they also share a number of other features with fish from the mainstream Virgin River and Meadow Valley Wash (e.g., caudal peduncle length and depth, Fig. 1, and scales in the lateral line, Table 5), which dilute significance of this apparent relationship.

Variation among populations within the Little Colorado River, each from a separate, north-flowing tributary, is great (e.g., pre- and post-dorsal lengths and length of caudal peduncle, Fig. 1; lip morphology, Fig. 3; and fin sizes, Figs. 4-6). These facts mask distinctiveness of the Little Colorado River form, and cast doubt upon Minckley's (1973) proposal that fish from that river basin constitute an undescribed species.

Specimens from creek mouths within Grand and Glen canyons also are unique, especially in head measurements (Fig. 2), in having small fins (Figs. 4-6), and in having relatively high lateral-line counts (Table 5). In many respects these fish tend to be intermediate between populations of the Little Colorado River and those from upstream. However, these were the largest specimens examined, and large size undoubtedly influences the degree of differences indicated by morphometry (Table 1).

Populations from the upper Colorado River basin share many features with those from the Virgin River, especially in their large heads (Fig. 2), lips (Fig. 3), and fins (Figs. 4-5). However, they have spectacularly high numbersof scales in the lateral line (Table 5), and their fins, although elongate, are not expansive (Fig. 6).

Populations of fishes of the genus Catostomus from the Grand Canyon region are thus highly variable, quite unlike the uniformity implied for Catostomus latipinnis in available literature. A complex of forms is obviously present, and this cursory survey of their morphology can only point toward the need for additional work. Type material of C. latipinnis from the San Pedro River, southern Arizona, must be examined so definition of that taxon may be solidified. Comparative material from geographic extremes of the Colorado River basin must also be examined. Perhaps

variation in C. latipinnis is equally pronounced elsewhere in the basin. If not, a number of alternatives exist: 1) presence of a "middle Colorado River" catostomid fauna, including one or more undescribed forms; 2) presence of a "Catostomus latipinnis superspecies," consisting of a number of environmentally induced and maintained "morphs;" 3) introduction, and spread of a non-native Catostomus, with subsequent hybridization and introgression of alien genes into native populations; or 4) some combination of the above.

Precedence exists for a middle Colorado River fish fauna (Smith 1966, Minckley and Brown 1981). The minnow genus Lepidomeda is endemic to that region, with distinctive species and/or subspecies in each major tributary (Miller and Hubbs 1960). Lepidomeda vittata Cope occupies the Little Colorado River basin, L. mollispinis Miller and Hubbs is in the Virgin River system (with two subspecies), and L. albivallis and L. albivelis (with additional subspecies) are in the Pluvial White River drainage. Thermal waters of Pluvial White River and Moapa River (former tributaries to the lowermost Virgin River in Pleistocene and prior to impoundment of Lake Mead, respectively) support springfish Crenichthys baileyi (Gilbert), and Moapa dace, Moapa coriacea Hubbs and Miller. The genus Gila is represented by the nominal G. robusta jordani T[illegible] Pluvial W[illegible] R[illegible], G. r. seminuda Cope and Yarrow in the Virgin River, and G. r. robusta Baird and Girard elsewhere, including the mainstream Colorado River. The population of Gila robusta in the upper Little Colorado River has scarcely been studied (see Rinne 1976), and may be extinct (original data). A complex of Pantosteus also exists in the region, although synonymized or aligned if undescribed with P. clarki (Baird and Girard) and P. discobolus

(Cope). The nominal Pantosteus intermedius (Tanner) is in Pluvial White River, undescribed forms exist in the Virgin River (all considered P. clarki by Smith 1966), and a distinctive, stubby-bodied population of P. discobolus is in the Little Colorado River (see below). Pantosteus discobolus also exists as two "morphs" in the mainstream Colorado River, one stubby and thick, and the other elongated, with a pencil-thin caudal peduncle (Minckley 1973, Suttkus and Klemmer 1979).

The above discussion applies equally well to the presence of "super-species" in the Grand Canyon region. Most of the cognate forms just discussed would be considered by some systematists as well-marked "morphs," or subspecies, of polymorphic species. Smith et al. (1979) recently referred big-river chubs of the Colorado River basin to such a category, after convincingly demonstrating their distinctiveness in special habitats of the region. In the pristine Colorado River basin, bonytail chub, Gila elegans Baird and Girard, humpback chub, G. cypha Miller, and round-tail chub, G. r. robusta, maintain their integrity and co-exist as species. With modifications of the system, reduced flows, controlled conditions, and reduced turbidities and temperatures, all resulting from extensive impoundment, species barriers (be they genetic, behavioral, environmental, etc.) begin to deteriorate, and hybridization results.

Minckley (1973) suggested that bicolored suckers in the Santa Clara River, Utah, might result from introduction of another species "perhaps C. ardens Jordan and Gilbert." Koehn (1967 et seq.) demonstrated that suckers of the genus Pantosteus had indeed been transferred from the Virgin River to the Siever River basin, Utah, so a reciprocal transfer is certainly possible, and Miller (1952) noted thattheVirgin River is subject

to commercial bait operations. Catostomus ardens now has been recorded from Lake Mohave, Arizona-Nevada (Gustafson 1975). That species is far too coarse-scaled (61 to 89 scales in the lateral line; LaRivers 1962) to likely be involved in production of the form(s) now present in the Virgin River system (see Table 5). In the Little Colorado River basin, Smith (1966) demonstrated the probable interbasin migration before historic times of Pantosteus plebeius Baird and Girard from the uppermost Rio Grande basin. He found an up- to downstream **cline** in certain characters of Pantosteus discobolus that certainly may indicate such an event. If the white sucker, Catostomus commersoni Lacepede, is also native to the upper Rio Grande as indicated by Lee and Kucas (1980), such circumstances might also explain some unique features of the Catostomus now inhabiting the Little Colorado River watershed. Catostomus commersoni is another coarse-scaled species (58 to 75 scales in the lateral line; Simon 1951) that has been introduced into the uppermost Colorado River basin (Minckley and Holden 1980) where it hybridizes with C. latipinnis (Holden and Stalnaker 1975). Its presence in the lower Colorado River basin has not been demonstrated. On the basis of evidence on hand, production of the variations in Catostomus sp. from the middle Colorado River region is not attributable to introductions ofHspecies from other geographic areas.

I speculate that a combination of the first two alternatives - the presence of a middle Colorado River ichthyofauna composed of "superspecies," now under influence of man's modification of the system - provides an acceptable explanation for the situation observed. Only additional work can test the following hypothesis.

The taxon Catostomus latipinnis presumably evolved in swifter waters of the Colorado River basin, developing distinctive features allowing it

to exploit that severe, highly variable environment. The Virgin River obviously represents a special part of the Colorado River basin. Endemism and reliction is high there, as detailed above, and the population of Catostomus latipinnis in the channel may have differentiated to special conditions, or may have been influenced by genetic introgression with the bicolored form of the Virgin River headwaters subsequent to isolation of that drainage by impoundment of Lake Mead in 1935.

I still consider the Little Colorado River form of Catostomus as distinct from C. latipinnis (s.s.), and submit that its presence may have effected changes in mainstrem populations of the Colorado River after closure of Lake Powell in the early 1960s. The Colorado River in Grand Canyon was vastly changed by that event (Kubly and Cole 1979). Variation, in discharge of the river became almost tidal, temperatures were vastly reduced and ameliorated to a narrow range, chemistry changed, and sediment transportwas curtailed resulting in consistently clear water. Habitats in the upper Little Colorado River basin, with the exception of discharge relations, resemble present conditions in the mainstream Colorado River far more than they did in the past. Suckers in the Little Colorado River inhabit clear, cold, relatively stable headwater streams, generally above 1,500 m elevation. They were thus "pre-adapted" to conditions that resulted from Glen Canyon Dam, and could have invaded the mainstream. Variation in present, mainstream Colorado River populations of Catostomus, and their generally intermediate characteristics between stocks from the Little Colorado River and those in yet-uncontrolled, upstream tributaries, both may thus be attributed to hybridization and introgression in the presently-modified, Grand Canyon reach. Catostomus

within Grand Canyon generally spawn in tributary streams (Suttkus and Klemmer 1979), and this would tend to promote such hybridization assuming the Little Colorado River form retains a proclivity for such smaller habitats.

I recommend that additional studies be made utilizing specimens taken from the middle Colorado River region prior to impoundment and attendent changes in environmental conditions. This will necessitate travel to pertinent museum facilities and search for specimens, including examination of type material of Catostomus latipinnis as noted before. Additional specimens from within Grand Canyon and its environs also must be examined to detail variations which occur. Until such investigations are complete the suckers of the genus Catostomus within Grand Canyon should be designated as members of the "Catostomus latipinnis complex" to underline their apparent differences from that conceptualized taxon.

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