

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 129

**Distribution and Evolution of the
North American Catostomid Fishes of the
*Subgenus Pantosteus, Genus Catostomus***

BY
GERALD RAY SMITH
University of Kansas

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
NOVEMBER 1, 1966

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DISTRIBUTION AND EVOLUTION OF THE
NORTH AMERICAN CATOSTOMID FISHES OF THE SUBGENUS
PANTOSTEUS, GENUS *CATOSTOMUS*

THE SUBGENUS *Pantosteus* comprises the mountain suckers of the genus *Catostomus*, family Catostomidae, and order Cypriniformes. They are terete, generally small freshwater fishes with characteristic protractile jaws and large lips. Phylogenetically they are nearest the suckers of the subgenus *Catostomus* with which they hybridize, and from which they differ primarily in the possession of trophic specializations. These include: development of cartilaginous scraping edges on the jaws; lateral notches at the junctions of the upper and lower lips; a shallow, posterior median incision of the lower lip; a long intestine, at least 4 times the standard length in adults; and a black peritoneum. The lip and jaw modifications seem to adapt these fishes to scraping algae, diatoms, and other organic matter from the substrate. The long intestine and black peritoneum are characteristic of many herbivorous fishes.

Most species of *Pantosteus* are mountain-stream inhabitants, usually associated with cool waters and moderate current, although they are occasionally found in mountain lakes or in rivers of moderately high temperature or slow current. They are usually vernal spawners with two- to four-year life cycles. The adult size varies from less than 100 mm to approximately 400 mm in total length, depending upon the population.

Eight species have been recognized recently in the genus *Pantosteus* (Bailey *et al.*, 1960). They are distributed, usually allopatrically, from southern British Columbia, Alberta, and Saskatchewan south to central Mexico, and from certain Pacific coast drainages east to New Mexico, Colorado, and the Black Hills of South Dakota. They are characteristic elements of the faunas of the Great Basin, Colorado River, and Columbia River; they occur also in headwaters of the North Platte River, Missouri River, Fraser River, Santa Ana system, Rio Grande and Pleistocene connectives, and Rio Mezquital. Sympatry among species of the subgenus occurs only in the northern Great Basin, upper Colorado, and Columbia systems (Fig. 1). In the present paper the group is recognized as a subgenus including five species embracing the previously recognized eight, and an additional species formerly considered unrelated.

The taxonomy of *Pantosteus* has been unusually difficult. Keys to the recognized species ultimately have been based on distribution (Simon, 1951:59; Eddy, 1957:74; Moore, 1957:91). There has long been an awareness of the need for systematic revision of the group, and data for this study were

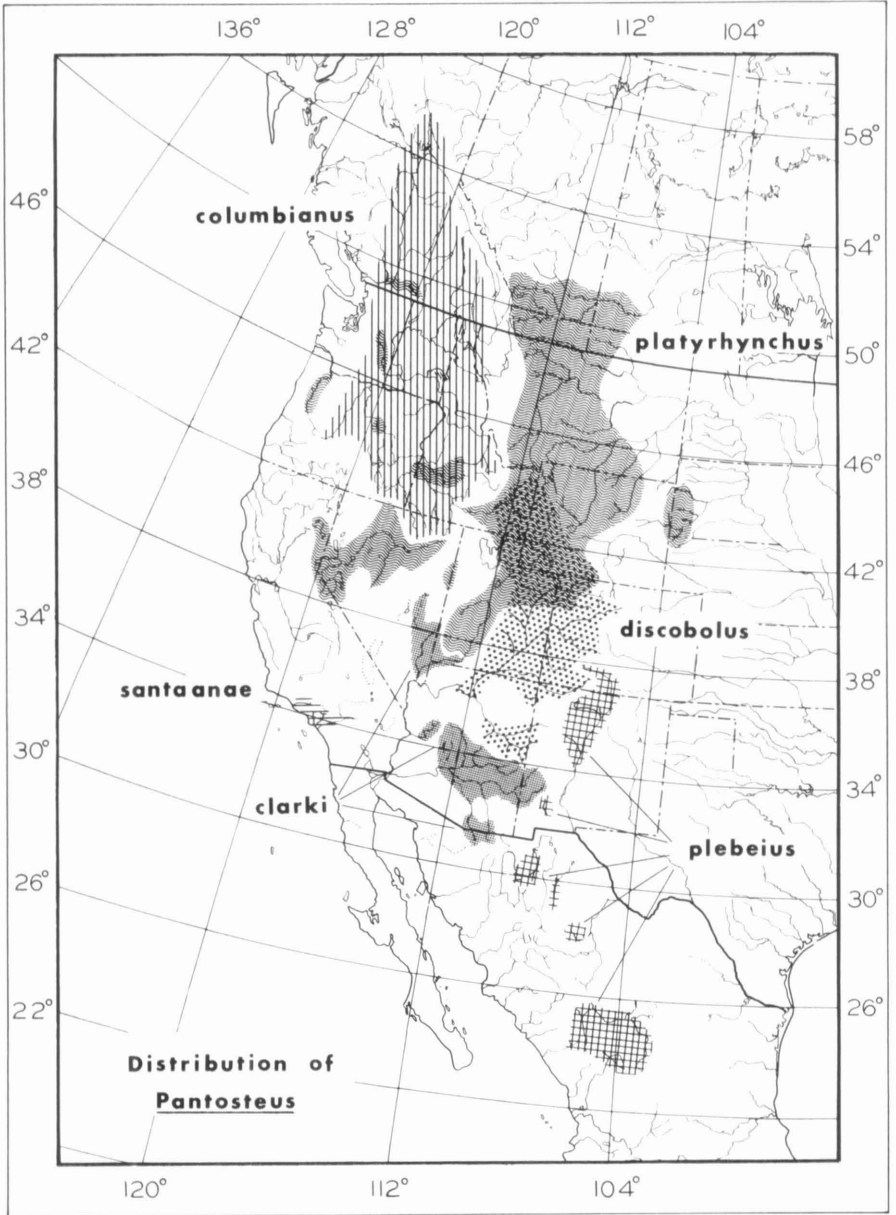


FIG. 1. General distribution of the fishes of the subgenus *Pantosteus*

collected with intent to clarify some of the taxonomic problems. The result has not been simplification of the problems, but rather an increase in complexity of explanations required by the data. The complexity is a result of lack of coincidence in the degree of evolution of morphological divergence and reproductive isolation. The assortment and distribution of characters throughout the genus suggest a history of reticulate evolution in which geographically isolated, diverging phyletic lines have been brought variously into secondary contact. The outcome of contact—either genetic mixture or sympatric species—is not simply a function of degree of divergence, but seems to be the result of interaction of time, space, genetic, and ecological factors, all of which are given some attention in this analysis.

The objectives of this study are: first, to describe the variation and distribution of morphological characteristics in populations of *Pantosteus*; second, to attempt to define phyletic lines and patterns and to reconstruct their evolutionary histories; and last, to try to classify the phyletic lines in a system consistent with current taxonomic concepts.

GEOGRAPHICAL CONSIDERATIONS.—The distribution and evolution of *Pantosteus* is intimately associated with mountains. The ecological reasons for this involve specializations adaptive to cool waters, moderate to rapid current, and rocky substrate, and correspondingly reduced adaptation to other conditions. Mountains are important in another significant way, however. The primary barriers isolating populations of *Pantosteus* are the more or less mountainous divides separating drainage basins. The efficiency of this type of barrier is relatively high; crossing by means of stream capture is uncommon. Furthermore, when a drainage transfer occurs, it may have the unique effect of bringing a more or less small breeding population and its habitat into contact with a new ecological and genetic environment.

Mountain-stream fishes are subject to other unusual properties of barriers. Impassable falls create obstacles which may be absolute in one direction and partial in the opposite, thereby facilitating unidirectional gene flow. Ecological barriers may be created by environmental differences in the lower parts of streams, where the waters may be less habitable owing to warmer, more turbid, or sluggish conditions, or to unsuitable bottom type. Intermittent streams whose lower reaches may be seasonally, or more or less permanently, dry are characteristic of the arid West and are important in isolating populations of *Pantosteus*. A related phenomenon is the isolation of fishes occupying the tributaries to Great Salt Lake, which is uninhabitable because of the high salt concentration.

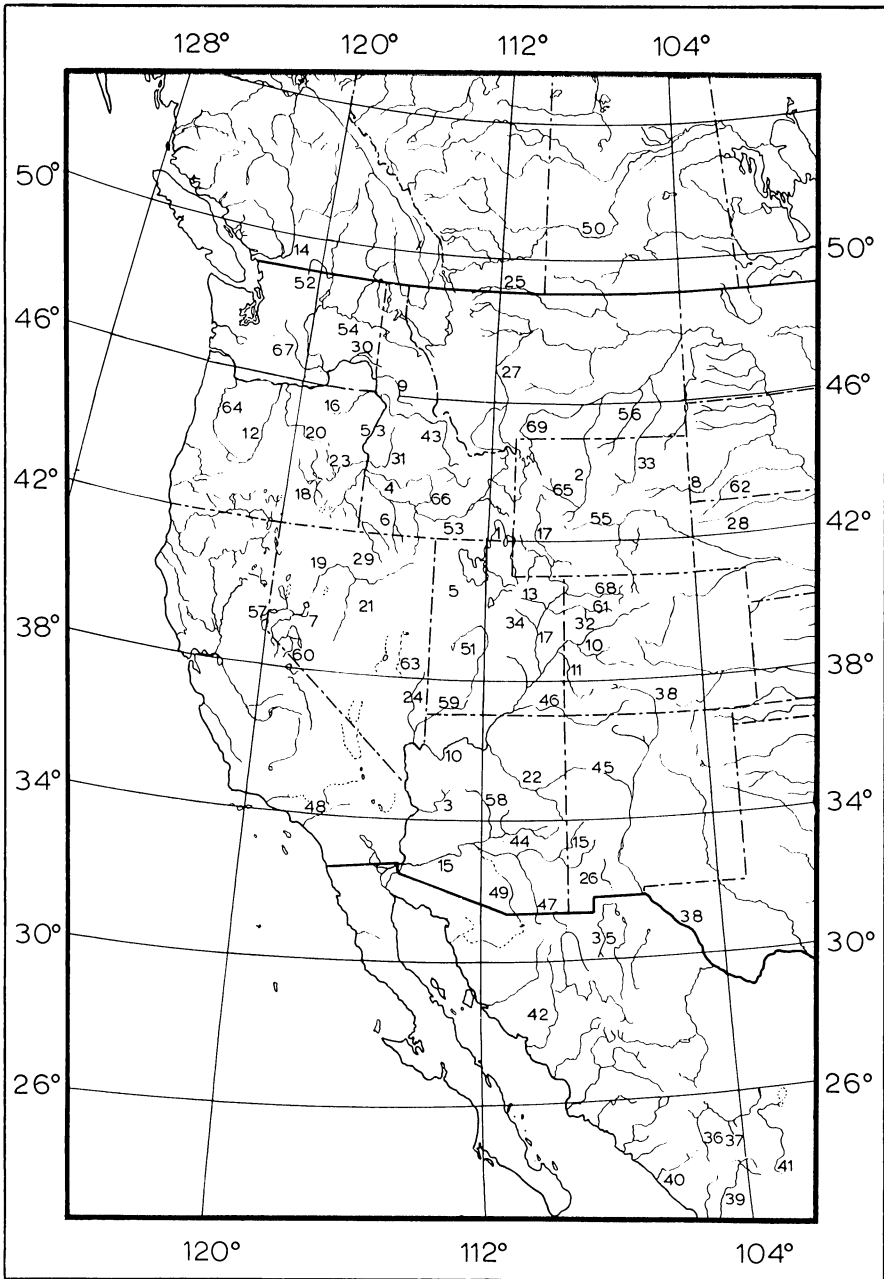
A final consideration is the linear nature of mountain-stream distribution patterns and its effect upon gene flow. In a river system a zone of intergradation may consist of a corridor many miles long, but only a few feet wide. The distance factor may be combined with other barriers to effect various degrees of population isolation.

These aspects of the environment have undoubtedly been among the prime determinants of gene flow and evolution in *Pantosteus*. It is apparent that the history of the subgenus is closely tied to the history of mountains and drainage basins of Western North America. Perhaps the most interesting feature encountered in this study is that the distributional limits of the biological units are not coincident with the limits of the existing hydrographic units. Thus, it is obviously unsatisfactory to use the patterns of modern surface features as the basis for classifying and understanding these fishes. The hypothesis to be presented here is that the phylogenetic groups of *Pantosteus* are older than the recent geographic patterns. Where geological data are available to explain geographically nonconterminous biological distribution patterns they will be discussed. When these data are inadequate or controversial, biological facts may be offered as possible bases for inferences relating to past geography.

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FIG. 2. Guide to some of the rivers and basins mentioned in this report.

- | | | |
|------------------------|------------------------|------------------------------|
| 1. Bear R. | 24. Meadow Valley Wash | 47. San Pedro R. |
| 2. Big Horn R. | 25. Milk R. | 48. Santa Ana R. |
| 3. Bill Williams R. | 26. Mimbres R. | 49. Santa Cruz R. |
| 4. Boise R. | 27. Missouri R. | 50. Saskatchewan R. |
| 5. Bonneville basin | 28. Niobrara R. | 51. Sevier R. |
| 6. Bruneau R. | 29. Owyhee R. | 52. Similkameen R. |
| 7. Carson R. | 30. Palouse R. | 53. Snake R. |
| 8. Cheyenne R. | 31. Payette R. | 54. Spokane R. |
| 9. Clearwater R. | 32. Piceance Cr. | 55. Sweetwater R. |
| 10. Colorado R. | 33. Powder R. | 56. Tongue R. |
| 11. Dolores R. | 34. Price R. | 57. Truckee R. |
| 12. Deschutes R. | 35. R. Casas Grandes | 58. Verde R. |
| 13. Duchesne R. | 36. R. de Ramos | 59. Virgin R. |
| 14. Fraser R. | 37. R. de San Juan | 60. Walker R. |
| 15. Gila R. | 38. R. Grande | 61. White R., Colo. |
| 16. Grande Ronde R. | 39. R. Mezquital | 62. White R., Neb. and S. D. |
| 17. Green R. | 40. R. Piaxtla | 63. White R., Nev. |
| 18. Harney basin | 41. R. Trujillo | 64. Willamette R. |
| 19. Humboldt R. | 42. R. Yaqui | 65. Wind R. |
| 20. John Day R. | 43. Salmon R. | 66. Wood R. |
| 21. Lahontan basin | 44. Salt R. | 67. Yakima R. |
| 22. Little Colorado R. | 45. San Jose R. | 68. Yampa R. |
| 23. Malheur R. | 46. San Juan R. | 69. Yellowstone R. |



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It would be improper to fail to acknowledge the efforts of the collectors of the fishes studied here. These contributors are comprised primarily of Carl L. Hubbs, his family, his students, and his friends. This study would not have been possible without their efforts.

METHODS AND MATERIALS.—The methodology employed in this study is basically the traditional systematic procedure of measuring characteristics of samples of populations, inferring the characteristics of natural populations, and interpreting the distribution of characters and character complexes in terms of biological units or phyletic lines. In the present case the apparent phyletic lines, based on the distribution of morphological characters and inferred breeding data, are not always satisfactorily expressible in terms of the taxonomic units—species and subspecies—of the accepted classification system. Though the conventional nomenclature is used, a tendency evolved

to think in terms of populations which may or may not belong to species, as rigidly defined. Populations are designated by geography.

The characters employed were chosen in a preliminary search for morphological attributes which seemed to vary significantly between populations. The preliminary survey was, of course, inadequate, and non-discriminative characters were measured while certain useful characters undoubtedly have yet to be discovered. In that sense, this paper represents a preliminary survey. All characters are not given equal treatment; sample size often varies for different characters. Economy of measurement and importance to the problem were influencing factors. Some characters, such as scale counts, are less reliable when taken from very young fishes, and are accordingly omitted where suspect. Certain characters show allometry, and some samples were chosen and graded by size in order to provide an estimate of the kind and degree of limitations on comparisons of samples of specimens of different sizes. Bias due to discrepancies in sample size within pooled samples, or allometric effects between samples, are considered. Osteological characters were examined on dry skeletons prepared with the help of dermestid beetles, or cleared and stained specimens prepared by the method of Hollister (1934). Vertebrae were counted from radiographs (Miller, 1957), and the number given is exclusive of the Weberian apparatus (which comprises 4 vertebrae).

The number of specimens at hand determined the sample size for areas represented by inadequate collections. Samples of 25 to 30 adult individuals were arbitrarily chosen from areas of uniform populations represented by abundant material. Data were collected from specimens from 558 samples which were subsequently consolidated into 200 morphological-geographical groups on the basis of homogeneity. The limits of sample pooling were decided after consideration of both geography and character uniformity, and were hopefully intended to approximate Mendelian populations. After statistical analysis (Smith, G. R., "Distribution and evolution of the North American fishes of the subgenus *Pantosteus*," 359 pp. Univ. Mich. Ph.D. Thesis, 1965) the data were again consolidated into 25 population groups, the ranges and means of which are summarized here (Table 1).

Counts and measurements follow the procedures given by Hubbs and Lagler (1958:19-26), except for certain modifications which are indicated in the discussions of individual characters. Statistical calculations of the mean, standard deviation, standard error, and 95 per cent confidence intervals were conducted according to standard procedures as outlined in Simpson, Roe, and Lewontin (1960). Graphical presentation (Figs. 7, 8) follows the revised method of Hubbs and Hubbs (1953), except that the standard error of the mean is converted to 95 per cent confidence intervals by means of "Students' T" table (Simpson *et al.*, *ibid.*). The danger of admitting unreal differences between

populations was minimized by searching for trends in groups of samples and by recognizing deviations in several characters as indications of genetic differentiation.

ANALYSIS OF CHARACTERS

OSTEOLOGY

Osteological differences are well developed at the subgeneric level and provide useful characters for distinguishing between *Pantosteus* and *Catostomus* (*s.s.*). Interspecific and population differences exist in the bone morphology, but are not particularly useful because at about this level the diversity is diminished to a point where statistical analysis becomes necessary. The usual method of preservation of fish specimens, the problem of obtaining series of skeletons, and the statistical difficulties due to the lack of definitive size in fishes, tend to prohibit the use of osteological characters in interpopulation geographical studies, although the variation in the characters is no less meaningful than in the commonly used external features. The use of radiographs offers a partial solution to the problem; however, mensurative difficulties here restrict the methods to subjective evaluation of bone shape and enumeration (see vertebral number, treated here as a meristic character).

THE OSTEOCRANIUM (Fig. 3).—The configuration of the skull of *Pantosteus* is similar to that of other species of *Catostomus* with three primary excep-

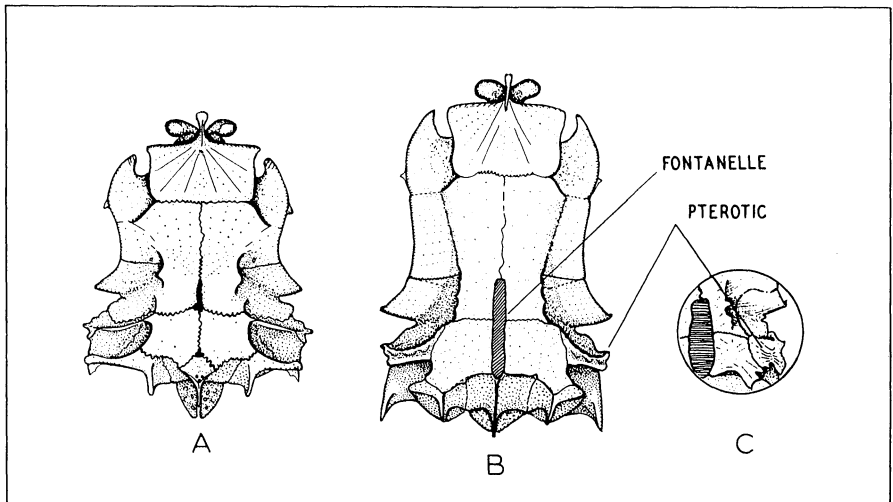


FIG. 3. Dorsal view of neurocrania of A, *Catostomus* (*Pantosteus*) *clarki* ($\times 2$); B, *Catostomus* (*Pantosteus*) *columbianus* ($\times 4$); C, *Catostomus* (*Catostomus*) *commersoni* (Lacépède) (part, actual size), showing relative width of frontoparietal fontanelle and shape of dorsal part of the pterotic bone (the latter is reduced to a thin, transverse ridge in *C. clarki*).

tions. First, as viewed in the dorsal aspect, the skull is broad and relatively short, reflecting the short, flat, broad head which is distinctive of *Pantosteus*. Second, the frontoparietal fontanelle is closed or reduced to a narrow slit in *Pantosteus*, and is broadly open in all other species of *Catostomus* except *C. rimiculus*, and all other suckers except *Cycleptus elongatus* and certain species of *Moxostoma* (*Thoburnia*). The restriction of the fontanelle was the major generic character in the early taxonomic history of the group, as well as being the basis for the generic name *Pantosteus* (=“whole-bone”), and has otherwise been a useful character in the study of suckers (Hubbs, Hubbs, and Johnson, 1943:53, fig. 6; Bailey, 1959:2, fig. 2; Miller, 1952:15, figs. 14, 15). The fontanelle exists by means of the separation by connective tissue of the median edges of the posterior part of the frontals and of the parietals. Restriction takes place by the replacement of the connective tissue by growth of the frontal and parietal bones. The obliteration is usually complete and the bones united by suture in adults of *C. santaanae*, *plebeius*, *discobolus*, and *clarki*, though the latter often retains a small opening between the frontals at the anterior end of the closure. In *C. platyrhynchus* the fontanelle is usually represented by a narrow slit. In *C. columbianus* the fontanelle is well developed, being intermediate between the restricted condition in most species of *Pantosteus* and the open condition in most other species of *Catostomus*. Individual and interpopulation variation is greatest in *C. platyrhynchus*.

The third important feature involves the relationship between the pterotic and two opercular muscles, the dilator operculi and adductor operculi. The species of *Pantosteus* are unique among the members of the Catostomini (*Catostomus*, *Chasmistes*, *Deltistes*, and *Xyrauchen*) in that the dorsal part of the pterotic is usually represented by a simple, transverse, vertical ridge separating the dilator operculi and the adductor operculi. In the remainder of the tribe the dorsal part of the pterotic is a more or less rectangular, horizontal roofing bone that broadly separates and partly overlies the origins of the two muscles. *Pantosteus columbianus* is intermediate in that the transverse ridge is narrow (Fig. 3B).

The dorsal aspect of the pterotic in *Pantosteus* is similar to that in *Hypentelium*, *Lagochila*, and probably all of the species of *Moxostoma* except *M. anisurum* and *M. collapsum*, and is, in turn, somewhat suggestive of the form found in the primitive ictiobine suckers—*Carpiodes*, *Ictiobus*, *Myxocyprinus*, and the aberrant *Cycleptus*. Other characters suggest that *Pantosteus* is a specialized derivative from a *Catostomus*-like ancestor and therefore gained this characteristic secondarily.

The phylogeny of the character is thus viewed as having had its origin in a form similar to *Carpiodes*, in which the pterotic is a simple skull-roofing bone, scarcely involved in the origin of the dilator operculi anteriorly, but

forming the anterodorsal edge of the posttemporal fossa and, consequently, an anterodorsal surface for the origin of the adductor operculi. A modification of this pattern probably consisted of the development of an anterodorsal transverse ridge on the pterotic to provide an increased area of attachment of the origin of the dilator operculi. Illustration of this stage may be seen in *Ictiobus cyprinellus* and (possibly secondarily) in the subgenus *Scartomyzon* of *Moxostoma*. From this stage the elaboration of the pterotic could develop in two directions. The form in most catostomines involves the simple increase in anterior extent and strength of the anterodorsal ridge (Fig. 3C). The condition in which the pterotic is represented dorsally by a single ridge (Fig. 3A) could be achieved from the previous form by the expansion of the field of origin for the two muscles involved and the concomitant reduction in the dorsal part of the pterotic to a single ridge with muscle origins on both sides.

Although the function of the fontanelle is not known it is possible that its closure in the small riffle forms (subgenera *Pantosteus* and *Thoburnia*) is correlated with the relative expansion of the opercular muscles and the reduction in the size of the pterotic. The adductor operculi, especially, is more extensive, originating in part on the dorsal surface of the parietal in certain species of *Pantosteus*—those which show the most complete closure of the fontanelle.

OROMANDIBULAR REGION.—The most striking adaptations in the evolution of *Pantosteus* have been trophic-oriented, and the most distinct osteological features are found in the jaw bones. The dentaries of all species of *Pantosteus* are distinct from those of other *Catostomus* in the sharp ventral deflection of the gnathic ramus (Figs. 4, 5). This feature, along with others, seems to be correlated with the adaptation of the jaws as scrapers of the substrate. The jawbones are also more robust, reflecting increased musculature and probably selective pressure for increased strength of the entire oromandibular mechanism. *C. plebeius*, and to a lesser extent *C. columbianus*, are the most *Catostomus*-like species of the subgenus, whereas *C. discobolus* and *C. clarki* are the most specialized.

The maxillae of *Pantosteus* are specialized in the same direction as the dentaries. The bone is robust and the points of insertion of the major muscles and ligaments are enlarged and strengthened. This is reflected in the enlargement of the anterodorsal facet for the insertion of the palatamaxillary ligament, and in the ventral process of the maxillary ramus, which possesses a strong ridge and is distinctly attenuate posteriorly. The ridge serves as the point of insertion for the maxillaris dorsalis muscle. The posteroventral end of the maxilla is thickened and bifurcate; anteroventrally it serves as the point of attachment of the rictal cartilage of the upper jaw. The antero-medial maxillary process is nearly perpendicular to the plane of the maxilla,

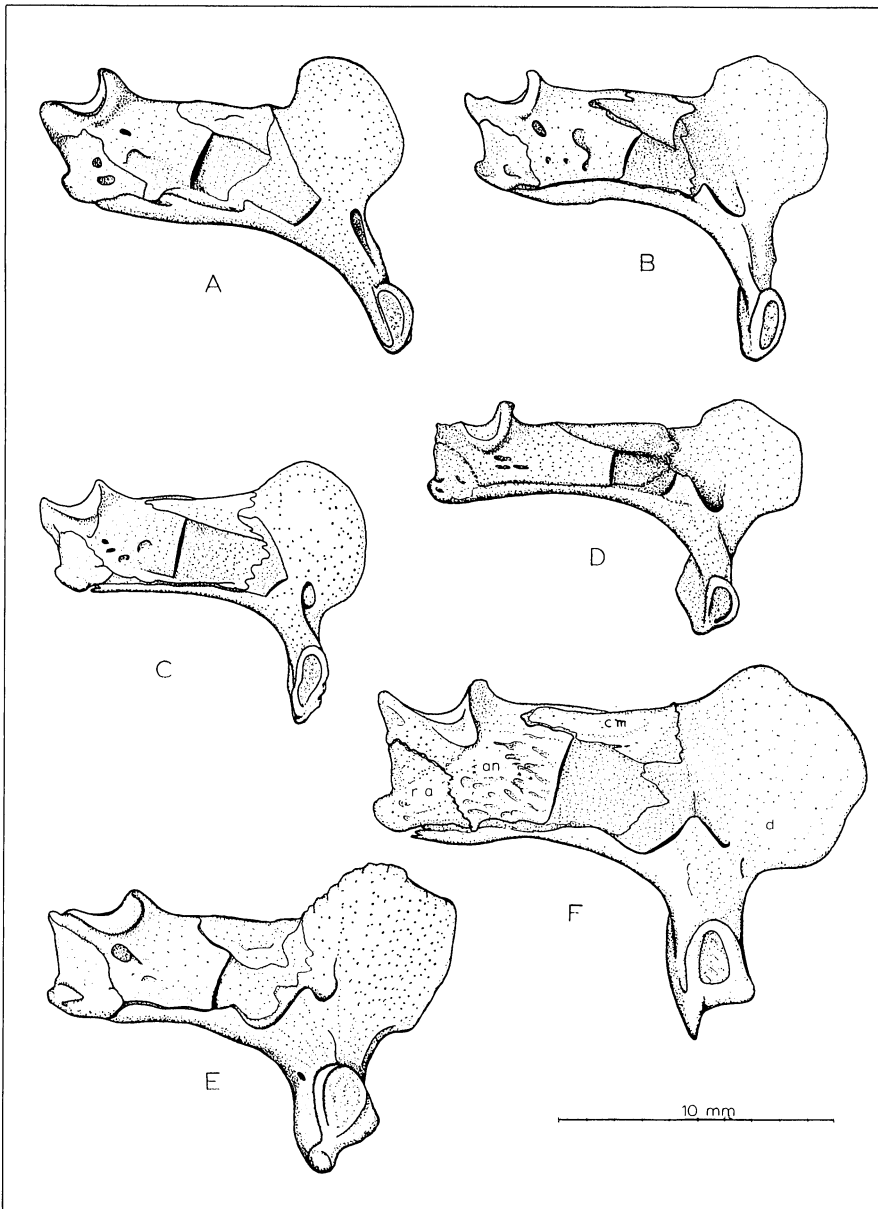


FIG. 4. Mesial view of left mandibles of A, *Catostomus (Catostomus) tahoensis* (Lahontan basin); B, *C. (Pantosteus) plebeius* (Rio Grande drainage); C, *C. (Pantosteus) columbianus* (Columbia River drainage); D, *C. (Pantosteus) platyrhynchus* (Bonneville drainage); E, *C. (Pantosteus) clarki* (Virgin River drainage); F, *C. (Pantosteus) discobolus* (Bonneville drainage). The bones of the lower jaw are indicated on F. They are the angular (an) with which the articular is fused (Haines, 1937), coronomeckelian (cm), retroarticular (ra), and dentary (d).

in contrast to the ventral deflection in most catostomines. The interspecific variation in specialization corresponds with that of the dentaries.

The palato-pterygoid series in *Pantosteus* differs from that of other species of *Catostomus* in several associated features. The longitudinal lateral ridge of the palatine is absent or reduced in *Pantosteus* and present in other species of *Catostomus*. The most specialized forms are *C. discobolus* and *C. clarki*; those most like other species of *Catostomus* are *C. columbianus* and *C. plebeius*.

The outstanding feature of the pterygoid complex in *Pantosteus* is the simulation of a right angle by the dorsal and lateral parts of the mesopterygoid (endopterygoid) and the metapterygoid. In addition, both bones have developed a vertical ridge at the vertex of the angle. In *Catostomus* (*s.s.*) the angle formed by the dorsal and lateral aspects of the pterygoids is obtuse and no ridges for muscle attachment are developed.

OPERCULAR SERIES.—The bones of the opercular series of the Catostomidae have been treated in detail by Nelson (1949). The relationship of *Pantosteus* in the tribe Catostomini was supported. However, variation and diagnostic differences remain to be discussed. *Pantosteus* is distinctive within the tribe in the rather quadrate form and tendency toward a convex anterior margin of the opercle, and in the short, rather deep proportions of the interopercle and (especially) the preopercle (Fig. 5). The trends in variation within the genus contrast somewhat with other characters in that *C. plebeius* is among the most extreme or specialized in form. *C. columbianus* is the most *Catostomus*-like (Fig. 5B).

WEBERIAN APPARATUS.—This complex has been the subject of an analytical study within the family Catostomidae (Nelson, 1948, 1955) and an embryological investigation in *C. plebeius* (Butler, 1960). Nelson's study indicates the close relationship of *Pantosteus* and *Catostomus* in the Catostomini. The species of *Catostomus* vary in the patency of the 2-3 intervertebral articulation. *C. catostomus* and *C. microps* have the articulation unfused, and the remainder of the subgenus *Catostomus* examined have the articulation fused. *Pantosteus* also shows variation. Species with the articulation fused are *C. columbianus*, *C. clarki* (except certain Virgin River specimens), and *C. discobolus* (except in the Little Colorado River). The remainder of the species have the 2-3 articulation unfused.

Pantosteus appears to be distinguishable from other *Catostomus* in the degree of divergence of the pleural ribs of the Weberian apparatus. Using the center of the centrum as the apex and the distal tips of the pleural ribs to define the angle, in *Catostomus* (*s.s.*) the angle of divergence varies between 65° and 90°. In *Pantosteus* the angle is between 90° and 110°; *C. columbianus* again is the most *Catostomus*-like representative.

AXIAL AND APPENDICULAR SKELETON.—Examination of the vertebral

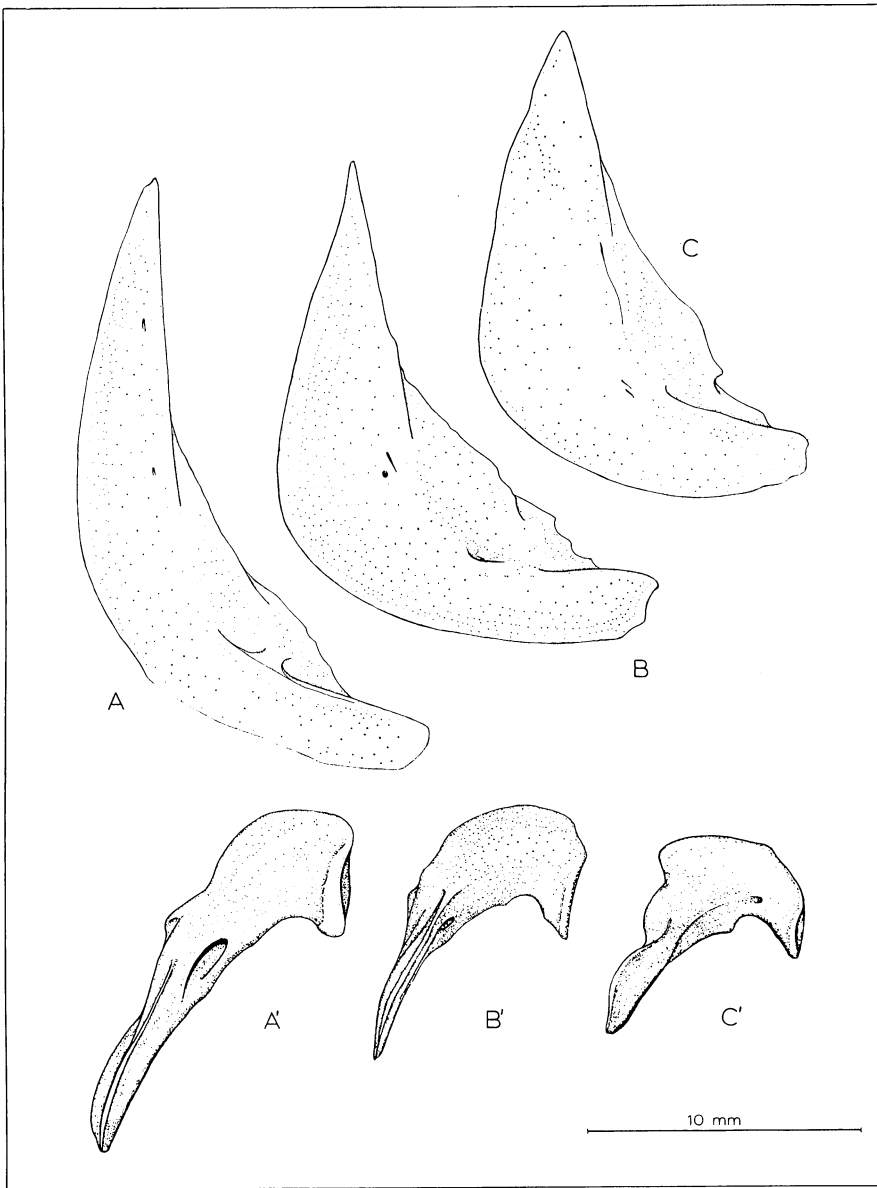


FIG. 5. Mesial view of left preopercles of A, *Catostomus (Catostomus) tahoensis*; B, *C. (Pantosteus) columbianus*; C, *C. (Pantosteus) platyrhynchus*; and anterodorsal view of left dentaries of A', *C. tahoensis*; B', *C. columbianus*; C', *C. platyrhynchus*.

column and the fins reveals no outstanding structural characters except those based on the numbers of elements. The number of vertebrae, dorsal fin rays, and pelvic fin rays are analyzed in the section on meristic characters. The pectoral fin ray number appears to be of limited value. Within the Catostomini the number of anal fin rays is consistently seven with only occasional individual variants. The number of caudal fin rays shows remarkable uniformity, with 18 principal rays as usual in the family Catostomidae, in contrast to the related Cyprinidae, which have 19 principal caudal rays (Gosline, 1961:8).

GENERAL MORPHOLOGY

VISCERAL ANATOMY.—The relative inaccessibility of internal characters limited their use to indicators of general relationship in this study. Features which were examined are size and shape of the swimbladder, pigmentation of the peritoneum, and length of the intestine.

The swimbladder is often reduced in *Pantosteus*, a fact which led Evermann (1893a:52; 1897:172) to use it as a generic character. Normally in the subgenus *Catostomus* it is a two-chambered structure, with the anterior chamber short and bulbous and the posterior chamber longer, several times the length of the anterior, round in cross section, and somewhat larger in diameter than the eye. The anterior chamber is connected to the Weberian apparatus and the posterior chamber occupies the dorsal part of the visceral cavity, extending somewhat posterior to the origin of the pelvic fins. The reduction of the swimbladder in *Pantosteus* may be correlated with adaptation to occupation of riffles and swiftly flowing waters. Under these circumstances the length of the swimbladder may be reduced to 15 per cent of the standard length and the diameter to about equal to that of the pupil of the eye. Specimens from slow-water situations may have swimbladders approaching the proportions described above for other *Catostomus*. There may be wide variation within a single species, for example, between the swift-water and slow-water forms of *C. discobolus*. Occasionally, variation may exist within a single sample.

An elongated intestinal tract, presumably correlated with a more vegetarian diet, is one of the primary characteristics of *Pantosteus*. In *Catostomus* (s.s.) the length of the gut is usually from $1\frac{1}{2}$ to 5 times the standard length of the fish. In adult *Pantosteus* the gut is relatively longer, usually 5 to 8 times the standard length. Ontogenetically, the pattern of the gut begins as a simple sigmoid curve and elongates by means of simultaneous growth and coiling (Kafuku, 1958). Thus, the relative length of the intestine may be measured by the extent of coiling. A simple method derived for use here consists of counting the number of loops of the coil anterior to the anterior section of the liver, which is situated in the double vortex of the coil.

Most species of *Catostomus* have 4 to 6 intestinal loops anterior to the liver. This state seems to be reached early in life, usually when the animal is between 50 and 100 mm in standard length. An exception to the major division is *C. (C.) tahoensis* (Kafuku, 1958, fig. 16), which commonly develops 8 or occasionally 10 anterior loops.

C. (P.) plebeius and *C. (P.) santaanae* usually have 6 or 8 anterior loops, the latter otherwise increasing the gut length by means of an extensive left dorsal loop which may lie partly above the left gonad. *C. (P.) platyrhynchus* usually has 6, 8, or 10 anterior loops, and *C. (P.) discobolus* and *clarki* have between 6 and 16, usually 10. *C. (P.) columbianus* shows some geographic variation in this character. Most populations have between 6 and 14 anterior loops, but *C. columbianus* from the Wood River, Idaho, possesses 6 or 8. In contrast to the ontogenetic pattern in most *Catostomus*, there seems to be continued allometric growth in intestinal length in *Pantosteus* up to a standard length of about 100 mm, after which the relative rate of increase in intestinal length decreases.

The occurrence of the long gut and a black peritoneum in herbivorous fishes appears to be correlated but the reasons are not yet known. Most species in the subgenus *Catostomus* have a dusky or silvery peritoneum, though in *C. catostomus* and *C. warnerensis* it may be dusky or black; in *C. tahoensis* it is usually black. With few exceptions the species of *Pantosteus* have a black peritoneum. *C. (P.) plebeius* is distinct in the absence of the black peritoneum; it exhibits a silvery, dusky, or speckled condition. Specimens of *C. (P.) discobolus* from the Little Colorado River, especially in the headwaters of the Zuni River, possess reduced pigmentation. *C. (P.) columbianus* of the Wood River system may have a black or dusky peritoneum.

LIP AND JAW STRUCTURE.—(Pl. I). As previously mentioned under OSTEOLOGY, *Pantosteus* is most distinct from other *Catostomus* in the modification of the oromandibular apparatus. The gnathic edges of the dentaries are augmented with cartilaginous ridges and a tough epidermal covering. The lower jaw is truncate in the most specialized forms but is rounded in two species, *C. plebeius* and *C. columbianus*. These forms are approached within *Catostomus (s.s.)* by *C. rimiculus* and *C. catostomus*.

The lips of *Pantosteus* are large. The upper is full and pendant with a smooth anterior face and a papillose oral face. The lateral junctures with the lower lip are marked by re-entrant angles. The third major lip notch is in the lower lip, which is shallowly emarginate posteromesially.

C. plebeius and *columbianus* are again most *Catostomus*-like, having smaller lips with the anterior face as well as the oral face of the upper lip tending to be papillose. The median incision of the lower lip is deep, leaving only 2 or 3 rows of papillae anterior to the notch. In *C. columbianus* the lateral notches are often indistinct or absent.

Variations in the size and number of papillae are significant. *C. discobolus* and *C. clarki* have smaller and more numerous papillae than is usual in the other species. In *C. platyrhynchus* an interesting pattern has evolved in which the papillae of the lower lip are large and arranged in a convex arch anteriorly, leaving the anterolateral corners of the lip without papillae. The specimens from the Missouri River drainage commonly appear to be intermediate between *C. platyrhynchus* and *C. discobolus* because of the presence of small papillae in the anterolateral spaces of the lower lip. The convex pattern of *C. platyrhynchus* is occasionally suggested in examples of the other species, especially *C. santaanae*. The usual condition in the remainder of the species is concentricity of the anterior row of papillae and the jaw.

WIDTH OF LOWER JAW.—The width of the cartilaginous sheath of the lower jaw was shown by Hubbs *et al.* (1943) to be useful in separating species of *Pantosteus* from those of other *Catostomus* and for recognizing hybrids between them. Specimens of several species of *Pantosteus* were shown to have wide jaws; the width of the cartilaginous sheath varying from 4.3 to 7.7, usually about 5.5 to 6.5, per cent of the standard length. Specimens of *Catostomus*, excluding *C. catostomus* and *C. syncheilus* (= *columbianus*), have narrower jaws; the width of the cartilaginous sheath being 3.0 to 5.5, usually about 3.5 to 5.0 per cent of the standard length. *C. catostomus*, with a sheath width of 4.1 to 6.2 per cent, and *C. columbianus*, with a width of 3.1 to 5.7 per cent, were shown to be intermediate.

The width of the cartilaginous sheath was measured in a number of population samples within species of *Pantosteus* in the present study. As a character of interspecific worth within the subgenus, its greatest value appears in the characterization of *C. plebeius* and *C. columbianus*. These species possess small, rounded lower jaws; the width never over 6 per cent of the standard length in *plebeius* and probably less than 6 per cent in *columbianus*. One population of *santaanae* ranged from 4.6 to 6.8 per cent with the mean near 5.6. Populations of *C. clarki* vary considerably. Specimens from Nevada possess small jaws similar to those of *santaanae*. In contrast, those of the Gila River drainage are large, with the population mean usually near 7.0 per cent.

The majority of measurements for most of the populations of *platyrhynchus* and *discobolus* are between 6 and 8 per cent, though outstanding exceptions exist. The most notable of these include a small sample of *platyrhynchus* from the Fraser River, British Columbia, in which 8 specimens all have wide jaws, more than 8 per cent of the standard length, and another group of specimens, from the Little Colorado River drainage, which show a gradation from *plebeius*-like jaws upstream to *discobolus*-like jaws downstream (Fig. 18).

Considerable variability exists within and between populations of *platyrhynchus* from some areas, for example, the Missouri River drainage. This may be contrasted with greater homogeneity and almost no significant differences between populations from such areas as the Lahontan basin in Nevada and California. Nothing is known of the adaptive significance or the environmental effects on development of this character.

HEAD SIZE.—As shown by Hubbs *et al.* (1943) and others the relative size of the head in the *Pantosteus* group of species differs on the average from that in most species of *Catostomus*. Most *Catostomus* have large heads, usually longer than one-fourth the standard length. In most species of *Pantosteus* the head is usually smaller than one-fourth the standard length. However, there is overlap between the two groups. Furthermore, the relative head length seems to be readily influenced by size and environmental effects on the condition of the fish, rendering the character somewhat untrustworthy.

WIDTH OF THE ISTHMUS.—The width of the isthmus between the ventral corners of the gill apertures was shown by Hubbs *et al.* (1943) to differ significantly within many sympatric species pairs of *Catostomus* and *Pantosteus*. Species of *Catostomus* are usually characterized by a narrow isthmus. Taken as a proportion of the standard length, a series of small samples of several species of *Catostomus* varies between 3.2 and 8.1 per cent, usually from 4.0 to 7.0 per cent. Similar samples of *Pantosteus* species varied from 5.6 to 13.5 per cent, usually between 8.0 and 11.0 per cent (Hubbs *et al.*, 1943).

In the present study the width of the isthmus was measured in specimens from a number of populations of *Pantosteus* (Table 1). The various recognized species generally show a characteristic though not diagnostic range. *C. columbianus* is distinctly *Catostomus*-like, with the great majority of specimens (included by 1 standard deviation either side of the mean) having the width of the isthmus between 5.5 and 8.2 per cent of the standard length. Specimens of *C. plebeius* usually appeared between 6 and 9 per cent in this character, thus approaching *C. columbianus*.

The most interesting aspect of the variation in this character is the possible correlation between variability and known hybridization. For example, in samples where hybrids between *Catostomus* and *Pantosteus* are unknown the variation in this character is usually low. By contrast, in areas where hybridization is known, populations usually show greater variation. For example, in the samples of *santaanae* from the Santa Clara River variation in this character is $4\frac{1}{2}$ per cent of the standard length ($S = 1.20$), but in other populations of the species the variation is 2 to $3\frac{1}{2}$ per cent and $S=0.59$ to 0.91. This is a population in which most specimens show other characteristics of hybridization (p. 56). Populations of *C. columbianus* from the Grand

Ronde and Palouse rivers also show variation of over 4 per cent with skewness and extremes varying toward the *Catostomus* (lower) range, whereas other populations show a variation of 2 to 3½ per cent of the standard length. These are also localities from which hybrids between these species and related *Catostomus* were obtained. The specimens producing this variation toward *Catostomus* (*s.s.*) were not recognizable as F₁ hybrids. This conclusion was reached after consideration of the character patterns to which putative F₁ hybrids would be expected to conform, according to the criteria provided by the exhaustive treatise of Hubbs *et al.* (1943). Lacking a better explanation for this circumstantial correlation, it is proposed that the evidence suggests at least occasional backcrosses between hybrids and members of the *Pantosteus* population.

PELVIC AXILLARY PROCESS.—Populations of *Pantosteus* vary in the development of the pelvic axillary process. The presence or absence of the character is not easily determined or described in some species. However, where *C. platyrhynchus* overlaps with closely related species the character is of definite taxonomic worth. It has been used by La Rivers (1963) for distinguishing *Pantosteus* from *Catostomus* in Nevada (although not all *Pantosteus* in Nevada possess the process).

The structure, the adaptive significance of which is unknown, consists of a small, fleshy flap of skin in the axil of the pelvic fin, dorsal to the first pelvic rays. In *C. platyrhynchus*, especially adults, the structure is an actual projection with a distinct, free posterior end. In populations of *C. discobolus* and most *columbianus* the process is absent. Intermediate degrees of development may occur in *C. plebeius*, *santaanae*, *clarki*, and some *columbianus* where an axillary fold with no free posterior end may be present.

DEPTH OF CAUDAL PEDUNCLE.—It has been observed many times that fishes with the ability to swim rapidly have slender caudal peduncles as one of the apparent adaptive modifications. Considerable variation in this depth relative to the standard length exists between populations of *Pantosteus*. The character was measured in numerous populations with the hope of relating interpopulation differences to ecological conditions and possible adaptive significance (Table 1; Figs. 9, 16, 19).

Examination of the data of Hubbs *et al.* (1943) reveals that the species of *Pantosteus* (as recognized here) usually have slenderer caudal peduncles than do those of *Catostomus* (*s.s.*) with which they are sympatric. The exceptions to this are in the Virgin River where *C. latipinnis* has a slenderer peduncle than *C. clarki* (*P. d. utahensis* of Hubbs *et al.*) and in the Columbia drainage where *C. macrocheilus* has a slenderer peduncle than *C. columbianus* (= *C. syncheilus*). The habitat of the species of *Pantosteus* usually consists of swifter waters than those occupied by *Catostomus* (*s.s.*).

Within *Pantosteus* some examples of *discobolus* and a population of

clarki show outstanding reduction in the depth of the caudal peduncle. Here, the presence of a slender peduncle is associated with the torrential habitat of the Green and Colorado rivers (Fig. 19). The areas with populations showing slender peduncles—the Hideout Canyon-Flaming Gorge Dam area on the Green River, parts of the Colorado River above the Green River confluence, the San Juan River in Utah and New Mexico, the Grand Canyon of the Colorado, and the Virgin River “Narrows” in Utah and Arizona, are all areas known for torrential rapids or swift waters of moderate volume. Examination of U. S. Geological Survey maps shows that these areas contain long stretches of river with an average drop in elevation of 10 to 30 feet or more per mile. This much gradient under normal river volumes of several thousand, up to 25,000, cubic feet per second creates a habitat of moving water that must make considerable selective demands on the adaptation of the inhabitants. Strong swimming ability must be at a premium in such an environment. The hydrodynamic advantages inherent in the extreme fusiform shape with a slender caudal peduncle and large fins undoubtedly have significant survival value.

By contrast, the headwaters in the Colorado River system may be characterized by equal or greater gradient; but the much smaller volumes and the mountain stream habitat, with alternating pools and riffles, offers a moderation of the current not found in the larger rivers. Hence, the populations of *discobolus* which inhabit these areas show less extreme development of the “fast-water” morphotype.

An interesting possible relationship between the center of selective pressure for the fast-water ecotype and gene flow between adjacent areas of unlike habitat is suggested by a situation in the Virgin River drainage in Arizona. The fishes in the Virgin River near the mouth of Beaver Dam Creek inhabit swift water with an estimated current of around 6 feet per second. They possess slender caudal peduncles unique for the species *clarki*. Specimens taken from the small, quiet stream at the mouth of Beaver Dam Wash show greater similarity to the adjacent, highly specialized Virgin River population than to populations at the head of Beaver Dam Creek. This is probably a result of genetic exchange between the adjacent populations which are not actually separated except by habitat. The resulting characters may not be ultimately adaptive in lower Beaver Dam Creek. Repopulation of the smaller stream following flood or desiccation might be the source of the traits otherwise characteristic of fishes from the Virgin River (Fig. 16).

Populations of *C. discobolus* from the Snake River and rivers of the Bonneville drainage, and *C. columbianus* from the Columbia River drainage, possess slenderer caudal peduncles than any *Pantosteus* populations except the extremes already mentioned. With few exceptions the mean depths of the caudal peduncles in these populations fall between 8 and 9 per cent of

the standard length. *C. columbianus* encounters habitats similar to those occupied by *C. discobolus* in the Colorado River. It may be significant that the specimens of *C. columbianus* with the slenderest caudal peduncles inhabit the Salmon River, known for its swift waters and rapids.

C. platyrhynchus populations from the Colorado River drainage are largely restricted to headwater situations and possess caudal peduncles hardly slenderer than those from other drainages. However, specimens from Bitter Creek, Wyoming, have slenderer caudal peduncles and other characters which probably indicate introgressive hybridization with *C. discobolus*.

The remainder of the populations are comprised of fishes with depths of the caudal peduncle usually between 8 and 10, most often 9 to 10 per cent of the standard length. Uniformity is the rule, with isolated instances of variation probably occurring in response to isolated local conditions, especially in *C. santaanae* and *C. plebeius*, and *C. clarki* of the White River drainage and Meadow Valley Wash.

CAUDAL FIN PIGMENT.—In suckers related to the genus *Catostomus* the caudal fin is usually rather uniformly pigmented (Fig. 9). Among some species of the subgenus *Pantosteus*, however, there is a tendency for the interradial membranes to be sparsely pigmented or immaculate. *C. clarki*, *C. discobolus*, and *C. columbianus* have fully pigmented caudal fins with the interradial membranes as densely pigmented as the rays. In *C. santaanae* and *C. plebeius* the interradial membranes tend to be less pigmented than the caudal rays. Often there is an unpigmented, longitudinal strip in the center of the membrane.

Specimens of *C. platyrhynchus* tend to have a sharp demarcation between the heavily pigmented caudal rays and unpigmented interradial membranes. This demarcation is quite complete in populations from the Great Basin. However, populations from the Columbia, Missouri, and occasionally the Colorado river drainages may show varying degrees of sparse pigmentation on the interradial membranes. In the Colorado River drainage this sparse pigmentation occurs irregularly and often takes on peculiar configurations which may be suggestive of introgressive hybridization with *C. discobolus* (pp. 93–107; Fig. 22). In the Missouri River drainage the interradial pigmentation is usually sparse and occasionally absent. In a few specimens from populations of the Columbia drainage it may appear dense enough to be difficult to distinguish from the condition in *C. columbianus*.

Individuals shorter than 30 mm in standard length rarely have pigmented interradial membranes. However, a related pigment character is present which differentiates small specimens of *platyrhynchus* from those of *discobolus* and *columbianus*. In *platyrhynchus* the ventral edge of the lower principal caudal ray has no pigment, whereas *discobolus* and *columbianus* have the lower and upper edges of the caudal fin distinctly and about equally

TABLE 1
COMPARISON OF CHARACTERS IN POPULATIONS OF THE SUBGENUS *Pantostomus**

	Number of vertebrae	Predorsal scales	Dorsal rays	Lateral-line scales	Caudal peduncle depth	Isthmus width	Gill rakers, ext. int.
<i>Catostomus santaanae</i>							
	38-42 (39.4-40.3)	27-41 (31.7-34.7)	9-11 (9.9-10.2)	67-86 (72.8- 77.6)	8.3-11.1 (9.0-10.2)	5.4-11.0 (7.7- 9.4)	21-28 27-36
<i>Catostomus plebeius</i>							
Rio Grande	38-41 (39.4-39.6)	40-52 (44.8-46.0)	8-10 (9.0- 9.3)	75-94 (81.1- 87.0)	8.4-10.5 (9.1- 9.6)	4.9- 9.5 (6.7- 7.7)	20-24 27-32
Mimbres and Mexico	38-42 (39.1-40.2)	32-55 (37.6-49.1)	8-10 (8.8- 9.5)	70-103 (77.0- 94.8)	7.1-10.6 (8.8- 9.7)	5.4- 9.8 (6.9- 8.3)	20-27 26-37
<i>Catostomus platyhynchus</i>							
Missouri R.	40-44 (41.3-42.7)	40-60 (47.3-53.2)	9-12 (9.9-10.5)	76-96 (80.4- 88.2)	7.7-10.8 (8.3- 9.5)	5.8-11.0 (8.4-10.2)	26-35 35-46
Columbia (lower)	40-44 (41.6-42.1)	41-58 (43.0-51.6)	10-12 (10.0-11.5)	70-91 (77.4- 81.3)	7.2- 9.8 (8.2- 9.1)	7.6-10.8 (8.9-10.1)	29-37 35-51
Upper Snake R.	39-42 (40.2-41.2)	36-48 (42.7-43.6)	9-11 (9.9-10.4)	77-95 (83.1- 85.7)	7.6-10.5 (9.1- 9.9)	7.0-10.5 (8.2- 9.2)	23-31 33-39
Colorado R.	38-43 (40.3-41.4)	41-62 (43.5-50.5)	9-13 (9.8-10.2)	78-106 (86.4- 97.2)	7.5-10.4 (8.9- 9.4)	4.2-11.1 (7.7- 9.6)	24-36 33-41
No. Bonneville	39-43 (40.2-41.1)	36-51 (42.4-44.8)	9-11 (10.0-10.3)	77-91 (81.6- 86.9)	8.4-11.3 (9.0- 9.8)	6.6-10.8 (8.5- 9.4)	24-33 32-42
So. Bonneville	40-43 (40.7-42.0)	37-53 (41.6-46.6)	9-11 (9.9-10.3)	70-99 (77.4- 85.7)	7.4-11.4 (9.0-10.2)	6.0-10.5 (8.6- 9.4)	26-35 31-45
Lahontan	39-43 (40.1-41.1)	38-54 (41.7-47.1)	8-12 (9.8-10.2)	72-100 (77.2- 90.0)	7.4-10.6 (8.4- 9.8)	7.1-11.1 (8.5- 9.8)	25-35 35-46
<i>Catostomus columbianus</i>							
Wood R.	40-43 (41.8-42.3)	51-65 (55.6-56.9)	10-12 (10.7)	93-112 (98.6-102.4)	8.0- 9.7 (8.9- 9.0)	5.4- 7.6 (6.2- 6.4)	24-31 34-41
Palouse R.	39-46 (43.0)	49-75 (59.7)	10-13 (11.2)	89-119 (104.9)	7.7- 9.4 (8.5)	4.2- 8.6 (7.1)	33-39 42-52
Crooked R.	41-45 (42.3)	52-63 (57.5)	10-12 (10.8)	97-107 (101.7)	8.0- 9.1 (8.7)	5.0- 7.3 (6.3)	30-36 41-47
Harney basin	41-44 (42.3-43.0)	43-54 (46.3-50.2)	7-13 (11.3)	77-92 (78.0- 87.8)	8.0-10.0 (8.3- 9.5)	5.1- 8.2 (5.7- 7.2)	34-38 47-48
Lower Columbia	42-46 (43.5-45.3)	50-72 (57.1-63.2)	10-14 (11.4-12.5)	82-121 (98.1-104.6)	6.9- 9.6 (7.6- 8.5)	4.4- 8.6 (6.8- 7.6)	30-42 41-55
<i>Catostomus discobolus</i>							
Bonneville	43-46 (44.3-44.5)	50-62 (56.3-47.0)	10-12 (10.4-11.0)	90-107 (95.8-100.1)	7.6- 9.3 (8.4)	7.8-10.6 (8.8- 9.3)	33-44 46-59
Snake R.	43-46 (43.9-44.7)	45-58 (50.5-54.4)	10-12 (10.6-11.2)	78-97 (86.4- 91.5)	7.9- 9.5 (8.5- 8.8)	7.0-11.5 (8.6- 9.6)	36-37 47-48
Colorado (upper)	41-46 (43.3-44.7)	44-75 (54.2-62.4)	9-12 (10.2-11.0)	83-122 (90.0-105.9)	4.2- 8.9 (5.4- 8.3)	6.5-11.2 (8.0- 9.8)	28-43 37-60
Colorado (middle)	42-46 (42.9-43.7)	47-64 (53.6-54.0)	9-11 (10.0-10.3)	80-98 (86.6- 91.0)	5.0- 8.0 (5.7- 7.2)	7.9-10.9 (9.3- 9.7)	28-35 37-45
Little Colorado R.	39-43 (40.5-41.3)	47-70 (53.8-60.3)	8-12 (9.3-10.2)	84-122 (95.4-106.5)	7.4-10.0 (8.3- 9.1)	6.2-11.2 (8.5- 9.0)	26-38 34-52
<i>Catostomus clarki</i>							
Virgin R.	41-45 (43.0-43.7)	29-52 (32.2-45.7)	9-12 (9.8-10.4)	72-103 (79.5- 95.0)	6.9-10.2 (7.7- 9.3)	7.6-11.3 (8.9-10.0)	27-40 36-51
Meadow Valley	41-44 (42.4-43.2)	29-42 (33.8-35.9)	8-11 (9.9-10.1)	70-93 (79.5- 83.6)	7.9-10.3 (8.7- 9.4)	7.5-11.1 (8.9- 9.9)	29-37 38-50
White R.	43-46 (43.6-44.4)	21-32 (25.2-26.7)	9-11 (9.8-10.1)	63-85 (72.8- 74.8)	7.7- 9.8 (8.5- 9.0)	6.8-11.4 (8.8- 9.5)	31-43 39-51
Bill Williams R.	42-43 (43.2-44.1)	23-36 (27.2-32.6)	9-11 (9.9-10.4)	72-104 (80.4- 92.1)	8.0-10.5 (9.2- 9.5)	7.6-11.4 (9.2- 9.9)	30-39 42-57
Gila R.	42-47 (43.6-45.2)	13-33 (16.6-27.6)	9-12 (9.9-11.0)	61-84 (67.2- 77.6)	7.3-11.2 (8.7-10.0)	6.9-11.8 (8.9-10.5)	28-42 39-59

* The sample ranges and ranges of means of subsamples (in parentheses) are given. See Figures 7 or 8 for size and localities of subsamples. *Italics* indicates sample size of fewer than 30; **bold face** indicates fewer than 10 specimens in the sample.

Counts of gill rakers are based on specimens 70 mm in standard length or over. For statistical treatment of subsamples see the appendix to "Distribution and evolution of North American fishes of the subgenus *Pantostomus*," 359 pp. Ph.D. Dissert., Univ. of Mich., G. R. Smith, 1965.

pigmented. This is a useful character for distinguishing postlarval specimens in areas of sympatry.

Such variation in a pigment character is suggestive of a visual isolating mechanism. It may be significant, therefore, that hybridization between *Pantosteus* and *Catostomus* (*s.s.*) has never been recorded from the eastern Great Basin, where the immaculate caudal interradiial membrane of *platyrhynchus* is best developed and where the sympatric *C. ardens* has a distinctly dark fin pigmentation. However, the imperfect correlation of the character with the distribution of sympatry throughout the range of *Pantosteus* and the lack of evidence for its visibility or association with spawning behavior weaken the hypothesis. It may be an example of a potential isolating mechanism which natural selection could reinforce if the necessary sensory-behavioral responses happened to involve it as a recognition character.

MERISTIC CHARACTERS

NUMBER OF GILL RAKERS.—This is one of the few meristic characters which appears to have direct selective value. The gill rakers serve as food tasters (Iwai, 1964) and strainers and the coarseness or fineness of the straining comb is probably related to food getting, although no such relationship has been actually demonstrated for these fishes.

Catostomids possess four pairs of gill arches, each with two rows of gill rakers, one on the anterior or outside edge of the arch, the other on the posterior or inside edge. The rakers extend toward the sensitive, fleshy pad comprising the dorsal part of the pharynx. In *Pantosteus* the gill rakers are shorter and generally more numerous than in *Catostomus* (*s.s.*). This is probably correlated with the primary dependence of *Pantosteus* upon periphyton for food.

In this study the number of gill rakers on both the anterior (or external) and posterior (or internal) rows of the first arch were counted (Table 1). The number on the posterior row is greater, but the two values are correlated on an individual as well as population level. Both were counted in order to increase the analytical power of the character. A factor which must be considered in taxonomic use of the character is that the number may be correlated with the size of the fish. Figure 6 illustrates the increase in the number of gill rakers with size in several populations of two species.

Pantosteus may be grossly divided into species with numerous gill rakers and species with fewer gill rakers. The first category includes *discobolus*, *clarki*, and most of *columbianus*. Species with fewer gill rakers are *plebeius*, *santaanae*, *platyrhynchus*, and *columbianus* from the Wood River drainage of Idaho. The differentiation within *columbianus* is marked, allowing nearly 100 per cent identification of individuals of the Wood River populations. Within *platyrhynchus* there is also a slight difference between populations

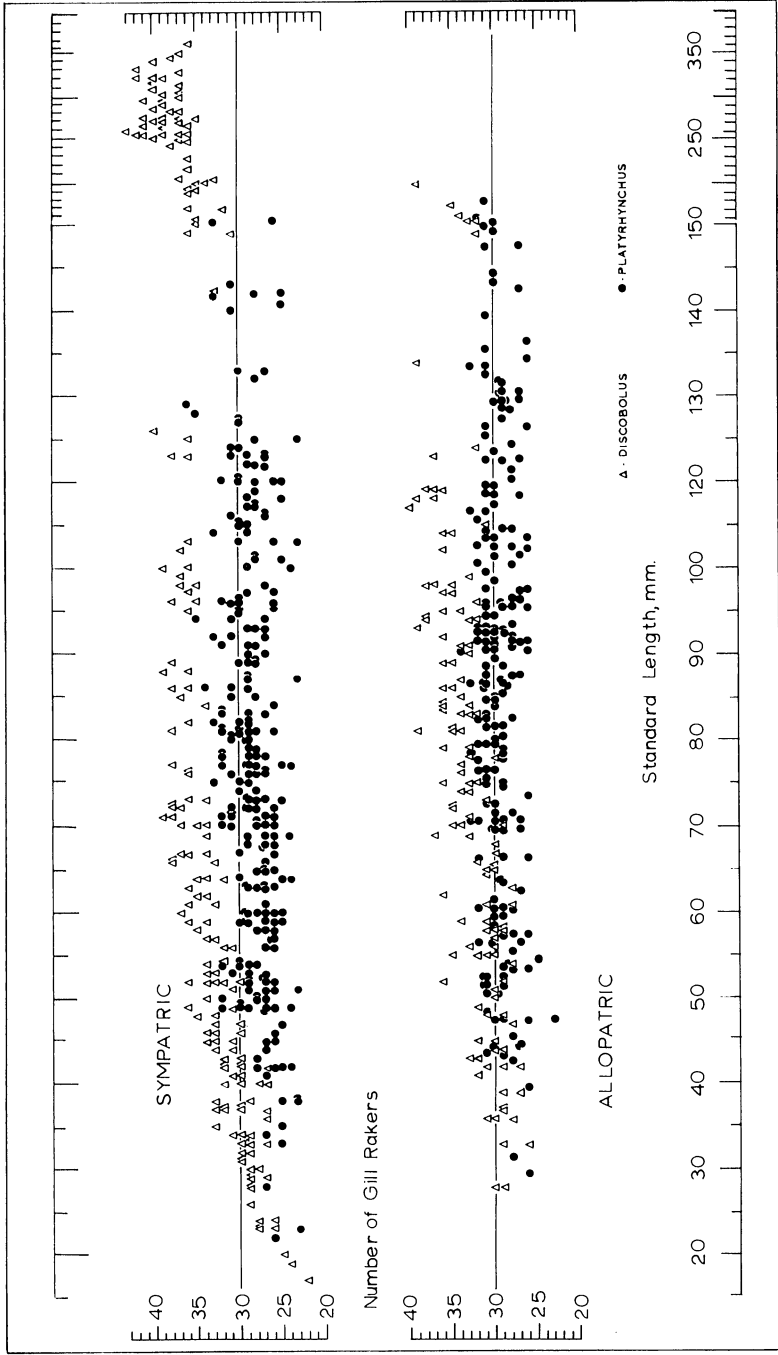


FIG. 6. The number of gill rakers in the external row on the first arch as related to the size of the fish. The graph compares *C. platyrhynchus* (round symbols) with *C. discobolus* (triangles) from the Green and upper Snake river drainages where the two species are sympatric (upper graph) and the same two species from allopatric populations in the middle Colorado and San Juan drainages and the Sevier River drainage (lower graph). It appears that overlap is reduced between the sympatric populations. (See text, p. 28. Compare Fig. 22).

from the Great Basin, which have few gill rakers, and those of the Missouri and Columbia river drainages which average somewhat more.

The differences between sympatric and allopatric populations of species with high and low numbers of gill rakers suggest selective effects of competition. Figure 6 illustrates the occurrence of different levels of separation between *C. platyrhynchus* and *C. discobolus* in different localities. It would appear that this is the result of the operation of selection favoring nonoverlap in competition-related trophic structures, and that the equilibrium attained is a function of local conditions somewhat independent of the norm for the species as a whole. It appears that the maximum number of gill rakers is reached earlier in life in populations of *C. discobolus* that are sympatric with *C. platyrhynchus*. The slope of the regression of number of gill rakers on size in the sympatric sample of *C. discobolus* is 0.196 ± 0.025 for individuals 70 mm and shorter in standard length. The corresponding slope of the regression in the allopatric sample is 0.081 ± 0.047 . In general, the number of gill rakers in sympatric populations of *C. platyrhynchus* is lower than that in the allopatric populations. The relationship of this phenomenon to the food habits of the populations involved has not been studied. No sympatry exists between species of *Pantosteus* which have similar numbers of gill rakers.

POST-WEBERIAN VERTEBRAE.—The Weberian apparatus in the Catostomidae invariably consists of four vertebrae. Some authors have expressed total vertebral counts as the number counted plus some number for the Weberian apparatus, but nothing has been gained by this except, occasionally, confusion. The post-Weberian number expressed here is that actually counted and includes the elements within which variation occurs. The first vertebra posterior to the Weberian apparatus is usually the first one bearing a normal pair of ribs and is readily determined on properly executed radiographs. The counts given in Figure 7 and Table 1 were taken from dry skeletons and radiographs. The centrum to which the uroneural is fused and to which the hypurals attach is counted as the terminal vertebra.

The range of normal variation in the number of post-Weberian vertebrae in *Pantosteus* appears to be from 38 to 47. Within a single population the variation usually encompasses three or four elements. On the basis of this character the subgenus may be divided into two divisions which correspond to the two possible divisions based on caudal pigment and number of gill rakers. *C. santaanae*, *C. plebeius*, and *C. platyrhynchus* have fewer vertebrae, usually 39 to 43. *C. clarki*, and most *C. discobolus* and *C. columbianus* have more vertebrae, usually 43 to 45. *C. discobolus* in the Little Colorado River drainage usually has from 40 to 42. *C. columbianus* shows extreme variation. Specimens from the Wood River system form a group with 40 to 43, and a mode of 42. Low counts for this species also occur in the Harney basin and

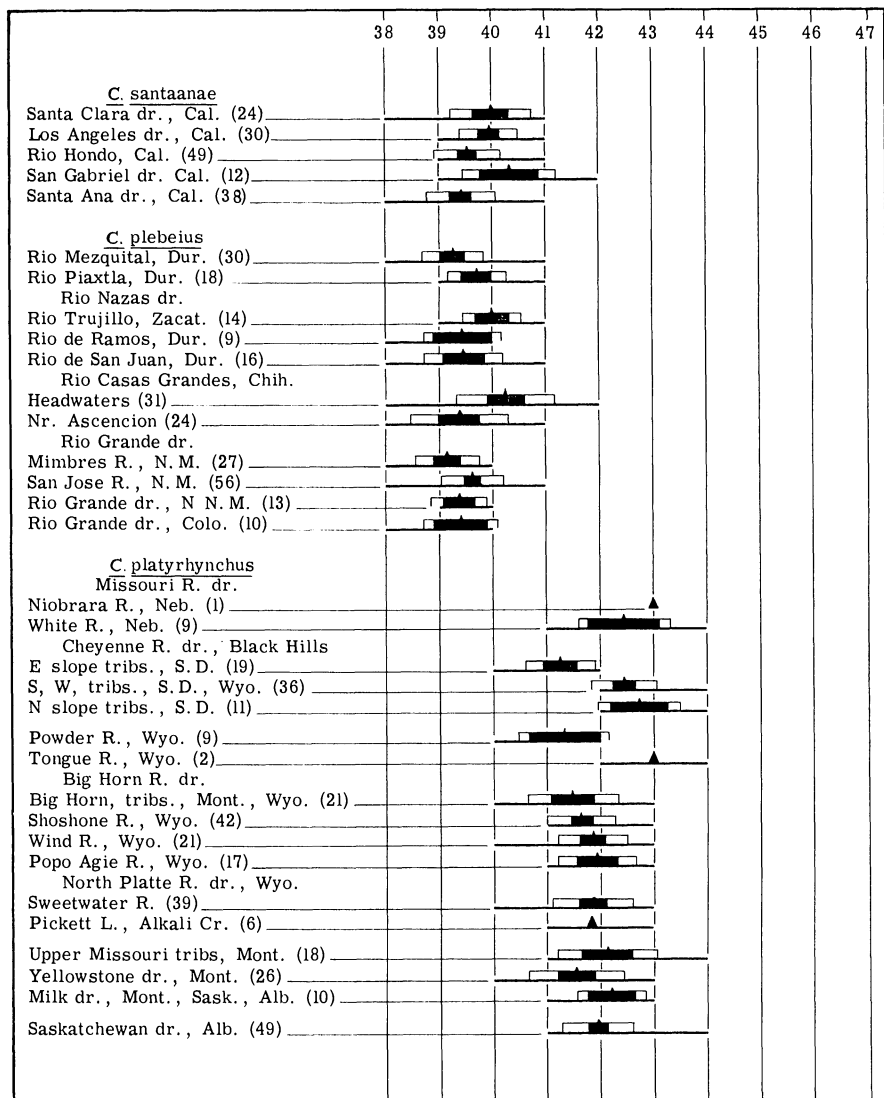


FIG. 7. Variation in the number of post-Weberian vertebrae in the subgenus *Pantosteus*. The diagrams indicate the mean (center point), 95 per cent confidence limits of the mean (black rectangle), one standard deviation on either side of the mean (outer limits of open rectangle), and sample range (basal line). The sample size is given in parentheses following the sample locality. The sequence of the populations is based on relationship between species and geographic propinquity between and within drainage basins, where possible. Exact localities are plotted on maps with each species account. An index to names and locations of some of the rivers and streams is given in Fig. 2.

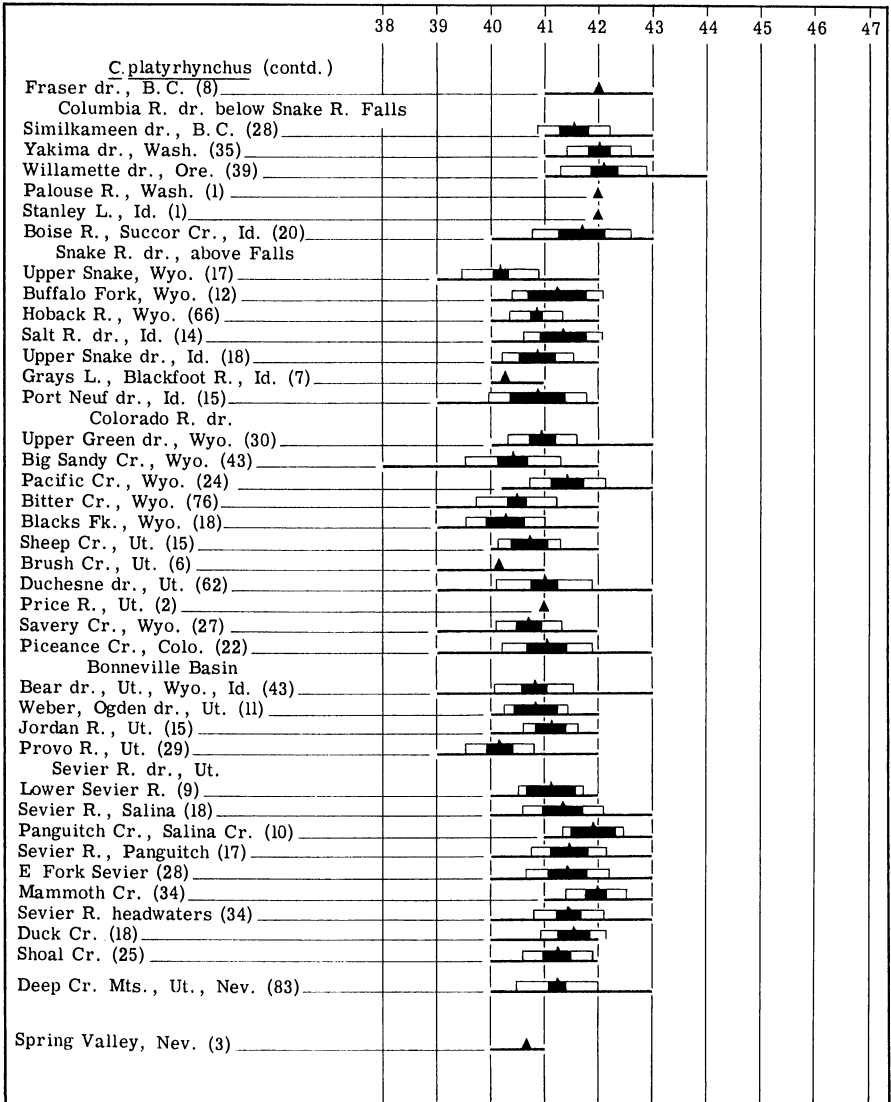


FIG. 7 (continued)

the adjacent upper Deschutes River drainage, Oregon. The Palouse River, Washington and Idaho, contains specimens of *columbianus* with the unusually great range of 39 to 46. This extreme variation and the occurrence of other unusual character distributions suggests introgressive hybrid influence in this population.

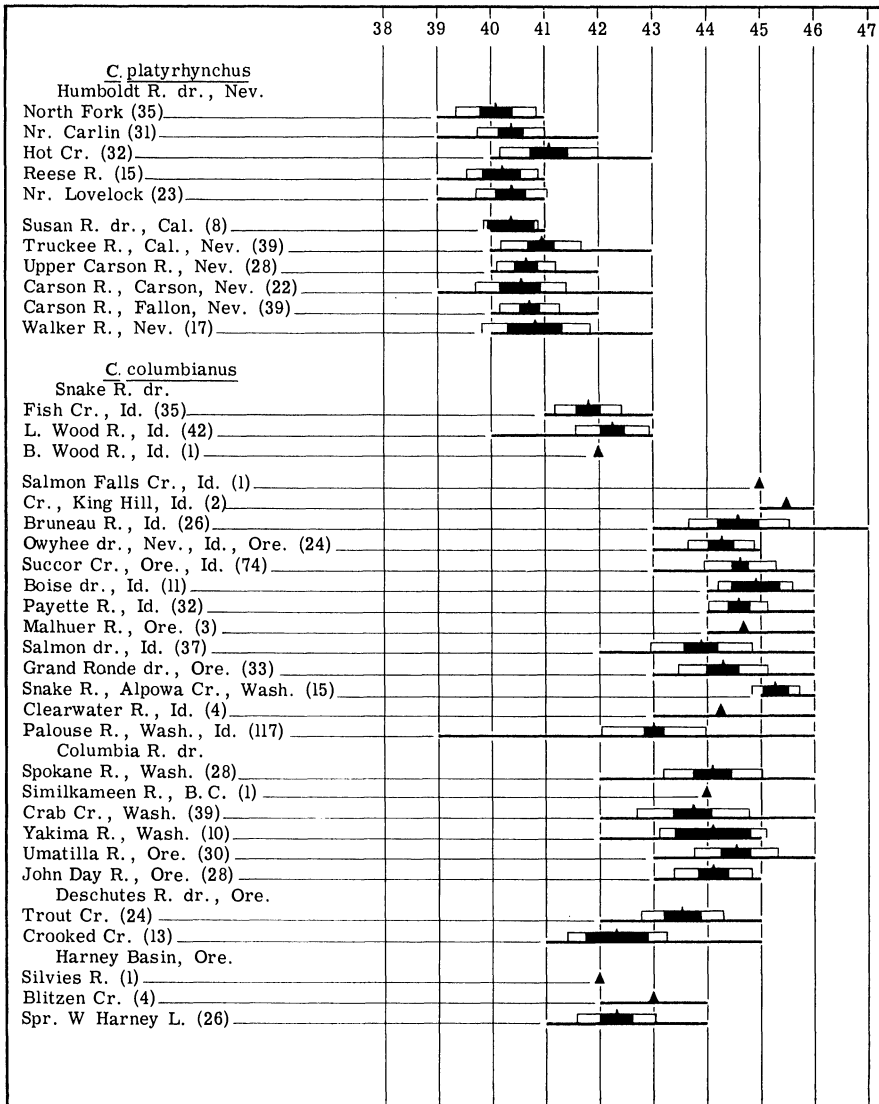


FIG. 7 (continued)

The modal vertebral number in *C. santaanae* and *C. plebeius* is usually 40 and occasionally 39. The usual variation extends from 39 to 41, rarely 42; the lowest values in *Catostomus*. It may be significant that these species are also made up of the smallest individuals in the genus, only occasionally attaining standard lengths over 130 mm.

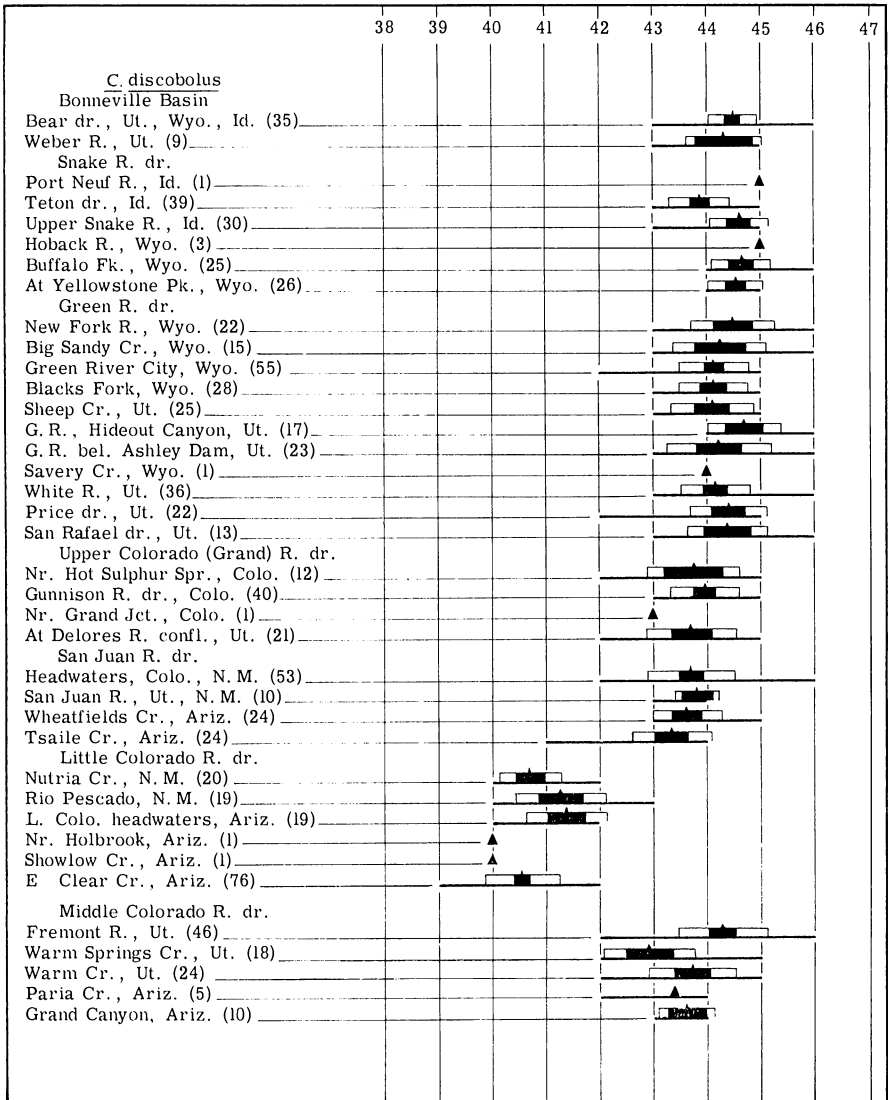


FIG. 7 (continued)

C. platyrhynchus contains the next larger individuals and has the next higher average number of vertebrae. The species may be divided into two groups on the basis of vertebral numbers. Populations from the Missouri, Lower Snake, and Columbia river drainages form a group with the mode usually 42. The populations from the northern Great Basin, Upper Snake

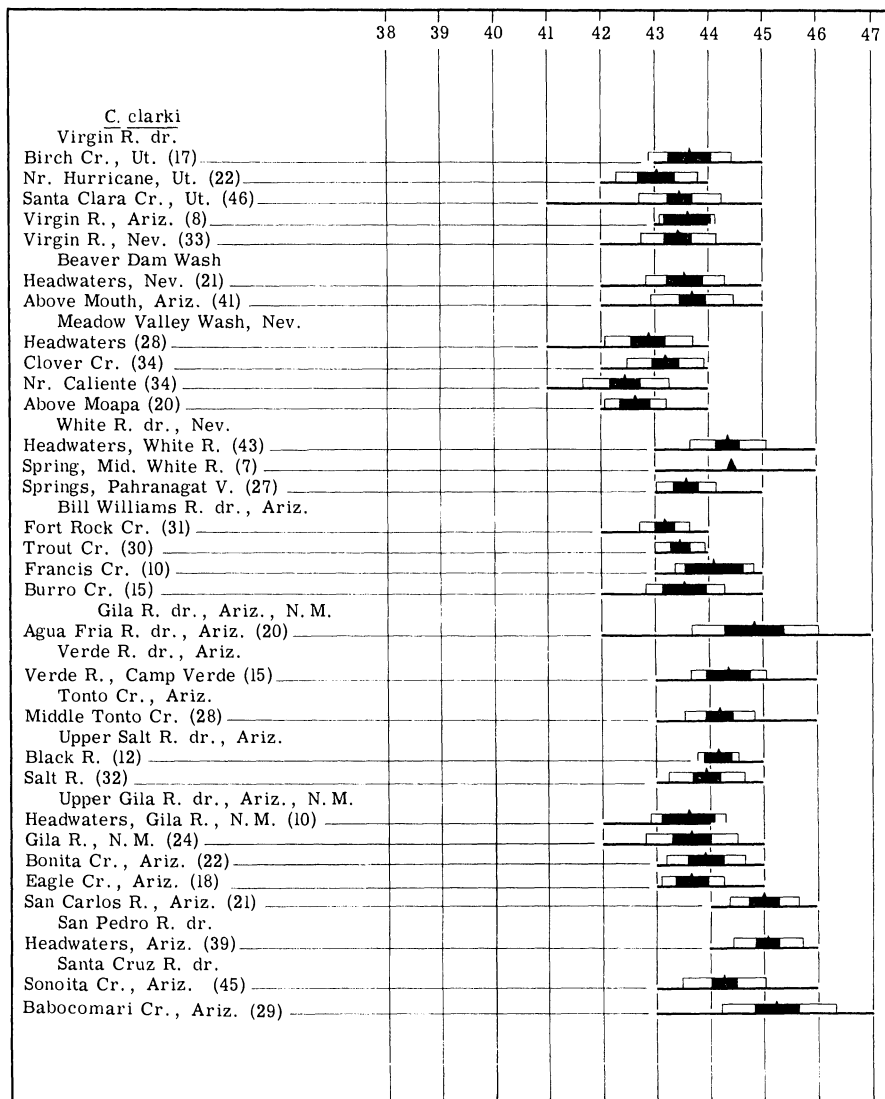


FIG. 7 (continued)

River, and Colorado River usually have modes of 40 or 41. The populations from the Sevier River drainage of the southern Bonneville basin are exceptional, having modes of 41 and 42, similar to those of the Missouri and Columbia river populations.

Populations of *C. discobolus* have modes of 43 to 45, usually 44 vertebrae

except in the Little Colorado River where the mode is 41. The latter situation may be explained by isolation from other populations of *discobolus* and introgression from *C. plebeius* (pp. 86-90, 110).

Specimens of *C. clarki* possess from 41 to 47 vertebrae. Population modes are usually 43 to 45, though specimens from Meadow Valley Wash, Nevada, tend to have fewer, modally 42 or 43.

PREDORSAL SCALES.—(Fig. 8; Table 1). The number of scale rows from the dorsal origin to the occiput, counted slightly to the left of the middorsal line, proved to be a morphological feature with moderate intrapopulation variation and great interpopulation variation. The subgenus *Pantosteus* as a whole displays a range of variation from 13 to 75 predorsal scales. The trends in variation in this character seem to be correlated with temperature through latitude and altitude.

C. santaanae, *C. plebeius*, and *C. platyrhynchus* are characterized by a moderate predorsal scale size. *C. santaanae* from coastal streams in the vicinity of Los Angeles, California, has the fewest predorsal scales in this group. The range of variation in 353 specimens is 27 to 41, the means for the five populations are between 31 and 35. The localities are at about 34° North Latitude and from elevations of 800 to 2,000 feet.

Populations of *C. plebeius* are found in Mexico, New Mexico, and Colorado from 24° to 38° North Latitude and from elevations of 4500 to 8000 feet. Specimens from the Rio Mezquital, a Pacific drainage stream, possess the fewest predorsal scales, 32 to 45, with a mean of about 37. The few specimens from the Rio Piaxtla appear to be in about the same range, and the single specimen seen from the Rio Yaqui has 41 predorsal scales. The last two localities are also in the Pacific drainage. In the eastern drainage streams the range usually is from 40 to 55 with means usually between 44 and 49. The known exception is the sample from the Rio de San Juan, Durango, which has a range of 38 to 47 and a mean of about 42.

C. platyrhynchus, with populations directly north of the previous two species, ranges from 37° to 53° North Latitude and from less than 200 feet to over 8000 feet in elevation. *C. platyrhynchus* may be divided into a generally southern (except the upper Snake River populations) group with large scales and a generally northern (except the Green River populations) group with slightly smaller scales. Populations of the Great Basin and the faunistically related Upper Snake drainage comprise the former group with a range of 36 to 54 and sample means usually between 40 and 47. These populations occupy elevations between 4000 and 8000 feet. The populations of the Lower Snake, Columbia, Colorado, and Missouri rivers, and associated drainages, have slightly smaller scales, the range being 40 to 62, and the sample means falling between 45 and 55. The populations of *platyrhynchus* from the Colorado River drainage show affinities with the Missouri River populations in

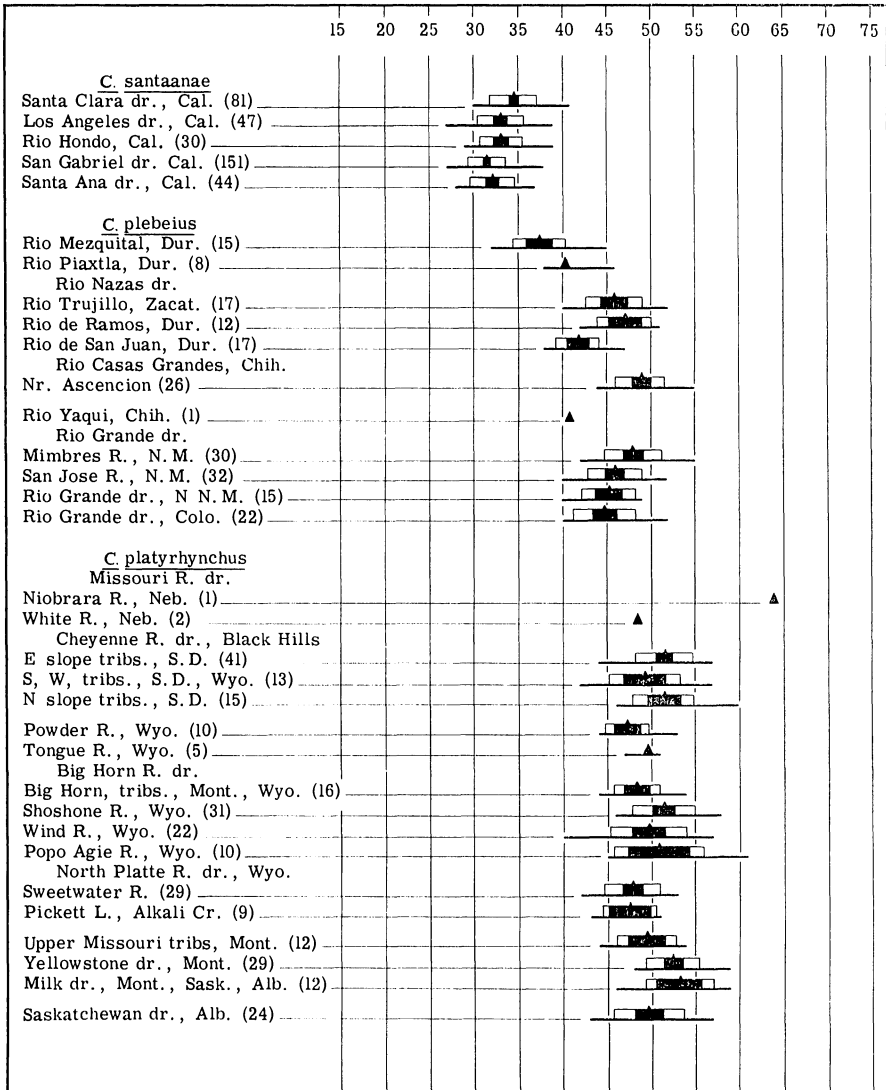


FIG. 8. Variation in the number of scales before the dorsal fin in the subgenus *Pantosteus*. See legend for Fig. 7 for explanation of the diagrams.

this character, whereas the affinities appear to be with the Great Basin populations when the vertebral number is considered. The Missouri River populations range between 3000 and 7000 feet in elevation, the Colorado River populations range between 5500 and 8000 feet, and the Columbia drainage populations range from below 200 to usually no higher than 3000 feet.

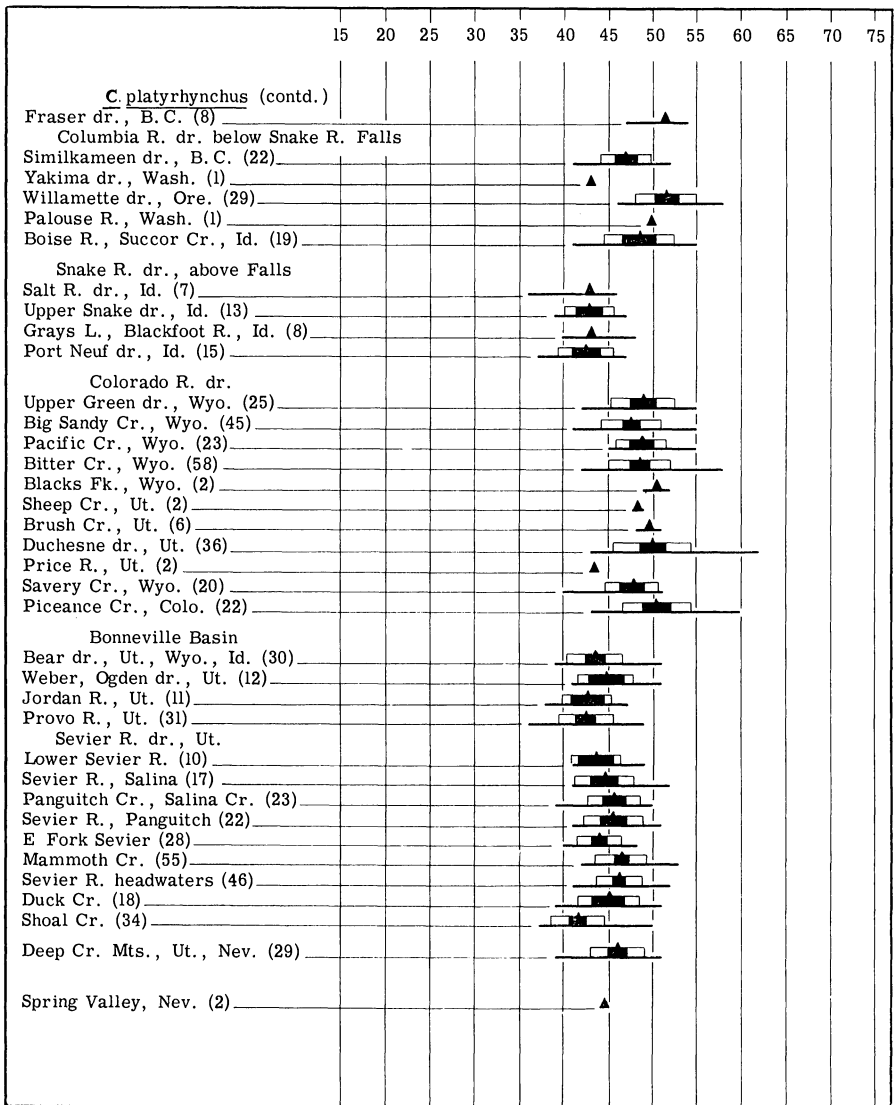


FIG. 8 (continued)

C. clarki, *C. discobolus*, and *C. columbianus* exhibit extreme variation in the number of predorsal scales. The southern *C. clarki* of the lower Colorado River drainage has extremely large scales in the Gila River drainage, the extreme counts ranging from 13 to 33. The population means are between 17 and 24 except in three localities, Sycamore Creek tributary to the Agua

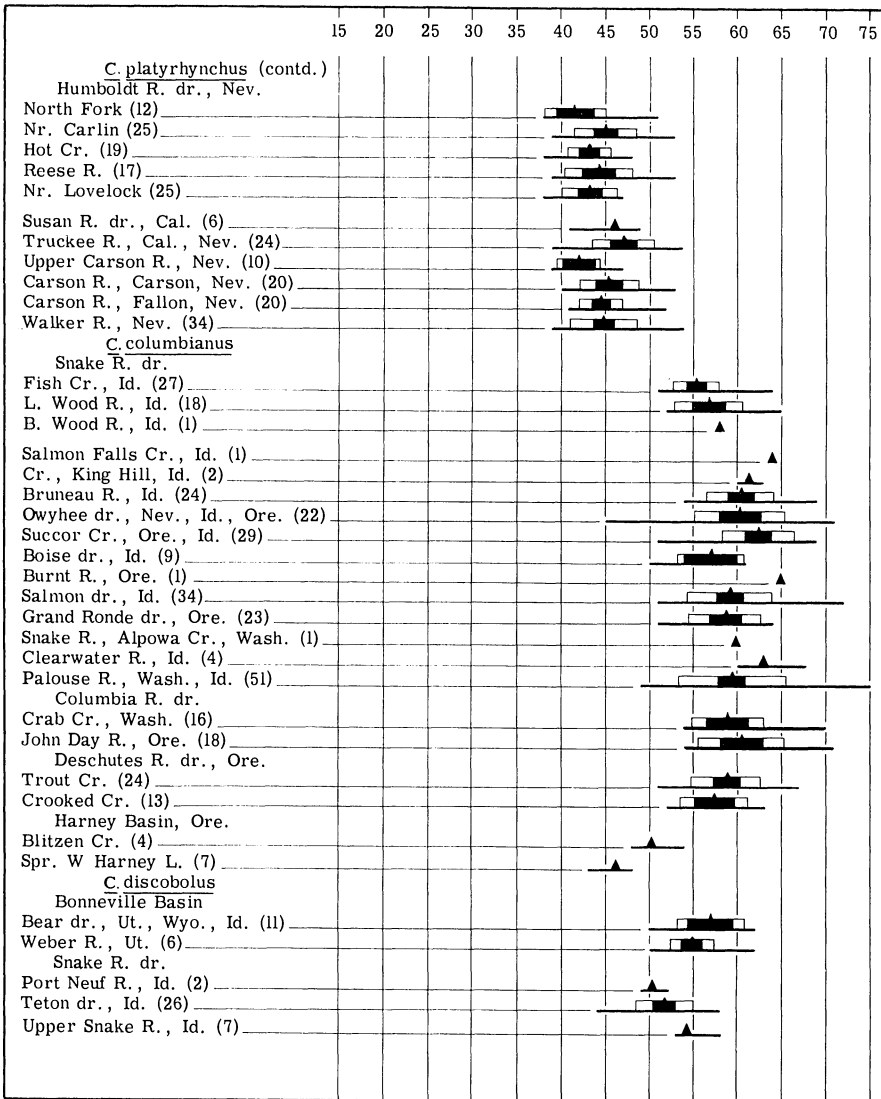


FIG. 8 (continued)

Fria, the Tonto Creek headwaters, and the San Carlos River, where the means are 27 or 28. The Agua Fria, Tonto Creek, and the Verde River are south-flowing tributaries which show a distinct correlation between elevation and the number of predorsal scales of the resident populations of *C. clarki*. The correlation with altitude holds true within stream drainages but not between

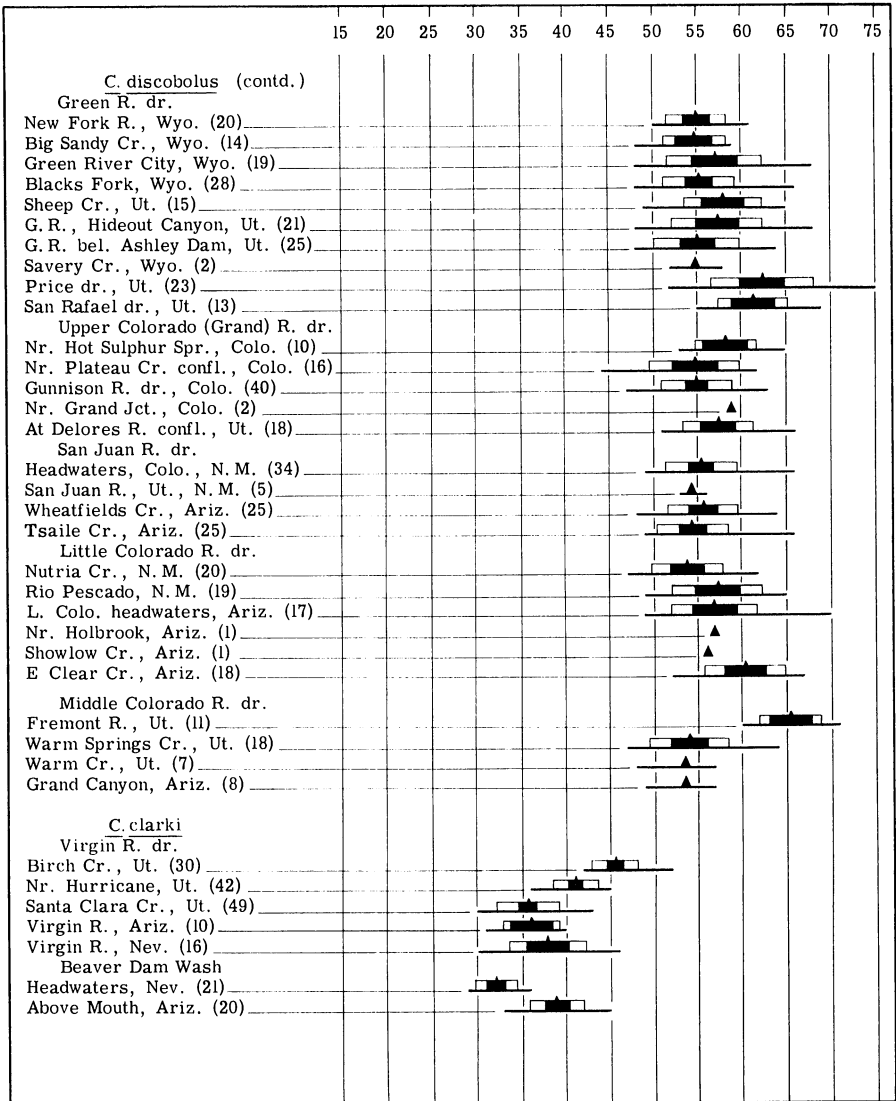


FIG. 8 (continued)

drainages. The altitudinal range of populations in these drainages runs from 2000 to 4500 feet. The eastern populations seem to be relatively stable in this character regardless of altitude. Populations of the upper Gila River above the confluence with the Salt River are relatively uniform with the exception of the San Carlos population, notwithstanding the altitudinal range of from 2000 to nearly 8000 feet.

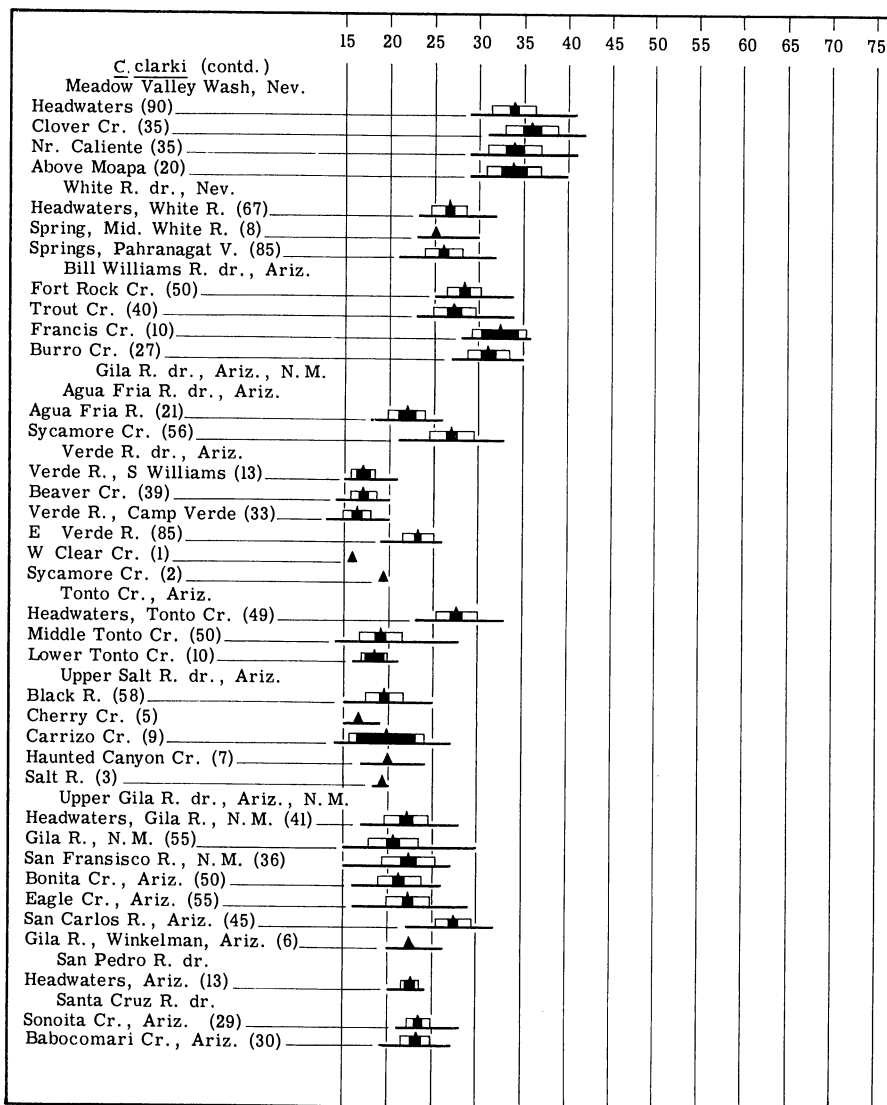


FIG. 8 (continued)

Specimens in the Bill Williams River drainage, Arizona, have smaller scales, ranging from 23 to 34, with population means between 26 and 29 in the Trout Creek section, and 27 to 36 with the means between 30 and 35 in the southern, Burro Creek section. In the White River drainage, Nevada, the scale size is intermediate between values from the Gila and Bill Williams

ivers. Three population samples comprised of 160 counts are between 21 and 32, with sample means at 26 and 27.

From the White River east, there is a trend toward higher numbers of predorsal scales in *clarki*. Specimens from the Meadow Valley Wash, Nevada, have smaller scales, ranging from 29 to 42, with sample means between 33 and 37. Specimens from the head of Beaver Dam Wash, just to the east, fall in the same range, but specimens from the mouth of Beaver Dam Creek have scale numbers near those of the adjacent populations of the cooler Virgin River. This may indicate genetic as well as environmental influence.

Populations of fishes from the Virgin River possess still smaller scales, ranging from 30 to 55. In the Santa Clara River of Utah and the Virgin River in Arizona and Nevada the population means are between 33 and 40, but samples from the Virgin River and tributaries farther upstream in Utah show much higher values, about 41 near Hurricane and 45 or 46 at Birch Creek in Zion Canyon. The last sample was taken from a cool spring in the steep and shaded Zion Canyon bottom and might reflect the influence of temperature on the development of this character. Populations in this section of the Virgin River may have been influenced by introgression with populations of *platyrhynchus* of the Sevier River drainage by means of possible drainage connections in the vicinity of Kanarraville (Hubbs and Miller, 1948:30). Although the upper Virgin River populations overlap with *C. discobolus* in this character the geographic pattern suggests no genetic connections.

Populations of *C. discobolus* possess small predorsal scales. Except for populations associated with hybridization most specimens have more than 50 (some specimens from the mouth of Plateau Creek, Colorado, and the Teton drainage, Idaho, have as few as 44). Population means are usually between 53 and 60, and extreme individual counts are as high as 65 to 75.

Specimens of *C. columbianus* have predorsal scale counts ranging from 43 to 75 with most of the specimens falling between 53 and 67, and with population means between 54 and 64. Exceptions are specimens from the Harney Lake basin where two small samples range from 43 to 54.

The extreme variation in predorsal scales makes it a sensitive character for analysis. Before too much reliance can be placed on the character, however, experimental data must be obtained on the influence of developmental temperature upon the number.

NUMBER OF SCALES IN THE LATERAL LINE.—This character, counted according to the method of Hubbs and Lagler (1958), is classically one of the most useful in ichthyology. Within the populations studied here, however, it had the interesting difficulty that the variation did not conform to the patterns displayed by the other characters examined (Table I). Great variation was found occasionally within populations and between populations otherwise

expected to be closely related. Knowledge of the source of this variability is essential to understanding its distribution among populations, but so far it is not known to what extent the variation is environmental or genetic in origin.

The number of lateral-line scales is only loosely correlated with the number of predorsal scales. *C. santaanae* has from 67 to 86. *C. plebeius*, extremely variable between populations, has between 70 and 103, with little discernible pattern to the variation (Fig. 11). *C. platyrhynchus* is variable, but most specimens usually have fewer than 90 lateral-line scales, contrasted with *discobolus* and *columbianus* which usually have more than 90. Populations of *C. clarki* (Fig. 15) usually have fewer than 75 lateral-line scales in the Gila River drainage and more than 75 in the Bill Williams and Virgin river tributaries, except that specimens from the White River average 75 and range from 63 to 85.

Although this character has been widely used to define taxonomic groups in *Pantosteus*, the variation and overlap is so great that no exclusive use can be made of it.

NUMBER OF DORSAL RAYS.—This is another classical ichthyological character which has been widely used in the taxonomy of *Pantosteus*. It can be considered a partial measure of the size of the dorsal fin, and thus, related to selective value, but it may also be under an independent meristic influence.

The total observed range within *Pantosteus* (Table 1) is from 7 to 14 principal dorsal rays. The usual range is 8 to 13. Specimens with as few as 8 dorsal rays are, with few exceptions, confined to populations of *C. plebeius*. Within this species the range is 8 to 10 and the population modes are usually 9 with means from 8.9 to 9.5. *C. santaanae* has a range of 9 to 11 and a mean of about 10.

Populations of *C. platyrhynchus* almost invariably have a mode of 10 dorsal rays. Exceptions are Lower Snake and Columbia river populations which tend to have means between 10.5 and 11, and specimens from the Fraser River, a small sample of which had 11 and 12 in equal proportions. Most populations show a range of 9 to 11. Lower Snake and Columbia river populations range from 10 to 12.

Variation in this character in *C. columbianus* indicates two general groups (Fig. 21). The first, comprising the majority of the species, characteristically has a mode of 12 dorsal rays. The second group, inhabiting various isolated areas, has a mode of 11 dorsal rays. The isolated populations are in the Wood River, Idaho, the Palouse River, Washington and Idaho, and Crooked Creek, Oregon, above barrier falls, and the Harney basin, Oregon, which is separated from former connectives by a lava flow. This distribution pattern is repeated in other characteristics suggesting the presence in isolated headwaters of the Columbia drainage of relicts of an older stage in the evolution of *C. columbianus*.

Populations of *C. discobolus* of the Green and Colorado rivers above the San Juan River have 10 to 12 dorsal rays with the mean value near 11, occasionally 10 or 10.5. Specimens from the middle Colorado and San Juan drainages have 9 to 11, modally 10, dorsal rays. They are similar in this respect to the adjacent representatives of *C. clarki* of the middle Colorado River drainage area. Farther south in the Gila drainage *C. clarki* may have 10 to 12 dorsal rays, the mean being between 10 and 11, usually near 10.5.

The number of dorsal rays is usually conservative in intrapopulation variation. The reduced variability tends to establish single-value modes with sample means approximating whole numbers.

NUMBER OF PELVIC RAYS.—This is a conservative character with little analytical value. Broad overlap exists between all species, though some differences exist between modes and means of samples. The trends in variation follow the same patterns as do the other meristic characters. *C. santaanae*, *C. plebeius*, and *C. platyrhynchus* have 8 to 10 pelvic rays, modally 9. The unusual group of populations of *platyrhynchus* from the east slope of the Black Hills differs in having usually 10 pelvic rays. *C. discobolus* and *C. clarki* from middle Colorado River drainages have 8 to 10 with the means around 9 or between 9 and 10. *C. clarki* from the Gila River drainage has 9 to 11 with a strong mode on 10. *C. columbianus* has a range of 9 to 12 and sample means between 10 and 11. This character shows the smallest variance of those analyzed in the study.

GENERIC STATUS OF *PANTOSTEUS*

In 1854 Baird and Girard named *Catostomus clarkii* and *C. plebeius*, including them with other relatively fine-scaled suckers. Girard, in 1856, placed these two species and *C. insignis* in the genus *Minomus*, with lips tuberculated and moderately bilobed, separate from the genus *Acomus*, with lips papillated and very deeply cleft. He then included *C. latipinnis* and synonyms of *C. catostomus*, as well as the newly described species *guzmaniensis* and *generosus*, in *Acomus*. Parts of this same arrangement were perpetuated by Girard in 1858 and 1859.

Cope (in Cope and Yarrow, 1875:673) erected the genus *Pantosteus* to include fishes with most of the characteristics of *Catostomus*, but which have the fontanelle obliterated by the complete union of the parietal bones. The genus thus constituted included five species: *P. platyrhynchus*, *P. jarrovii*, *P. virescens*, *P. delphinus*, and *P. bardus*. *Catostomus discobolus* Cope was not included, although it was noted that its fontanelle was reduced to a narrow slit. Jordan (1877:81) in a key to the genera of Catostomidae "accepted by Prof. Cope and the writer" recognized *Pantosteus* with the diagnosis: "Fontanelle obliterated by the union of the parietal bones." The following year Jordan (1878a) included *C. plebeius* within *Pantosteus*. *C. clarki* was

not included, probably owing to confusion over the type (see Cope and Yarrow, 1875:673) and *C. discobolus* was excluded, although it was noted to be a *Pantosteus* in all features except the fontanelle character (Jordan, 1878*b*, see quotation, p. 83, this report).

By 1908 all of the species recognized in this revision had been named at least once and the genus was understood in essentially its modern interpretation, primarily through the researches of Jordan (1878*b*), Evermann (1893*a*, 1897), Snyder (1908*a*), Jordan and Gilbert (1882), and Jordan and Evermann (1896).

Fowler (1913) initiated an abortive attempt to recognize two genera within the group. Specimens with large predorsal scales were called *Notolepidomyzon*. This classification was supported by Snyder (1915), Jordan, Evermann, and Clark (1930), and Tanner (1932, 1936, 1942), but has not been otherwise accepted.

One other sequence of taxonomic events is pertinent. Eigenmann and Eigenmann, in 1893, described *Pantosteus columbianus*. The systematic placement of this species is supported by the facts submitted in the present study. However, Hubbs and Schultz (1932) rediscovered and renamed the same species *Catostomus syncheilus* although they indicated that its closest relative might be "*Pantosteus*" *plebeius*. The species has been known as *Catostomus columbianus* since the discovery of the identity of the two forms by Miller and Miller (1948).

The generic validity of *Pantosteus* has been questioned by those who have been most familiar with the group. Hubbs and Schultz (1932:11) noted that *plebeius* and *columbianus* tend to bridge the gap between *Catostomus* and *Pantosteus* and stated that "It is clear that the current classification of the Western suckers in genera does not adequately indicate their resemblances or probable relationships." Hubbs, Hubbs, and Johnson (1943:33), in describing numerous hybrid crosses between *Catostomus* and *Pantosteus* in nature, mildly qualified the generic status of "these combinations, intergeneric according to the present nomenclature of the family." In the same paper (p. 73) it was noted that *Catostomus syncheilus* (= *columbianus*), being intermediate between *Catostomus macrocheilus* and *Pantosteus jordani*, also of the Columbia River drainage, may have arisen through hybridization of those forms.

Thus, it is seen that *Pantosteus* has been usefully regarded as a phylogenetic unit with definable limits except for one or two borderline species. The characters on which the generic delimitations have been based have never been given thorough analysis or comparison with closely related species. The data presented here are intended to relate to the problem of whether or not the species group is definable by character complexes which

suggest monophyly and whether or not the species group is sufficiently separate from its closest relatives to warrant generic recognition.

The following characters may be used to define *Pantosteus* as here constituted: Skull with frontoparietal fontanelle usually obliterated; pterotic dorsally a more or less vertical transverse ridge rather than a horizontal, quadrate roofing bone; maxilla short and broad; dentary with abrupt angle between gnathic ramus and body of the bone; longitudinal labial ridge of the palatine reduced; dorsal and lateral aspects of the mesopterygoid and metapterygoid meet at right angles and form a ridge at the apex; pleural ribs of Weberian apparatus diverge at an angle greater than 90°; swim-bladder reduced; intestine long, six or more loops in the coil; peritoneum usually black or dusky; mouth large, edges of jaws with well-developed cartilaginous sheaths; lips large, pendant, with notches separating upper and lower lips at lateral corners; median notch of lower lip shallow, not extending to base of lip.

These morphological characters define a probably monophyletic assemblage of species. Yet, a review of the analysis of characters shows that two of the six species considered are consistently borderline, that is, very close to *Catostomus* (*s.s.*) in these delimitations. In fact, if *C. columbianus* (which has the fontanelle present) were removed, the definition could be restricted, and additional characters could be listed which would define the remaining five more thoroughly, and if *C. plebeius* (which does not have the black peritoneum) were removed the remaining four likewise could be more completely defined. Such a procedure, if carried out, would perpetuate increasingly homogeneous genera at the cost of failure to show relationship.

Furthermore, many of the characters forming the above definition appear in possibly closely related species of *Catostomus* (*s.s.*). *C. rimiculus* has a closed frontoparietal fontanelle; *C. catostomus* has a rather sharp angle to the ramus of the dentary, and a dusky to black peritoneum; *C. warnerensis* and *C. tahoensis* have a dark peritoneum; *C. tahoensis* often has a long gut; and several of these species may have a somewhat reduced notch in the lower lip and more or less extensive development of the cartilaginous jaw sheaths.

It may be concluded that the morphological evidence indicates that the species *santaanae*, *platyrhynchus*, *discobolus*, and *clarki* form a phylogenetically close group of species. The species *plebeius* and *columbianus* are slightly separate and are shown to be a part of the *Pantosteus* complex by the possession of most of the characters that define the group. Yet the latter two species may be almost as closely related to *C. catostomus* and *C. rimiculus* and more distantly related to *C. warnerensis* and *C. tahoensis* according to the number of shared characters.

The resolution of the question of generic status depends on the opposition

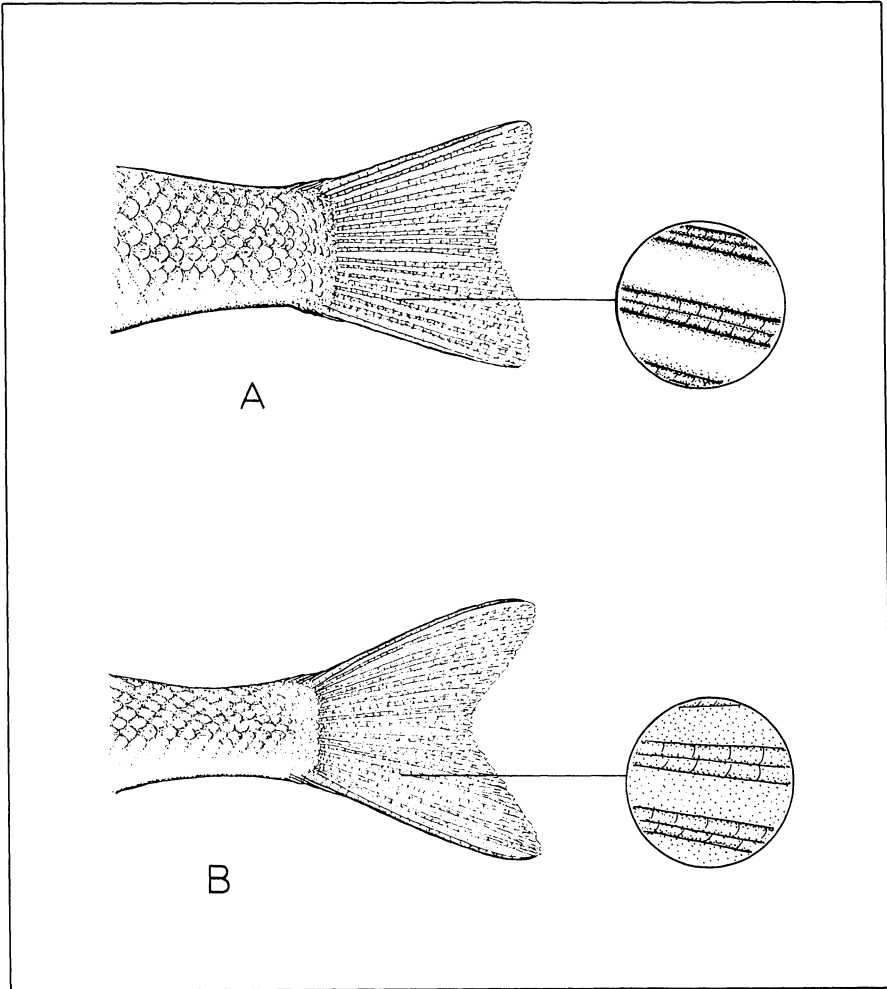


FIG. 9. Caudal peduncles and caudal fins of A, *C. platyrhynchus* from the Bonneville basin, and B, *C. discobolus* from the Green River, Utah, showing comparative depths of caudal peduncle and caudal fin pigmentation (insert). The caudal fin pigmentation shown in B, insert, is also representative of that in *C. clarki*.

of two considerations. On one hand is the utility of recognizing monophyletic, morphologically definable species groups. On the other hand is the utility of recognizing the evolutionary closeness of *Pantosteus* and *Catostomus* and the continuum among the borderline species of the groups. The choice is a difficult one, but the latter solution is favored here and is supported by an independent body of information.

The remarkable frequency of hybridization must be considered strong evidence for phylogenetic closeness of *Pantosteus* and *Catostomus*. Furthermore, backcrossing and limited introgression is suggested by the skewness, or unilateral extensions of variation of certain characters in populations known to be involved in hybridization. If this level of fertility can be experimentally verified, such conclusive evidence for genetic closeness would seemingly forbid taxonomic separation of the groups at the generic level.

In summation, the existing morphological and genetic data suggest that the relationship of *Pantosteus* and *Catostomus* can be best expressed as subgenera within the genus *Catostomus*. The previous use of the subgenus *Decactylus* Rafinesque to separate coarse-scaled from fine-scaled *Catostomus* is here regarded as obsolete, since the relationships of suckers within *Catostomus* (*s.s.*) are discordant with the scale-size character.

KEY TO THE SPECIES OF THE SUBGENUS *PANTOSTEUS*

- 1 a. Lower jaw rounded vertically and horizontally (Pl. I, A); dorsal rays usually 9 (8-10); predorsal scales usually 40-50 (32-55); gill rakers on arch 1 always fewer than 27 (outer row) and 37 (inner row); lower lip deeply incised, 2 or 3 rows of papillae crossing midline. *plebeius*
- b. Lower jaw truncate (Pl. I, B-E); dorsal rays usually 10 to 12; predorsal scales and gill rakers variable; lower lip usually with more than 3 rows of papillae crossing midline (except in *columbianus* which usually has more than 55 predorsal scales). 2
- 2 a. Anterior lower lip papillae grouped in a convex arch leaving anterolateral corners of lower lip bare or with minute papillae (Pl. I, D); caudal pigment restricted to rays, interradiated membrane immaculate or with sparse, superficial melanophores (Fig. 9A); pelvic axillary process well developed. *platyrhynchus*
- b. Anterior row of lower lip papillae usually concentric with margin of lower jaw (Pl. I, B, C, E); caudal interradiated membranes pigmented (Fig. 9, B); pelvic axillary process absent or represented by a simple fold. 3
- 3 a. Predorsal scales large, in 42 or fewer rows. 6
- b. Predorsal scales small, in 43 or more rows. 4
- 4 a. Lips weakly notched or entire at corners (Pl. I, B); lower lip with 2 or 3 rows of papillae crossing midline; outer face of upper lip often papillose; gill rakers with spines arranged in rosette clusters; dorsal rays, 10 to 13; isthmus narrow, width entering head length $3\frac{1}{2}$ to 4 times. *columbianus*
- b. Notches at lateral junctures of upper and lower lips well developed (Pl. I, E); lower lip not deeply incised, more than 3 rows of papillae crossing midline; outer face of upper lip usually smooth; gill rakers usually with spines in double row; dorsal rays, 10 or 11, rarely 12; isthmus broad, width usually entering head length $2\frac{1}{2}$ to 3 times. 5
- 5 a. Predorsal scales usually more than 50 (44 to 75); caudal peduncle slender, least depth entering standard length more than 12 times (except in some Great Basin and Snake River specimens [which have more than 45 gill rakers in inner row of arch 1] and some Little Colorado River specimens [which have a tendency toward *plebeius*-type lips]). *discobolus*

- b. Predorsal scales fewer than 47 (except in certain headwater populations in the Virgin River, Utah, which may have as many as 52, but which have fewer than 46 gill rakers in inner row of arch 1); caudal peduncle not slender, least depth entering standard length fewer than 12 times. *clarki* (part)
- 6 a. Gill rakers usually 30 to 43 (27 to 43) in outer row, and usually 40 to 59 (36 to 59) in inner row on arch 1; number of post-Weberian vertebrae usually more than 42; predorsal scales, 13 to 52. *clarki* (part)
- b. Gill rakers, 21 to 28 in outer row and 27 to 36 in inner row on arch 1; post-Weberian vertebrae usually fewer than 42; predorsal scales 27-41. *santaanae*

SPECIES ACCOUNTS

Catostomus plebeius Baird and Girard

NOMENCLATURE.—Lectotype (herein designated) USNM 168, a specimen 104.5 mm in standard length with 9 dorsal rays, 84 scales in the lateral line, 46 predorsal scales, and 23 gill rakers in the outer row of the first arch. The remaining 5 specimens of the original syntypes, USNM 168, are now USNM 196398. The type locality, somewhat confused in the original description and subsequent literature, is the Rio Mimbres, just east of the headwaters of the Gila River in New Mexico, but tributary in the past to Laguna de Guzman, Chihuahua, Mexico (Girard, 1856:165[sep., page 1]; Hubbs and Miller, 1948:116).

SYNONYMY

Catostomus plebeius Baird and Girard, 1854:28 (original description; Rio Mimbres trib. to Gila R. [=Mimbres R., New Mexico, a past trib. to L. de Guzman, of the Rio Casas Grandes dr., Chihuahua, Mexico]. Agassiz, 1855:208.

Minomus plebeius, Girard, 1856:173 (characters; Rio Mimbres). Girard, 1859:38, pl. 22, figs. 1-4 (characters; Rio Mimbres, trib. to L. Guzman [Chihuahua, Mexico]).

Catostomus (Acomus) guzmaniensis Girard, 1856:173 (original description; Rio Janos, trib. to L. de Guzman, Chihuahua, [Mexico]).

Catostomus (Acomus) generosus Girard, 1856:174 (original description; Cottonwood Cr., Utah [=Utah Cr., Rio Grande dr., Colorado; Snyder, 1921:28]).

Acomus guzmaniensis, Girard, 1858:39, pl. 23, figs. 6-10 (characters; Rio Janos [Chihuahua, Mexico]).

Pantosteus jarrovii, Cope and Yarrow, 1875:674 (misidentification in part; Costilla, Taos, San Hdefonso, and Tierra Amarilla [Rio Grande dr., New Mexico]).

Catostomus plebejus, Jordan and Copeland, 1876:156.

Catostomus generosus, Jordan and Copeland, 1876:156.

Pantosteus plebeius, Jordan, 1878a:416 (Colorado basin, [New Mexico?]). Jordan, 1878b:184 (characters, misidentification in part [Chihuahua, Mexico]). Jordan and Gilbert, 1882:122 (characters; L. Guzman, Mexico). Jordan, 1885:805. Jordan, 1891a:19, 20 (characters; Rio Grande basin). Evermann, 1893a:54 (synonymy; Rio Grande basin). Evermann and Kendall, 1894:98 (characters, synonymy; Rio Grande and basins of Mexico). Jordan and Evermann, 1896:170 (characters; Rio Grande basin). Bean, 1898:167 (characters; San Diego, Chihuahua). Jordan and Evermann, 1902:46. Evermann and Goldsborough, 1902:146 (Rio Piedras Verdes, Colonia Garcia; Rio Casas Grandes, old Casas Grandes, Chihuahua). Meek, 1902:75 (characters; Colonia Juarez, Ahumada, San Andres, Miñaca, Mexico). Meek,

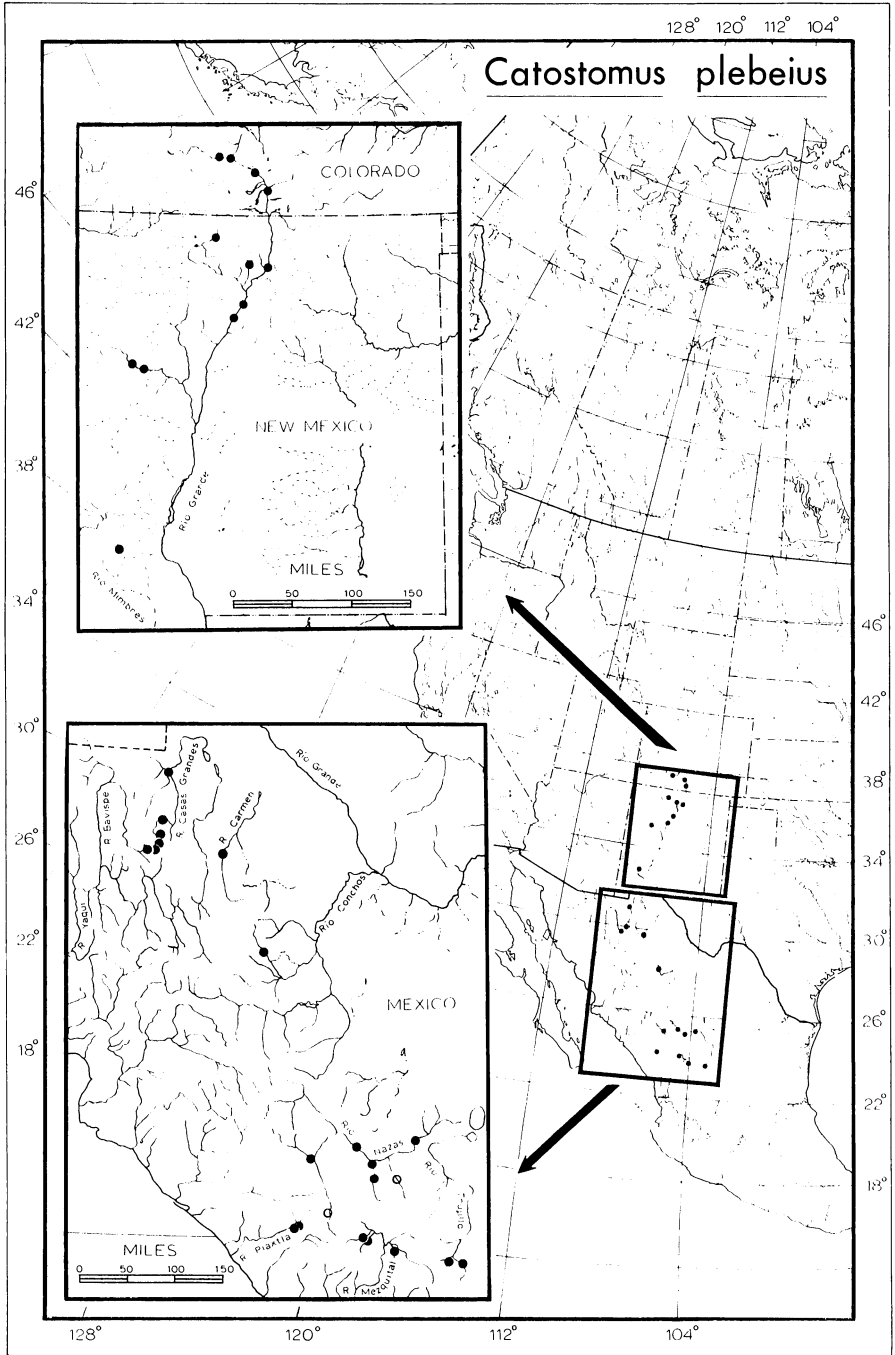


FIG. 10. Distribution of *Catostomus plebeius*. Closed circles represent specimens examined, open circles represent records of specimens not seen (see additional specimens, p. 53).

1904:30 (characters, synonymy; Rio Santa Cruz [Rio Grande dr.], San Andres; Rio Mimbres; Rio Janos; Casas Grandes at Colonia Garcia, San Diego, Casas Grandes, and Colonia Juarez; Rio Carmen, Ahumada; Rio Sauz, Sauz; Rio Nazas at Lerdo, Santiago Papasquiario, and Durango; Rio Mezquital, Durango; Rio Yaqui, Miñaca). Fowler, 1913:47 (Watrita Cr., Colo.). Ellis, 1914:28 (characters, color description, food habits; Rio Grande, Alamosa, Colorado). Hubbs and Miller, 1948:116 (Rio Mimbres, New Mexico). Beckman, 1952:36, 1 fig. (characters; Rio Grande dr., Colorado). Miller, 1952:28, fig. 17 (characters, habitat, distribution; bait introduction, Colorado R.). Moore, 1957:92 (characters; Rio Grande basin; northern Mexico). Eddy, 1957:75 (characters; Rio Grande, Colorado to Mexico). Koster, 1957:46 (characters, ecology; New Mexico; also reported in Gila R.). Miller, 1958:214 (Rio Grande dr.; Rio Yaqui, Chihuahua, Mexico; zoogeography). Bailey *et al.*, 1960:18 (common name: Rio Grande sucker).

Pantosteus generosus, Jordan, 1878a:416 ([Rio Grande dr.], New Mexico). Jordan, 1878b:183 (characters, misidentification in part; Rio Grande [dr., Colorado, New Mexico, Mexico]). Jordan and Gilbert, 1882:123 (characters, misidentification in part; Rio Grande [dr., Colorado, New Mexico, Mexico], Mojave Desert [*sic*]). Jordan, 1885:805. Snyder, 1921:27 (suggestion that the type locality for *A. generosus* Girard is Utah Cr., Colorado, rather than Cottonwood Cr., Utah).

Catostomus nebuliferus Garman, 1881:89 (original description; Rio Nazas, Coahuila [Mexico]).

Pantosteus guzmaniensis, Jordan, 1885:805. Jordan and Evermann, 1896:171 (characters; Rio Grande basin, Coahuila and Chihuahua). Jordan and Evermann, 1902:46.

Notolepidomyzon plebeius, Snyder, 1915:578 (characters; Rio Grande basin). Jordan, Evermann, and Clark, 1930:104 (synonymy; Rio Grande basin, Colorado to Chihuahua; Rio Piedras; Rio Casas Grandes). Tanner, 1942:29 (characters; Rio Grande basin, Colorado to Chihuahua).

Notolepidomyzon generosus, Snyder, 1915:578 (characters; Bonneville basin [in error]). Jordan, Evermann, and Clark, 1930:104 (Colorado basin [erroneous locality]). Tanner, 1942:29 (characters; Rio Grande basin in Colorado).

Pantosteus species, Rostlund, 1952:267, map 15 (distribution).

RANGE.—Rio Grande drainage, northern New Mexico and Colorado; Rio Mimbres, southwestern New Mexico; tributaries to Laguna de Guzman, Chihuahua; Rio Yaqui headwaters, Chihuahua; Rio Nazas headwaters, Durango; Rio Trujillo headwaters, Zacatecas; Rio Mezquital headwaters, Durango; Rio Piaxtla headwaters, Durango (Maps, Figs. 1, 10).

DESCRIPTION.—Catostomid fishes of small size, up to approximately 160 mm in standard length; lips small, papillose over all, the lower with a rather deep median cleft, two or three rows of papillae between median cleft and lower jaw; anterolateral notches present at junctions of upper and lower lips; cartilaginous ridge of lower jaw rounded, narrow, width 4 to 6 per cent of standard length; isthmus relatively narrow, width usually 6 to 9 per cent of standard length; gill rakers few, 20 to 27 on external row and 26 to 37 on internal row of first arch in specimens longer than 70 mm in standard length (smaller specimens may have as few as 18 on the outer row and 24 on the inner row of the first arch); gill rakers with spines in series, not in clusters; frontoparietal fontanelle nearly closed in young, closed in larger young and

adults except for occasional specimens with narrow frontal slit; peritoneum silvery with scattered melanophores; intestine long, 4 to 8 loops anterior to liver; swimbladder variable, usually reaching to above the pelvic fin insertion, but often reduced to one-fourth or less of the standard length or occasionally reaching beyond pelvic insertion; lateral-line scales moderate, 70 to 103, usually 75 to 95; predorsal scales, 32 to 55, usually 40 to 50; post-Weberian vertebrae, 38 to 40, rarely 42; dorsal rays, 8 to 10, modally 9; pelvic rays, 8 to 10, occasionally 11, modally 9; pelvic axillary process absent; caudal peduncle deep, usually 9 to 10 (7.2–10.5) per cent of standard length; color dusky brownish or greenish above, lighter below, often sharply bicolor; melanophores tend to concentrate in spot at base of dorsal and caudal fins in many populations; caudal interradiial membranes usually unpigmented except for sparse melanophores posteriorly, especially on the medial membranes, caudal rays always strongly pigmented.

COMPARISON.—Differs from *santaanae* which has truncate lower jaw; black peritoneum; usually fewer than 40 predorsal scales; modally 10 dorsal rays.

C. platyrhynchus differs in the possession of papillae-free outer face of upper lip and anterolateral corners of lower lip; lower jaw truncate; gill rakers usually more than 26 on external row and usually more than 35 on internal row of first arch; peritoneum black; dorsal rays modally 10; pelvic axillary process present.

C. discobolus outside the Little Colorado River drainage differs in the possession of papillae-free outer surface of the upper lip; wide, truncate edge of lower jaw; gill rakers more than 28 on external row and 37 on inner row of first arch; peritoneum black; predorsal scales usually more than 50 (44–75); post-Weberian vertebrae usually more than 43 (41–46); dorsal rays usually modally 10 or 11; depth of caudal peduncle usually less than 8 per cent of standard length (except in certain slow-water situations); caudal interradiial pigment dense.

C. discobolus from the Little Colorado River drainage differs in the possession of more gill rakers, 26–38 on the external row and 34–52 (usually more than 38) on the internal row of the first arch; usually more than 50 predorsal scales (47–70); caudal interradiial membranes more densely pigmented.

C. clarki differs in the possession of nonpapillose outer face of the upper lip; truncate edge of lower jaw; gill rakers usually more than 30 on external row (27–43) and 40 on internal row (36–59) of first arch; peritoneum black; predorsal scales usually less than 40 (13–53); post-Weberian vertebrae usually more than 42 (41–47); dorsal rays modally 10 or 11; caudal interradiial membranes densely pigmented.

C. columbianus differs in the possession of fewer papillae on outer face of upper lip; edge of lower jaw more truncate; gill rakers more than 29

on external row and more than 40 on internal row of first arch (except in populations from the Little Wood River, which have 24–31 and 34–41); fontanelle open; peritoneum black; predorsal scales usually more than 50 (45–75); post-Weberian vertebrae more than 42 in most populations; dorsal rays modally 11 or 12; caudal interradiial pigment dense.

VARIATION.—This species has not evolved into clearly defined subspecific groups. Interpopulation variation exists, but is not generally geographically concordant.

The number of lateral-line scales is the characteristic with the broadest interpopulation differences (Fig. 11). In this feature there is little overlap between the sample from the upper Rio Grande drainage and the sample from the Casas Grandes drainage, for example. Yet populations from other scattered geographical areas overlap so extensively between these extremes that a meaningful evolutionary pattern does not seem clear. In this character and others the samples from the Lake Guzman, Rio Grande, and Nazas drainages, though presently geographically isolated from each other, show less variation between groups than between samples within these hydrographically defined groups.

The Rio Mimbres population, presently isolated but historically a part of the drainage of Lake Guzman (Hubbs and Miller, 1948), shows closer morphological similarity to Lake Guzman drainage populations than do those of the Rio Grande in three characters, the caudal peduncle depth, the number of predorsal scales, and the number of dorsal rays. Other characters of the Mimbres population are more or less intermediate.

Samples from the southernmost Pacific Coast drainages, the Rio Mezquital and Rio Piaxtla, appear extreme in several meristic characters, especially the number of predorsal scales and dorsal rays. More collections from the

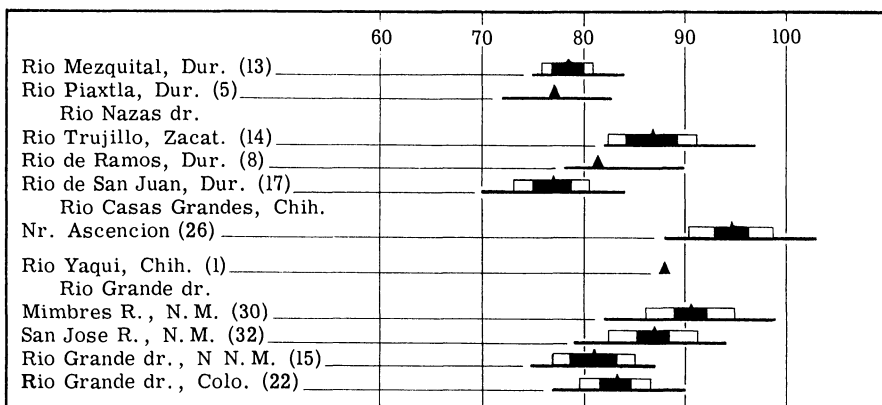


FIG. 11. Number of scales in the lateral line in populations of *C. plebeius*.

southern part of the range are needed to ascertain the significance of this variation.

HYBRIDIZATION.—*C. plebeius* is the only species in the subgenus *Pantosteus* which has not been reported to hybridize.

ECOLOGY.—This species is found in small to large streams, commonly those with widths of 30 to 75 feet. The current of streams from which samples have been taken ranges from slight to moderate or swift. Depth of water may be six inches to three feet. Summer water temperatures are commonly between 15°–19° C (59°–66°F). Winter temperatures have been recorded near 7°C (45°F). Bottom conditions encountered include stones, sand, and mud, usually with sparse vegetation, but occasionally with abundant *Chara* or *Potamogeton*.

At a collection site on the Rio Grande, 18 miles north of Monte Vista at an elevation of 7600 feet, the river had the following ecological characters: width up to 75 feet; bottom consisting of sand, stones, mud, few boulders; vegetation consisting only of a trace of *Chara*. Pools up to six feet deep were fished, but the fishes were found in a pool three feet deep with sparse vegetation and slight current (C. L. Hubbs, field notes).

A collection was taken in swift water from Vallecitos Creek, New Mexico, where the creek is narrow with only one-half to two feet of water. Apparently, food usually consists of periphyton. Specimens taken from the Rio Mimbres in June contained small fingernail clams in the intestine. This species may be more omnivorous than other species of *Pantosteus*.

Specimens of *C. plebeius* mature at a length of 60 to 80 mm for males and 70–90 mm for females. Ripe, tuberculate, and probably spawning specimens have been taken in February and March in the southern part of the range. Specimens taken February 14 in the Rio Trujillo, Zacatecas, contained ova 1.6 mm in diameter and were probably spawning, since some specimens had ova in the pharynx. Spawning probably occurs progressively later to the north.

Ova size at spawning seems to be approximately 1.5 mm. Ova this large have been observed in specimens taken in September in the Rio Grande drainage. However, elsewhere in the same drainage specimens with ova 0.5 mm in diameter have been recovered the same month. Koster (1957:46) has suggested that spawning occurs in the spring and fall in this species.

Embryological development has been described by Butler (1960). Larval specimens approximately 20 mm in standard length have been collected in February in the Nazas and Lake Guzman drainages and in May and July in the Rio Grande drainage. It would appear that some specimens may mature at one year of age, but most probably do not mature until the second year.

The usual tubercle pattern consists of the presence of large tubercles on the lower part of the caudal peduncle in females and large tubercles on the

anal fin, caudal peduncle, and caudal fin of males. Smaller tubercles may be present distally on the dorsal side of the pectoral and pelvic fins of males, and rarely on the anal fin of females.

SPECIMENS EXAMINED

RIO MEZQUITAL DRAINAGE.—Mexico, Durango: UMMZ 157682 = USNM 132444 (Rio Nayar, 5 mi. S Durango, R. G. Miller, V:10:1946); UMMZ 161681 (Rio Graceros, 2 mi. W Vicente Guerrero, J. T. Greenbank, II:15:1951); MSU 3215-19 (Rio de Santiago, 4 mi. E, 7 mi. S Durango, R. H. Baker, IV:24:1961).

RIO PIAXTLA DRAINAGE.—Mexico, Durango: UMMZ 166460 (trib., 2.5 mi. W San Luis, I. J. Cantrall, III:25:1953).

RIO TRUJILLO DRAINAGE.—Mexico, Zacatecas: UMMZ 161676 (Rio Atotonilco, 4 mi. W El Sauz, J. T. Greenbank, II:14:1951); UMMZ 161669 (Rio Trujillo [Rio Florida], 1 mi. W Rancho Grande, J. T. Greenbank, II:14:1951).

RIO NAZAS DRAINAGE.—Mexico, Durango: UMMZ 161709 (Rio de Ramos, Atotonilco, J. T. Greenbank, II:17:1951); UMMZ 161714 (Rio de San Juan, ca. 15 mi. N Menores, J. T. Greenbank, II:18:1951); UMMZ 161703 (Rio de Santiago, Navarros, J. T. Greenbank, II:17:1951); UMMZ 161721, 179641, 180130 (Rio Nazas).

RIO YAQUI DRAINAGE.—Mexico, Chihuahua: UMMZ 165027 (Rio Gavilan, ca. 10 mi. S Gavilancito sawmill, W. P. Knoch, II:22:1953).

RIO CASAS GRANDES DRAINAGE.—Mexico, Chihuahua: UMMZ 133039, 162620, 165028, 165030, 180323, USNM 50512.

RIO MIMBRES DRAINAGE.—New Mexico: USNM 168, 196398, UMMZ 124740 (Rio Mimbres near Grant-Luna Co. line, 30 mi. NW Deming, C. L. Hubbs, VI:30:1938).

RIO GRANDE DRAINAGE.—New Mexico: Valencia Co.: UMMZ 94889, 179561. Santa Fe Co.: USNM 131881. Sandoval Co.: UMMZ 178709. Rio Arriba Co.: UMMZ 120070, 180126, USNM 18009. Taos Co.: UMMZ 87189, 121630. **Colorado,** Conejos Co.: UMMZ 180127. Alamosa Co.: UMMZ 66186, 117814, 180129, USNM 41645, 41659, 125263. Rio Grande Co.: UMMZ 142521, USNM 125262. Co. unknown: USNM 18008.

RIO CONCHOS DRAINAGE.—Mexico, Chihuahua: UMMZ 182369 (Rio Santa Isabel at General Trias, 30.5 mi. SW Chihuahua City, R. R. Miller, VI:18:1964).

RIO CARMEN DRAINAGE.—Mexico, Chihuahua: UMMZ 182396 (Rio del Carmen, 39 mi. W. El Sueco at Ricardo Flores Magon, R. R. Miller, VI:21:1964).

ADDITIONAL RECORDS.—Rio Nazas Drainage, Durango; Rio del Peñon de Cavadonga, Peñon Blanco, S. Weitzman, VIII:1:1952, and Rio Arenales, 33 mi. NW Otinapa, S. Weitzman, VII:12:1952, identified by R. R. Miller; UMMZ file (specimens at California Academy of Sciences).

Catostomus santaanae (Snyder)

NOMENCLATURE.—Holotype: USNM 61675; **Paratypes:** USNM 62312. The specific name has been emended to eliminate the hyphen (*santa-anae*). Inclusion of *santaanae* in the genus *Catostomus* represents a new combination.

SYNONYMY

Pantosteus generosus, Jordan, 1878a:416 (southern California).

Pantosteus santa-anae Snyder, 1908a:33 (original description; Santa Ana R., Riverside, California). Fowler, 1913:48. Hubbs, Hubbs, and Johnson, 1943:47, fig. 6; pl. 1, fig. 1c;

pl. 7, fig. 1c (characters, hybridization with *Catostomus* species; Santa Clara R. system, California). Shapovalov and Dill, 1950:385.

Notolepidomyzon santa-anae, Snyder, 1915:578 (characters; Santa Ana R.). Tanner, 1942:29 (characters).

Notolepidomyzon santae-anae, Jordan, Evermann, and Clark, 1930:104 (southern California).

Pantosteus (Notolepidomyzon) species, Rostlund, 1952:267, map 15 (distribution).

Pantosteus santaanae, Moore, 1957:92 (characters; southern California). Miller, 1958:215 (zoogeography). Shapovalov, Dill, and Cordone, 1959:71. Bailey *et al.*, 1960:18, (common name: Santa Ana sucker).

Pantosteus santanae [*sic*] Eddy, 1957:75 (southern California).

RANGE.—Santa Clara, Los Angeles, San Gabriel, and Santa Ana drainages of southern California (Maps, Figs. 1, 12).

DESCRIPTION.—Small catostomids, ranging up to approximately 150 mm in standard length; lips moderate in size; lower lip papillae large, with tendency to be arranged in convex arch anteriorly and with papillae occasionally sparse on anterolateral corners of lower lip; outer face of upper lip often somewhat papillose; lateral notches at junction of lower and upper lip strong; median notch of lower lip weak, with approximately four rows of papillae separating notch and edge of lower jaw; edge of lower jaw truncate, width moderate, 4.5 to 7 per cent of standard length (one sample only); width of isthmus variable, 5.5 to 11 per cent, usually 7 to 10 per cent of standard length; gill rakers, 21–28 on external row of first arch and 27–36 on internal row of first arch in specimens greater than 60 mm in standard length, no apparent increase in number above the 60-mm size; spines of ventral rakers occasionally arranged in rosette-like clusters; fontanelle closed in adult specimens over approximately 70 mm in standard length; peritoneum black; intestine long, with up to 8 coils anterior to liver, unique in the possession of an extension of the leading coil, which may extend dorsal to the left gonad; swimbladder reduced; scales large, 67 to 86 in the lateral line; predorsal scales, 27 to 41, usually 29 to 37; post-Weberian vertebrae, 38 to 42; dorsal fin short, usually with 10 rays, occasionally with 9 or 11; pelvic rays, 8 to 10; pelvic axillary process usually foldlike; caudal peduncle rather deep, 8.3 to 11.1 per cent of standard length; color silvery below, darker above, with irregular dorsal blotches; melanophore pattern on scales often gives the impression of longitudinal lateral stripes; caudal interradiation pigment present but occasionally sparse, especially on dorsal and ventral interradial membranes of smaller (less than 70 mm S. L.) specimens.

COMPARISON.—Differs from *plebeius* which has somewhat narrower and less truncate development of the lower jaw; a deeper incision in the lower lip; a silvery or speckled peritoneum; smaller predorsal scales (*santaanae* usually has fewer than 40; *plebeius* usually more than 40, except in some of the southernmost populations in Mexico).

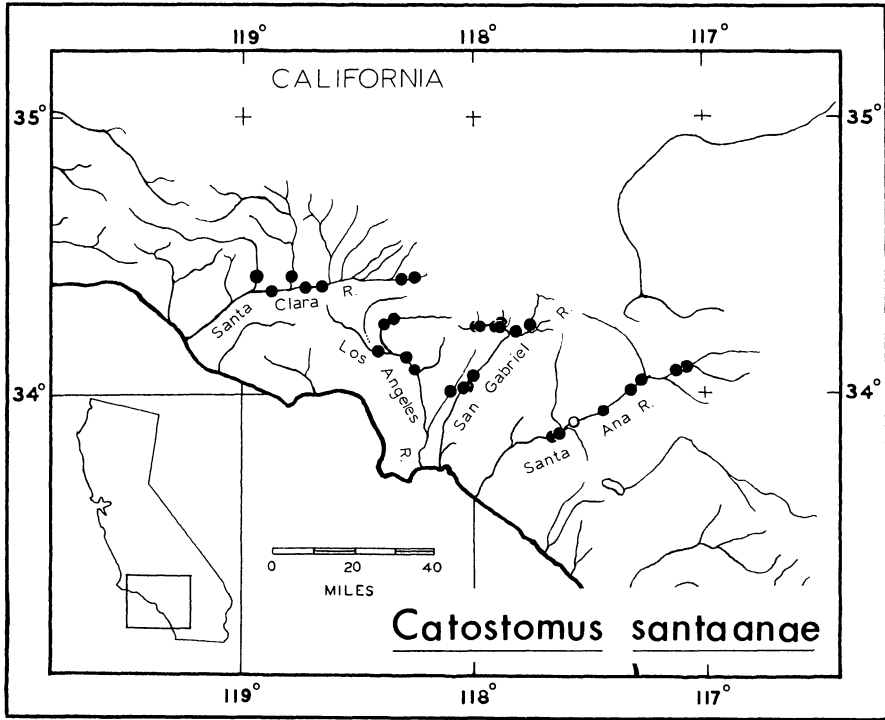


FIG. 12. Distribution of *Catostomus santaanae*. Closed circles represent specimens examined, open circles represent records of specimens not seen.

C. platyrhynchus has more pronounced papillae-free anterolateral corners of the lower lip; pelvic axillary process well developed; usually more than 26 gill rakers on external row of first arch and usually more than 35 gill rakers on internal row of first arch (except in some Bonneville basin and upper Snake River populations); usually more than 40 predorsal scales; caudal interradial membranes usually unpigmented.

C. discobolus has more gill rakers, always more than 36 on the internal row of the first arch (except specimens in Nutria Creek, New Mexico, which possess rounded lower jaws); more than 86 lateral-line scales (except in certain lower Colorado River populations); always more than 43 predorsal scales; usually more than 42 vertebrae (except in populations in the Little Colorado River drainage); depth of caudal peduncle usually less than 8.5 per cent of the standard length (except populations in the Little Colorado River drainage).

C. clarki has more gill rakers, 27 to 43, usually more than 30 in external row, and 36 to 59, usually more than 40 in internal row, of first arch; usually

more than 42 vertebrae; usually fewer than 42 predorsal scales (except in some populations in the Virgin River drainage).

C. columbianus usually has less developed lateral notches at both junctions of the upper and lower lip; more gill rakers, 30 or more on the external row and more than 40 on the internal row of the first arch (except in *C. c. hubbsi* from the Wood River drainage, Idaho); fontanelle open; lateral-line scales usually more than 86; predorsal scales always more than 43; post-Weberian vertebrae usually more than 42.

VARIATION.—Populations of *C. santaanae* possess variation in characters which have attained homogeneity elsewhere in the subgenus. For example, the tendency toward papillae-free anterolateral corners of the lower lip, immaculate caudal interradiial membranes, and development of the pelvic axillary process are variable features in *santaanae* which have attained a sufficient level of homogeneity to be regarded as specific characters in the related *platyrhynchus* to the north. The generalized nature of variability plus the affinities shown by *santaanae* with *clarki* to the east, *platyrhynchus* to the north and *plebeius* to the south suggest that *santaanae*, in restricted isolation, has failed to develop the degree of specialization found in the other, more widespread species. Yet, it is at the same time reasonable to recognize the variation as an indication of heterozygosity, and possibly, stable polymorphism.

A possibly different type of problem is suggested by the variation in degree of papillation of the outer face of the upper lip. Although all populations of *santaanae* show some development of small papillae on the outer face of the upper lip in some specimens, those from the Santa Clara River in Los Angeles and Ventura counties show it to a marked extent. Some populations (UMMZ 133854) show 100 per cent incidence of the character. In view of the fact that the Santa Clara River is the site of hybridization between *santaanae* and a *Catostomus* (*s.s.*) species, the high incidence of the *Catostomus*-like character in *santaanae* may possibly be attributable to introgression.

Five meristic characters show a slight tendency toward numerical increase with northward latitudinal progression. These characters are: number of lateral-line scales, number of predorsal scales, dorsal rays, pelvic rays, and post-Weberian vertebrae. The depth of the caudal peduncle also shows a northward cline, decreasing in proportional depth. It is not known whether these differences (to the extent that they may actually exist) result from genetic differences between populations or are phenotypic differences caused by environmental effects on development. There is some circumstantial evidence that the populations in the Santa Clara River, northernmost of the streams inhabited by *santaanae*, are not indigenous. This evidence is of the nature of negative data from early-day collections (Robert R. Miller, personal communication). If this is correct, it would support the view that the clinal

differences which show ultimate expression in the Santa Clara River are phenotypic, resulting from environmental influence.

HYBRIDIZATION.—Hybrids between *C. santaanae* and species of *Catostomus* have been reported by Hubbs, Hubbs, and Johnson (1943:47) from the Santa Clara River drainage. It has already been noted that certain populations of *santaanae* from this drainage show a striking prevalence of papillae on the anterior face of the upper lip—a *Catostomus* (s.s.) character perhaps gained through introgression (see also page 21).

ECOLOGY.—*C. santaanae* inhabits small to medium-sized streams, usually less than 20 feet in width with slight, moderate, or swift current. Water conditions range from clear or greenish to stained or silty and easily roiled, occasionally turbid, but never foul. Bottom conditions range from boulders to rubble and sand. Shifting sand bottom or mud is occasionally encountered. Often collections are associated with algae and *Chara*, though occasionally macroscopic vegetation is apparently absent. Water depths range from a few inches to several feet. One sample (UMMZ 131657) in the Santa Clara drainage was found by Robert R. Miller in a pond measuring approximately 20 by 45 feet in a sandy wash of Piru Creek. The bottom consisted of rocks and mud with some algae and the water temperature was near 70° F (21° C). A collection from a spring-fed tributary to the Rio Hondo was found in water with a temperature of 16.8° C in May.

Study of the available collections has not yet yielded a clear picture of the life history of this species. Mature females with near-ripe ova up to 1.5 mm in diameter have been collected in May and July. Larvae as small as 20 mm in standard length have been collected in July and November. These data suggest dual spawning in spring and fall, or protracted spawning. The length frequency data are inconclusive in their information relative to age distribution. The maximum size for most populations increases from approximately 100 mm in early spring to approximately 150 mm in August. This age class apparently dies in late summer or fall. Tuberculate males as small as 70 mm are known. Mature females between 81 mm and 131 mm have been observed. Spawning may be possible at the end of the first year, at least in males.

The tubercle patterns appear in early spring. Males have strong contact organs or tubercles on the rays of the anal fin, the caudal peduncle, and the caudal fin, especially the lower half. Females have tubercles on the caudal peduncle and the caudal fin. Both sexes have smaller tubercles on the head and dorsal and lateral scales at breeding time. Small tubercles on the dorsal surfaces of the pectoral and pelvic rays have been observed in males of several samples. A sample taken from the San Gabriel River in late August (UMMZ 131760) contained a male 89 mm long with tubercles on both sides of all fins plus small tubercles on the sides, dorsum, head, snout, and gular regions.

SPECIMENS EXAMINED

SANTA CLARA DRAINAGE.—California, Ventura Co.: UMMZ 130713, 131654, 131657, 131660, 131664, 132960, 132962, 133854, 136285, 138341, 140417, 140485. Los Angeles Co.: UMMZ 138338, 138339.

LOS ANGELES DRAINAGE.—California, Los Angeles Co.: UMMZ 131765, 132987, 132992, 133162, 133858, 136288, USNM 94342.

SAN GABRIEL DRAINAGE.—California, Los Angeles Co.: UMMZ 131668, 131671, 131760, 132710, 132712, 132948, 132953, 132980, 132990, 134673, 134676, 156998.

SANTA ANA DRAINAGE.—California, Los Angeles Co.: UMMZ 132944. Riverside Co.: UMMZ 131697, 132985, USNM 61675, 62312 (Santa Ana R., Riverside, Holotype). San Bernardino Co.: UMMZ 131701, 131705, 131753, 131756.

ADDITIONAL RECORD.—Santa Ana River at Norco, Riverside Co., Cal., K. H. Walker, X:28:1950, identified by R. R. Miller; UMMZ file.

Catostomus platyrhynchus (Cope)

NOMENCLATURE.—Lectotype (herein designated): USNM 15763, a specimen 135 mm in standard length, with about 83 scales in the lateral line, 39 predorsal scales, 11 dorsal rays, 27 and 38 gill rakers on the two rows of the first arch, 41 post-Weberian vertebrae, fontanelle reduced to a narrow slit, and caudal interradiial membrane without pigment. Paralectotypes (from syntypes): USNM 196399, 3 specimens 60 to 100 mm in standard length. Type locality: Provo, Utah. Specimens collected by Yarrow and Henshaw, November, 1872.

Concurrently with the discovery that the name *Catostomus discobolus* Cope 1872 applied properly to the species previously known as *Pantosteus delphinus* it was realized that the names *Minomus delphinus* Cope 1872 and *M. bardus* Cope 1872 did not apply to that species. The type specimens of *M. delphinus* and *M. bardus* have been lost at least since 1878 (Jordan, 1878b). The original descriptions of *M. delphinus* and *M. bardus* (Cope 1872:435, 436) apply to specimens of *C. platyrhynchus* more closely than they do to specimens of the species long called *Pantosteus delphinus* of the Colorado River drainage. The name *delphinus*, which has page priority over *bardus*, is not here employed as a recognized senior synonym to *platyrhynchus* owing to the original lack of locality data, the absence of the specimens, and the inadequacy of the description, allowing reasonable doubt as to the actual identity of the types.

The previously recognized species, *P. platyrhynchus* Cope, 1874, *P. jordani* Evermann, 1893a, and *P. lahontan* Rutter, 1903, are here considered to constitute a single species which takes the name *Catostomus platyrhynchus* (Cope), a new combination. The name *Pantosteus generosus* was applied to this species throughout much of the older literature, but *generosus* was shown to be a synonym of *plebeius* by Snyder (1921:28).

SYNONYMY

?*Minomus delphinus* Cope, 1872:435 (original description; “. . . in Professor Hayden’s collection without locality. This should be probably a tributary of the Green River.” [type lost, type locality unknown, identity uncertain]).

?*Minomus bardus* Cope, 1872:436 (original description; “From the same locality as *M. delphinus*.” [type lost, type locality unknown, identity uncertain]).

Minomus platyrhynchus Cope, 1874:134 (original description; Provo, Utah).

Pantosteus platyrhynchus, Cope and Yarrow, 1875:673, pl. 29, figs. 3, 3a (characters; Provo R., Utah). Jordan and Copeland, 1876:156. Jordan, 1878a:416 (“Utah”). Jordan, 1878b:183 (characters; Utah L. and tribs., Utah). Jordan and Gilbert, 1882:123 (characters; Utah L.). Snyder, 1915:578 (characters; Bonneville basin). Snyder, 1917:49 (characters, comparison with *P. lahontan*; Bonneville basin). Snyder, 1924:4–6 (characters, comparison with *P. virescens* [=discobolus]; Provo R., Weber R., and Sevier R., Utah). Jordan, Evermann, and Clark, 1930:104 (synonymy; Provo R. and Sevier R., Utah). Tanner, 1936:165 (characters, distribution). Simon, 1951:59, fig. 34 (characters, ecology; Snake and Bear R. drs., Wyoming). Miller, 1952:27, fig. 14 (characters; use as bait, lower Colorado R.; [misidentification, in part, of *C. clarki*, Lake Mead, September 8, 1938, collected by J. Weston]). Moore, 1957:92 (characters; Bonneville basin, Utah; Columbia R. dr.; Colorado R. dr.). Eddy, 1957:75, fig. 180 [sic] (Bonneville basin and Snake R. dr., Utah and Wyoming). Miller, 1958:211 (Colorado R. dr., Great Basin). Bond, 1961:22 (characters; Columbia R. dr., including Willamette R., Oregon). Bailey and Allum, 1962:87 (characters, synonymy, distribution; South Dakota, Nebraska). Sigler and Miller, 1963:98, 1 fig. (characters, ecology; Bonneville basin, Snake R. dr. above Shoshone Falls).

Catostomus (Acomus) guzmaniensis, Cope and Yarrow, 1875:679 (Utah L., Utah).

Pantosteus generosus, Jordan, 1878b:183 (characters, misidentification in part; Great Basin, Utah). Jordan and Gilbert, 1882:123 (characters, misidentification in part; Great Basin, Utah). Jordan, 1891a:20, 31 (characters; Provo R., Jordan R., Sevier R., Utah). Evermann, 1893a:55 (synonymy; Great Salt Lake Basin, Utah). Jordan and Evermann, 1896:170 (characters; Great Basin, Utah). Jordan and Evermann, 1902:45. Fowler, 1913:47 (Weber R., Echo; Logan, Utah).

Jordan and Evermann, 1902:45. Fowler, 1913:47 (Weber R., Echo; Logan, Utah).

Catostomus araeopus Jordan, 1878b:188 (original description, based on *C. occidentalis*, Kern R., California, and *C. (Pantosteus) platyrhynchus* of the Carson R., Nevada).

Pantosteus virescens, Jordan, 1878c:780 (characters; “Sweetgrass Hills,” Montana).

Catostomus discobolus, Evermann, 1892:41, pl. 18, fig. 1 (characters; Red Rock R., Red Rock; Beaverhead R., Dillon, Montana).

Pantosteus jordani Evermann, 1893a:51, 1 fig. (original description; Red Rock R., Red Rock; upper Missouri R. dr.). Evermann, 1893b:77 (Black Hills, South Dakota). Eigenmann, 1894:107 (characters, misidentification of *P. columbianus*; Boise R.). Gilbert and Evermann, 1894:189 (characters, distribution, Columbia R. dr.; based on misidentification of *P. columbianus* in part). Jordan and Evermann, 1896:171, fig. 73 (characters, upper Missouri R. dr., Columbia R. dr.). Evermann and Cox, 1896:389 (characters, variation; Missouri R. dr.). ?Evermann and Meek, 1898:68 (Wallowa L., Oregon). Jordan and Evermann, 1902:45, 1 fig. Henshall, 1906:3 (distribution, Montana). Halkett, 1913:17, 58 (distribution, habitat). Snyder, 1915:578 (characters; Columbia R. dr.). Jordan, Evermann, and Clark, 1930:104 (upper Missouri and Columbia R. basins). Churchill and Over, 1933:29, fig. 15 (characters, ecology; streams of Black Hills, South Dakota). Schultz and DeLacy, 1935:376 (Columbia R. dr.). Schultz, 1936:143 (characters; Columbia R. and upper Missouri R. basins). Hubbs, Hubbs, and Johnson, 1943:37, 58, pl. 4, fig. 3; pl. 7, fig. 3c (characters, hybridization with *Catostomus commersonnii sucklii*; Grace Coolidge Cr., French Cr., South Dakota; hybrid-

zation with *Catostomus catostomus griseus*; Sweetwater R., Wyoming). Rawson, 1947:5 (Cypress Hills, Saskatchewan). Dymond, 1947:14 (characters; Battle and Belanger crs., Saskatchewan). Simon, 1951:61, fig. 36 (characters, ecology; Missouri R. dr., Wyoming). Beckman, 1952:35, fig. 10 (characters; occurrence in S. Platte R. dr. of Colorado [unsubstantiated; specimen presumed to be that reported is here identified as *C. plebeius*, see p. 70, this report]). Bond, 1953:116 (Willamette R. dr.; possible recent invader) Lindsey, 1957:674, table 1; 665 (Similkameen R., near Princeton, British Columbia). Moore, 1957:92 (characters; upper Missouri basin; Willamette dr., Oregon). Eddy, 1957:75 (characters; upper Columbia R. dr.; headwaters, Missouri R.). Slastenenko, 1958a:167 (characters; distribution). Slastenenko, 1958b:6 (distribution). Carl, Clemens, and Lindsey, 1959:94, fig. 16b, 17 (characters, ecology; distribution in British Columbia; Similkameen R. system between the mouth of Otter Cr. on the Tulameen R. and Wolfe Cr. east of Princeton; North Thompson R., Heffley, Fraser R. system). Reed, 1962:30 (Swift Current Cr., Saskatchewan dr., Saskatchewan).

Catostomus griseus, Eigenmann, 1894:108 (Swift Current R., Saskatchewan).

Pantosteus araeopus, Jordan and Evermann, 1896:172 (characters; Kern R., California [= *C. occidentalis*]; Carson R., Reece R., Nevada). Jordan and Evermann, 1902:45 (in part).

Pantosteus lahontan Rutter, 1903:146, 1 fig. (original description, comparison with [*platyrhynchus*]; Susan R., Little Truckee R., Prosser Cr., California [misprint for *lahontan*]).

Pantosteus lahontan, Rutter, 1908:120 (North Fork Feather R., California). Snyder, 1915:578, pl. 76, fig. 2 (characters; Lahontan basin). Snyder, 1917:49 (characters, comparison, ecology; Long Valley Cr., Carson R., Quinn R., and Humboldt R., Nevada). Jordan, Evermann, and Clark, 1930:105 (Lahontan basin, Nevada). Murphy, 1941:167 (characters; North Fork Feather R., California). Hubbs, Hubbs, and Johnson, 1943:54, pl. 1, fig. 2c; pl. 7, fig. 2c (characters, hybridization with *Catostomus tahoensis*; Carson R. 2 mi. W Fallon, at Coleman Dam, and at Carson City; East Fork Carson R., Douglas Co.; Humboldt R., 3 mi. NE Lovelock; North Fork Humboldt R. near mouth; Hot Cr., 31.6 rd. mi. S Carlin; Truckee R., 3.3 mi. above Wadsworth, Nevada; Prosser Cr., 4.5 mi. N Truckee; Little Truckee R., 7 mi. E Truckee, and 14 mi. N Truckee; Buckeye Cr., 3 mi. N Bridgeport, and tributary below Highway 395, California). Moore, 1957:92 (characters; Lahontan basin, Nevada). Eddy, 1957:75 (Lahontan basin, Nevada). Bond, 1961:22 (characters; Lahontan basin in southeastern Oregon near McDermitt).

Pantosteus delphinus, Fowler, 1913:48 (Provo, Utah). Simon, 1951:60 (lakes of Green R. drainage, Wyoming). Sigler and Miller, 1963:101, 102 (upper Green R. dr., in part; Green R. L., Wyoming [after Simon, 1946]).

Pantosteus sp., Miller, 1946:518, table 1 (Feather R. dr., perhaps introduced). Miller, 1952:fig. 13 (Spring Valley, Nevada). Rostlund, 1952:267, map 15 (distribution). Miller, 1958:216 (zoogeography; Spring Valley, Great Basin). Miller, 1961:381 (Spring Valley, Nevada).

Pantosteus delphinus jordani, Miller, 1946:519 (headwaters of the Missouri R.).

Pantosteus [jordani = platyrhynchus], Miller, 1958:218 (zoogeography; Missouri R. headwaters).

RANGE.—Streams of the Great Basin in Utah, Nevada, and California; headwaters, North Fork Feather River, California; headwaters of the Green River in Utah, Colorado, and Wyoming; parts of the Columbia River drainage in Wyoming, Idaho, Washington, Oregon, and British Columbia; Fraser River drainage, British Columbia; upper Saskatchewan River drainage, Saskatchewan and Alberta; Milk River drainage, Montana and Saskatchewan; upper Missouri River drainage, Montana and Wyoming, and the

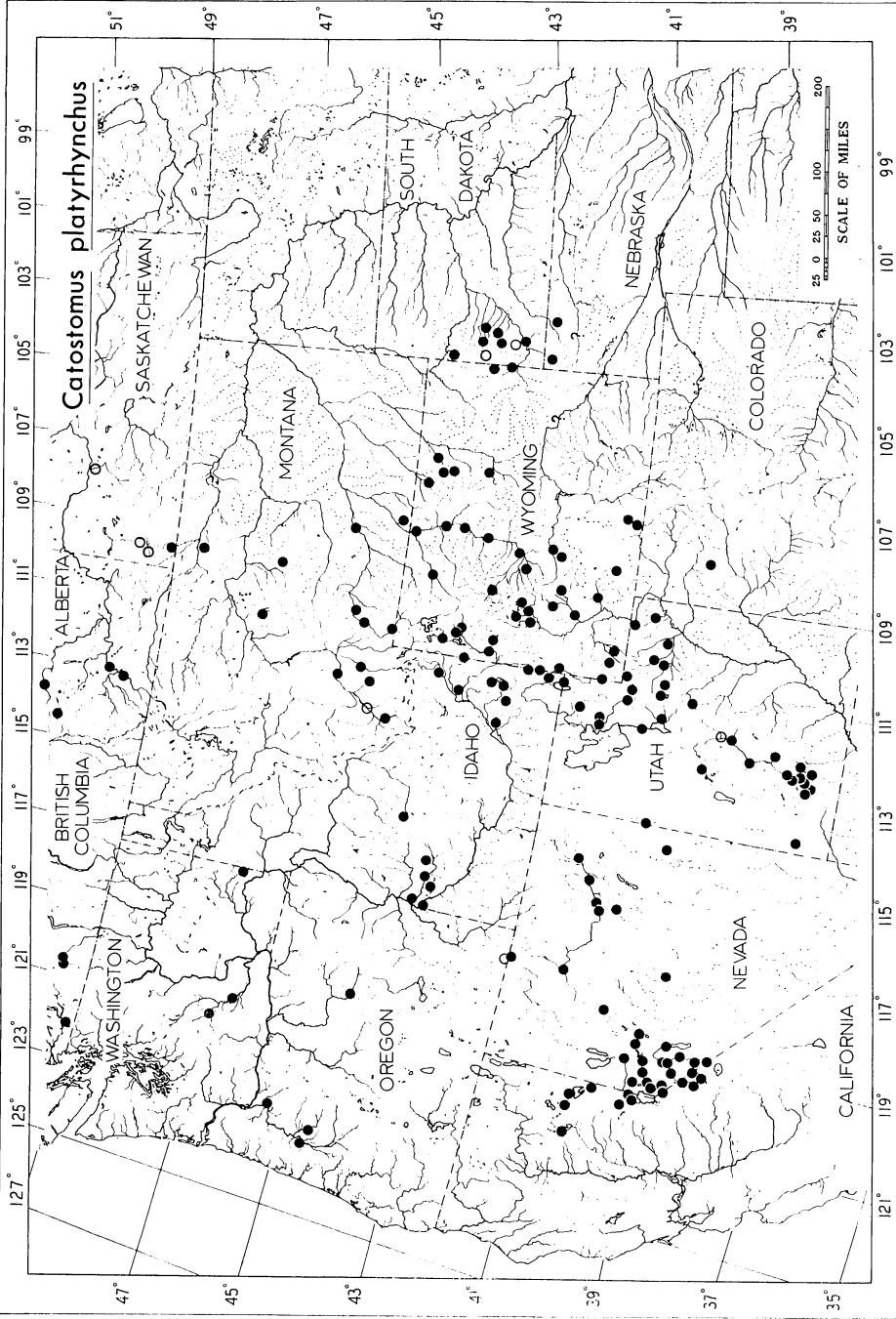


FIG. 13. Distribution of *Catostomus platyrhynchus*. Closed circles represent specimens examined, open circles represent records of specimens not seen. Question marks indicate questionable records (see p. 69-70).

Black Hills, South Dakota; White River and formerly, possibly, the Niobrara River, Nebraska (Maps, Figs. 1, 13).

DESCRIPTION.—Small catostomids, up to 175 mm in standard length; lips moderate in size; lower lip with large papillae except on anterolateral corners, the anteriormost of these arranged in a convex arch of about seven papillae; outer face of upper lip without papillae; lateral notches at juncture of upper and lower lips well developed; median notch of lower lip shallow, separated from lower jaw ridge by 3 or 4 rows of papillae; edge of lower jaw truncate, width moderate, usually 5 to 8 per cent of standard length; width of isthmus variable, usually 7 to 10 per cent of standard length; gill rakers, 23 to 37 on external row of first arch, 31 to 51 on internal row of first arch, with gill raker spines in two rows; fontanelle reduced to narrow slit, occasionally obliterated; peritoneum black or dusky; intestine long (6 times standard length in Black Hills, South Dakota, specimens, Bailey and Allum, 1962:78), 6 or 8, occasionally 10 intestinal coils anterior to liver; swimbladder moderately reduced, usually extending to origin of pelvic fins; scales in the lateral line, 60–108, usually 75–92; predorsal scales, 34–63, usually 44–55 in the Missouri, Green, and Columbia river drainages, usually 34–50 in the Great Basin and Upper Snake River; post-Weberian vertebrae, 38–44, usually 40–43; dorsal rays, 8–13, usually 10; pelvic rays usually nine; pelvic axillary process well developed; caudal peduncle usually deep, 8 to 10 per cent of standard length; color in life light yellowish ventrally, dusky brownish gray appearing abruptly on sides and thence over dorsum, melanophores with tendency to form pattern of diagonal lines determined by underlying scales, concentrating into a dark lateral band and/or 5 dorsal blotches, fins colorless or with faint reddish tinge, breeding specimens more highly colored including a deep red lateral band (see breeding coloration, ecology section); caudal pigmentation concentrated on rays, interradial membranes without pigment or with sparse or superficial melanophores.

COMPARISON.—See *plebeius*, p. 50; *santaanae*, p. 55.

C. discobolus adults are usually much larger; have smaller papillae which are more evenly dispersed over lower lip; gill rakers usually more than 30 on external row of first arch and usually more than 40 on internal row of first arch; fontanelle usually closed in adults; predorsal scales usually more than 50; post-Weberian vertebrae usually more than 42; dorsal rays usually 11; no pelvic axillary process; caudal interradial membranes heavily pigmented.

C. clarki has smaller papillae which are more evenly dispersed over lower lip; gill rakers usually more than 30 on external row of first arch and usually more than 40 on internal row of first arch; fontanelle usually closed in adults; predorsal scales often fewer than 35; post-Weberian vertebrae usually more than 42; pelvic axillary process absent; caudal interradial membranes heavily pigmented.

C. columbianus has papillae evenly dispersed over lower lip; lateral notches at juncture of upper and lower lips less developed; gill rakers with spines in clusters; gill rakers (except in Wood River populations) 30 or more on external row and more than 40 on internal row of first arch; fontanelle clearly open; lateral-line scales usually more than 90; predorsal scales usually more than 50; post-Weberian vertebrae usually 43–46; dorsal rays usually 12; no pelvic axillary process. Caudal interradiation membranes heavily pigmented.

Small *platyrhynchus*, 20–25 mm in standard length, can be distinguished from small *discobolus* or *columbianus* where sympatric by the lower vertebral number (see above); caudal pigment concentrated into vertical bands (not so in *discobolus* and *columbianus*); 12–13 ribs anterior to origin of pelvic fins (14–15 in *discobolus* and *columbianus*); lobes of lower lip separated by small median lobe; lower caudal rays relatively immaculate (pigment nearly equal on upper and lower lobes in *discobolus* and *columbianus*); melanophores smaller and tending toward cross-hatched pattern (larger and tending toward blotches in *discobolus* and *columbianus*).

VARIATION.—Intraspecific geographical variation is pronounced in *C. platyrhynchus*. The first of the major definable population groups is that of the Missouri River and Columbia River drainages, including populations from the Fraser and Saskatchewan rivers, but excluding those from above the falls of the Snake River. This large complex was formerly known as *Pantosteus jordani*. A second group is that from the Great Basin and upper Snake River, formerly separated as *Pantosteus lahontan* of the Lahontan basin and *Pantosteus platyrhynchus* of the Bonneville basin and upper Snake River. The third, somewhat intermediate series of populations, is in the upper Colorado River drainage.

These subdivisions of the species might be recognized as subspecies except that at no level of subdivision are the between-group differences significantly greater than the within-group variation. Therefore they are treated here as population groups to be recognized by average morphological distinctness and referred to by geography rather than formal nomenclature.

The Missouri drainage and Columbia drainage populations differ from other *platyrhynchus* groups in having, on the average, more post-Weberian vertebrae (Fig. 7), more predorsal scales (Fig. 8), and sparse pigment on the caudal interradiation membranes. Within this complex the Fraser River sample, though small, stands out with a mean of 11.5 dorsal rays. This population is also notable for the possession of wide lower jaws. Samples from tributaries of the east slope of the Black Hills, South Dakota, have a significantly higher number of pelvic fin rays ($\bar{X} = 9.8 \pm 0.10$) than other populations of the species ($\bar{X} =$ usually 8.9–9.4).

Specimens from the Saskatchewan drainage are notably undifferentiated from populations from the adjacent Missouri drainage. The similarity is

greatest in the direction of the Milk River samples. In fact, no significant differences exist between Saskatchewan and Milk River samples in any of the characters yet studied.

The samples from the Columbia River drainage below the falls of the Snake River tend to be extreme, for this species, in the slightly higher number of gill rakers and dorsal rays and the low number of lateral-line scales. This group of populations consists of widely scattered, possibly isolated representatives, and variation between demes is extreme in a number of characters.

The characteristics of specimens from the Colorado River drainage differ from those of the Missouri drainage and Columbia drainage groups primarily in the narrower average width of the isthmus and the lower average number of post-Weberian vertebrae. It is significant that the samples from the Sweetwater drainage, though geographically adjacent to the Green River drainage and by water only remotely connected to the rest of the Missouri drainage populations by the North Platte River, are still distinctly similar in these distinguishing characters to populations of the Missouri drainage. The vertebral number and widths of isthmus suggest that populations of the Colorado drainage are allied to those of the Great Basin. However, the higher number of predorsal and lateral-line scales indicates closer relationship to populations of the Missouri drainage. This discordance of characters suggests that *platyrhynchus* has been in the Colorado drainage long enough to have developed distinct character patterns and is not simply a recent derivative or an introduction from an adjacent drainage. The distribution of characteristics within the Colorado drainage is uniform with the exception of the high number of scales in the lateral line in the sample from Piceance Creek, Colorado, the most isolated population of the species in this drainage (range = 87–106, $\bar{X} = 97.2 \pm 2.3$; \bar{X} is less than 90 in other populations in the drainage).

An opportunity to check character stability over a short time interval resulted from the collection by Robert R. Miller, in 1960, of a sample from Bitter Creek, Wyoming, which repeated a series collected by Seth Benson in 1935. Comparisons of 7 characters in samples of 30 specimens from each collection showed remarkable homogeneity in each of the characters except width of isthmus, which showed a significant difference. Predorsal scales and dorsal rays show some difference in the range but none in the sample means. The depth of the caudal peduncle, number of scales in the lateral line, number of pelvic rays, and number of vertebrae show no significant differences between sample ranges, variance, or means.

Populations from the northern Great Basin and upper Snake River show a concordance of characters that suggests relatively recent genetic connections. The complex is marked primarily by the low number of predorsal scales and the immaculate caudal interradiial membranes. An unexpected

differentiation is the slightly higher number of vertebrae in populations from the southern Bonneville basin. The separation of the Sevier River system from the northern Bonneville basin is one of the most recent of the succession of isolating breaks in the pluvial Great Basin. Since no other such recently isolated population has differentiated, this variation may antedate the last pluvial period.

Three isolated population groups are associated with the Sevier drainage system. They are from Shoal Creek, Duck Creek, and Deep Creek Mountain. Of these, the Shoal Creek population in the extreme southeastern part of the Bonneville basin is most distinct. Specimens are distinguishable from other *platyrhynchus* by their dark pigmentation. In addition they have a higher average number of gill rakers, fewer lateral-line scales, narrower lower jaws, and deeper caudal peduncles. Apparently, Shoal Creek has been isolated from the Sevier River system at least since pluvial times.

The Duck Creek population from near the headwaters of the Sevier River differs from other Sevier River populations primarily in the greater average depth of the caudal peduncle, a characteristic in which it resembles the Shoal Creek population. The sample was collected at an elevation of about 8400 feet by Carl L. Hubbs who recorded the following observation (quoted with slight alteration from Hubbs' field notes):

The Duck Creek bottom is flooded by Duck Springs Reservoir. About two miles farther Duck Creek disappears in the Duck Creek Sinks, but soon reappears to enter Strawberry Creek which joins with Asay Creek, tributary to the upper part of the Sevier River. Prior to the relatively recent lava flow the bed of Navajo Lake formed the upper part of Duck Creek. The Creek consists of isolated pools above the area of seining which is about one tenth mile above the reservoir. It seems obvious that the fauna remains from what existed before the lava flows formed the sink and also formed Navajo Lake.

Other native fishes collected here were *Richardsonius balteatus hydrophlox*, *Gila atraria*, and *Gila copei*. The geology of this lava flow has been reported by Gregory (1949:979).

The populations inhabiting streams of the Deep Creek mountains, on the Utah-Nevada border at 40° North Latitude, show few distinctive features and appear to be more similar to the Sevier River populations than to those of the northern Bonneville or Lahontan basins according to vertebral number and number of predorsal scales.

A population of *platyrhynchus* formerly existed in the north end of Spring Valley, White Pine County, Nevada (Hubbs and Miller, 1948:56-57; Miller, 1952: fig. 13; Miller, 1961). These fishes are known from three specimens which possess typical *platyrhynchus* characters with an apparent tendency toward a thick caudal peduncle, as in the Shoal Creek and Duck Creek populations, and large lateral-line scales as in those from Deep Creek. Since this

valley (called Schell Creek Valley) was reported fishless by Cope and Yarrow (1875:668), the populations since recorded may have been introduced (R. R. Miller, personal communication).

Very little variation is apparent among populations within the streams of the Lahontan basin. Specimens from the Truckee River possess a slightly higher average number of dorsal rays and lateral-line scales. There is an apparent tendency for populations from the Truckee, Carson, and Walker rivers to have deeper caudal peduncles than those from the upper Humboldt (specimens from Hot Creek were emaciated, with slender caudal peduncles probably reflecting this physiological condition). In general, very little differentiation appears to have occurred in populations in the Lahontan basin. These fishes are remarkably similar to their counterparts in the northern Bonneville basin, differing only in the slightly lower average number of post-Weberian vertebrae.

Populations from the upper Snake River show clear affinities with those of the northern Bonneville basin. In contrast, they differ from adjacent populations of the lower Snake River and the Colorado drainage to the east in most of the characters studied. The upper Snake River has had recent hydrographic connections with the Bonneville basin (see p. 120).

Sharp interpopulation variation in the number of vertebrae occurs in the upper Snake drainage. Variation in other characters has not yet been analyzed in adequate series owing to the small size of the specimens presently in collections.

The specimens from the upper Snake River in Wyoming show a significantly lower number of vertebrae. Such tributaries as the Salt River and the Buffalo Fork contain specimens which appear to have the highest vertebral numbers. In general, the populations with fewest vertebrae are those which live in association with populations of *Catostomus discobolus*, which usually have 43 to 45 post-Weberian vertebrae in this drainage. The shift in number thereby results in reduced overlap in areas of sympatry. The selectional value of this character, although not yet known, is probably associated with growth and size parameters. Owing to the paucity of specimens the correlation suggested here is tentative.

HYBRIDIZATION.—The hybrid combination, *Catostomus platyrhynchus* × *Catostomus tahoensis* has been recorded from 13 localities in the Carson, Humboldt, Truckee, and Walker river drainages by Hubbs, Hubbs, and Johnson (1943:54). In all, 28 hybrid specimens were found in the collections which also contained approximately 2000 of each of the parental species. While recording data from specimens of *C. platyrhynchus* during the present study it was noted that certain populations showed skewness or otherwise unusual variation patterns in certain characters. This usually involved populations in or near areas of known hybridization. The extreme characters are

typical of *C. tahoensis* rather than *C. platyrhynchus* of the Lahontan basin. For example, UMMZ 140303, from the Carson River east of Carson City, Nevada, contains 6 of 20 specimens with sparse pigment on the caudal interradial membranes, a high incidence of abnormal pelvic fins, and a distribution of post-Weberian vertebral numbers of 39(2), 40(8), 41(11), 42(0), 43(1). *C. tahoensis* has pigmented caudal interradial membranes, usually more pelvic fin rays, and more vertebrae. The specimens which are extreme in the above characters are usually normal in all but one or two and are not, on the basis of the whole character system, interpreted as F_1 hybrids. Two well-marked F_1 hybrids were collected with the above sample and were recorded by Hubbs *et al.*, *ibid.* Such variational patterns in association with known hybrids are interpreted as circumstantial evidence for limited introgression.

Catostomus platyrhynchus has been reported in two additional crosses with species in the subgenus *Catostomus*—*C. commersoni* and *C. catostomus* (Hubbs *et al.*, 1943:37, 58). The former hybrids occurred at two localities in the Black Hills, South Dakota, and the latter in the headwaters of the Sweetwater River, Wyoming. The possibility of another record of the latter cross is discussed on p. 69.

The combination, *C. discobolus* \times *C. platyrhynchus* is recorded from localities in the Snake and Colorado River drainages in the species account of *C. discobolus*. Hybridization between *C. columbianus* and *C. platyrhynchus* has not been reported (see section on *C. columbianus*).

C. platyrhynchus is not known to hybridize in the Bonneville basin. The reproductive barriers between *C. platyrhynchus* and *C. ardens* in that drainage seem to be sufficient to prevent crossing. However, a single specimen taken from the Green River below the Farson road bridge, Sublette County, Wyoming, by Robert R. Miller and party, September 5, 1962, is here tentatively referred to that combination. The specimen has the following characteristics: standard length, 249 mm; depth of caudal peduncle, 9.2 per cent; width of isthmus, 4.4 per cent; width of lower jaw cartilage, approximately 5.2 per cent of standard length; scales in the lateral line, 72; scales before the dorsal fin, 37; scales around the caudal peduncle, 22; dorsal rays, 11; pelvic rays, 10–9; gill rakers, 33 on the external row and 40 on the internal row of the first arch; post-Weberian vertebrae, 43; caudal and dorsal interradial pigment present; pelvic axillary process present; fontanelle reduced to a narrow slit; intestine elongate, 8 anterior intestinal loops; peritoneum dark brown near gut, fading to hyaline dorsoposteriorly; gonad abnormal, apparently testicular but with several possible abnormal ova; lips with weak lateral notch; lower median notch separated from lower jaw by three rows of papillae; cartilaginous sheaths of jaws weakly developed. The deep peduncle, low scale counts, and presence of the pelvic axillary process coupled with the *Pantosteus*-like lip characters definitely indicate *C. platy-*

rhynchus as one of the hybrid parents. The other parent is a *Catostomus* (*s.s.*) with a deep peduncle and large scales, undoubtedly *C. ardens* or *C. commersoni*, each of which has been unofficially reported from the Green River drainage. Neither species is native there. *C. ardens* is tentatively suggested as the other parent on the basis of the presence of interradiial pigment in the dorsal fin, a characteristic of *C. ardens* but not of *C. commersoni* or *C. platyrhynchus*. The entire character complement of this hybrid specimen fits the expected intermediacy between *C. platyrhynchus* and *C. ardens*. The rarity of one of the parent species (*C. ardens*) in the drainage is conducive to the formation of a mixed breeding population (Hubbs, 1955).

ECOLOGY.—*C. platyrhynchus* has been collected in a wide variety of habitats. It is usually encountered in small mountain streams, 10 to 40 feet wide. However, a series was collected from the Yellowstone River by R. M. Bailey where the stream was 400–600 feet wide and the depth of capture was up to 8 feet. More often the depth of capture is less than 3 feet. Usual current conditions are moderate to swift, occasionally slight. Bottom type ranges from mud or sand to gravel and boulders, usually rubble. Associated vegetation includes *Potamogeton*, *Chara*, and attached algae. Pondweed and cress are occasionally found. Macroscopic vegetation is sometimes absent altogether. Water conditions range from clear to easily roiled or turbid. The altitudinal range for the species appears to be from 3900 to 8400 feet in the Great Basin and from nearly sea level to about 7000 feet in more northern drainages. Daytime summer water temperatures range from 10° to 28° C (50°–77° F), usually 15° to 23° C (60°–74° F). Winter temperatures extend to just above freezing. Specimens have been observed in Lower Green River Lake, Wyoming (Simon 1951: 61, as *P. delphinus*), and from Stanley Lake and Bear Lake, Idaho. The occurrence in lakes is rare but perhaps more common than for other species of the subgenus.

Food consists of algae and diatoms, and secondarily, small invertebrates. Other microscopic organic matter is undoubtedly of great importance. Large quantities of sand and silt are ingested.

Spawning apparently occurs during the late spring and summer months. Simon (1951:60) recorded spawning near Moran, Wyoming, on June 25, and spawning has been observed near Salt Lake City, Utah, in late May. Females containing well-developed eggs were taken in the Bonneville basin from the Sevier River near Hatch on June 9, from Deep Creek on June 9, from the Provo River on June 19, and from Duck Creek on June 26. Fry, 15 mm in standard length, were taken from the Sevier River on July 31. In Fremont Lake, Wyoming, of the Colorado drainage, specimens have been recorded (as *P. delphinus*) with well-developed eggs on July 14 (Simon, 1951:61). Specimens collected on July 22, from Bitter Creek, Wyoming, were spent. Fry, 9 mm in standard length, were collected in the Duchesne drainage, Utah,

August 13. In the Missouri River drainage, specimens taken in Rapid Creek on July 8 had well-developed eggs. Numerous other July collections from throughout that drainage contained spent adults.

Maturity is apparently reached at the end of the second or occasionally the first year. Nuptial males as small as 64 mm in standard length were collected in Bitter Creek, Wyoming, and Shoal Creek, Utah. Mature males are usually 80–110 mm and occasionally 140 mm in standard length, rarely larger. Females are usually larger, ranging from about 90 to 120 mm and up to 175 mm. A female from the Bear River drainage, Utah, 175 mm in standard length, appeared to be in the fourth or fifth year, and a male 127 mm in standard length from the Sevier River drainage, Utah, had three annuli on the scales.

Breeding coloration differs from the usual pattern primarily by the presence of a reddish lateral stripe. Mature specimens collected from Duck Creek, Utah, on June 26, 1950, by Carl L. Hubbs are described in the field notes as follows:

A greenish black stripe from the tip of the snout to just below the caudal base.

Above this is a very conspicuous golden orange-red stripe with even edges. The back is moss-green. Smaller fish with little of bright colors.

The primary, large breeding tubercles appear on the anal fin and lower caudal lobes of males and on the caudal peduncle above the anal fin of females. Smaller tubercles often appear on the sides, dorsum, head, gular, region, and all fins of both sexes. Dorsal fin tubercles are rare and pelvic and pectoral tubercles are usually limited to the distal part of the dorsal surface of the fins.

REMARKS.—Several doubtful records and collections of this species require special discussion. The record of occurrence in the Niobrara River at Marsland, Nebraska, is based on a single specimen, 105 mm in standard length, in the United States National Museum, USNM 76037. The specimen bears a paper field tag no. 407 and data indicating collection in 1893 by B. W. Evermann. However, the specimen was not reported by Evermann and Cox in the Missouri River basin Report (1896). Though the specimen appears to approach Missouri drainage *platyrhynchus*, certain characters, for example the depth of the caudal peduncle, the width of the lower jaw, and the number of predorsal scales, are not in agreement with observed characteristics of other Missouri drainage specimens. Dr. W. R. Taylor of the National Museum has searched accession papers at that institution and found that the original field number appeared to be 107, which was later changed on one of two copies to 407. Numbers 108 and 109 were assigned to *Catostomus commersoni* from the Marsland locality. The total combination of characters shown by the specimen does not exactly fit any known population of suckers. The closest agreement to a known specimen, in fact,

is to the hybrid between *Catostomus catostomus griseus* and *Pantosteus jordani* recorded from the North Platte drainage, Wyoming, by Hubbs, Hubbs, and Johnson (1943:58). Since *Catostomus catostomus* is also unknown from the Niobrara River, the status of the specimen must remain in question.

In the collection of the University of Michigan Museum of Zoology is a single specimen of *C. platyrhynchus* (UMMZ 87003 = MCZ 24908) collected by Samuel Garman in "Indian Creek, Northeast Wyoming Territory before 1880," and identified by Garman as *Catostomus griseus*. Of the several Indian Creeks in Wyoming the most likely localities for this collection are tributaries to the Cheyenne and North Platte rivers. The record is here questionably referred to the North Platte tributary on the basis of the possible association in the same collection of *Fundulus sciadicus* (*Zygonectes lineatus* Garman, 1881:88, Evermann and Cox, 1896:359), which is known from the North Platte but not the Cheyenne drainage.

The characteristics of *C. platyrhynchus* in the Sevier River drainage, Utah, are such that the presence of *C. discobolus* in that drainage would be significant. Such an occurrence would also be of importance to the interpretation of past hydrographic events in the northern Bonneville basin where *C. discobolus* lives at the present time. It is therefore of interest that in the collection of the U. S. National Museum is a series of four specimens (USNM 42703, F.C. 3118), one of which is *Catostomus discobolus*. Collector and date are not given, but the series was probably a part of the Jordan collections of 1889. However, the validity of these data is subject to question. Somewhat later a specimen of *C. platyrhynchus* was found in a series (USNM 104879) of *C. discobolus* from Delta, Colorado, also collected by D. S. Jordan and party, probably in 1889. The possibility of transposition renders the unique samples questionable.

A record of the occurrence of *Pantosteus jordani* in the South Platte drainage, Colorado, has been published by W. C. Beckman (1952). A specimen collected by the Colorado Game and Fish Department and sent to the University of Michigan Museum of Zoology (UMMZ 160745) bears the data "probably Antero Reservoir, adjacent to South Platte River, Park Co. 1950?" The specimen, 95 mm in standard length, has 9 dorsal rays, 43 predorsal scales, 21 gill rakers on the external row and 29 gill rakers on the internal row of the first arch, and is here reidentified as *Catostomus plebeius*. If the locality data are correct the specimen was probably the result of an introduction.

SPECIMENS EXAMINED

?NIOBRARA RIVER.—Nebraska, Dawes Co.: USNM 76037 (?Niobrara R. at Marsland, B. W. Evermann, 1893).

WHITE RIVER.—Nebraska, Dawes Co.: USNM 76036 (Chadron Cr., Chadron, B. W. Evermann, 1893).

CHEYENNE RIVER DRAINAGE.—**Nebraska**, Sioux Co.: UMMZ 134473 (Sowbelly Cr., trib. to Hot Cr., NE Harrison, R. E. Johnson, VII:1:1939). **South Dakota**, Lawrence Co.: UMMZ 161904, 163809, 166783, 177409. Pennington Co.: UMMZ 120386, 126925, 126929, 126932, 127505, 177400. Custer Co.: UMMZ 116373, 120382, 127501, 177406 = USNM 76033. Fall River Co.: UMMZ 177407. **Wyoming**, Weston Co.: UMMZ 120378, 127510, 127513.

POWDER RIVER DRAINAGE.—**Wyoming**, Johnson Co.: UMMZ 162417, 162424, 162425. Sheridan Co.: USNM 59145.

TONGUE RIVER DRAINAGE.—**Wyoming**, Sheridan Co.: UMMZ 160297, 162435.

BIG HORN RIVER DRAINAGE.—**Montana**, Big Horn Co.: UMMZ 173877. **Wyoming**: USNM 104810. Washakie Co.: UWZM 2075. Hot Springs Co.: UWZM 2077. Park Co.: UMMZ 159943, 159946, 159951. Big Horn Co.: UMMZ 159979, UWZM 2082. Fremont Co.: UMMZ 113444, 114636, 114647, 127563, 127566.

NORTH PLATTE RIVER DRAINAGE.—**Wyoming**, ?Converse Co.: UMMZ 87003 ("Indian Cr., NE Wyo. territory" S. Garman, before 1880). Fremont Co.: UMMZ 127540, 127547, 127556, 162931. Co.?: UMMZ 86679.

UPPER YELLOWSTONE RIVER DRAINAGE.—**Montana**, Yellowstone Co.: UMMZ 179515. Park Co.: UMMZ 105706, 156933, 173876.

MISCELLANEOUS UPPER MISSOURI RIVER TRIBUTARIES.—**Montana**, Fergus Co.: UMMZ 173875 (Beaver Cr., trib. Judith R. nr. Lewistown, C. J. D. Brown, VIII:13:1948). Cascade Co.: UMMZ 173872 (Otter Cr., trib. Belt Cr., N. Thoreson, VIII:26:1958). Jefferson Co.: UMMZ 94083 (S Channel Jefferson R., Cardwell, C. L. Hubbs, VI:13:1926). Madison Co.: UMMZ 173874 (Warm Springs Cr., S Sheridan, P. Graham, VII:2:1957); UMMZ 105562 (Madison L. nr. mouth of Meadow Cr., C. J. D. Brown, V:30:1936). Beaverhead Co.: USNM 43953, 125265 (Red Rock R. at Red Rock, B. Clapham, B. W. Evermann, VII:26:1891).

MILK RIVER DRAINAGE.—**Montana**, Blaine Co.: UMMZ 173873. **Canada**, **Saskatchewan**: UMMZ 164907 (trib. to Battle Cr., E Willow Creek Port of Entry, S. W. Corner, prior to 1928). **Alberta**: BC 56-6, 57-357.

SASKATCHEWAN RIVER DRAINAGE.—**Canada**, **Alberta**: BC57-359, 57-375, 57-361 (High Wood R., S Calgary, VI:16:1957); BC 56-616 (Bow R., Carseland, VII:21:1956); BC 57-362 (junction Blindman and Red Deer R., VI:17:1957).

GREEN RIVER DRAINAGE.—**Wyoming**, Sublette Co.: UMMZ 110094, 110129, 110132, 110140, 178623, 182484, 182491, UU 750. Sweetwater Co.: UMMZ 112922, 113436, 136939, 178619, 178630, 182505. Uinta Co.: UMMZ 92249 (Black's Fork, Fort Bridger, L. P. Schultz, VI:22:1931); USNM 104398, UMMZ 106409. **Utah**, Daggett Co.: UMMZ 167579, 179557. Uintah Co.: UMMZ 178660. Wasatch Co.: UMMZ 167594, (S51-28). Duchesne Co.: UMMZ 178636, 178655, 180070. Carbon Co.: UMMZ 176905. **Wyoming**, Carbon Co.: UWZM 2105, 2109 (Big Savery Cr., trib. to Little Snake R., trib. to Yampa R., WGF, VII:15:17:1956); UWZM 2098, 2116. **Colorado**, Rio Blanco Co.: UMMZ 178669 (Piceance Cr., 24 road mi. S St. Hwy 64, R. R. Miller, V:17:1960).

BEAR RIVER DRAINAGE.—**Wyoming**, Lincoln Co.: UMMZ 156945, 161797. Uinta Co.: UMMZ 132199. **Idaho**, Bear Lake Co.: UMMZ 141819, 141829. **Utah**, Summit Co.: UMMZ 176933, 176942. Rich Co.: UMMZ 141837. Cache Co.: UMMZ 158436, 160655.

OGDEN RIVER DRAINAGE.—**Utah**, Weber Co.: UMMZ 87005, 86855 (Ogden R., 12 mi. above Ogden, J. A. Allen, X:1871).

WEBER RIVER DRAINAGE.—**Utah**, Summit Co.: UMMZ 168969, 178647. Weber Co.: UMMZ 86900.

JORDAN RIVER DRAINAGE.—**Utah**, Salt Lake Co.: UMMZ 141450.

PROVO RIVER DRAINAGE.—**Utah**, Utah Co.: USNM 15763, 30807, 125264, 196399, UMMZ 85936, 87042, 141470, 141477, ANSP 18727-8, 18731-2.

SEVIER RIVER DRAINAGE.—**Utah**, Juab Co.: USNM 42703, 63291, 63322 (part). Millard Co.: UMMZ 141440. Sevier Co.: UMMZ 117853, 141689, 176870, 176872. Garfield Co.: UMMZ 85953, 117843, 117849, 141676, 141681, 141686, 156717, 156718, 156720, 176885, 176887, 176895. Kane Co.: UMMZ 156719, 160721, 176877. Piute Co.: UMMZ 176899. Beaver Co.: UMMZ 87109. Washington Co.: UMMZ 124776, 124777.

DEEP CREEK MOUNTAINS.—**Utah**, Tooele Co.: UMMZ 141407, 141414, 141415. **Nevada**, White Pine Co.: UMMZ 141409, 141411.

SPRING VALLEY.—**Nevada**, White Pine Co.: UMMZ 124785, 173944.

HUMBOLDT RIVER DRAINAGE.—**Nevada**, Elko Co.: UMMZ 124911, 141525, USNM 75273, 75281, 75755, 75757. Eureka Co.: UMMZ 124920, USNM 75846. Pershing Co.: UMMZ 124869, 141333. Lander Co.?: USNM 102090, 131314. Nye Co.: UMMZ 124891, 136210. Humboldt Co.: USNM 76290, 104878. Humboldt Co.?: USNM 75754.

SUSAN RIVER, TRIBUTARY TO HONEY LAKE.—**California**, Lassen Co.: USNM 50587, 75753, 76289, UMMZ 141552.

TRUCKEE RIVER DRAINAGE.—**California**, Sierra Co.: UMMZ 140236. Nevada Co.: UMMZ 133690, 140244, 162274, USNM 73670. **Nevada**, Washoe Co.: UMMZ 141541, 141634.

WALKER RIVER DRAINAGE.—**California**, Mono Co.: UMMZ 133111, 140352, 140364, 140368, 140392. **Nevada**, Douglas Co.: UMMZ 133087, 140335. Lyon Co.: UMMZ 133080, 133824, 140316, 140342, USNM 75752. Mineral Co.: UMMZ 133108, 140323, 140330, USNM 75756.

CARSON RIVER DRAINAGE.—**Nevada**, Douglas Co.: UMMZ 140272, 140286, 140291. Lyon Co.: UMMZ 136257, 140303, 140310, 141530. Churchill Co.: UMMZ 124856, 133809, 133817, 136234, 141341. Ormsby Co.: UMMZ 136250, 140296.

FEATHER RIVER DRAINAGE.—**California**, Plumas Co.: USNM 61190 (Warner Co. trib. to Feather R., Johnson's Reh. [NW Chester], Rutter and Chamberlain, IX:11:1898).

FRASER RIVER DRAINAGE.—**British Columbia**: BC58-321 (North Thompson R. 1 mi. S Hefley, VIII:24:1958); BC59-605 (Vedder R. at confluence with Fraser R., Lower Mainland, VIII:31:1958).

SIMILKAMEEN RIVER DRAINAGE.—**British Columbia**: BC56-89, BC56-413, BC56-488, BC55-398, BC56-89, BC59-477, BC56-374, UMMZ 179425.

YAKIMA RIVER DRAINAGE.—**Washington**, Yakima Co.: USNM 103659 (Yakima R., Zillah, L. A. Royal, XII:16:1930); UMMZ 98806 (Naches R., 5 mi. above Naches, L. P. Schultz, IX:2:1932).

WILLAMETTE RIVER DRAINAGE.—**Oregon**, Clackamas Co.: UMMZ 162983. Linn Co.: UMMZ 162982. Benton Co.: UMMZ 162981.

PALOUSE RIVER.—**Washington**, Whitman Co.: UMMZ 95039 (S Fk. Palouse R. 2 mi. above Pullman, L. P. Schultz, VI:15:1932).

STANLEY LAKE.—**Idaho**, Custer Co.: UMMZ 118079 (Stanley Lake, head of Salmon River, Challis Nat. For., I. A. Rodcheffer, VII:28:1934).

BOISE RIVER DRAINAGE.—**Idaho**, Boise Co.: UMMZ 144820. Ada Co.: UMMZ 141788, 169800, 169802. Canyon Co.: UMMZ 136227, 146675, 169803. Owyhee Co.: UMMZ 136200, 158895.

UPPER SNAKE RIVER DRAINAGE.—**Wyoming**, Teton Co.: UMMZ 110118, 127569, 156958, 156963. Sublette Co.: UMMZ 110106. **Idaho**, Caribou Co.: UMMZ 162327, 169806, 170946, 170954. Madison Co.: UMMZ 161816. Fremont Co.: UMMZ 157017, 169801. Teton Co.: UMMZ 169804. Bonneville Co.: UMMZ 162307. Bingham Co.?: USNM 48051, 48083, 48086, 48099, 48116.

JOHN DAY RIVER DRAINAGE.—**Oregon**, Grant Co.: USNM 104808 (John Day R., Dayville, L. P. Schultz, VI:11:1933).

Catostomus clarki Baird and Girard

NOMENCLATURE.—Syntypes: USNM 166, 167; *Catostomus clarki* Baird and Girard, 1854, is here employed as the specific name for the species previously divided as *P. clarki*, *P. intermedius* Tanner, 1942, *P. delphinus utahensis* (Tanner), 1932, and known but unnamed populations from the Bill Williams River drainage of Arizona.

SYNONYMY

Catostomus clarkii Baird and Girard, 1854:27 (original description, Rio Santa Cruz). Agassiz, 1855:208. Jordan and Copeland, 1876:156. Jordan, 1878a:416 ("Gila Basin").

Minomus clarkii, Girard, 1856:173 (characters; Rio Santa Cruz).

Minonus clarki, Girard, 1859:38, pl. 22, figs. 5–8 (characters; Rio Santa Cruz).

Catostomus clarki, Jordan, 1878b:165 (characters; Santa Cruz R., Arizona). Jordan, 1885:805. Kirsch, 1889:556 (Fort Thomas, Arizona).

Pantosteus arizonae Gilbert, in Jordan and Evermann, 1896:170 (original description; Salt R., Arizona). Gilbert, in Gilbert and Scofield, 1898 (description; Tempe, Arizona). Jordan and Evermann, 1902:45. Fowler, 1913:47 (Rio San Francisco, New Mexico).

Pantosteus clarki, Jordan and Evermann, 1896:172 (characters; Gila R. basin). Jordan and Evermann, 1902:46. Hubbs, Hubbs, and Johnson, 1943:40, pl. 1, fig. 3c, pl. 6, fig. 3c (characters, hybridization with *Catostomus insignis*; Taylor Cr., Gila National Forest, New Mexico; Middle Fork and West Fork of East Branch of Black R., Apache National Forest; Beaver R. and Verde R., Camp Verde, Arizona). Winn and Miller, 1954:284, figs. 3D, 4D (larval characters, Gila R. dr.). Eddy, 1957:75 (characters; lower Colorado R.). Moore, 1957:92 (characters; Gila R. system). Koster, 1957 (characters, ecology, New Mexico). Bailey *et al.*, 1960:18 (common name: Gila sucker). Miller, 1961:376, table 2; 378, table 3; 379 (San Pedro R., Salt R., Santa Cruz R., Ariz.).

Notolepidomyzon clarki, Snyder, 1915:575, pl. 76, fig. 1 (characters; lower Colorado R. basin). Jordan, Evermann, and Clark, 1930:104 (synonymy; Gila R. dr., Arizona). Tanner, 1942:29 (characters, Gila R. basin, Arizona).

Notolepidomyzon utahensis Tanner, 1932:135 (original description, comparison with *P. clarki*, *P. santanae*, and *P. delphinus*; Virgin R.; Fremont R. [misidentification?], Utah). Tanner, 1936:165 (Virgin R., Utah). Tanner, 1942:29 (characters; Virgin R. north to Green R. [misidentification?], Utah).

Notolepidomyzon intermedius Tanner, 1912:29 (original description, White R. Valley, Lund and Preston, Nevada).

Pantosteus delphinus utahensis, Hubbs, Hubbs, and Johnson, 1943:60 (characters, hybridization with *Catostomus latipinnis*; Virgin R., La Verkin, Utah); Wallis, 1951:87 (Santa Clara R., Utah; use as bait fish in Lake Mead). Miller, 1952:27, fig. 15 (characters; Virgin R., Utah). Winn and Miller, 1954:283, figs. 3B, 4B (larval characters; Burro Cr., Arizona). Miller and Hubbs, 1960:20 (Virgin R. dr., Utah, Arizona, Nevada).

Pantosteus platyrhynchus, Wallis, 1951:89 (misidentification of bait fish; L. Mead).

Pantosteus sp., Rostlund, 1952:267, map 15 (distribution). Miller, 1952:28 (characters; attributed to Spring Valley, [probably from Meadow Valley Wash, in part], Nevada). Winn and Miller, 1954:283, figs. 3C, 4C (larval characters; Williams R. system, Arizona). Miller and Hubbs, 1960:22 (Meadow Valley Wash, Nevada).

Pantosteus intermedius, Moore, 1957:93 (characters; White R., Nevada). Bailey *et al.*, 1960:18 (common name: White River sucker). Miller and Hubbs, 1960: 25, 27, 28 (White River., Nevada). La Rivers, 1963:337 (characters, distribution).

Pantosteus delphinus, Sigler and Miller, 1963:99, 101, 102 (characters [in part]; L. Mead, Bill Williams R., Arizona; [Virgin R., Utah]).

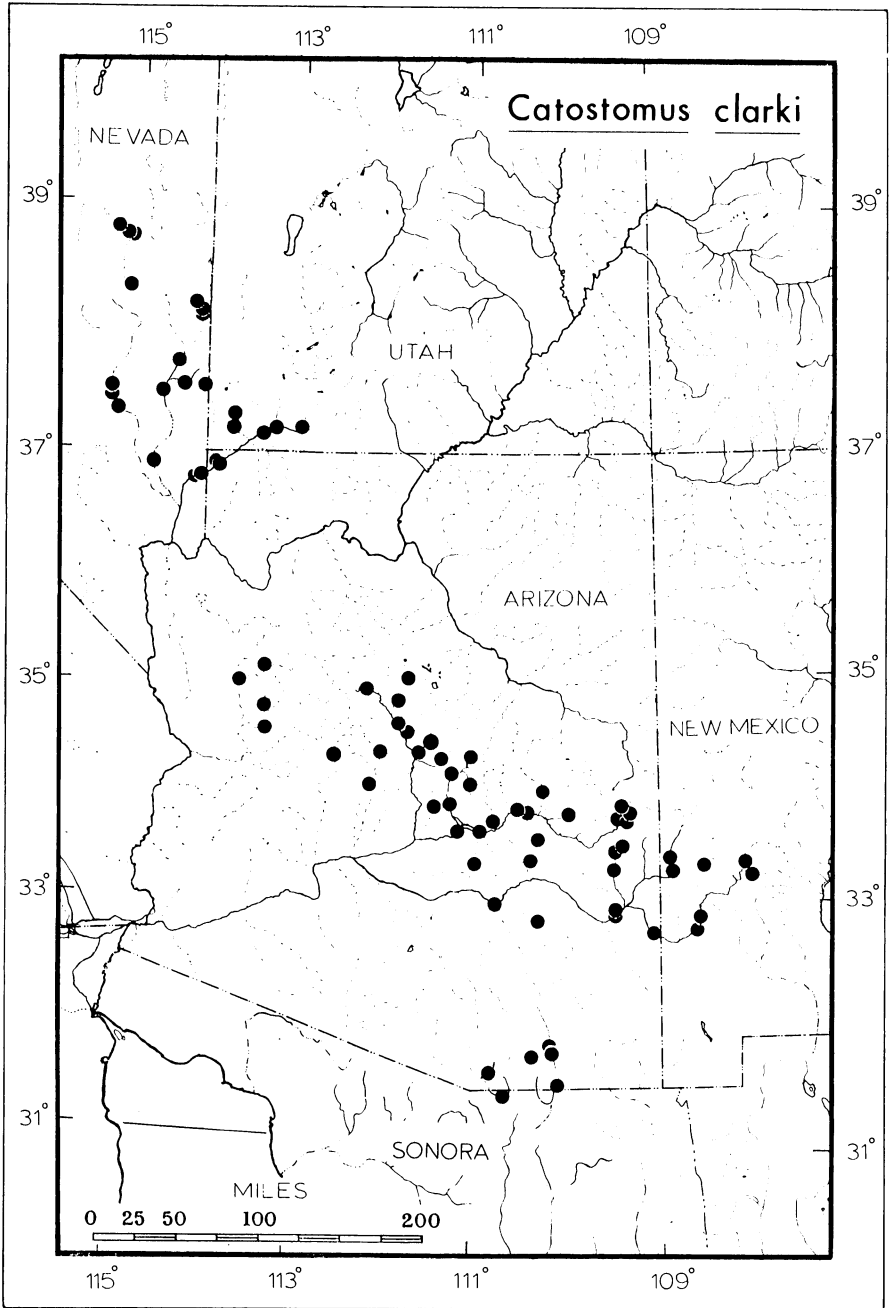


FIG. 14. Distribution of *Catostomus clarki*

RANGE.—Colorado River drainage below Grand Canyon; Gila River drainage, New Mexico, Arizona, and Sonora; Bill Williams River drainage, Arizona; White River drainage, Nevada; Meadow Valley Wash, Nevada; Virgin River drainage, Utah, Arizona, and Nevada (Maps, Figs. 1, 14).

DESCRIPTION.—Medium-sized catostomid fishes, attaining adult size of 100 mm to 280 mm in standard length; lips large with small papillae evenly dispersed over lower lip and oral face of upper lip, but absent from anterior face of upper lip; lateral notches at juncture of lower and upper lip well developed; median notch in lower lip shallow, separated from upper by 4 to 7 rows of papillae; ridge of lower jaw truncate, 4.1 to 8.7, usually 5 to 8 per cent of standard length; width of isthmus, 6.9 to 11.9, usually 8 to 11 per cent of standard length; gill rakers, 28–43 (usually 30–40) on external row and 38–59 on internal row of first arch in specimens over 70 mm in standard length; gill rakers with spines in two rows; frontoparietal fontanelle usually closed in adults, reduced in young specimens; peritoneum usually black, occasionally dusky; intestine long, up to 8.8 times standard length, with 6 to 16 coils anterior to liver, usually 10 or more coils in specimens over 70 mm in standard length; swimbladder reduced or not, length 15 to 30 per cent of standard length; scales in the lateral line, 61 to 104, usually 65 to 80 in the Gila drainage, 70 to 80 in the White River drainage, 75 to 90 in the Meadow Valley Wash and Beaver Dam Wash, and 80 to 100 in the Virgin River and Bill Williams River drainages; predorsal scales, 13 to 52, usually 15 to 30 in the Gila River drainage, 25 to 35 in the White and Williams River drainages, 30 to 40 in the Meadow Valley Wash, and 30 to 45 in most of the remainder of the Virgin River drainage (except 42 to 52 in Birch Creek); post-Weberian vertebrae, 41 to 47, usually 43 to 46 in the Gila River drainage and 42 to 45 elsewhere; dorsal rays, 8 to 12, usually 10 or 11; pelvic rays, 8 to 12, usually 9 or 10; pelvic axillary process reduced to a simple fold or absent; caudal peduncle, 6.9 to 11.2, usually 8.5 to 10 per cent of standard length; coloration silvery tan to dark greenish above, silvery to yellowish below; caudal pigment dispersed over fin rays and membranes.

COMPARISON.—See *plebeius*, p. 50; *santaanae*, p. 55; *platyrhynchus*, p. 62.

Differs from *C. discobolus* which usually has 50 or more scales before the dorsal fin. The overlap is graphed in Figure 8. All populations of *discobolus* except that of Plateau Creek on the upper Colorado have 47 or more predorsal scales. All *clarki* except the population from Birch Creek have 46 or fewer predorsal scales. Populations of *discobolus* in the vicinity of contiguity have slender caudal peduncles, the depth being less than 8 per cent of the standard length. The populations of *clarki* displaying overlap in the predorsal scale character all have deeper caudal peduncles, the depth being greater than 8 per cent of the standard length. The population of *clarki* from the Virgin River in Arizona and the adjacent population at the mouth of the

Beaver Dam wash show a reduction in caudal peduncle depth and therefore overlap with specimens of *discobolus* in this character. The populations of *clarki* in question have fewer than 45 predorsal scales (the adjacent Grand Canyon sample of 8 *discobolus* ranges from 49 to 57 with a mean of 53.6). Populations of *clarki* with the typical deep caudal peduncle (8 to 9.9, mean approximately 9 per cent of the standard length) exist in the Virgin River geographically between the populations of *clarki* with slender caudal peduncles and *discobolus* in the Colorado River. *C. clarki* from the Gila River drainage differs from *discobolus* in that they never have more than 85 lateral-line scales. Very few populations of *discobolus* contain specimens with fewer than 85 lateral-line scales.

C. clarki may be distinguished from *C. columbianus* which has less prominent lateral notches at the juncture of the upper and lower lips; less prominent and narrower lower jaw ridge; the frontoparietal fontanelle present in adults; predorsal scales usually more than 50; lateral-line scales usually more than 90; dorsal rays usually 11 or 12.

VARIATION.—*C. clarki* is composed of several geographical population groups, formerly considered species, which may be recognized by variation in the number of predorsal and lateral-line scales, the number of vertebrae, the width of the lower jaw, and the depth of the caudal peduncle. Notwithstanding the wide range of variation, none of the population groups is given taxonomic recognition here owing to the extensive overlap that exists in all of the known discriminating characters.

The largest group of populations with any degree of variational homogeneity is that of the Gila River drainage. Characterized by large lateral-line scales, wide jaws, modally 9 pelvic rays, and large predorsal scales, these fish are among the most highly specialized of the subgenus. The most striking characteristic is the large size of the predorsal scales. Most specimens have fewer than 25 scales before the dorsal fin, though three populations, Sycamore Creek of the Agua Fria drainage, the head of Tonto Creek, and the San Carlos River may have up to 33, with sample means of about 27. The sample means for the remainder of the populations range from 16 to 23. The variance is not great. The sample means for the number of scales in the lateral line are with few exceptions between 68 and 72.

Relatively little interpopulation variation occurs within this drainage. However, specimens from the Salt River seem to have more expansive, falcate fins, and some of the extreme southern populations have narrow jaws.

The fish most similar to the Gila River specimens are those from the White River drainage, Nevada, paradoxically, the populations farthest removed geographically. These formerly were known as *Pantosteus intermedius*. White River specimens have from 21 to 32 predorsal scales, the mean values being approximately 26 or 27. They have from 63 to 85 lateral-line scales, with

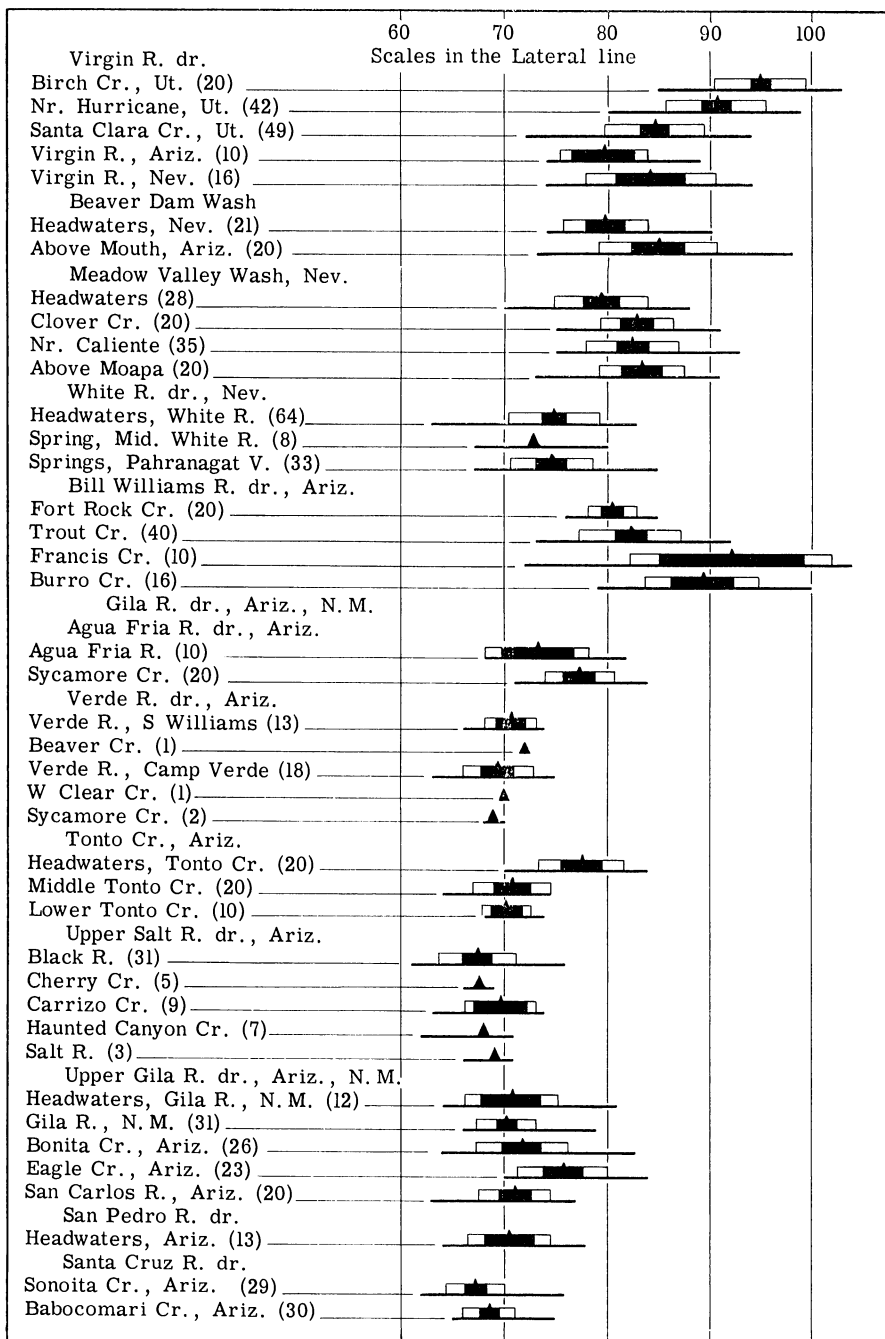


FIG. 15. Variation in the number of scales in the lateral line in *Catostomus (Pantosteus) clarki*.

means of approximately 75. The White River specimens also tend to have slenderer caudal peduncles, narrower jaws, and fewer pelvic rays than most *clarki* of the Gila River. However, all of the characters studied show nearly total overlap.

Just east of the White River drainage in Nevada is the Meadow Valley Wash. The stream of the Meadow Valley Wash harbors several populations of *Pantosteus*. Morphologically, these specimens tend to be intermediate between those of the White River drainage and certain populations of the Virgin drainage to the east, and show strong similarities to certain samples from the Bill Williams drainage to the south. However, part of the Meadow Valley Wash samples, especially from the lower part of the stream, show a tendency toward fewer vertebrae, being more extreme in this character than any other population group within *C. clarki*. The Meadow Valley Wash populations differ from those of the White River in the number of predorsal scales, having 29 to 42, with means of 34 to 36 in four populations, hence with little overlap. They also differ in having fewer vertebrae, more scales in the lateral line, and thicker caudal peduncles (although the sample of 41 specimens from near Caliente have slender peduncles). These differences between the White River and Meadow Valley Wash populations mark the sharpest break within the variational cline which characterizes *C. clarki*, and might be considered the basis for taxonomic recognition except that the differences are spanned by variation within other drainages, particularly the Bill Williams drainage.

The populations of the Bill Williams River drainage in western Arizona are geographically interjacent between southern (Gila River) and northern (Utah and Nevada) populations of *clarki*. Four samples from this drainage show considerable variation although they are in close proximity to each other and isolated from other populations. These samples include two from the north, Fort Rock Creek and Trout Creek, and two from the south, Burro Creek population from the other three which are probably the same. They differ in the number of predorsal and lateral-line scales, and possibly, the number of pelvic rays. The southern samples have the higher values in each of the scale characters. However, each of these characters indicates a different direction of resemblance when compared with the other populations of *clarki*. The measurements of the width of the mandible distinguish the Burro Creek population from the other three which are probably the same. The small sample from Francis Creek displays an abnormal range of variation in the number of scales in the lateral line, from 72 to 104 in 10 specimens. The same 10 specimens failed to show abnormally high variance in the other characters examined, however, and there was no correlation of extremes in this character with patterns shown by other characters within the sample.

The next major drainage system to the east of the Meadow Valley Wash in the Virgin River drainage is the Beaver Dam Wash. Two samples were available, from the headwaters and from the mouth of the stream. The headwater population shows its greatest similarity to the samples of the adjacent Meadow Valley Wash, but fish from the mouth of the stream show some morphological similarity to the adjacent population of the Virgin River (p. 23). The vertebral number in the specimens of the Beaver Dam Wash is discordant with the general pattern. The sample from the headwaters indicates affinities to the east in the Virgin River drainage rather than to the west.

Within the Virgin River drainage, variation occurs in the number of predorsal scales and depth of the caudal peduncle. The number of scales shows a general tendency to be greater in populations higher in the headwater streams (Fig. 8). The extreme known population, in Birch Creek, is not particularly high, but happens to be in a cool spring effluent in Zion National Park, Utah (with late afternoon temperature of 16.5° C on May 13, 1964). It is probable that the unusually high number of scales is a response to local temperature conditions rather than an indication of relationship. It appears that the headwater populations of the Virgin River in general have a higher number of scales than do those of the Santa Clara River. The latter have the same number as do samples from the lower Virgin River and the western Beaver Dam Wash and Meadow Valley Wash. Specimens from the Virgin River drainage, including the Santa Clara, have reduced numbers of gill rakers compared with the remainder of the *clarki* populations, including those from the Beaver Dam Wash and the Meadow Valley Wash.

As the Virgin River traverses the Utah-Arizona state line it passes through a canyon of rapids commonly called "the narrows." Within this canyon the river drops approximately 33 feet per mile for 12 miles. This gradient is comparable to that of the Green River in the canyon areas (12 feet per mile) and the Grand Canyon of the Colorado (approximately 25 feet per mile). It is therefore interesting that a swift-water form which parallels the swift-water fishes known from the Green and Colorado rivers has evolved in this section of the Virgin River. The primary characteristics of this adaptation to rapids include increase in fin size and decrease in the depth of the caudal peduncle. Figure 16 shows the statistics for the slender caudal peduncle in the sample from the Virgin River in Arizona. The intermediate depth of peduncle in the specimens from the mouth of the Beaver Dam Wash indicates intergradation between the tributary form and the population in the Virgin River in Arizona. The populations live within a few feet of each other where the Beaver Dam Wash joins the Virgin River.

HYBRIDIZATION.—This species hybridizes with *C. insignis* in the Gila River drainage, New Mexico and Arizona. Six hybrid occurrences have been documented (Hubbs, Hubbs, and Johnson, 1943:40). A single hybrid speci-

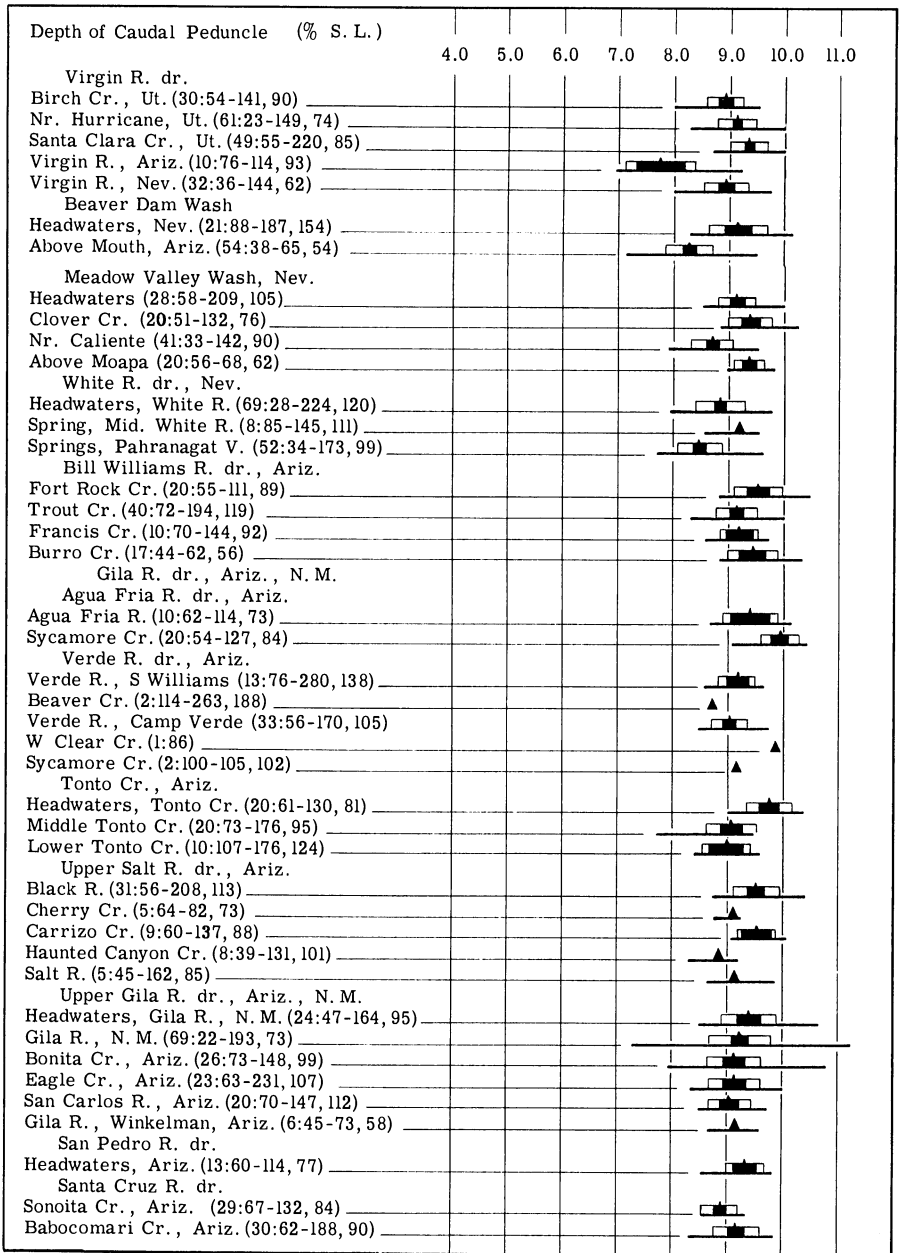


FIG. 16. Variation in the depth of the caudal peduncle in *Catostomus clarki*. The stability of this character in this species contrasts markedly with the wide variation in *C. discobolus* (Fig. 19). The sample from the mouth of Beaver Dam Wash is intermediate between the extreme form in the adjacent Virgin River in Arizona and the population in the headwaters of Beaver Dam Wash.

men between *C. clarki* and *C. latipinnis* is also known from the Virgin River drainage, Utah (*ibid.* p. 60).

An additional record of the *clarki* × *insignis* hybrid cross is represented by a 90-mm specimen (UMMZ 182083) from the Gila River, T.15S, R.17W, Grant Co., New Mexico, collected by C. L. Hubbs, June 30, 1938. The specimen has the depth of caudal peduncle 10.4, isthmus width 8.3, and width of lower jaw 5.8 per cent of the standard length; 69 scales in the lateral line; 25 predorsal scales; 29 gill rakers on the external row and 36 gill rakers on the internal row of the first arch; a rounded jaw and intermediate lips; only 3 rows of papillae separating the lower lip incision from the lower jaw (4 to 8 rows in the remainder of 25 specimens examined); and 43 post-Weberian vertebrae. The caudal peduncle, isthmus, and lower jaw measurements plus the gill-raker counts and lip characteristics, compared with the *clarki* and *insignis* characters (see Hubbs, *et al.* 1943:40) mark the specimen as a hybrid.

ECOLOGY.—*C. clarki* is found in a variety of large and small desert and mountain streams. Current velocity is variable, ranging from the swift waters of the Virgin River in Arizona (observed current velocity of 4 to 6 feet per second) and the montane tributaries of the Gila system to pools or sluggish streams with little current. Depth of capture is usually less than 2 feet. Observed bottom materials include sand, rubble, boulders, mud, and bedrock. Associated vegetation types include algae, watercress, and pondweed. The known altitudinal range is approximately 2000 to 8000 feet. Winter temperatures approach freezing in northern and high-altitude habitats. Daytime summer temperatures have been observed between 16° and 28° (61–83° F).

Food consists of microscopic periphyton and other microscopic organic matter, occasionally invertebrates. Much sand and silt is ingested and passes through the alimentary tract.

C. clarki spawns in early spring. Specimens from Babocomari Creek, at the southern part of the range, were spent on April 2, when postlarvae 10 mm and longer were taken. Spent individuals have been collected April 8 in the Bill Williams drainage and in May at many localities in the southern as well as northern parts of the range. Postlarvae 10 to 20 mm and longer have been collected from many parts of the range in April, May, and June. The major part of the year's growth occurs in June, July, and August according to population histograms prepared from preserved collections. Maturity is reached at the end of the second year, usually at a size of about 100 mm in standard length, but varying from 85 to 120 mm depending on the population. Females appear to be slightly larger than males. The maximum recorded size is about 380 mm. Specimens over 200 mm in standard length are usually three to five years old. In at least the northern populations the breeding coloration of both sexes includes an orange-red lateral stripe.

SPECIMENS EXAMINED

SALT RIVER DRAINAGE.—**Arizona**, Coconino Co.: USNM 131855, UMMZ 162809, 162812. Yavapai Co.: UMMZ 120079, 120093, 120103, 125015, 125027, 125034, 146700, 162817, 162826, 162836, USNM 39583, 39590, 41573, 146106. Gila Co.: UMMZ 94878, 94884, 113537, 120087, 120089, 131101, 131107, 131119, 162759, 162772, 162776, 162786, 162792, 162802, 162805, 162822, USNM 129960, 130006, 130014, 130016, 130019. Maricopa Co.: UMMZ 131115, 162797, USNM 48126. Apache Co.: UMMZ 121637, 121639, 121640, 121645, 121659, 121664. Navajo Co.: UMMZ 162765. Pinal Co.: UMMZ 176177, 176178.

GILA RIVER DRAINAGE.—**New Mexico**, Catron Co.: UMMZ 110432, 118167, 118171, 118176, 118185, 120085, 162726, 162732. Grant Co.: UMMZ 124743, 162723, 162737, USNM 132253. **Arizona**, Greenlee Co.: UMMZ 102865, 131124, 162714, 162718, 162741. Graham Co.: UMMZ 162708. Gila Co.: UMMZ 162755, 162756. Pinal Co.: UMMZ 146664.

SAN PEDRO RIVER DRAINAGE.—**Arizona**, Graham and Pinal Cos.: UMMZ 162750. Cochise Co.: USNM 129975, 129978, 130205, UMMZ 137064, 137065.

SANTA CRUZ RIVER DRAINAGE.—**Arizona**, Santa Cruz Co.: USNM 132360, UMMZ 85817, 125044, 129998. Cochise Co.: UMMZ 162691, 162694, 162697. Co. unknown: USNM 166, 167, 129985. **Mexico**, **Sonora**: UMMZ 157238.

BILL WILLIAMS RIVER DRAINAGE.—**Arizona**, Yavapai Co.: UMMZ 162829, 162830. Mohave Co.: UMMZ 157683 (=USNM 146095), 162651, 162658, 165920, 165921, (=USNM 146100).

VIRGIN RIVER DRAINAGE.—**Utah**, Washington Co.: UMMZ 85952, 124759, 124763, 124768, 141671, 156716, 162848, 170977, 177098, USNM 104416, 132852. **Arizona**, Coconino Co.: UMMZ 141660, 141664, 141665. **Nevada**, Clark Co.: UMMZ 105494, 125012, 141657. Lincoln Co.: UMMZ 177458.

MEADOW VALLEY WASH DRAINAGE.—**Nevada**, Lincoln Co.: UMMZ 124791, 124794, 124795, 124797, 124800, 124825, 177092.

WHITE RIVER DRAINAGE.—**Nevada**, White Pine Co.: USNM 120169, UMMZ 124976, 124979, 124983, 126166, 132179. Nye Co.: UMMZ 124988. Lincoln Co.: UMMZ 124802, 124806, 124811, 125000.

Catostomus discobolus Cope

NOMENCLATURE.—Holotype: apparently lost, but may be in the collection of the Academy of Natural Sciences of Philadelphia. The original description is repeated here from Cope, 1871 (1872): 435, in Hayden's Geological Survey of Wyoming, etc.

Remarkable for its very large lips especially the upper. In general it is allied to *griseus*, being of the same cylindrical form. Upper lips pendant, and somewhat expanded all round. Its margin extends outside that of the lower lip, where it joins it, thus forming an entering right angle with it. The commissural margins of both are wide and abruptly separated from the tuberculated portion. Tubercles sub equal; those of lower jaw projecting in a convex enlargement, concentric with the lower commissure; behind deeply incised. Muzzle projecting a little beyond upper lip; head wide, flat above; eye superior, small, entering length of head 5.5 times; three times in muzzle. Pharyngeal bones expanded below; teeth delicate laminar, with acute inner cusp. Length of head entering total to end of caudal scales, four and a half times; ventral fins originating opposite posterior third of dorsal, barely reaching vent; pectorals well separated; isthmus very wide. Radii D.11; A.8; V.9; scales in 38-40, longitudinal series between dorsal and ventral fins; color olive brown above, black on head, passing into light yellow below, gradually on the body, abruptly on the head.

The description applies best to the large *Pantosteus* of the Green River drainage, previously called *Pantosteus delphinus*. The characterization of the lips, particularly, is probably the best in the literature for the distinctive *Pantosteus* lip configuration. Cope and Yarrow (1875:673) referred to the fact that the fontanelle is reduced in *Catostomus discobolus*, and Jordan (1878b:179) remarked that "*C. discobolus* . . . is a *Pantosteus* in all but the technical character of the open fontanelle . . . really intermediate as the fontanelle, in the adult at least, is reduced to a narrow slit."

Catostomus discobolus is here intended to include *Pantosteus* "*delphinus*" populations of the Colorado River drainage above Grand Canyon, *Pantosteus* "*virescens*" of the Weber and Bear rivers of the Bonneville basin, and also several populations from the upper Snake River formerly misidentified as *P. platyrhynchus* or *P. jordani* (but not misidentified by Jordan who apparently had examples of this species from the Snake River in hand when he wrote the above remarks on *C. discobolus*).

A gill tag discovered by Robert R. Miller under the opercle of the type specimen of *P. virescens* gives the locality as Pagosa, Colorado, thus making the name *virescens* unavailable for application to the Bonneville basin populations should these be judged taxonomically distinct in the future.

Specimens taken from the headwaters of the Zuni River, tributary to the Little Colorado River, are here referred to *Catostomus discobolus* although they show extraspecific variation (see p. 86). Some comments on the taxonomic history of these populations may be useful in this connection. Jordan, Evermann, and Clark, 1930:105 placed *Minomus jarrovi* Cope in the synonymy of *P. platyrhynchus*, gave the original type locality as "near Provo," and reported that the types were lost. The original description, which contains the information "Radii D.9," and "Commissure with acute cartilaginous edge, regularly convex forwards," can only apply to *Catostomus plebeius* or the populations from the headwaters of the Zuni River, recently rediscovered by W. J. Koster (but since destroyed by stream reclamation, R. R. Miller, personal communication). The correction of the type locality by Cope and Yarrow (1875:675) to the Zuni River, New Mexico, though long ignored by ichthyologists, thus allows the correct application of the name *jarrovi* to the Zuni River populations, should anyone wish to recognize these taxonomically.

SYNONYMY

Catostomus discobolus Cope, 1872:435 (original description; "Two specimens, one certainly, the other probably, from the Green River, Wyoming"). Cope and Yarrow, 1875:677 (Zuni R., New Mexico, Arizona). Jordan and Copeland, 1876:156. Jordan, 1878a:416 ("Colorado basin; Snake River, Idaho"). Jordan, 1878b:179 (characters: Idaho to Arizona). Jordan and Gilbert, 1882:125 (characters; "Idaho to Wyoming and Arizona"). Jordan, 1885:805.

Minomus jarrovi Cope, 1874:135 (original description: "obtained by messrs. Yarrow

and Henshaw at Provo," [Utah]; but attributed to the Zuni R., New Mexico, by Cope and Yarrow, 1875:675).

Pantosteus jarrovi, Cope and Yarrow, 1875:674, pl. 29, figs. 2, 2a (characters; Zuni R. in part; misidentification of *P. plebeius* in part).

Pantosteus virescens Cope, in Cope and Yarrow, 1875:675 (original description; "One species [*sic*] accompanying an *Amiurus*, which is marked Arkansas River, at Pueblo," however, a gill tag of the Wheeler survey gives the locality as Pagosa, Colorado). Jordan and Copeland, 1876:156. Jordan, 1878a:416 ("Arkansas River"). Jordan, 1878b:182 (characters; Arkansas R.). Evermann, 1893a:54 (synonymy; "not sure that this is really distinct from *P. discobolus* and doubt if the specimen came from the Arkansas River"). Snyder, 1924:1-8 (characters; comparison with *P. platyrhynchus*; Weber R., Bear R., Utah). Jordan, Evermann, and Clark, 1930:105 (Weber R., Bear R., Utah). Moore, 1957:92 (characters; Weber R., Bear R., Utah). Miller, 1958:212 (zoogeography; Bonneville basin, upper Snake R.). Sigler and Miller, 1963:103, 1 fig. (characters, ecology; Bear R., Utah, Idaho, and Wyoming; Weber R., Utah; upper Snake R. dr., Idaho).

Pantosteus yarrowi, Jordan and Copeland, 1876:156.

Pantosteus plebeius, Jordan, 1878b:184 (characters, misidentification in part; Colorado basin). Fowler, 1913:47, 48 ([Rio Puerco?], Fort Wingate; [Nutria Cr.], Nutria, New Mexico).

Pantosteus generosus, Jordan, 1878b:183 (characters, misidentification in part; Colorado basin).

Pantosteus delphinus, Jordan, 1891a:20, 27 (characters, habits, Colorado). Evermann and Rutter, 1895:481 (synonymy; distribution in Colorado R. basin). Jordan and Evermann, 1896:171 (characters; Colorado R. dr.). Jordan and Evermann, 1902:46. Ellis, 1914:29, fig. 9 (characters, color description, food; Colorado). Snyder, 1915:577 (characters, comparison; Colorado R. dr.). Jordan, Evermann, and Clark, 1930:104 (synonymy; upper Colorado R. dr., Colorado and Wyoming). Nelson, 1948: pl. 3, fig. 8 (morphology of Weberian apparatus). Simon, 1951:60, fig. 35 (characters, ecology; Green R. dr., Wyoming). Moore, 1957:92 (characters; Colorado R. dr.). Eddy, 1957:74, [fig. 180 misidentified] (characters; upper Colorado R. dr.). Miller and Hubbs, 1960:31 (Little Colorado R. dr., Arizona). Sigler and Miller, 1963:100, 1 fig. (characters, ecology; upper Colorado R. dr.). Miller, 1963:5 (Clear Cr., Little Colorado R., Arizona).

Pantosteus discobolus, Evermann, 1893a:55 (synonymy, characters; *C. discobolus* Cope selected as senior synonym in taxon including *M. delphinus* Cope and *M. bardus* Cope. [Construed as action of first reviser]). Miller, 1964:28 (fig., ecology, Green R.).

Pantosteus delphinus delphinus, Hubbs, Hubbs, and Johnson, 1943:39, pl. 5, fig. 3 (characters, hybridization with *Catostomus commersonnii sucklii*; Colorado R., Hot Sulphur Springs, Colorado; Gunnison R., Olathe, Colorado). Hubbs and Hubbs, 1947:147 (hybridization with *Catostomus latipinnis discobolus*; Beaver Cr. and Gunnison R., Colorado). Beckman, 1952:34, 1 fig. (characters, ecology; Colorado dr., Colorado). Miller, 1952:27, fig. 16 (Colorado R. dr.; use as bait, L. Mead).

Pantosteus sp., Rostlund, 1952:267, map 15 (distribution).

RANGE.—Colorado River drainage above the mouth of Grand Canyon, Wyoming, Colorado, New Mexico, Arizona, and Utah; Snake River drainage above the great falls, Idaho and Wyoming; Bear River drainage and Weber River drainage of the Bonneville basin, Idaho, Wyoming, and Utah (Maps, Figs. 1, 17).

DESCRIPTION.—Small to medium catostomid fishes, attaining adult size of

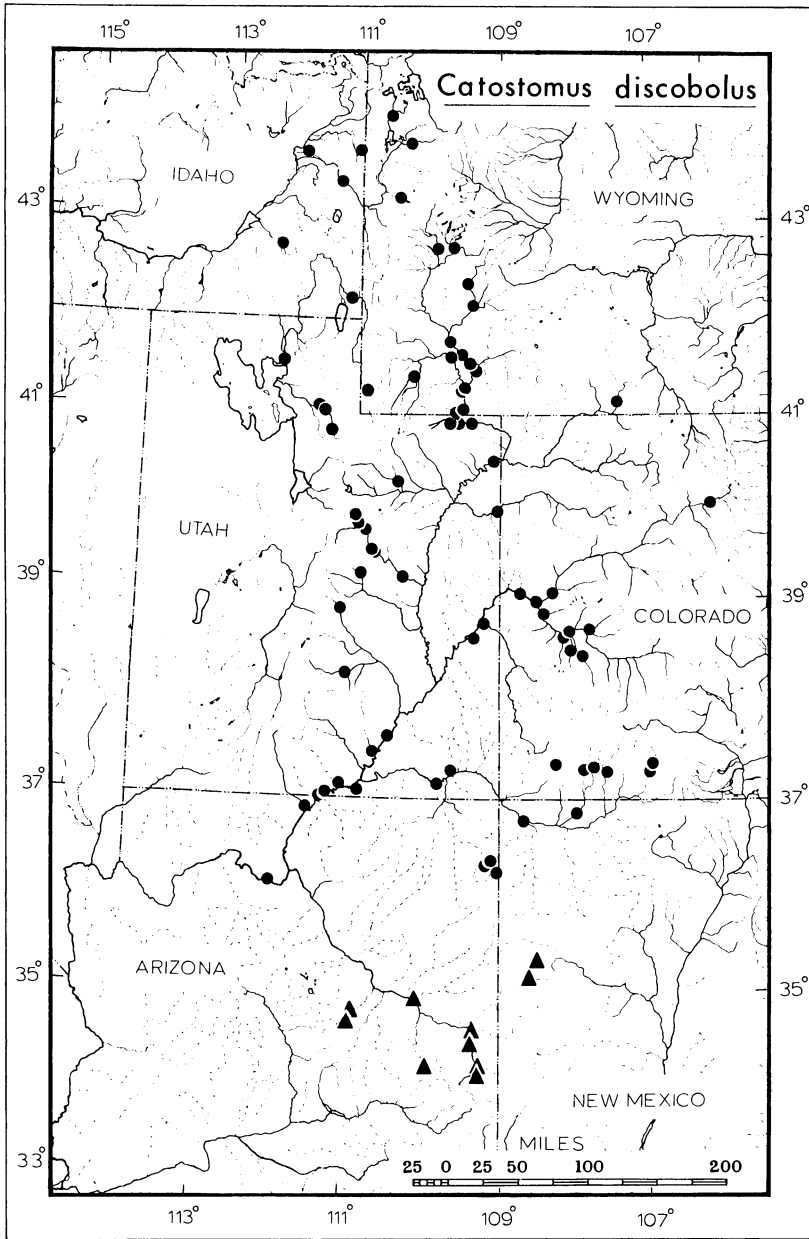


FIG. 17. Distribution of *Catostomus discobolus*. Triangles represent records in the Little Colorado River drainage.

80 to 400 mm in standard length; lips large, with small papillae evenly dispersed over lower lip and oral face of upper lip, but absent from anterior face of upper lip; lateral notches at juncture of upper and lower lips well developed; median notch in lower lip shallow, separated from lower jaw ridge by 3–5 rows of papillae; ridge of lower jaw truncate, width, 4.8 to 8.3, usually 6 to 7.5 per cent of standard length; width of isthmus, 6.2 to 11.5, usually 7.5 to 10 per cent of the standard length; gill rakers, 28 to 44 (usually more than 30) on external row and 37 to 60 (usually more than 40) on internal row of first arch in specimens over 70 mm in standard length (except in the Little Colorado River drainage where counts as low as 26 on the external row and 34 on the internal row have been recorded); gill rakers with spines in two rows; frontoparietal fontanelle usually closed in adults, reduced in immature specimens; peritoneum dusky to black (but silvery or speckled in parts of the Little Colorado River drainage); intestine long, 6 to 14 loops anterior to liver; swimbladder reduced, diameter of posterior chamber often reduced to diameter of eye, correlated with habitat; lateral-line scales, 78 to 122, usually 90 to 110; predorsal scales, 44 to 75, usually 50 to 65; post-Weberian vertebrae, 39 to 46, usually 40 to 42 in the Little Colorado drainage, 43 to 45 elsewhere; dorsal rays, 8 to 12, usually 10 to 12 (greater variability in the Little Colorado drainage); pelvic rays, 7 to 11, usually 8 to 10; pelvic axillary process absent; caudal peduncle often slender, 4.2 to 10 per cent of standard length, correlated with habitat; coloration silvery tan to dark green above, silvery to yellowish below, depending on habitat; caudal pigment dispersed over interradiial membranes as well as rays.

COMPARISON.—See *plebeius*, p. 50; *santaanae*, p. 55; *platyrhynchus*, p. 62; *clarki*, p. 75.

Differs from *columbianus* which has smaller, rounded lips with reduced notches at the juncture of the upper and lower lips, or such notches absent; jaw narrower, usually less than 6.5 per cent of standard length, less truncate; fontanelle always well developed; dorsal rays usually 11–13; pelvic rays usually 10 or 11; head often larger, usually more than one-fourth standard length (usually less than one-fourth standard length in adult *discobolus*), but much overlap exists.

VARIATION.—Isolation of populations within this species is extensive and considerable variation is probably associated with it. However, two additional factors are of unique importance. They are: the local effect of introgression of *C. plebeius* characters on the populations of the Little Colorado River, and the relationship between habitat and caudal-peduncle depth throughout the species.

The Little Colorado River is a northwest-flowing tributary to the Colorado River above Grand Canyon, with headwaters in east-central Arizona and west-central New Mexico. A barrier falls well above the river mouth prevents

upstream movements of Colorado River fishes in the Little Colorado River. Transient barriers also exist between populations within the system as a result of desiccation of much of the river except during floods.

It is reasonable to assume that the original stock of *Catostomus discobolus* in the Little Colorado River gained access to the system before the advent of the falls and was at least as generalized as present day populations in the headwaters of the San Juan River system, the next major upstream tributary to the Colorado River. It is not likely that traits of *C. plebeius* were original in the population in the Little Colorado for two reasons. First, the distribution and characters within *Pantosteus* indicate that *C. plebeius* and *C. discobolus* are not closely related, but are phylogenetically diverse representatives of the subgenus. Second, extreme variation between populations probably would not have been maintained during the pluvial periods of the Pleistocene when the increased river flow would have eliminated the present desiccation barriers.

The remarkable pattern of variation at the present time consists of the presence of two populations in the headwaters in New Mexico with traits otherwise characteristic of *C. plebeius*, the species which occupies the drainage just over the low continental divide to the east, and south. These *plebeius*-like characters occur almost uniformly in the headwater populations and with decreasing penetrance in populations farther downstream (Fig. 18, Table 1). The explanation suggested here may be summarized in four hypothetical stages:

1. A stream capture, bringing part of the headwaters (and resident fish populations) of San Jose Creek of the Rio Grande drainage into the headwaters of the Zuni River, tributary to the Little Colorado River.

2. Hybridization between *C. plebeius* in the extreme headwaters and *C. discobolus* in the newly connected streams.

3. Selective introgression of the genetic material for various character complexes by backcrossing between surviving hybrids and the parental populations.

4. Downstream penetration of *plebeius* characters to produce a polymorphic pattern perhaps balanced by the interaction of the selective value with the rate of influx from upstream populations. (This "balance" would tend to fluctuate because the degree of contact with the more *plebeius*-like upstream populations would vary with the transient barriers, which are a function of the volume of the river. Assuming that this balance is under the same influences now, this part of the hypothesis might be tested over a long term period.)

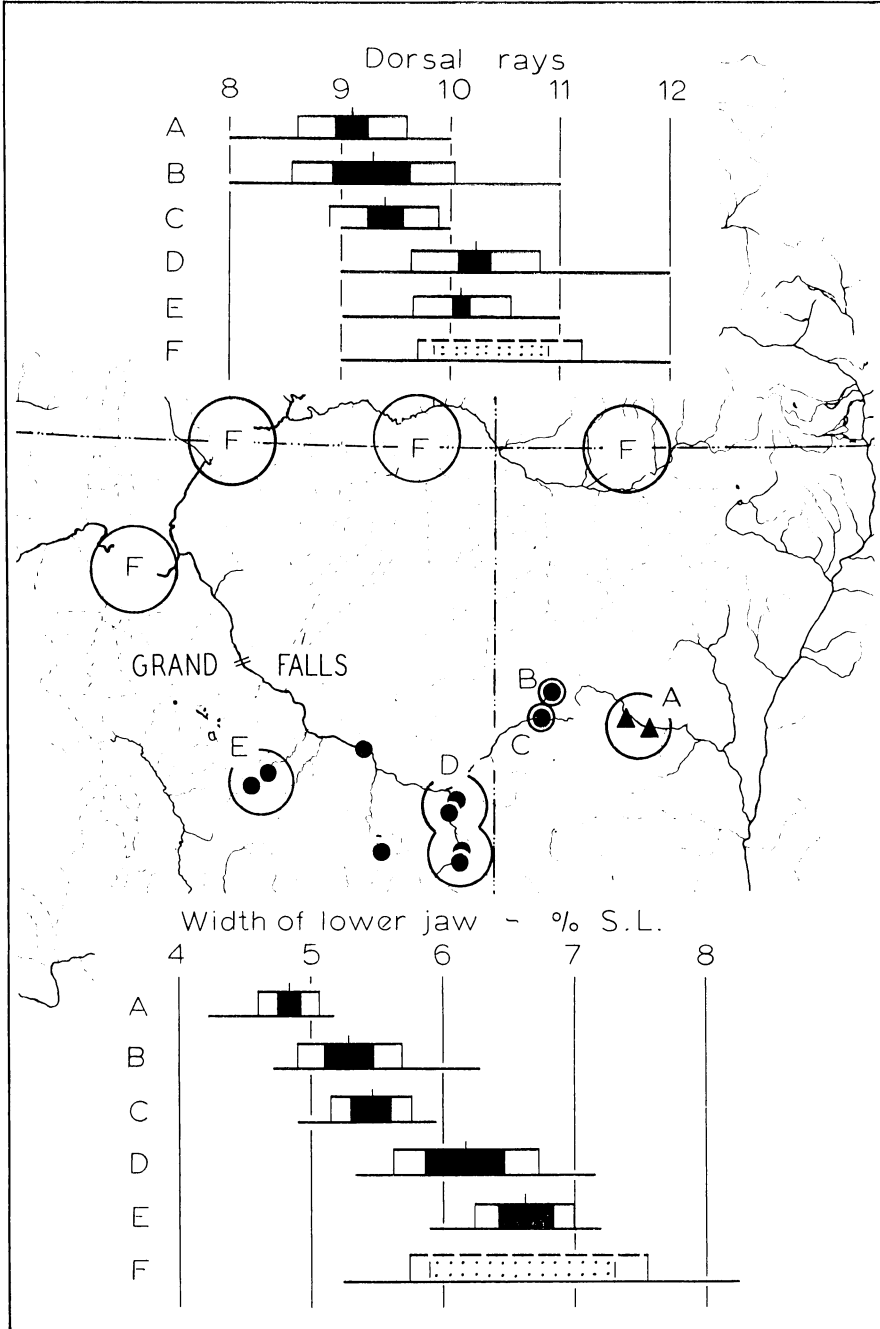
This situation and the explanatory hypothesis is somewhat similar to the introgression patterns described by Baker (1951). The discordance of the character distribution patterns are of special interest in the present case. Such

characteristics as lip and jaw development show gradients in downstream penetration, as do most of the meristic characters (Fig. 18). In contrast, among the populations, numbers of vertebrae tend toward the *plebeius* norm, but the numbers of gill rakers are distinctly closer to the *discobolus* norm. These patterns of variation, if they are a function of introgressive penetrance, are probably related directly to selective value and the filter effect of barriers. However, another influencing factor, suggested by Baker (*loc. cit.*), is the effect of different linkage patterns on the rate of movement of genes through an introgressive system. Unfortunately, the present ignorance of the genetics of these fishes prohibits the immediate analysis of this possibility. It can be supposed that selection is operating on known and unknown characteristics and that linkage and the effect of selection on pleiotropic systems has effected the known character distributions.

The essential geological corroboration of the above hypothesis is lacking. However, the data are suggestive of an introgressive influence originating near Nutria Creek, New Mexico (locality "B," Fig. 18). After study of maps of the area, Robert R. Miller kindly conducted a brief field study of some of the geology between valleys of the Nutria Creek drainage and the adjacent Rio Grande drainage basin southeast of Gallup, New Mexico, and reported the possibility of past stream capture across the continental divide. Relatively recent lava flows are known to have caused drainage changes in this vicinity (Nichols, 1946) and the removal of a Tertiary erosion surface in the Gallup-Zuni area (McCann, 1938) might have affected the position of the divide.

The patterns of variation in the populations of *C. discobolus* in the Little Colorado River are of biological interest whatever the final explanation may be. (The possibility of introduction by man is considered remote because *plebeius*-like fish were collected in the Zuni drainage as early as 1873. See page 99). It is not felt that interest or understanding of the problem can be enhanced at this point by assigning subspecific names to the groups of populations involved. From the standpoint of taxonomy, perhaps the most

FIG. 18. (opposite) Distribution and variation in *Catostomus discobolus* in the Little Colorado River drainage (B, C, D, E) compared with samples of *C. plebeius* of the Rio Grande drainage (A) and *C. discobolus* from the middle Colorado and San Juan river drainages (F). (Compare with Fig. 17.) The variation within the system suggests introgression of *plebeius* characteristics from the headwater populations into the downstream populations of *discobolus*. The variation diagrams indicate the range (basal line), the mean (center line), one standard deviation either side of the mean (outer limits of open rectangle) and the 95 per cent confidence limits of the mean (dark rectangles). The outer limits of the 95 per cent confidence intervals (not lumped) of the four samples from the San Juan River are indicated by the stippling; the outer limits of the standard deviations are indicated by the open rectangle. The round symbols between D and E represent single specimens.



serious question pertains to the justification of separate names for *C. discobolus* and *C. plebeius* as distinct species in light of the data presented and the explanation favored. As mentioned earlier, *C. discobolus* and *C. plebeius* are morphologically clearly distinct outside the limited area of introgression and they are clearly on opposite sides of a fundamental phylogenetic division in the subgenus *Pantosteus*. To unite them as one species would render the definition of the other species in the subgenus extremely difficult and arbitrary. The taxonomic arrangement presented here at least avoids that problem and further allows the clear morphological separation of all specimens of *discobolus* and *plebeius* on the basis of the number of gill rakers. All of the characters except the vertebral number, which overlaps, favor the alignment of the Little Colorado River population complex with *C. discobolus*.

Variation in the remainder of the known *C. discobolus* populations seems to be related more to local ecological parameters than to broader geographical patterns of isolation and gene flow. The most striking morphotype is the form with a long, slender caudal peduncle and large fins. The slender peduncle is the anatomical result of reduction in the volume of muscle mass in the posterior part of the caudal peduncle and the corresponding reduction in the angles of the neural and hemal processes of the caudal vertebrae. The most extreme examples of this form are found in the Green River in the canyon area at the east end of the Uinta Mountains and in the Grand Canyon of the Colorado, Arizona. Rather extreme representatives are also found in the main channels of the San Juan and the Colorado rivers wherever the fluvial environment consists of large volume and rapid or at least persistent current. The aquatic environment here is commonly sand-bottomed with active *kolks*.

Specimens with slender caudal peduncles also occur in small tributaries when adjacent to large river populations which show the characteristic, for example the populations in Warm Creek, Warm Springs Creek, and the Paria River. Figure 19 shows the variation in depth of caudal peduncle in *C. discobolus*.

The opposite morphotype is typified by the rather stout, more normal-shaped caudal peduncle. These fishes are found in headwater streams of the Colorado River system and in the Weber, Bear, and Snake river drainages. The fluvial habitat of these populations is characterized by smaller volume with riffles and pools.

The samples between the headwater tributaries and the Green River at Flaming Gorge Dam show the trend in variation in depth of caudal peduncle. The factors governing this trend seem to be habitat and genetic exchange. The correlation indicates that the size of the caudal peduncle is under selective control. The hydrodynamics of the characteristic are not under-

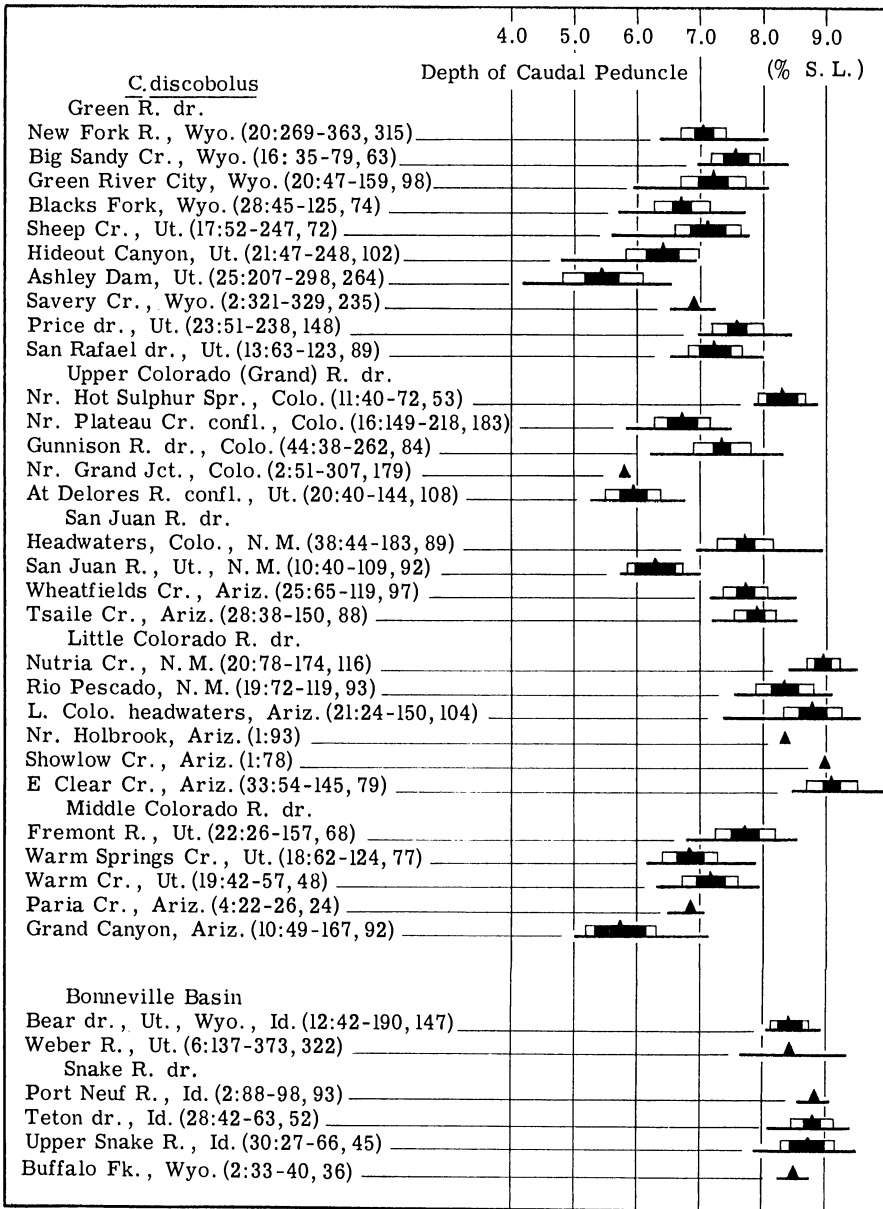


FIG. 19. Variation in the depth of the caudal peduncle in *Catostomus discobolus*. Samples from large, swift rivers in canyon areas tend to have slender peduncles.

stood, but in general the more powerful swimmers among the world's fish species have slender caudal peduncles and enlarged caudal fins. Long, slender caudal peduncles are characteristic of two other species in the Colorado River, *Catostomus latipinnis* and *Gila robusta elegans*. No other river in the world is known to have species so extremely modified in this characteristic. The slender caudal peduncle is therefore thought to be an adaptive response to high volume and velocity characteristics peculiar to the Colorado River and its larger tributaries.

An interesting corollary to the habitat and depth of caudal peduncle relationship is the general coloration of specimens. Those from headwaters and other generally clear waters are dark green above and yellowish below. Specimens from the sand- and silt-laden channels of the Green, Colorado, and San Juan are silvery tan, blending with their environment. The forms with the slender caudal peduncles are also among the larger of the *C. discobolus* specimens.

In a few instances stunting occurs in very small habitats. One such dwarf population existed in Warm Springs Creek, a small tributary to the Colorado River in Glen Canyon, Utah, now inundated by Lake Powell. Males of this population were beginning to mature in July when as small as 62 mm in standard length. Northern members of the species commonly reach standard lengths of 300 to 400 mm.

The number of dorsal rays shows a general correlation with size and perhaps, indirectly, with latitude. This character shows a slight trend from 11 dorsal rays in northern populations to means of approximately 10.5 in middle drainages and around 10 in some of the southernmost populations.

Specimens from the Price and San Rafael, tributaries to the Green River, and the Muddy and Fremont (Dirty Devil), tributaries to the Colorado River, at the western part of the Colorado Plateau and east slope of the Wasatch Mountains in Utah, show an interesting tendency toward higher numbers of predorsal scales. The number of scales in the lateral line is not generally correlated with the number of predorsal scales in this species. Unexplained reduction in the number of scales in the lateral line occurs in the Snake River and in the Glen Canyon area.

The discordance of the variation of *C. discobolus* suggests that little is to be gained by the use of subspecies names at this time. Subspecies based on the most significant varying characteristic, the depth of the caudal peduncle, would be polytopic and would not necessarily enhance further study of the significance of this character or the populations.

HYBRIDIZATION.—See "Variation," p. 87. The hybridization of *C. discobolus* with *C. commersoni* and with *C. latipinnis* was reported by Hubbs, Hubbs, and Johnson (1943:39) and Hubbs and Hubbs (1947:147), respectively. In the present study, hybrids between *C. discobolus* and *C. platyrhynchus*

have been recognized from the Green River drainage, and the strong possibility occurs that these same species also hybridize in the upper Snake River drainage. However, the recognition of hybrids between these species is more subjective than is the recognition of hybrids between species of the subgenera, *Catostomus* and *Pantosteus*. In the Green River, for example, there is overlap between most of the characters which differentiate *platyrhynchus* and *discobolus*. The three most distinct characters are the caudal-fin pigment (Fig. 9), the size and distribution of the lower-lip papillae (Pl. I), and the presence of a pelvic axillary process in *platyrhynchus*. Variation in these characters is so widespread in the Green and Snake rivers that specimens have not been recognized as hybrids unless they possess either intermediacy in several of these characters or a mixture of characters typical of both species. In practice, the latter type of hybrid is most common, and offers the difficulty of distinguishing between F_1 and F_2 hybrids and backcross products.

For example, UMMZ 178663, from Blacks Fork, tributary to the Green River, contains a specimen 110 mm in standard length with depth of the caudal peduncle equal to 7.8 per cent of the standard length (*discobolus*-like, but almost intermediate); 104 lateral-line and 65 predorsal scales (clearly *discobolus*-like); 36 and 47 gill rakers in the 2 rows of the first arch (*discobolus*-like); caudal interradiation pigment *discobolus*-like; the size and distribution of the papillae of the lower lip definitely *platyrhynchus*-like; 42 post-Weberian vertebrae (*platyrhynchus*-like); pelvic axillary process intermediate. The specimen is considered a hybrid even though only two or three characters are actually intermediate. Nevertheless, it is clear that a hybrid index based on summed values for each character would suggest intermediacy.

A contrasting specimen is UMMZ 176904 taken from Pondtown Creek in the Price River drainage. This fish, 139 mm in standard length, has a caudal-peduncle depth equal to 8.8 per cent of the standard length (*platyrhynchus*-like, almost intermediate); 88 lateral-line scales (*platyrhynchus*-like, almost intermediate); 53 predorsal scales (in overlap zone, but more like *discobolus*); 34 and 41 gill rakers (*platyrhynchus*-like); pelvic axillary process developed (*platyrhynchus*-like); caudal interradiation pigment on basal third of caudal membrane (intermediate); 42 post-Weberian vertebrae (*platyrhynchus*-like, but close to intermediate); papillae of lower lip large, in central convex arch (*platyrhynchus*-like), but with numerous small papillae in anterolateral corners of lower lip (*discobolus*-like). In this case neither the intermediate lip form nor caudal pigment arrangement is expected in a normal specimen of *platyrhynchus* and this, taken with the near intermediacy of the other characters, suggests that the specimen is a product of hybridization.

A more complex situation is posed by five specimens, UMMZ 178625, from

Big Sandy Creek, tributary to the Green River. The five remain after allocating 8 specimens of the collection to *C. discobolus* and 29 specimens to *C. platyrhynchus*. Characteristics of the five specimens are distributed as shown in Table 2.

Specimen number one is predominantly *discobolus*-like, with exception of the low vertebral number, the presence of a pelvic axillary process, and intermediate lips. Specimens 2 to 5 are predominantly *platyrhynchus*-like, except for the intermediate lips in all, the high vertebral count in number 4, and high number of predorsal scales and absence of a pelvic axillary process on one side in number 3. The variational pattern presented by the five speci-

TABLE 2
CHARACTERS OF HYBRIDS (UMMZ 178625) BETWEEN *C. discobolus* AND
C. platyrhynchus FROM BIG SANDY CREEK, GREEN RIVER BASIN, WYOMING*

Character	X	1	2	3	4	5
Standard length	...	156	74	58	69	66
Caudal peduncle depth/S.L. $\times 100$	8.2	7.9	9.2	9.0	8.7	8.5
Lateral-line scales	90	96	89	84	87	82
Predorsal scales	52	50	48	56	48	51
Gill rakers, external	33	33	27	29	30	28
Gill rakers, internal	43	46	38	36	41	38
Caudal interradiial pigment	...	+	—	—	—	—
Pelvic axillary process	...	+	+	(+—)	+	+
Post-Weberian vertebrae	42.5	42	41	40	43	42
Lip form				intermediate in all		

*The "X" column gives values that are approximately intermediate between the two species.

mens appears too diverse to represent F_1 hybrids. The departure from intermediacy may indicate that the specimens are the products of backcrosses (Fig. 22).

ECOLOGY.—Populations of *C. discobolus* are found in a wide variety of fluvial habitats. Those in the Weber River, Utah, and the headwaters of the Green River, Wyoming, are living in cool, trout-stream environments, with temperatures usually less than 20° C (68° F) in summer, and high dissolved oxygen, usually more than 9 ppm during the day and 7 ppm at night (Smith, 1959, unpubl. MS thesis, Univ. Utah). Most of the Colorado River populations are living in habitats considerably warmer than trout streams. Summer temperatures where this species has been taken in the Green and Colorado rivers commonly ranged between 16° and 26° C (60°–79° F). Much lower temperatures exist now below the dams, however. Specimens in Warm

Springs Creek were taken from water which ranged from 20° to 28° C (68°–83° F) over a 24-hour period in July, 1958.

Stream volumes throughout the range of the species vary from several thousand cubic feet per second in the Snake, Green, and Colorado rivers to even less than one cubic foot per second in tributaries. Smaller tributaries often appear to be nursery grounds for populations of adjacent larger rivers. This sometimes serves to bring together young of this species with *C. platyrhynchus*, which usually occupies small streams. Adults of both species are found together in medium-sized waters of the Green River headwaters of Wyoming and the Weber River of Utah.

The range in current velocity occupied by members of this species is great but difficult to measure. Maximum currents are between 8 and 15 feet per second but the actual microhabitat current is probably somewhat less. The effective current is much greater in sand-bottomed streams. This undoubtedly accounts for at least part of the selective pressure for strong swimming adaptations in Green and Colorado river forms of this species. The torrential currents common to spring floods in the arid Colorado basin also may be a factor in the current-oriented adaptations of these fishes. Boulders and rubble on the stream bottom produce disrupted turbulence and thereby may provide zones of microhabitat with much less linear current energy to be combatted by the fish.

Associated vegetation consists primarily of algae and diatoms which, supplemented by the free-living bacterial flora and other microscopic organic matter, make up the food of these fishes. Much sand is ingested and passes through the alimentary tract. The shifting sand bottom of much of the Colorado River drainage is notoriously nonproductive of fish food organisms and does not support fish life. However, rocks which provide a stable base for periphyton, or settling areas where organic matter accumulates, may provide food sources for this species. In general, the adjacent tributaries tend to be much more productive than the sand-bottomed rivers (Woodbury, 1959). (Colorado River drainage ecological data from Smith, Musser, and McDonald, 1959; Gaufin, Smith, and Dotson, 1960).

As in other suckers, spawning appears to take place in the spring and early summer. A sample taken in the headwaters of the Price River, Utah, June 19, includes both ripe and partly spent individuals. Ova size was 1.3 to 1.6 mm in diameter. Specimens from elsewhere in the same drainage had ova 1.2 mm in diameter April 29. Fish from the Bear River appeared spent on June 29 and a population from the headwaters of the Little Colorado River contained ripe as well as spent individuals on June 6. Specimens taken July 15 from the headwaters of the Little Colorado River were spent. Postlarvae as small as 30 mm in standard length were collected in this drainage in August and September. Postlarvae, 26–63 mm in standard length, were taken

in the Snake River headwaters on September 15, and 213 postlarvae, 13–22 mm, were taken in the San Juan drainage October 11.

Age and size at maturity are variable. In Warm Springs Creek in July large adults were 106 and 124 mm in standard length, but specimens as small as 62 mm showed signs of approaching maturity. Possibly spawning adults in the Price River in June included four females 166–226 mm and two males 192 and 200 mm. Adults between 111 and 236 mm have been taken in the Price and San Rafael drainages. In the San Juan and Little Colorado rivers adults range from 90 to 200 mm, although mature males as small as 79 mm have been taken above Canyon de Chelly and the type specimen of *P. virescens*, probably from the San Juan drainage, is 293 mm in standard length. In the Colorado (Grand) River, observed adults range from 144 to 307 mm. Specimens from the lower Colorado at Grand Canyon were mature at 152 mm.

In the canyon section of the Green River mature specimens collected in early September included five tuberculate males, 245 to 293 mm, which appeared to be in their fourth and fifth summers. Immature specimens, 107 and 123 mm, appeared to be in their second summer. In the upper Green and New Fork tributary waters the maximum size was larger. A collection in early September included six tuberculate males, 269 to 323 mm, and five tuberculate females, 300 to 326 mm. One mature female, 319 mm in standard length, contained about 8500 ova 1.4 to 2.0 mm in diameter. A female 323 mm in standard length appeared to be in the fifth summer, and a 349-mm specimen appeared to be in the fifth or sixth summer. The largest specimen studied was a seven-year-old female, 400 mm in length, from the Weber River.

The pattern of the breeding tubercles is similar to that described for the previous species. The red lateral stripe of breeding specimens appears to be usually less prominent than in other species. However, adult specimens from above Canyon de Chelly display a brilliant red lateral stripe as late as September.

SPECIMENS EXAMINED

GREEN RIVER DRAINAGE.—**Wyoming**, Carbon Co.: UWZM 2178. Sublette Co.: UMMZ 178642, 182483, 182492, CAS 23017. Sweetwater Co.: UMMZ 86902, 113424, 132207, 132211, 162930, 178663, 182506, 182513, 182521, 183992, CAS 23022. **Utah**, Daggett Co.: UMMZ 160651, 167570, 167571, 167579, 178640, 182538, CAS 23012. Uintah Co.: UMMZ 136932, 178665. Carbon Co.: UMMZ 176923, 176926, 176930. Utah Co.: UMMZ 176917. Wasatch Co.: UMMZ 176913. Emery Co.: UMMZ 141694, 141697.

COLORADO RIVER DRAINAGE.—**Colorado**, Grand Co.: UMMZ 105639. Mesa Co.: USNM 133203, 143592, UMMZ 163903, 167561. Delta Co.: UMMZ 134655, 136916, 142914, USNM 104879. Montrose Co.: UMMZ 66195, 136914. Co. unknown: USNM 41631, 125260. **Utah**, Grand Co.: UMMZ 167560, 178672, UU33-1. Wayne Co.: UMMZ 177103. Emery Co.: UMMZ 141692. Garfield Co.: UMMZ 174576. Kane Co.: UMMZ 180193. **Arizona**, Coconino Co.: UMMZ 117837, 178686.

SAN JUAN RIVER DRAINAGE.—**Colorado**, Montezuma Co.: UMMZ 142532. La Plata Co.: UMMZ 66184, 117825, 152528. Archuleta Co.: UMMZ 117818, UMMZ 179541, USNM 16758. **New Mexico**, San Juan Co.: UMMZ 117828, 142536, 142540. **Utah**, San Juan Co.: UMMZ 167551, 178681. **Arizona**, Apache Co.: UMMZ 178699, 178701, 178703.

BEAR RIVER DRAINAGE.—**Wyoming**, Uinta Co.: UMMZ 173139, 176679, SU 37770, 37771. **Idaho**, Franklin Co.: SU 37760. Bear L. Co.: UMMZ 180118, 180119, USNM 104410. **Utah**, Box Elder Co.: BYU 4166, 4169, 4170, 4173.

WEBER RIVER DRAINAGE.—**Utah**, Summit Co.: LBSC Museum, UMMZ 178646, 180135, 180136. Morgan Co.: SU 37776.

SNAKE RIVER DRAINAGE.—**Idaho**, Bannock Co.: UMMZ 162314. Teton Co.: UMMZ 158908. Bonneville Co.: UMMZ 158915, 169805. Madison Co.: UMMZ 161816. **Wyoming**, Sublette Co.: UMMZ 180121. Teton Co.: UMMZ 180115, 180120.

LITTLE COLORADO RIVER DRAINAGE.—**New Mexico**, McKinley Co.: UNMCV (Nutria Cr. above upper Nutria, W. J. Koster, VI:6:1960); UNMCV (Rio Pescado, T. 10N, R. 17W, Sec. 3, W. Koster, IX:2:1948). (McKinley Co.): USNM 15783 (Zuni R., H. W. Henshaw, [1873]). **Arizona**, Apache Co.: UMMZ 124751, 137079, 178695, 178697. Navajo Co.: UMMZ 117833, 131098. Coconino Co.: UMMZ 178690, 179568, 180122.

ADDITIONAL RECORD. **Utah**, Duchesne Co.: Duchesne R. above Duchesne, W. Sigler, IX: 15:1951, identified by R. R. Miller: UMMZ file

Catostomus columbianus (Eigenmann and Eigenmann)

NOMENCLATURE.—Lectotype: USNM 125261; paralectotypes: British Museum number 1893, 2 specimens. The lectotype was designated by Miller and Miller (1948:179) upon discovery that *Pantosteus columbianus* Eigenmann and Eigenmann, 1893, and *Catostomus syncheilus* Hubbs and Schultz, 1932, applied to the same species, in part. The description of *Pantosteus columbianus*, based on specimens from the Boise River, was published in the American Naturalist, February 4, 1893, eight days after the publication of the description of *Pantosteus jordani* Evermann, January 27, 1893, from the Black Hills, South Dakota, in the Bulletin of the U. S. Fish Commission. Eigenmann unfortunately synonymized his species with *Pantosteus jordani* the following year and that terminology was followed until the correction by Miller and Miller (1948).

The existence of the additional species of sucker in the Columbia River was recognized by Hubbs and Schultz (1932), who described the *Pantosteus*-like species, *Catostomus syncheilus*, with a thorough discussion of its characters and relationships. The Palouse River population of this species was subsequently recognized subspecifically as *C. s. palouseanus* by Schultz and Thompson (1936). The present interpretation of the relationships of the species are expressed by inclusion in the subgenus *Pantosteus*.

SYNONYMY

Pantosteus columbianus Eigenmann and Eigenmann, 1893:151 (original description; Boise R., Caldwell, Oregon [=Idaho]). Jordan, Evermann, and Clark, 1930:105 (Columbia R. basin).

Pantosteus jordani, Eigenmann, 1894:107 (characters; Boise R., Caldwell, "Oregon"

[=Idaho]). Gilbert and Evermann, 1894:189 (characters; localities, Columbia R. dr., based on *C. columbianus* and *C. platyrhynchus*). Jordan and Evermann, 1896:171 (characters; Columbia R. dr.). Evermann, 1897:172 (characters: Idaho).

Catostomus catostomus, Gilbert and Evermann, 1894:189 (characters; Columbia R. dr.). Snyder, 1908b:83 (characters, comparison; southeastern Oregon). Evermann and Nichols, 1909:93 (characters; Crab Cr., Washington).

Catostomus syncheilus Hubbs and Schultz, 1932:6 (original description, comparison with *C. catostomus* and *C. rimiculus*; Crab Cr., 7 miles below Odessa, Washington; distribution). Schultz and DeLacy, 1935:377 (distribution), Schultz, 1936:143 (characters; middle and lower Columbia R. dr.). Hubbs and Miller, 1948:31 (Columbia R. dr.), p. 69 (relationship to *C. rimiculus*), p. 76 (Crab Cr., Washington), p. 77 (possibly distinct subspecies, Wood R. dr., Idaho).

Catostomus syncheilus palouseanus Schultz and Thompson, 1936:71 (original description, comparison with *C. s. syncheilus*; Palouse R., Washington). Hubbs, Hubbs, and Johnson, 1943:29, pl. 6, fig. 2c (characters, hybridization with *Catostomus macrocheilus*; South Fork Palouse R., Pullman; Palouse R., Palouse, Washington).

Catostomus syncheilus syncheilus, Schultz and Thompson, 1936:71 (comparison with *C. s. palouseanus*; distribution). Hubbs, Hubbs, and Johnson, 1943:19, pl. 2, fig. 1c, pl. 6, fig. 1c. (characters, hybridization with *Catostomus macrocheilus*; Wenatchee R., Wenatchee; Grande Ronde R.; Crab Cr., Washington; Grande Ronde R.; Umatilla R., Rieth, Echo, and Columbia R. confluence; Sucker Cr.; Jordan Cr., Oregon).

Catostomus columbianus, Miller and Miller, 1948:177 (characters, ecology, variation, hybridization, synonymy, designation of lectotype; Owyhee R., Bruneau R., and Salmon R., Nevada). Lindsey, 1956:781 (Fraser R. at Prince George, British Columbia). Lindsey, 1957:654, table 1 (Columbia R., Fraser R., British Columbia). Moore, 1957:89 (characters; Columbia R. dr.). Eddy, 1957:78 (characters; middle and lower Columbia R.). Miller, 1958:212 (zoogeography; Columbia R. dr.). Slastenenko, 1958a:160 (characters; distribution). Slastenenko, 1958b:6 (distribution). Carl, Clemens, and Lindsey, 1959:92, fig. 16a, 17 (characters, ecology; Erie L. and lower Arrow L., East Kootenay District; Osoyoos L.; Similkameen R., [Columbia R. dr.]. Nicola L.; North Thompson R., Heffley; Quesnel R. and tribs. to Fraser R. between Australian Cr. and Prince George; Wright Cr. east of Vanderhoof; several tribs. to West Road R., [upper Fraser R. dr.], British Columbia). Bailey *et al.* 1960:18 (common name: bridgelip sucker). Bond, 1961:22, fig. 7 (characters; Columbia R. dr., Harney basin, Oregon). La Rivers, 1962:342 (characters, synonymy, distribution; Nevada).

Catostomus columbianus columbianus, Miller and Miller, 1948:180 (characters, Columbia R. dr.).

Catostomus columbianus palouseanus, Miller and Miller, 1948:180 (characters, Palouse R., Washington).

RANGE.—Fraser River drainage, British Columbia; Columbia River drainage below the great falls of the Snake (including the Wood River system), Idaho, Nevada, Oregon, Washington, and British Columbia (Maps, Figs. 1, 20).

DESCRIPTION.—Small catostomid fishes, attaining maximum adult size of approximately 250 mm in standard length; lips variable, with small to large papillae on lower lip and the anterior and oral face of upper lip; lateral notches at juncture of upper and lower lips weak or absent on one or both sides; median notch in lower lip deep, separated from cartilaginous sheath of

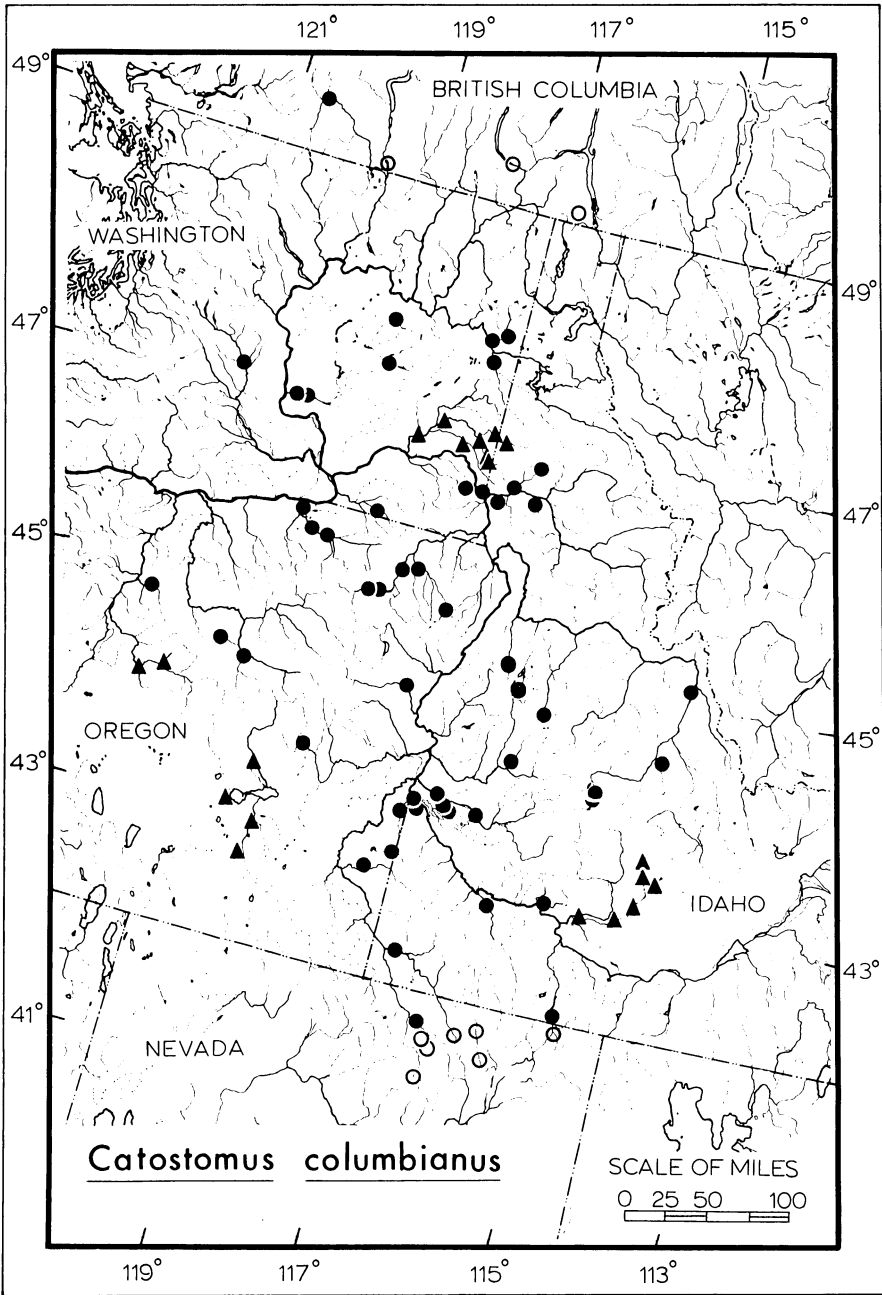


FIG. 20. Distribution of *Catostomus columbianus* in the Columbia River drainage. Solid symbols represent specimens examined, open circles represent records for specimens not seen. Triangles represent isolated headwater populations which possess a characteristic phenotype (see text). The distribution of this species north of the area shown here is recorded by Carl, Clemens and Lindsey (1959:92); see synonymy, p. 98, for list of northern localities.

jaw by two rows of papillae; ridge of lower jaw weak or well developed, more or less rounded, width, 4 to 6 per cent of standard length; width of isthmus, 4.2 to 8.6, usually 5.5 to 8 per cent of standard length; gill rakers, 24 to 42 (usually 25–30 in the Wood River drainage and 30–40 elsewhere) on external row and 34 to 55 (usually 35–40 in the Wood River drainage and 42–55 elsewhere) on the internal row of the first arch in specimens larger than 70 mm in standard length; gill rakers with spines in clusters rather than double row; frontoparietal fontanelle present but reduced; peritoneum black or dusky to black; intestine long, 6 to 14 loops anterior to liver; swimbladder usually not reduced but reaches posteriorly at least to the origin of the pelvic fins; lateral-line scales, 77 to 121, usually 90 to 110; predorsal scales, 43 to 75, usually 55 to 65; post-Weberian vertebrae, 39 to 47, usually 40 to 46 (geographically variable); dorsal rays, 7–14, usually 8 to 13 (geographically variable); pelvic rays, 9–13, usually 10 or 11; pelvic axillary process absent; caudal peduncle moderately slender, 7–10, usually 7.5–9.5 per cent of standard length; coloration greenish to brownish mottled above, yellowish below; caudal fin pigment dispersed over rays and interradiial membranes.

COMPARISON.—See *plebeius*, p. 50; *santaanae*, p. 56; *platyrhynchus*, p. 63; *clarki*, p. 76; *discobolus*, p. 86.

VARIATION.—The pattern of geographical variation in *C. columbianus* suggests a historical explanation. Isolated headwater populations differ from those of the central Columbia system in a similar manner, suggesting either long-term independence from the main stream of evolution of the central group or separate changes in the same direction as a result of similar selective pressures (Figs. 7, 8, 21).

The most distinctive populations are in the Wood River system of Idaho. The characteristics which distinguish this group are sufficiently concordant and discriminative to make recognition by a formal name useful.

Catostomus columbianus hubbsi, new subspecies
(Pl. IB)

DIAGNOSIS.—Populations of *Catostomus columbianus* which differ in the possession of 24 to 31 rakers on the external row and 34 to 41 rakers on the internal row of the first arch (contrasted with 30 to 44 and 41 to 59 for 26 other populations); post-Weberian vertebrae 40 to 43, and dorsal rays modally 11.

TYPE.—The holotype, UMMZ 182084, an adult female, 160 mm long, was taken from Fish Creek, one mile below the reservoir, T.1N, R.22E, Blaine County, Idaho, by Carl L. Hubbs and family, July 22, 1934. Taken with this specimen were 76 paratopotypes 41 mm to 195 mm long, UMMZ 130447.

CHARACTERS.—Meristic and morphometric characteristics are given in Figures 7, 8, 21, and Table 1. The lips (Pl. IB) are smaller and have larger

papillae than in most samples of *C. columbianus*. The distinctness of this population group suggests the possibility that *C. c. hubbsi* might actually be a unique species. In view of the slight character overlap and the absence of information on reproductive isolation, the populations are considered a subspecies of the species which comprises its nearest relatives.

DISTRIBUTION.—Restricted to the Wood River drainage, including now isolated Fish Creek, and isolated by barrier falls from the rest of the Snake River system.

ETYMOLOGY.—This subspecies is named in honor of Dr. Carl L. Hubbs in recognition of his work on fishes in Western North America and his leadership in ichthyology. Dr. Hubbs collected the majority of the known specimens of the subspecies.

DISCUSSION.—The Wood River system is also the range of the endemic sculpin, *Cottus leiopomus* Gilbert and Evermann, and one of the few natural localities for *Gila copei* (Jordan and Gilbert) outside the Bonneville basin. The age of the barrier falls is not known.

A similarly differentiated population, *C. c. palouseanus* Schultz and Thompson, also occurs above a barrier falls in the Palouse River of eastern Washington and western Idaho. This population also is characterized by fewer vertebrae and dorsal rays, though not fewer gill rakers. The other populations which show the same trend to a lesser degree are from Crooked Creek, tributary to the Deschutes River, and, possibly, the streams of the Harney basin, Oregon. The Deschutes River is marked by a series of falls below Redmond, Oregon, and the Harney or Malheur basin is an isolated fragment of the Columbia River drainage (Hubbs and Miller, 1948:75). Specimens from the Deschutes drainage below the falls (Trout Creek) do not show the same vertebral numbers and numbers of dorsal rays (Fig. 21) as populations from above the falls, but show increased variance and a possible shift in the mean which is suggestive of intergradation.

The occurrence of similar populations of the species in widely separated headwater streams above falls can best be explained by assuming that they are remnants of an older widespread form. Since the advent of the falls the headwater populations have been isolated from evolutionary changes taking place in the central part of the drainage system. The genetic changes in the larger, central populations were not available to the isolated headwater populations, although gene combinations evolved in the headwaters, if any, were potentially available to fishes in the central part of the drainage. The differences which exist between the fishes in the headwaters and those in downstream sections can be attributed to evolution which has occurred since the time of isolation. If this hypothesis is correct, the larger, central populations must have evolved more rapidly. The differences between isolated headwater populations, which consist primarily of varying degrees of differ-

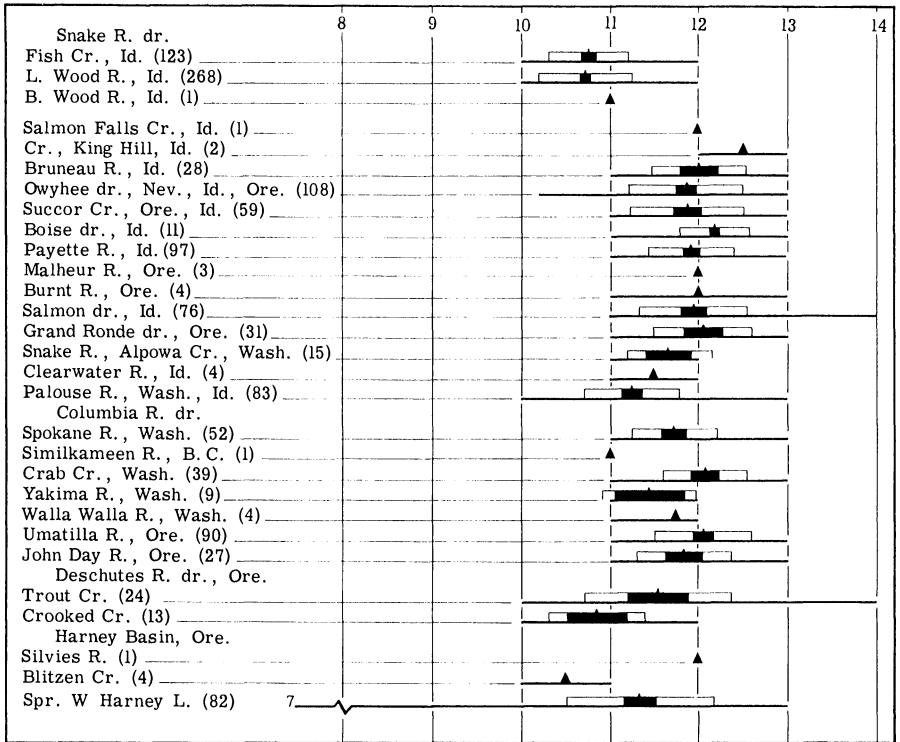


FIG. 21. Number of dorsal rays in *Catostomus columbianus*

entiation from the central population, are probably the result of a combination of variation in the time of isolation and degree of selective pressures.

According to the hypothesis, the different forms of *C. columbianus* can be viewed as representative of different stages in the evolution of the species. In this connection it is interesting to evaluate the frequency of the lateral notches of the lips in light of the problem of whether or not *columbianus* is a primitive or specialized member of the subgenus *Pantosteus*. For *Pantosteus*, except *C. columbianus* which is variable, is distinguishable from the subgenus *Catostomus* on the basis of the lateral lip notches. The percentage of specimens with at least one side of the lips notched was recorded for various populations. Among the isolated headwater samples, 19 per cent of 43 specimens from Fish Creek of the Wood River system and 70 per cent of 20 specimens from the remainder of the Wood River showed notches; 94 per cent of 49 specimens from the Palouse River and all of 13 specimens from Crooked Creek showed well-developed notches; 40 per cent of 25 specimens from Trout Creek, tributary to the Deschutes below the falls,

showed notches. Samples of 16 to 33 specimens each from 7 various non-isolated parts of the Columbia River system showed from 15 per cent to 62 per cent, and a mean of 40 per cent with notches. These included samples from nonisolated headwaters. The degree of fixation of the genes for lateral lip notches appears to be higher in isolated headwater populations (except in Fish Creek, a small population isolated from the rest of the Wood River system, Hubbs and Miller, 1948:77). These data suggest that *C. columbianus* might have been more typically *Pantosteus*-like and has since evolved toward the *Catostomus* (*s.s.*) ancestral type (perhaps with the added stimulus of hybridization, see p. 111). The alternative is that the headwater samples represent parallel evolution toward notched lips.

An interesting pattern which is comparable to the above is found in the distribution of a minnow, *Richardsonius balteatus*, of which one subspecies, *R. b. balteatus*, occupies the central Columbia River system and another, *R. b. hydrophlox*, the headwater streams of the Columbia River system including the Snake River above the falls and the Bonneville basin (Gilbert and Evermann, 1894; Eigenmann, 1895). The same hydrographic phenomena might have contributed to the patterns of distribution and variation in these two species.

The trinomial recognition of the other populations of *C. columbianus* poses a problem. Consistency seemingly demands placement of all populations of a species under the trinomial system if any part of it is so treated. However, the populations from the Palouse River and Crooked Creek are not really sufficiently distinct from others of the species or from each other to warrant recognition according to the modern ichthyological standards (93 per cent discrimination—Bailey, Winn, and Smith, 1954:148), although they are clearly part of an evolutionary system recognizably separate from the rest of the species. Therefore, if all of the populations must be covered by the trinomial it would seem expedient to recognize *C. c. hubbsi* in the Wood River system, *C. c. palouseanus* in the Palouse River, with a representative in the Crooked Creek tributary to the Deschutes, and the remainder in *C. c. columbianus*, with awareness that the treatment of the Harney basin populations, which will probably prove to be distinct, is provisional.

The three known populations in the Harney basin have not been adequately sampled. The unusual specimens from the warm spring west of Harney Lake probably represent a morphological response to the temperature conditions of their environment. The Silvies River and Blitzen Creek populations, when understood, will probably contribute much to the elucidation of the history of this hydrographically puzzling area (Snyder, 1908b).

HYBRIDIZATION.—Hybrids between this species and *Catostomus macrocheilus* have been recorded from 14 localities in the Columbia River drain-

age by Hubbs, Hubbs, and Johnson (1943:19-33). These records occur in the following drainages: Wenatchee, Grande Ronde, Umatilla, Palouse, Crab Creek, Sucker Creek, and Jordan Creek (tributary to the Owyhee). In the present study additional hybrid records are reported from the Bruneau and Deschutes drainages.

UMMZ 179584, collected in the Bruneau R. west of Bruneau, Owyhee County, Idaho, by R. R. Miller, August 4, 1961, contains two of four hybrid specimens with the following characteristics: Standard length, 58 54 mm; depth of caudal peduncle, 7.9, 8.3 per cent of the standard length; width of isthmus, 6.9, 7.6 per cent of the standard length; lateral-line scales, 77, 86; predorsal scales, 43, 51; dorsal rays, 13, 13; pelvic rays, 10-10, 11-11; gill rakers on the external row, 28, 29, on the internal row, 39, 38; lips intermediate; post-Weberian vertebrae, 45, 43. These specimens are either extreme or outside the normal variation for *C. columbianus* in the lateral-line and predorsal scale counts, the number of dorsal rays, and the number of gill rakers. In all cases the variation is toward *C. macrocheilus* (see Hubbs *et al.*, 1943:19).

UMMZ 179375, collected in Trout Creek, tributary to the Deschutes River northeast of Madras, Jefferson County, by R. M. Bailey, July 11, 1955, contains a specimen 55 mm in standard length with the following characteristics: depth of caudal peduncle, 9.6 per cent of the standard length; width of isthmus, 6.7 per cent of the standard length; 77 scales in the lateral line; 48 predorsal scales; 12 dorsal rays; pelvic rays 11-11; gill rakers, 28 and 37; lips and jaws intermediate between *C. columbianus* and *C. macrocheilus*; vertebrae abnormal and uncountable. The scale and gill-raker counts, as well as the lip and jaw form, possess the intermediacy expected of an F_1 hybrid. Abnormal vertebral columns are common, though not restricted, to hybrid specimens.

It has been suggested that one of the paratypes of *Pantosteus columbianus* (British Museum 1893. 2. 7. 647-8) may represent a hybrid between *C. columbianus* and *C. macrocheilus* (Miller and Miller, 1948:179).

Hybrids between *C. columbianus* and *C. platyrhynchus* are unknown and would be difficult to identify because of the overlap in characteristics of sympatric populations of these species. The populations of *C. columbianus* above barrier falls are especially similar to *platyrhynchus* in all characters except scale counts. *C. platyrhynchus* is sympatric with only one of these isolated *columbianus* populations, that of the Palouse River, and in this case *platyrhynchus* is known only from a single specimen. Collected with this unique specimen were 13 examples of *C. columbianus*. The data are: South Fork Palouse River 2 miles above Pullman, Whitman County, Washington, collected by L. P. Schultz and L. Erkkila, June 15, 1932. The characteristics of the single specimen of *platyrhynchus* and the range of variation (in

parentheses) of the 13 specimens of *C. columbianus* are as follows: Standard length, 49 (39–125); depth of caudal peduncle, 8.6 (7.7–9.1) per cent of the standard length; width of isthmus, 9.0 (6.7–8.6) per cent of the standard length; width of lower jaw cartilage, 6.1 (4.3–6.1) per cent of the standard length; lateral-line scales, 81 (89–104); predorsal scales, 50 (49–69); dorsal rays, 11 (11–12); pelvic rays, 9–9 (9–10 to 11–11); gill rakers, 29 and 36 (28–36 and 34–49); caudal interradiial pigment absent (absent to sparse); lateral lip notches present (present or absent); lower lip papillae arrangement normal for *platyrhynchus* (normal *columbianus* but with occasional tendency toward *platyrhynchus* type); post-Weberian vertebrae, 42 (39, 42–45). The specimen of *platyrhynchus* also differed in the possession of the reduced dorsal plate of the pterotic bone and a reduced swimbladder which fell short of reaching the insertion of the pelvic fins. In such characteristics as width of isthmus, scale counts, number of gill rakers, lip, and pigmental characters, and especially the number of vertebrae, the *columbianus* population contained variants with unexpected similarity to the *platyrhynchus* characteristics. Though only suggestive, the evidence indicates the possibility of gene exchange between these species in the Palouse River. It appears that the population of *platyrhynchus* may be in the process of being genetically absorbed.

ECOLOGY.—The primary ecological difference between fishes of the subgenus *Pantosteus* and their congeners in *Catostomus* is the preference of the former for small, more rapidly flowing streams. *Catostomus* (*s.s.*) are found in larger more sluggish streams and lakes, though there is broad ecological overlap in rivers. *Catostomus columbianus* has been noted for its proclivity to occupy *Pantosteus*-type habitat. Hubbs *et al.* (1943:21) recorded that “*Catostomus syncheilus* shows a greater preference for smaller and more rapid waters.” Miller and Miller (1948:180) stated:

In contrast to *C. macrocheilus*, the usual habitat preference of *columbianus* is for the more swiftly flowing portions of streams. At each of the four collecting stations [in Nevada] where the junior author secured this species, but not *macrocheilus*, he noted that the current was swift, and that the bottom was composed of boulders, rocks or gravel, except on the headwaters of the Bruneau River where the current was moderate and the bottom consisted of mud and sand . . . the water was cold, only 60° F. (Air 74° F.).

The temperature data are for the last station on August 20. The usual habitat is in cool waters. Food consists of periphyton, detritus, and occasionally small invertebrates.

Spawning occurs in the spring, probably in April and May. Ova size seems to be larger than in other species of *Pantosteus*. Eggs up to 2.8 mm in diameter have been observed. Specimens taken from the Palouse River in August and Crooked Creek in October contained ova up to 1.3 mm and 0.9

mm, respectively. A spent female was taken April 16 from Crab Creek. Young of the year were as small as 7 mm on July 10 and 20 mm on July 22 in the Little Wood River. Individuals may range from 40 to 80 mm by the end of the first summer of growth. Maturity is probably attained at the end of the second year at lengths of over 100 mm. A sample taken from the Crooked Creek drainage in August included specimens approximately 80 mm in length which were immature and specimens over 100 mm which were mature. No mature specimens under 100 mm have been recorded.

SPECIMENS EXAMINED

WOOD RIVER DRAINAGE.—**Idaho**, Blaine Co.: UMMZ 127625, 130447, 161846, (JCS 2), USNM 48046, 48055. Lincoln Co.: UMMZ 130453, 130459, 157013, 180149. Gooding Co.: UMMZ 144798.

SNAKE RIVER DRAINAGE (IN PART).—**Idaho**, Elmore Co.: UMMZ 92241. Twin Falls Co.: UMMZ 118114. Owyhee Co.: UMMZ 136199, 136224, 158878, 158883, 158894, 179585. Canyon Co.: UMMZ 136220, 146634, 146676, USNM 125261. Ada Co.: UMMZ 144789. Boise Co.: UMMZ 146689. Valley Co.: UMMZ 180442. **Nevada**, Elko Co.: UMMZ 160938. **Oregon**, Malheur Co.: UMMZ 130469, 130479, 130480. Baker Co.: UMMZ 179504. Harney Co.: UMMZ 106408, USNM 104780. **Washington**, Asotin Co.: UMMZ 179417, 179454.

SALMON RIVER DRAINAGE.—**Idaho**, Adams Co.: UMMZ 180134. Custer Co.: UMMZ 161850, 118094, 118110. Valley Co.: UMMZ 157036. Lemhi Co.: UMMZ 144824.

CLEARWATER RIVER DRAINAGE.—**Idaho**, Latah Co.: USNM 104809, UMMZ 162323. Nez Perce-Lewis Co. line: UMMZ 162304. Nez Perce Co.: USNM 35249, 35258, 35259, 35382.

GRANDE RONDE RIVER DRAINAGE.—**Oregon**, Union Co.: UMMZ 98748, 98758, 98760, 138601, 179489, USNM 104783. Wallowa Co.: USNM 73707.

PALOUSE RIVER DRAINAGE.—**Washington**, Whitman Co.: UMMZ 95037, 95039, 95055, 98701, 98707, 98716, 98722, 98723, USNM 104198, 104787. **Idaho**, Latah Co.: UMMZ 157021.

COLUMBIA RIVER DRAINAGE.—**Canada**, **B.C.**: UMMZ 179425. **Washington**, Spokane Co.: UMMZ 98666, 98683, 98684. Lincoln Co.: UMMZ 94075, 94076 (Crab Cr. below Odessa, C. L. Hubbs, VI:16:1926, types, *C. syncheilus* Hubbs and Schultz); UMMZ 98662. Grant Co.: UMMZ 95067, 95068, USNM 104784. Grant Co?: USNM 62971. Kittitas Co.: UMMZ 94074, USNM 104781, 184782. Walla Walla Co.: UMMZ 179478, USNM 134936.

UMATILLA RIVER DRAINAGE.—**Oregon**, Umatilla Co.: UMMZ 98775, 98778, 98791, 138614, USNM 48085, 104805.

JOHN DAY RIVER DRAINAGE.—**Oregon**, Wheeler Co.: UMMZ 132258. Grant Co.: UMMZ 106407.

DESCHUTES RIVER DRAINAGE.—**Oregon**, Jefferson Co.: UMMZ 179375. Crook Co.: OSU 525, UMMZ 141303.

HARNEY BASIN.—**Oregon**, Harney Co.: UMMZ 112917, 114106, 130499, 136696.

ADDITIONAL RECORDS PLOTTED (Fig. 20).—From Miller and Miller 1948: 179, 180. **Nevada**, Elko Co.: USNM 132186, E Fk. Owyhee R., upper end of Wild Horse Reservoir; USNM 146031, S. Fk. Owyhee R. 4 mi. ENE Tuscarora; USNM 146031, Deep Cr., trib. to S Fk. Owyhee R., 17 rd. mi. S White Rock; USNM 146041, Bull Run Cr., trib. to S Fk. Owyhee R., 6 mi. S White Rock; USNM 146046, Salmon R. W San Jacinto, 7 mi. NE Contact; USNM 146065, Bruneau R. 7 mi. E Gold Creek; USNM 146068, headwaters Bruneau R. at first crossing of rd. N from Deeth.

HYBRIDIZATION AND EVOLUTION IN *PANTOSTEUS*

The occurrence of natural hybridization in fishes has been rigorously demonstrated by C. L. Hubbs and his co-workers in numerous papers. Among the clearest of demonstrations were those involving *Pantosteus* and *Catostomus* (Hubbs, Hubbs, and Johnson, 1943; Hubbs and Hubbs, 1947). The Hubbs' studies firmly established two related principles: that the majority of characteristics in these fishes are the result of polygenic inheritance, and that F_1 hybrids are generally intermediate between the parental types. Although certain characters may show unilateral additive effect, the over-all intermediacy of an F_1 hybrid is clear when all characteristics are considered. While these studies elucidated the behavior of genetic characteristics in individual hybrid specimens, the effects of hybridization at the population level were demonstrated by Edgar Anderson (1949, 1953).

From these studies there emerged criteria for recognizing hybrids and methods of analysis of hybridization. Important foundations of the methodology are the facts relating to the behavior of characteristics in the F_1 , F_2 , and backcross products. The initial hybrid offspring (F_1 's) of a particular interpopulation combination tend to possess expected homogeneity; F_2 specimens display heterogeneity with some specimens approaching each parental phenotype. Backcross products are intermediate between the hybrid and the parent involved, and succeeding backcrosses to one side tend to dilute the strength of the extraneous characters proportionately (Hubbs, 1940), until the offspring become indistinguishable from the parental type. Subsequent recombination within the absorbing population may provide increased variability in the form of occurrence of characters common to the foreign species.

Of the characters used in the present analysis, only the pigment of the caudal fin seems to be under the control of a small number of genes. No indication of dominance was observed. The remainder of the characteristics appear to behave as quantitative characters under polygenic control.

Several observations on the pigment of the caudal fin are pertinent. In certain *platyrhynchus* populations, sparse pigment on the third, fourth, or fifth lowest interradiial membrane of the caudal fin occurs as a population variant. For example, this characteristic occurs in 3 of 10 specimens taken from Dry Gulch Creek, tributary to the Duchesne River of the Green River drainage. Presence of the same character in two collections from Bitter Creek, also in the Green River drainage, suggests that this is not simply random variation. Of 145 measurable specimens taken in 1935, seven, or 4.8 per cent, possessed this pigment character. In 1960, five, or 2.6 per cent, of 193 specimens from the same location possessed the character. The frequency of the character is not significantly different in the samples taken 25 years apart. Sparse pigment on the caudal interradiial membranes occurs

in several other populations of *platyrhynchus* in the Green River drainage and elsewhere, especially in areas of hybridization. Mutation is a likely explanation, but it is possible that the Bitter Creek population is retaining in equilibrium a pigment gene obtained through past hybridization with *C. discobolus*, which possesses this character. The Bitter Creek population is isolated from *C. discobolus*, except in times of flood when the usually dry lower section of the stream may be connected with the Green River.

It is probable that *C. discobolus* and *C. platyrhynchus* have had various interactions of evolutionary significance during their history of sympatry in the Green River drainage (where *C. discobolus* was probably the first of the two inhabitants; see p. 120) and in the northern Bonneville basin and upper Snake River (where sympatry has probably existed for at least 34,000 years; see pp. 119–121). The relative lack of overlap in this trophic-related character may be selective displacement as a result of competition between the two species. The overlap is greater in allopatric populations (see p. 28).

The reverse relationship exists in other characters. In areas of sympatry, there is broad overlap in characteristics which differ between allopatric populations. Figure 22 illustrates by scatter diagrams the relationship of three characteristics of the two species in selected allopatric populations, in two sympatric populations, and in a single-species population possibly subject to gene flow from both species.

The allopatric populations of *discobolus* from the Green River canyon area and *platyrhynchus* from the Bonneville basin are distinct. Different patterns appear where the species are in broad ecological contact as in the headwaters of the Green River and the headwaters of the upper Snake River.

The diagram illustrating sympatric populations in the Green River drainage is based on specimens taken from Sheep Creek and Big Sandy Creek, including five specimens from the Big Sandy which are interpreted as hybrids (page 93). Overlap exists in all three characters. The distribution of these and other characters (see page 94) indicates the occurrence of hybridization between the two species.

Although the characteristics of a few of the specimens are the direct result of their hybrid ancestry, the population average must ultimately be the result of selective action. It is proposed here that the selected genes which provide the sympatric populations with characteristics that differ from those of their allopatric counterparts were made available by hybridization. Hybridization would be expected to provide the source of the variation more rapidly than mutation (Stebbins, 1959). Owing to the independent assortment of genes on different chromosomes and, probably, the crossing over between genes on the same chromosomes, the extraneous genes of hybrid origin may be independently selected for or against in

the absorbing populations. This allows for the possibility of selective character displacement as well as introgressive influence in the ecological and genetic interaction between two species.

The sympatric populations from the upper Snake River (Fig. 22) show still a different relationship in the distribution of the characters in the diagram. The shift to deeper caudal peduncles in the *discobolus* population

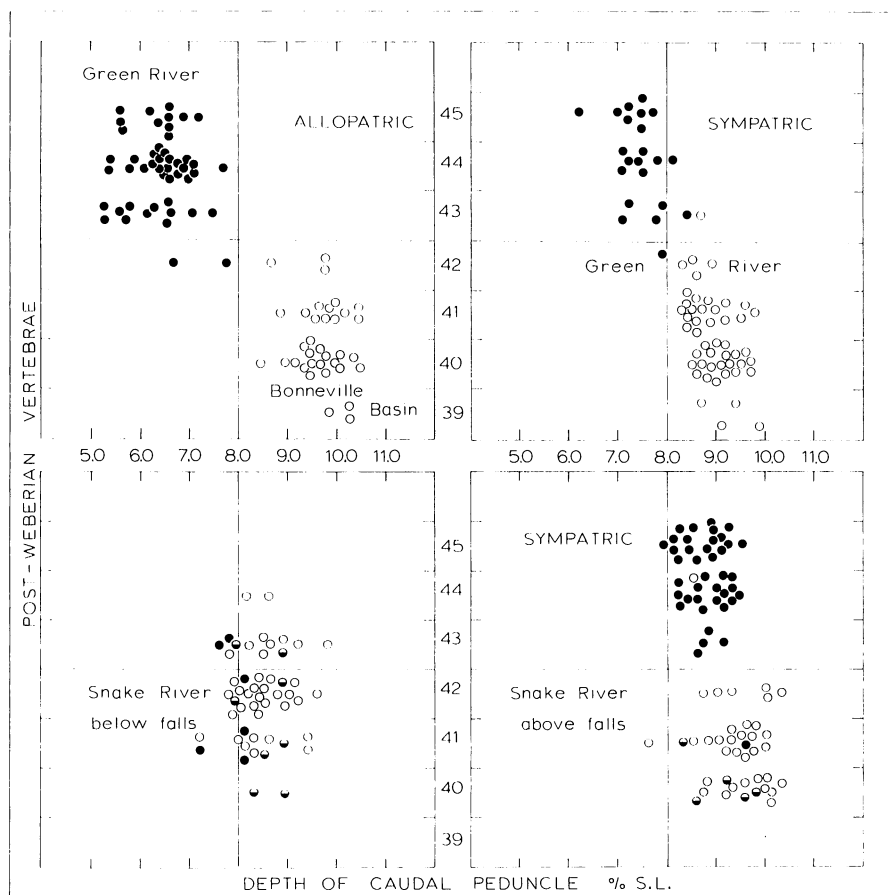


FIG. 22. Scatter diagrams showing the distribution of three characters in five selected situations. The legends, showing number of post-Weberian vertebrae on the ordinate and depth of caudal peduncle expressed as per cent standard length on the abscissa, are the same for each diagram. Black circles represent the presence of pigment on the caudal interradiial membranes, typically a *discobolus* character; open circles represent the restriction of such pigment to the rays, typically a *platyrhynchus* character; half-black circles represent intermediates (Fig. 9). The position of each specimen is plotted according to its depth of caudal peduncle and number of post-Weberian vertebrae. The specimens in the Snake River drainage below the falls are referred to *C. platyrhynchus*.

is most striking. The pattern of discordance in character alignment also strongly suggests introgressive hybridization. It is possible, as in the last case, that the genes for a deeper caudal peduncle have been made available by hybridization and proved selectively successful in the *discobolus* populations.

A series of populations exist in the Columbia and Snake River systems below the Snake River falls that are here referred to as *C. platyrhynchus*. These populations are separated from the sympatric populations upstream by barrier falls, but it is important to note that although gene flow from below to above the falls is impossible, limited gene flow in the reverse direction is possible and historically probable. The downstream populations are characterized by intermediacy and overlap in all of the characteristics which separate *C. discobolus* and *C. columbianus* from *C. platyrhynchus* (Fig. 22; Table 1). The downstream population is also polymorphic in the character, pigment of the caudal fin. The possibility that this is strictly the result of recent hybridization between *platyrhynchus* and *discobolus* is considered unlikely, because of the sporadic distribution pattern of the downstream populations and the great distances separating some of the populations. It is also possible that the lower populations are relicts of an older, intermediate ancestral type.

The presence of a *plebeius*-like phenotype in one of the headwater streams of the Little Colorado River drainage and the introgression of some of these characteristics into the downstream populations of *C. discobolus* in that drainage has been discussed (Fig. 18). Genetic exchange between two kinds of animals which differ as much as *C. plebeius* and *C. discobolus* is interesting, but more striking is the apparent degree of success of some of the characters of *plebeius* in populations of *discobolus*. The prevalence in the downstream populations of unusually low (for *discobolus*) vertebral numbers may be compared with only partial influx of low numbers of dorsal rays, lip and jaw shape, and a caudal pigment character. Furthermore, this contrasts with the presence of *discobolus*-like gill-raker numbers in the upstream, otherwise *plebeius*-like populations. These observations lead to several conclusions and concomitant considerations:

1. The introgression of the genes requires a relatively high selective value or fitness for the hybrid individuals. For example, if the relative hybrid fitness were 50 per cent of that of the normal genotypes, the hybrid characters would exist in the population at a frequency no higher than two times the quantity of new hybrids each generation. If the fitness of any of the hybrid gene combinations were equal to the fitness of the normal genotypes, the equilibrium established would be a function of the relative sizes of the parental populations. Unlike a mutation with a survival value equal to its allele, which will strike an equilibrium according to the rate

of reverse mutation, a small but constant (and equally fit) hybrid influx into a finite population will replace the original type if the hybrid source continues for a sufficient time.

2. The different rates of penetration of the various hybrid characters indicate the existence of at least several hybrid genotypes with high enough selective value to spread through downstream populations. The differential rate of spread is a function of the selective value of the character and its associated pleiotropic effects on the homeostatic system, and is also a function of linkage.

3. A polymorphic system of genes and characters typical of both parental types might be retained in the population, supported by heterozygotic advantage if any particular hybrid gene system were to have a higher selective value than any of the normal genotypes.

The possibility of introgression between species of different subgenera, *Catostomus* and *Pantosteus* (pp. 21, 56, 102, and especially, 66), is still perhaps too speculative to build on further. However, the possible evolutionary effects mentioned above might be considered, with the major reservation that the greater the phylogenetic gap the more unlikely is the occurrence of a hybrid gene combination with sufficiently high fitness. Part of *Catostomus columbianus* might be considered a possible product of introgressive influence between species of the subgenera, *Catostomus* and *Pantosteus*. The zoogeographical evidence for a more typical *Pantosteus*-like ancestry for the species (p. 103) and the known frequency of hybridization between *C. columbianus* and *C. macrocheilus* lend support to the possibility of introgressive modification of *C. columbianus columbianus*.

Mayr (1963:30-35) has thoroughly discussed the unlikelihood of introgressive influence in the evolution of higher animals. The reasons for this are: (1) the rarity of hybrids, and hence, introgression in animals; (2) the improbability of incomplete breakdown of species-isolating mechanisms; (3) the improbability of harmonious gene complexes, leading to selection against hybridization and introgression.

The possible examples of introgressive influence in *Pantosteus* evolution are based only on observations on museum specimens and require experimental verification. That these examples of the hypothesized phenomena might be real is given some support by the following conditions:

(1) Hybridization is not rare in the externally fertilized animals being considered (Hubbs, 1955). For example, quoting from Hubbs, Hubbs, and Johnson, 1943:63:

The 183 hybrids identified in this family constitute 11.5 and 7.2 percent of the specimens, respectively, of the more primitive and of the more specialized of the parental species with which they happened to be collected, but only 1.8 and 1.5 percent of the specimens of the two species from the same river systems . . . the hybrids between the not closely related species *C. macrocheilus* and *C. colum-*

bianus . . . constitute 15.1 and 21.6 percent of the individuals of the respective parental forms with which they were collected, and 6.4 and 4.2 percent of the total specimens at hand from the same river systems.

(2) The complete breakdown of the species-isolating mechanisms need not occur if the genetic contact is between the hybrid-influenced population and a sufficiently large parental gene pool where the hybrid genotypes are relatively less fit. The hybrid-derived genes will appear in the populations at a frequency determined by the interaction of influx rate and selection pressure. Because of the nature of fertilization in these animals, the population genetics may be similar to that in plants.

PHYLOGENY OF *PANTOSTEUS*

The evolution of *Pantosteus* as a specialized product from within the genus *Catostomus* is indicated by several lines of evidence, especially: (1) the morphological similarity of *Pantosteus* and *Catostomus*; (2) the common hybridization between species of the two groups; and (3) the specialized morphology and ecology of *Pantosteus* contrasted with the comparatively generalized morphology and ecology of other species of *Catostomus*.

The osteological structure of the oromandibular region of *Catostomus* (*s.s.*) is similar to that of the earliest known fossil suckers, *Amyzon* Cope, of early Tertiary age. In fact, this structural pattern is somewhat uniform throughout the family with the exception of the aberrant *Lagochila*, *Cycleptus* (Branson, 1962), *Pantosteus*, and several undescribed fossil forms (Miller and Smith, *ms.*). The sharp angle of the dentary (Fig. 4), the heavy maxilla, the cartilaginous jaw sheaths (Pl. I), the unusual lips, and the long gut of *Pantosteus* are specializations derivable from the more primitive form in *Catostomus*. The ecologically more generalized species of *Catostomus* (*s.s.*) occupy a wide range of habitats in lakes and rivers and use a wide range of plant, animal, and detrital food material. The forms of *Pantosteus*, by contrast, are mountain-stream inhabitants with a diet largely restricted to microscopic periphyton.

These differences within the relationship pattern of *Catostomus* and *Pantosteus* provide the background for the consideration of phylogeny. As mentioned in the discussion, reducing *Pantosteus* to subgeneric status (pp. 43-44), two species are intermediate, bridging the gap between the generalized forms and the specialized forms. These species, *C. columbianus* and *C. plebeius*, must therefore be considered representatives of the earliest offshoots of the line leading from *Catostomus* to *Pantosteus*. In all external characters, except the intermediate lip and jaw structure, however, these species are sharply divergent. *C. columbianus*, in the extreme northwestern segment (Columbia River drainage) of the range of *Pantosteus*, has high meristic characters; *C. plebeius*, the southernmost (Rio Grande and Mexico)

species, has low meristic characters. This divergence in range and characteristics suggests that the two species may be separate, early isolates from the stock that was to give rise to the most specialized populations of *Pantosteus*.

The central, specialized product of evolution in *Pantosteus* now consists of four species: *clarki* and *discobolus*, which probably evolved in the Colorado River drainage; *santaanae*, isolated in the Santa Ana system of streams on the Los Angeles Plain in southern California; and *platyrhynchus* of the Great Basin, Columbia, and Missouri systems, and several adjacent drainages. Of these species, *santaanae* is the most generalized in the characters that separate the other species. All morphological aspects considered, *santaanae* appears intermediate among three species: *plebeius*, *clarki*, and *platyrhynchus*. It is therefore considered that *santaanae* represents the closest living approximation to the ancestor of *santaanae*, *clarki*, *discobolus*, and *platyrhynchus*.

C. platyrhynchus is a widespread and variable species. On the basis of shared characters it appears to be phylogenetically closest to *santaanae*. However, Missouri drainage populations possess some characteristics of *discobolus*, and Columbia drainage populations are similar to some isolated headwater samples of *columbianus*. Certain southern Bonneville basin populations of *platyrhynchus* share characteristics with adjacent populations of *clarki*. These patterns are suggestive of reticulate evolution.

C. clarki and *C. discobolus* are the most closely related species within the subgenus. This fact is revealed by near identity of osteological features and mouth structure, but the relationship has not been previously recognized, owing to sharp dissimilarity in two characteristics: the depth of the caudal peduncle and the number of predorsal scales. However, these differentiated characters overlap and are probably not fundamental, except as responses to relatively recent selective pressures.

GEOLOGICAL CONSIDERATIONS.—Perhaps the most striking feature of the distribution of *Pantosteus* is the ecological affinity for mountain streams and the geographical association of populations with areas of orogeny. It may be noted from the distribution maps that most collections are from the slopes or bases of mountain ranges or other areas of uplift. It is therefore concluded that the specializations of *Pantosteus* and the evolutionary history of the group are closely tied to the history of mountains and plateaus in western North America.

Further inspection of the geographical distribution reveals that four of the six species exist within or on the borders of the Colorado Plateau. *C. discobolus* inhabits the Colorado River drainage throughout most of the Plateau and the Wyoming basin to the north, and has secondarily gained access to the upper Snake and northern Bonneville drainages. *C. clarki* inhabits the streams draining the Mogollon Rim, which forms the southern

boundary of the Plateau in Arizona, and the Virgin River, which drains part of the High Plateau section in southwestern Utah. The other populations of *clarki* are in the Bill Williams River west of the Plateau, the Western Virgin River drainage, and the White River drainage west of the Colorado Plateau in the Basin and Range Province. *C. plebeius* inhabits the southeastern border of the Plateau in the Rio Grande drainage and extends south into the mountains of Mexico. *C. platyrhynchus* inhabits the Great Basin side of the High Plateaus in central Utah and is present in the Colorado drainage on the northern part of the Colorado Plateau. It is otherwise distributed widely in the Great Basin, Columbia, Missouri, and associated drainages. Of the remaining two species, *C. columbianus* is in the Columbia and Fraser River drainages, far removed to the northwest, and *C. santaanae* is in southern California, but not far removed—its history may be associated with the history of the Colorado River.

The geological time during which the early evolution of *Pantosteus* occurred is suggested by observations on fossil catostomids as well as the history of the Colorado Plateau. The primitive sucker *Amyzon* Cope is known from early Tertiary strata in western United States variously considered as Eocene to Oligocene. No Miocene sucker is yet reported. Late Pliocene suckers, widespread in sedimentary deposits of the Columbia Plateau and associated areas (Miller and Smith, ms., Uyeno and Miller, 1963), contain some essentially modern morphotypes in addition to a diversity of extinct forms. Pleistocene suckers seem to illustrate more extinction than change from Pliocene forms. The only recognized fossil of *Pantosteus* is known from a dentary and maxilla, and is similar to *C. columbianus*. The fossil is from fluvial sediments of the Glens Ferry formation of southern Idaho, a lower section of which has been dated as over three million years in age (K:A determination, Evernden *et al.*, 1964). It is possible that the early evolution and differentiation of *Pantosteus* took place during the Miocene and/or Pliocene.

It was perhaps in early Miocene time that the Colorado Plateau became a well-defined structural unit at an altitude higher than the basins of the Basin and Range Province but not as high as the ranges. The major patterns, but not the present continuity, of the Colorado River drainage were formed by this time (Hunt, 1956:77, 82–83). The Miocene and early Pliocene was a time of aggradation over much of the inland area of western United States (Love, 1960; Love *et al.*, 1963; Van Houton, 1956). During Late Miocene to Middle Pliocene time, the Colorado River became ponded and deposited sediments, possibly as the result of northeastward tilting (Hunt, 1956:84–85).

At this time the Great Basin floor probably stood at an elevation of about 2000 feet with drainage to the Pacific. Floras indicate lowland conditions in

transition from temperate forest to drier continental climate (Axelrod, 1950, 1955, 1962). Fossil fishes also indicate lowland conditions (Hubbs and Miller, 1948:26).

Notwithstanding the extensive aggradation in Miocene time, montane drainage probably existed in association with such areas as the fault block mountains of the Great Basin, the Colorado Plateau, the San Juan Mountains of Colorado, the Uinta Mountains of Utah, and in the Yellowstone vicinity of Wyoming. The focus of the headwaters of the major drainages of western North America on the San Juan Mountains and the Yellowstone area indicates that uplands existed here throughout most of the Cenozoic (W. L. Stokes, personal communication, 1964).

It is hypothesized that the initial stage of *Pantosteus* evolution occurred in the vicinity of highland areas in the eastern Great Basin, the Colorado Plateau east to the San Juan Mountains, and north to the ancestral Snake and Missouri River headwaters in the Yellowstone region.

The Miocene uplift of the Colorado Plateau might have been important in the evolution of *Pantosteus*. As described by Hunt (1956:77) the "Plateau broke away from and was raised higher than the basins to the west, south and southeast; large areas of the Plateau must have begun draining to those basins." As pointed out earlier, three related species are adjacent to *C. discobolus*, the species of the Plateau. They are *platyrhynchus*, *clarki*, and *plebeius*, and are found just off the edge of the Plateau to the west, south, and southeast, respectively.

Several observations suggest that by middle Pliocene time much of the evolution might have already occurred. First, the southern Colorado Plateau already harbored a fish fauna with elements suggestive of the Colorado River fauna of today, although lacking suckers (Uyeno and Miller, 1965). Second, the geological events that probably separated *C. clarki* and *C. discobolus* appear to be no later than late Pliocene, suggesting that the ancestor of these closely related species must have separated from the *santaanae-platyrhynchus* stock prior to this time. Third, the existence in premiddle Pliocene times of drainage from the Colorado Plateau and possibly the Great Basin to the Pacific Ocean apparently offers the best opportunity for access of *Pantosteus* into the southern coastal area of California where *C. santaanae* is now isolated.

The subsequent history of the group is discussed from the standpoint of the individual species as presently recognized, beginning with the most primitive representatives.

Catostomus columbianus: The Snake and lower Columbia rivers are the seat of evolution of this species. It occupies the lower Snake River and one isolated headwater of the Snake above the falls, indicating former widespread occupation of this area. To the west it occupies most of the tribu-

taries to the lower Columbia, including some above barrier falls, suggesting long occupation of this part of the drainage. To the north it is in the Fraser River, indicating active postglacial dispersal. It appears to be absent from the upper Columbia drainage east of the Columbia Plateau. As previously noted, the fossil occurrence of a fish close to this species is known from the Glens Ferry formation, probably late Pliocene or early Pleistocene in age, in fluvial deposits of the ancestral Snake River.

The history of the Snake River Plain is well documented through several series of fluvial and lacustrine sediments and basalts dating from at least early Pliocene (Malde and Powers, 1962). However, the historical relationship of the Snake to the Columbia River has been a difficult problem.

Wheeler and Cook (1954) noted that Snake River canyons above and below Hells Canyon differ, and barbed tributaries below the oxbow indicate reversal of the stream. These authors suggested that the present course through Hells Canyon is a relatively young feature and that the Snake formerly may have had an outlet through southeastern Oregon, northern Nevada, and northeastern California through the Feather River to the Great Valley. Biogeographical data based on late Pliocene molluscs (Taylor, 1960) indicate, to the contrary, that the Snake outlet was independent of the Great Valley (see also Miller, 1965).

Catostomus columbianus occurs in the following drainages: throughout the lower Snake and lower Columbia basins; the Harney basin, once a part of the Snake drainage; above barrier falls in the Wood River tributary to the Snake; the Palouse River, tributary to the lower Snake; and the Deschutes River, tributary to the lower Columbia. Such a pattern, superimposed on the fossil occurrence of an ancestor to *C. columbianus* in the ancestral Snake River during Late Pliocene and Early Pleistocene times, suggests that the upper and lower Snake and the lower Columbia constituted a through-flowing system prior to the development of the barrier falls of the Palouse and Deschutes rivers.

The similarities of the isolated populations of the Wood, Palouse, and upper Deschutes River suggest that these are remnants of a formerly widespread ancestral type. Nonisolated headwater populations are similar to the central type, now widespread in most tributaries to the lower Snake and lower Columbia, indicating evolution of the latter group (page 101) since isolation of the headwater types; or since establishment of the Snake-Columbia as a through-flowing drainage. If this interpretation is correct, it leads to the conclusion that *C. c. columbianus* was formerly more *Pantosteus*-like, at least in the possession of lateral lip notches, for the isolated upstream populations show the highest incidence of this character. A possible explanation is subsequent introgressive effacement of this character in the downstream, presently widespread population (p. 111).

The local differentiation of the isolated Palouse River population has been recognized subspecifically (Schultz and Thompson, 1936), though the degree of distinction is not particularly high. The Wood River population, which is nearly 100 per cent distinct, is named *C. columbianus hubbsi* in the present paper. The isolated populations in the headwaters of the Deschutes River are distinct to about the same degree as those of the Palouse River. Populations of the Deschutes River below the falls are intergrades.

The known specimens of *C. columbianus* from the presently isolated Harney or Malheur basin tend toward the isolated headwater morphotype, with possible limited differentiation in certain isolated spring waters. The basin was a through-flowing tributary to the Snake River until isolated by lava flows (Hubbs and Miller, 1948:75).

Catostomus plebeius: This inhabitant of the Rio Grande and southern drainages shares with *C. columbianus* mouth characteristics intermediate between *Catostomus* and *Pantosteus*. In *plebeius*, however, the *Catostomus*-like character is the distinctly rounded lower jaw, which is curved dorsoventrally and anteroposteriorly rather than abutting against the upper jaw as a truncate ridge as in other species of *Pantosteus*. This characteristic suggests that *plebeius* was isolated very early in the history of *Pantosteus*. The line of isolation is, and likely was originally, the southeastern edge of the Colorado Plateau, which dates from the Miocene. *C. plebeius* shares more characters with and is more closely related to *platyrhynchus* and *santaanae* from west of the Plateau than to the more specialized *discobolus* and *clarki* of the Colorado River drainage.

The historical relationship between the populations in the Rio Grande and those of the presently isolated basins and streams to the south must involve former continuous occurrence associated with Pleistocene fluvial connections and cool, moist conditions. Contemporaneity of glaciation with pluvial conditions and lower summer temperatures, lower snowlines, and increased effective humidity in the southwest (Estancia, New Mexico) is shown by Leopold (1951). The extension of *plebeius* into Mexico is probably old—certainly prior to drainage changes which carried it across the continental divide into at least three Pacific drainage streams, Rio Mezquital, Rio Piaxtla, and Rio Yaqui. Limited differentiation has occurred in at least the southern pair of these streams.

The history of the Rio Grande offers clues to the relationship between the Rio Grande fishes and those of the Guzman basin area in northern Chihuahua. According to King (1958), it is possible that the Rio Grande once flowed south into the lake region of northwestern Chihuahua, but later shifted eastward through progressive basins to appear finally in its present course. Stream-worn gravel deposits in basins of northern New Mexico

indicate the presence of streams probably ancestral to the Rio Grande as early as lower Pliocene time. The degree of differentiation of *C. plebeius* in the Rio Grande and Guzman drainage is slight, but is sufficient to show that the Rio Mimbres, isolated in southwestern New Mexico, is a part of the Guzman drainage independent of the Rio Grande.

Fishes of the Rio Nazas and associated drainages show variation between populations but no broad patterns of differentiation. The apparent geographical gaps between these and other populations are partially a result of insufficient collecting, though the hypsithermal and postpluvial desiccation have constricted the habitable areas.

Catostomus santaanae: The range of this species is strikingly restricted and isolated from other kinds of *Pantosteus*. The area occupied, the Los Angeles Plain, was marine during the Pliocene and was uplifted during the Pleistocene (Reed, 1933). The populations of the four adjacent but isolated streams are little differentiated. These facts suggest that the species has been isolated for a relatively long period of time but the local populations are relatively new in the present area of occupation. Moderate uplands with permanent drainage might have harbored populations in the vicinity, but there is no direct distributional evidence for this. The original access to the coastal area might have been by way of an ancestral course of the Colorado River. This possibility is supported by the existence of extensive Pliocene (Reed, 1933:237) siltstone, indicating the discharge of a large, low-gradient river, perhaps the ancestral Colorado River, southwest of the Salton Sea (Woodring, 1932:9).

C. santaanae varies in structural features that are stabilized as specific characters in other species of *Pantosteus*, suggesting that *santaanae* is a generalized representative of an intermediate stage in the evolution of *Pantosteus*. The species shares some characters with *plebeius*, fewer with *platyrhynchus*, and still fewer with *clarki*, yet variation renders it close to overlap with each of these species.

Catostomus platyrhynchus: This species is best represented in the Great Basin and in the upper Missouri drainage from the Black Hills westward. Considered alone, these two groups of populations are fairly distinct, suggesting a relatively long period of isolation.

The Great Basin populations include a section associated with the Sevier River drainage, just off the west slope of the Colorado Plateau; a northern Bonneville section in the streams flowing west from the Wasatch Mountains; a Lahontan basin section, including inhabitants of the east-flowing drainages of the Sierra Nevada and the Humboldt River drainage of northern Nevada; and a few isolated population groups in the center, between the major sections. There has been little differentiation among these broader groups, the greatest being that between those of the northern and southern Bonne-

ville basin. Two isolated populations of the southern Bonneville group are even more differentiated. One is in Duck Creek, isolated by a late Tertiary lava flow (Gregory, 1949:979); the other is in Shoal Creek, a former tributary to the Escalante arm of Pleistocene Lake Bonneville.

The undifferentiated condition of the widely separated Great Basin populations argues for rather slow evolution. Determination of the age of drainage connections that might have connected the Bonneville and Lahontan basins would establish a length of time which is, in fact, insignificant in the evolution of the fishes involved.

Pantosteus is absent from the west slope drainage of the Sierra Nevada, with the exception of the reported occurrence of *platyrhynchus* in the Feather River system tributary to the Great Valley (Rutter, 1908:120). The Feather River was formerly a larger stream, probably antecedent to the Sierra uplift (Wheeler and Cook, 1954). Its source is east of the Sierra Nevada in what would otherwise be part of the Great Basin. The Sierra ridge, whose east-slope tributaries support *C. platyrhynchus* in abundance, may have reached an elevation of 6000 feet in Mio-Pliocene time (Axelrod, 1955) and was subject to great Pleistocene uplift, locally as much as 6500 to 7000 feet (Axelrod, 1962).

C. platyrhynchus of the Missouri drainage is most similar to populations of the lower Snake, Columbia, Green, and Sevier rivers. These populations are probably relatively old inhabitants of the western Wyoming area. The eastward spread to the Big Horn Mountains and the Black Hills probably did not occur until the rejuvenation of streams in late Pliocene-early Pleistocene times (Love *et al.*, 1963). *C. platyrhynchus* of the Saskatchewan drainage probably represents an undifferentiated postglacial derivative from the Missouri drainage.

The Green River populations of *platyrhynchus* are not obviously derived from those of the Great Basin, the upper Snake, or the Missouri drainages, notwithstanding the abundance of possible drainage connections with these areas. It is possible that a long history of reticulate evolution has occurred in conjunction with adjacent populations now in different drainages. The populations of the Green River drainage show relative morphological unity as well as obvious affinities with the surrounding populations.

The Columbia River drainage harbors populations of *platyrhynchus* of two kinds. Those below the falls of the Snake River are in sparse, scattered localities and possess affinities with the Missouri drainage populations. However, they share certain characteristics with *C. discobolus* and *C. columbianus*, species that are more or less genetically available to *platyrhynchus* at the present time. *C. columbianus* is sympatric; *C. discobolus* is above the falls and is available by way of accidental migration. The populations in the Fraser River drainage are probably postglacial derivatives from the Columbia

River drainage. Populations of *platyrhynchus* in the Snake River drainage above the great falls are largely undifferentiated associates of the Bonneville basin populations. A complex history is suggested, however, by examples of unusual interpopulation variation within the drainage. It is probable that the upper Snake had a resident population related to the fishes of the Green River or Missouri drainage and was invaded by Bonneville populations at the time of the Bonneville drainage into the upper Snake. According to Bright (1962), the Bear River drained to the Snake River prior to 34,000 years B. P. A succession of geological events eventually diverted the Bear River into the Bonneville basin, which later topped its rim and flowed into the Snake. The overflow into the Snake was a cataclysmic flood which may have exceeded 10 million cubic feet per second (Stearns, 1962). It is difficult to imagine the effect of such an event on the fish fauna; however, it is possible that a rather normal drainage connection might have existed for an extended period following the initial flood.

Catostomus discobolus: This species presently occupies the Colorado Plateau, the Colorado River drainage of the Wyoming basin, and the west slope of the Colorado Rockies. Additional populations are restricted to small ranges in the Bonneville and Snake drainages, more or less contiguous with the Colorado drainage.

The species is similar to *C. columbianus* in its meristic characteristics. Its closest relative, however, is *C. clarki* of the lower Colorado, from which it differs structurally only in depth of caudal peduncle and scale size. *C. discobolus* is the most specialized species of *Pantosteus*, the major specialization being adaptation to the extreme fluvial environment of the Colorado River—the torrential current and sand bottom. These conditions probably have been in existence through the period of canyon cutting, which is estimated to have occupied the past one or two million years (Stokes, 1964; Hunt, 1956). The major centers of distribution of the most specialized fluvial morphotype of this species are presently in the canyon areas of the Colorado drainage—at the east end of the Uinta Mountains, the Grand Canyon, and the San Juan River in the Monument Upwarp near Mexican Hat, Utah. Specimens from headwater areas are much less modified.

The populations of the west slope of the Colorado Plateau in the Price, San Rafael, and Fremont drainages have similar meristic characters. Specimens from small, spring-fed tributaries in Glen Canyon (now inundated by Lake Powell) possessed adaptations to these peculiar conditions, including small size and reduction of certain meristic elements.

Access into the Snake River and Bonneville basin, where the species exists in generalized form similar to the population from the upper Green River, has been through past drainage exchanges and connections. One such possible drainage connection of the Snake and Green rivers exists in the Kinky Creek

area, T.40 N, R.11 W (Driggs, Idaho; Wyoming Quadrangle, U.S.G.S. 1:250,000, 1962). The diversion of Bear River from the Snake to the Bonneville drainage (Bright, 1962) is discussed above. The occurrence in Weber River indicates access prior to the isolation of Bear and Weber rivers by the desiccation of the remnant of Lake Bonneville about 11,000 years ago (Broecker *et al.*, 1960).

The character gradient in populations of the Little Colorado River (pp. 86, 110) suggests a drainage transfer from the Rio Grande to the Colorado in the vicinity of Nutria, New Mexico. The McCarty's basalt flow in Valencia County, New Mexico, appears to have diverted part of the San Jose drainage into the Little Colorado River drainage within the last 1200 years (Nichols, 1946), but this is several miles south of the area of importance. It is possible that the rapid removal of the Tertiary erosion surface in the Gallup-Zuni area (McCann, 1938) could have effected drainage changes in the direction of slope, from east to west, in the Nutria area. The Little Colorado River is isolated from the rest of the Colorado River by Grand Falls. However, the lava flow that created these falls may be as young as 1100 years (Childs, 1948).

Catostomus clarki: The remarkable distribution of this close relative of *C. discobolus* provides definite clues concerning the evolution of the Colorado River and its fishes. As presently recognized, the species is found in the Gila River drainage, just off the southern edge (Mogollon Rim) of the Colorado Plateau; the Bill Williams River drainage just west of the Colorado Plateau; the Virgin River, which drains part of the High Plateaus; and remnants of the pluvial Carpenter and White rivers of the Basin and Range province south of the Great Basin. Stated otherwise, the species is found in connected and disconnected parts of the Colorado River system below Grand Canyon, a distribution pattern similar to that of the spiny minnows (Miller and Hubbs, 1960).

The differentiation of *C. clarki* and *C. discobolus* along with the lower and upper segments of the Colorado River fish fauna might be attributed to isolation during the Pleistocene by the Grand Canyon, but several things seem to suggest an alternative explanation. The torrential falls of the Grand Canyon are not a complete barrier to fishes. In addition, northern populations of *C. clarki* have been isolated perhaps for much of the Pleistocene by desiccation of the pluvial White and Carpenter rivers; yet the differentiation within *clarki* is not comparable to that between *clarki* and *discobolus*. Finally, the course of the Colorado River between Grand Canyon and the point of connection of the pluvial White River and lower Colorado River is a relatively new feature, dating only from the Pleistocene or late Pliocene (Blackwelder, 1934; Hunt, 1956). Longwell (1928, 1946) pointed out that the Colorado River and the Virgin River could not have existed in their present courses while the Pliocene (?) Muddy Creek formation and the overlying

limestone beds were being deposited in this area. The Muddy Creek deposits were not formed by the Colorado River. The drainages now occupied by *C. clarki* (Fig. 14) might have been an integrated system isolated from the upper Colorado River at this time. Hunt (1956:82-86) showed that during late Miocene to Middle Pliocene times the upper Colorado River no longer drained the Plateau into the area southwest of the present Grand Canyon, but was suspended and ponded by northeastward tilting and by the Kaibab Up-warp. Then, in late Pliocene time, drainage resumed through the old channel when the water was raised to that level by ponding and aggradation. This interpretation of the history of the Colorado River offers a period of isolation and evolution of *discobolus* and *clarki* in the upper and lower sections of the drainage.

The various populations of *C. clarki* extend over a linear range of about 800 fluvial miles. It is interesting that the most widely separated of these, the Gila and the White river populations, are the most similar. The geographically intermediate populations appear to be closer to *C. discobolus* to which they might have been genetically exposed since the initial isolation. The rapids of the canyon of the Virgin River in Arizona have produced a swift-water morphotype in *C. clarki* which parallels those in *C. discobolus*.

The isolated populations in the pluvial White River, the pluvial Carpenter River (Meadow Valley Wash), the Beaver Dam Wash, and the Virgin River form a series showing slight differences. Populations of the Bill Williams River are related to this series. Some of the apparent differentiation in the species seems to be partly correlated with altitude.

SUMMARY

The osteology, external anatomy, and internal anatomy of fishes of the genus *Pantosteus* and related suckers are analyzed for information on the levels of relationship within that section of the family Catostomidae. *Pantosteus* is seen to be a specialized product of *Catostomus* evolution and *Pantosteus plebeius* and *Catostomus columbianus* are found to be intermediate between the two genera. It is concluded that *Pantosteus* should rank taxonomically as a subgenus of *Catostomus*—an arrangement independently supported by the widespread hybridization between the two groups. The relationships of *C. columbianus* are with *Pantosteus*.

Analysis of the distribution and variation of populations of *Pantosteus* led to construction of descriptions, comparisons, keys, range statements, distribution maps, and synonymies for the species. Six species are recognized: *C. columbianus* of the Columbia River drainage below the falls of the Snake River, and the Fraser River; *C. platyrhynchus* of the Great Basin and the Columbia, upper Green, Missouri, Saskatchewan, and Fraser rivers; *C. discobolus* of the Colorado River drainage above Grand Canyon, the upper

Snake River drainage, and the northern Bonneville basin; *C. clarki* of the Colorado River drainage and Pleistocene connectives below Grand Canyon; *C. santaanae* of the Santa Ana system of streams, southern California; and *C. plebeius* of the drainage systems of the upper Rio Grande, Lake Guzman, Rio Nazas and associated streams, Rio Mezquital, Rio Piaxtla, and upper Rio Yaqui.

It is suggested that the early evolution of *Pantosteus* involved a *columbianus* ancestor in the north, a central ancestral form in the Great Basin-Colorado Plateau area, and a *plebeius* ancestor in the southern parts of the range, as sections of one of the products of *Catostomus* evolution. The history of these population groups has been closely tied to the history of the drainage patterns around areas of orogeny in western North America, particularly the Colorado Plateau. The range of *C. discobolus* is largely conterminous with the Colorado Plateau in the south and three species border on the rim of the Plateau in this area: *C. plebeius* to the southeast, *C. clarki* to the south and southwest, and *C. platyrhynchus* to the west. Drainage changes along the borders of the major river basins have probably transferred populations and contributed to reticulate evolution of the major population groups. Later drainage changes in the area between the Colorado Plateau and the Yellowstone area have resulted in the transfer of *C. discobolus* populations into the Snake River and Bonneville basin and *C. platyrhynchus* into the Green River drainage, leading to sympatry and some hybridization.

An example of introgressive hybridization between *C. discobolus* and *C. plebeius* exists in the Little Colorado River drainage, probably as a result of a drainage transfer. Hybridization might have played a role in the evolution of some populations of *C. columbianus*. Two general forms of *C. columbianus* are known as a result of past isolation of several similar populations above barrier falls. The isolated populations seem to have been removed from the mainstream of evolution of *C. columbianus*, and may represent an older historical stage. Hybridization has probably influenced the evolution of some populations of *Pantosteus*, but the major factors have been adaptation of populations to local environmental conditions and the restriction or causation of gene exchange by the changing geography of the drainage patterns.

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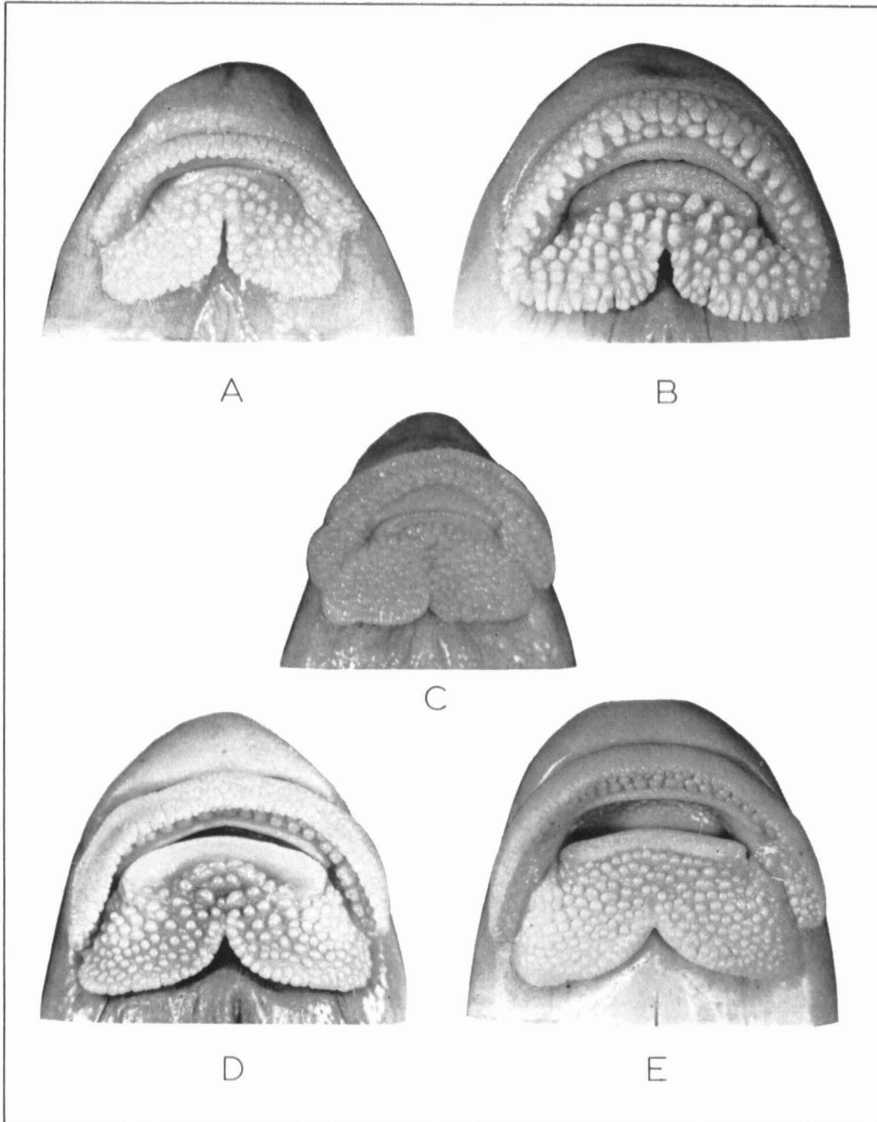


PLATE I

Ventral view of the jaws and lips of suckers of the subgenus *Pantosteus*. A, *C. plebeius*; B, *C. columbianus*; C, *C. santaanae*; D, *C. platyrhynchus*; E, *C. discobolus*. B represents *C. columbianus hubbsi*, new subspecies (UMMZ 157013). *C. clarki* is similar to E, *C. discobolus* and is not figured.

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