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Middle Pliocene Cyprinid Fishes from the Bidahochi Formation, Arizona

TERUYA UYENO AND ROBERT RUSH MILLER

Significant differences have been noted between fish faunas of Pliocene and Pleistocene times. Consequently, study of Pliocene fishes may be expected to contribute importantly to an understanding of the evolutionary history of the living American fish fauna. Four species of cyprinids are described from Arizona, of which 3 are new—including a new genus. A K–Ar dating of 4.1 million years establishes, along with evidence from fossil biotas (mammals and mollusks), the Middle Pliocene age of the Bidahochi formation. All 4 species are illustrated. *Ptychocheilus preluclus* is regarded as ancestral to the living Colorado squawfish, *P. lucius*; ?*Gila cristifera* and *Evomus navaho* represent extinct species and an extinct genus. *Gila* cf. *G. robusta* indicates, along with *P. preluclus*, that the Colorado River had, by Middle Pliocene time, attained the swift-river habitat to which the modern representatives are so admirably adapted. Absence of suckers from the Bidahochi formation may be explained on the basis that *Amyzon*, an early evolutionary line of the Catostomidae representing species found in lacustrine deposits, did not survive the Miocene, whereas other suckers evidently reached the area later.

INTRODUCTION

ALTHOUGH our knowledge of Cenozoic freshwater fishes is still meager, results of recent studies tend to indicate that Pleistocene ichthyofaunas are, with few exceptions, similar to or identical with those of the Recent (Uyeno and Miller 1963). This also seems to be true of other cold-blooded vertebrates (Holman 1962), but is in marked contrast to the great changes that took place in mammals and, to a lesser extent in birds, during about the same time span (Wetmore 1956, Hibbard 1958). There are, however, some significant differences between the fish faunas of the Pleistocene and the Pliocene. Many species and some genera became extinct around the close of the Pliocene or in the early Pleistocene (Uyeno 1961; C. L. Smith 1962; Uyeno and Miller 1962, 1963; Table 1). This circumstance has suggested that an extensive study of fossil fishes of Pliocene age would contribute importantly to an understanding of the evolutionary history of much of the Recent North American fish fauna.

In this report, we describe 4 species of cyprinid fishes from the Middle Pliocene Bidahochi formation in northeastern Arizona—3 of which are new, including a new genus. These fossils provide an insight into the changes undergone by the fish fauna of the Colorado River basin since Pliocene times.

Our deep appreciation is expressed to Carl L. Hubbs, who examined some of the first

Bidahochi specimens and who has critically read the manuscript. We are particularly grateful to Charles A. Repenning, of the U. S. Geological Survey, who discovered some of the fossil-bearing beds, made valuable collections from them, and gave us the benefit of his knowledge of the geology of the Bidahochi formation. John F. Lance, of the University of Arizona, provided age information on the fossil beds and the associated fauna, and further guided one of us to the fossil localities with William J. Breed, of the Museum of Northern Arizona, and Neal McClymonds, of the U. S. Geological Survey, in the summer of 1960. Mr. Breed generously accompanied us to the Roberts Mesa locality in the summer of 1961, and arranged for a loan of specimens from the Museum of Northern Arizona. Collecting in the Navajo Indian Reservation was carried out under the sponsorship and with personnel of the Museum of Northern Arizona, which has authorization from the Navajo tribe to make surface collections in the area. Richard O. Witten of the Amerada Petroleum Corporation collected the specimen illustrated in Fig. 5B. William G. Melton, Jr., Preparator of The University of Michigan Museum of Paleontology, painstakingly exposed a critical part of one fossil. The photographs were taken by Karoly Kutasi, Preparator of the Museum of Paleontology, through the courtesy of C. W. Hibbard.

This contribution was made possible by the continuing support of the National

Science Foundation (G-15914 and GB-735), which is gratefully acknowledged. Gifford H. Miller served ably as field assistant.

LOCALITIES AND PRESERVATION

The Bidahochi formation extends over a wide area in the upper part of the drainage basin of the Little Colorado River, chiefly in northeastern Arizona but extending into adjacent parts of extreme western New Mexico, a short distance west and southwest of the Zuni Mountains (Repenning and Irwin 1954, Fig. 1; Repenning, Lance, and Irwin 1958, Fig. 3). Its age was reported as Middle Pliocene (or Hemphillian) by Stirton (1936), who described a new beaver of the Pliocene genus *Dipoides* from White Cone, one of several known fossil-bearing localities in the formation. Subsequent age determinations from mollusks and mammals other than beaver are consonant with this dating (Lance 1954, Taylor 1957), which has recently been determined as 4.1 million years on the basis of potassium-argon analysis (Evernden *et al.* 1964).

The Bidahochi formation is divisible into a lower sedimentary member, a middle volcanic member, and an upper sedimentary member. Details of the composition and distribution of the formation and references to earlier geological work in the region are given in the papers by Repenning *et al.* cited above. All the fossil fishes came from the basal part of the upper member of the Bidahochi formation. This level represents mixed lacustrine and fluvial deposition, whereas the higher parts of the upper member appear to be entirely fluvial. Possibly, the fish from Steamboat Wash was found higher in the section than were the other fossils. Most of the lower member is lacustrine except near the margins of the basin. The specimens from the Coliseum Diatreme (see below) lived in an isolated small pond rather than in the main lake, but the pond was doubtlessly connected to the lake by a stream or estuary. Examination of available material from the diatreme does not indicate that the 2 species collected there reflect marked ecological differences in habitat.

The fossils reported here are from 4 localities within the Bidahochi formation, 3 of which are described in detail below (the exact location of the fourth is unknown). The materials are deposited in the Museum of Northern Arizona (MNA), The University of Michigan Museum of Paleontology

(UMMP), and the United States National Museum (USNM). Specimens cataloged without reference to locality are all from Roberts Mesa.

1. Roberts Mesa locality (UM-ARIZ-2-60, 61), Navajo Co., Arizona (Fig. 1). On south-facing slope of Roberts Mesa in Sec. 22, T 26 N, R 21 E, approx. 4.5 airline mi NW of White Cone Peak. To reach, take dirt road leading W from main N-S hwy. just N of turnoff to White Cone Trading Post; after 2.1 mi, turn right (N) at crossroads and go up old Keams Canyon road 1.6 mi (near crest of switchbacks) where, leading NE at top of mesa, is a trail that may be followed for a little less than a mile into scattered junipers. Fossiliferous area lies about 100 yards SE.

Fossils were relatively abundant over a restricted area of the eroded southern surface of the mesa (Fig. 1), occurring both as float material (especially around ant hills) and as bones in place. Where exposed, they are weathered whitish. Specimens were collected by Repenning and Lance in 1950, by W. J. Breed, C. L. Hubbs, J. F. Lance, Neal McClymonds, and R. R. and G. H. Miller in 1960, and by Breed, the Millers, and T. Uyeno in 1961.

A basalt unit exposed in the road cut near the crest of the switchbacks and underlying, by a few feet, the fossiliferous strata has been dated at 4.1 million years by K-Ar analysis (Evernden *et al.* 1964:190 and Table 6). This basalt separates the upper member of the Bidahochi formation from the lower and is essentially correlative to the basaltic agglomerate 20 ft below the lowest vertebrate fossils of the White Cone local fauna.

2. White Cone Peak (UM-ARIZ-3-60), Navajo Co., Arizona. Taylor (1957) named this the White Cone local fauna; contained fossils (mollusks, fishes, and mammals) are from upper member of Bidahochi formation at White Cone Peak, in Sec. 12, T 25 N, R 21 E, 1.5 mi S of White Cone Trading Post, about 40 mi N of Holbrook. The peak is a prominent topographic feature of the region (see Gregory 1917: Pl. 14, Fig. B).

The condition of the material is similar to that from Roberts Mesa. Specimens were taken by Lance in 1950 (or 1953), and those who visited Roberts Mesa also collected there in 1960.

3. Coliseum Diatreme locality (UM-ARIZ-4-60), Navajo Co., Arizona. Locality is in Sec. 20, T 23 N, R 21 E, approx. 14 airline

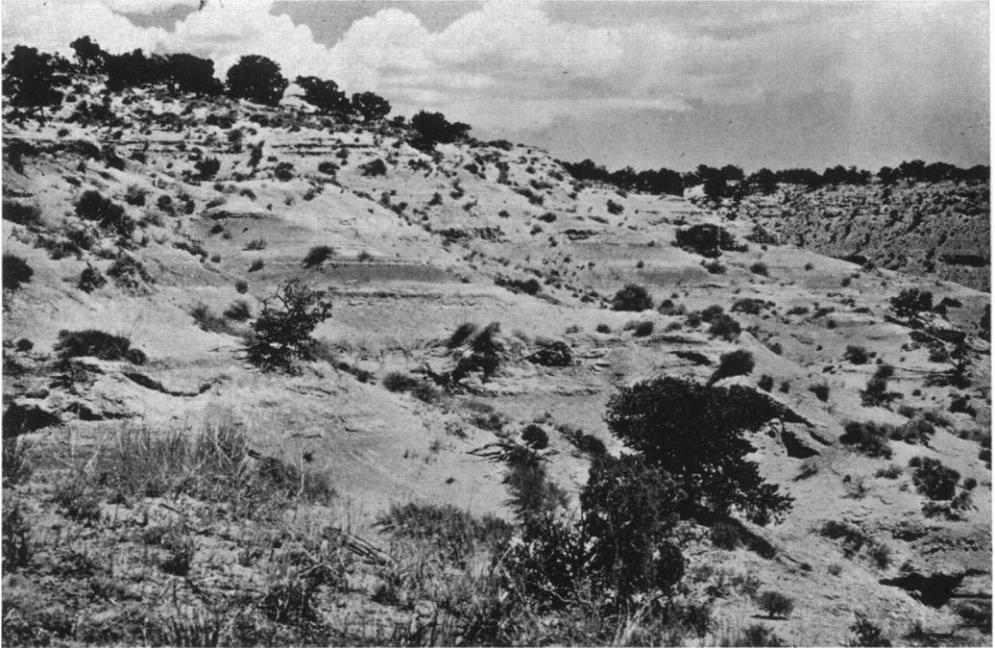


Fig. 1. View eastward of south-facing slope of Roberts Mesa (UM-ARIZ-2-61), Navajo Co., Arizona. From Kodachrome by T. Uyeno, 18 July 1961.

mi SSW of White Cone Peak. To reach, turn W off (new) Keams Canyon road 31.2 mi N of U. S. Hwy. 66 toward Indian Wells Trading Post, but take left fork (rather than going into trading post). About 1.5 mi from Keams Canyon road, cross main road from Indian Wells T. P., and turn left. After about 3 mi, turn right (N) on dirt road leading up wash and continue for about 0.8 mi to below rock dam; exposures are on left (S) wall of crater.

The fish fossils occur in deposits on the steep slopes of the inner wall of a crater (which has been cut directly through by Lokasakad Wash) in a thin-bedded limey clay interbedded with tuff. They are embedded in brittle, loose, reddish-white slabs, and are mostly represented by skeletal casts. Subsidence within the diatreme has tilted the beds about 25°, so that the structure is bowl-shaped; the fossils were found about halfway up the southern side of the "bowl." The age is approximately the same as that of the White Cone local fauna (Repenning, pers. comm.). The diatreme was mapped and described by Hack (1942:354, Pl. 1, Fig. 8) as diatreme number 3. The 2 species from this locality were collected by C. A. Repenning, E. M. Shoemaker, and Richard O. Witten, in

1958, and by W. J. Breed, C. L. Hubbs, J. F. Lance, Neal McClymonds, and R. R. Miller in 1960.

DESCRIPTIONS

When fossil remains consist of numerous, isolated bones belonging to several different species, it is often difficult or even impossible to assign each bone to its respective species, especially when the bones include several new species that are extinct, since no equivalent material is available for comparison. Describing a new taxon on the basis of a single element of the skeletal system thus presents certain problems. A major difficulty is trying to match isolated bones with the proper species in the absence of (1) an articulated specimen of the species in question, or (2) abundant remains representing only a single species. When several species are present, assignment can be reasonably assured if the remains represent taxa sufficiently distinct to render highly improbable their identity with the other species in the locality. Another pitfall is the possibility of applying different specific names to isolated bones of the same species. This type of error, however, can generally be obviated by thorough studies of the age and geography

of the fossil beds and by careful comparison of remains with specimens collected from the type locality.

If only disarticulated material is available, and careful study shows that some bone is strikingly different from that of any known species, either Recent or fossil, we feel that there is justification in describing the taxon. The bone designated for the holotype preferably should be one selected from 2 or more individuals in order to avoid the possibility of describing an abnormal structure.

Among the available bones from the Bidahochi formation, the dentaries, cleithra, and pharyngeals are the most diagnostic. Only a single family, the minnows (Cyprinidae), is represented among the abundant remains collected thus far. Four kinds, including a new genus and 3 new species, are identified as follows: *Ptychocheilus preluceus*, *Evomus navaho*, ?*Gila cristifera*, and *Gila* cf. *G. robusta*. In the following descriptions, the specimens are usually incomplete, unless otherwise indicated.

Since 2 new species are herein based on the cleithrum, it was necessary to work out a detailed terminology for the parts of this bone that are important in the descriptive morphology. This terminology is most readily presented by 2 illustrations based upon a composite cyprinid cleithrum (Fig. 2).

Ptychocheilus preluceus, new species

(Fig. 3A-B)

Holotype.—MNA G2.7819, a nearly complete right dentary, collected by J. F. Lance in 1953. Middle Pliocene, Bidahochi formation. Locality UM-ARIZ-2-60, 61, Roberts Mesa, Sec. 22, T 26 N, R 21 E, Navajo Co., Arizona.

Paratypes.—UMMP 45501a, fragments of 4 left and 3 right dentaries, collected from Roberts Mesa by R. R. Miller and party in 1960 and 1961.

Nontypes.—MNA G2.7822, fragments of 1 left and 1 right dentary, collected from White Cone Peak by J. F. Lance in 1953.

Description of holotype.—The holotype, a virtually complete right dentary, weathered whitish, is 48 mm long (to last sensory pore). The 15 sensory pores are aligned with the curvature of the bone. The area traversed by the pores is folded inward to form a broad ventral surface which becomes especially wide and flattened posteriorly, between pores 7 and 15. There is a prominent process at the

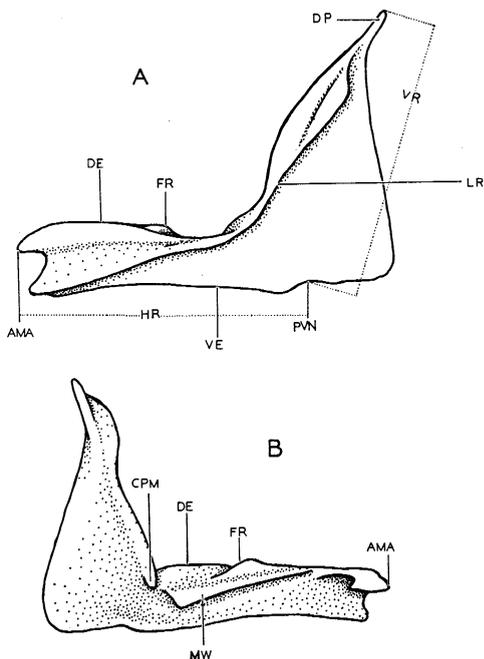


Fig. 2. Schematic drawing of a composite cyprinid cleithrum. A, lateral view; B, mesial view. See text for explanation. AMA, antero-mesial angle; CPM, contact point with mesocoracoid; DE, dorsal edge; DP, dorsal process; FR, free ridge; HR, length of horizontal ramus; LR, lateral ridge; MW, mesial wing; PVN, posteroventral notch; VE, ventral edge; VR, length of vertical ramus.

anteroventral corner. The anterolateral foramen lies within the anterior fourth of the length of the dentary at a point about one-third the distance from the anterior tip to the origin of the dorsal process. A section of the upper part of the dorsal process and a piece at the posterior end of the bone are missing. The height of the anterior ramus is greatest (8 mm) just before the anterolateral foramen and least (5 mm) near the base of the dorsal process. The height of the anterior end (including its process) is 9 mm. The greatest width of the ventral surface, measured across the posterior end, is 10 mm. The paratypes are too fragmentary to add significantly to the above description.

Etymology.—The specific name is formed by adding the Latin prefix *pre-*, meaning before, to *lucius*, the specific name of the representative now inhabiting the Colorado River system, thereby suggesting that the fossil species is ancestral to *Ptychocheilus lucius*.

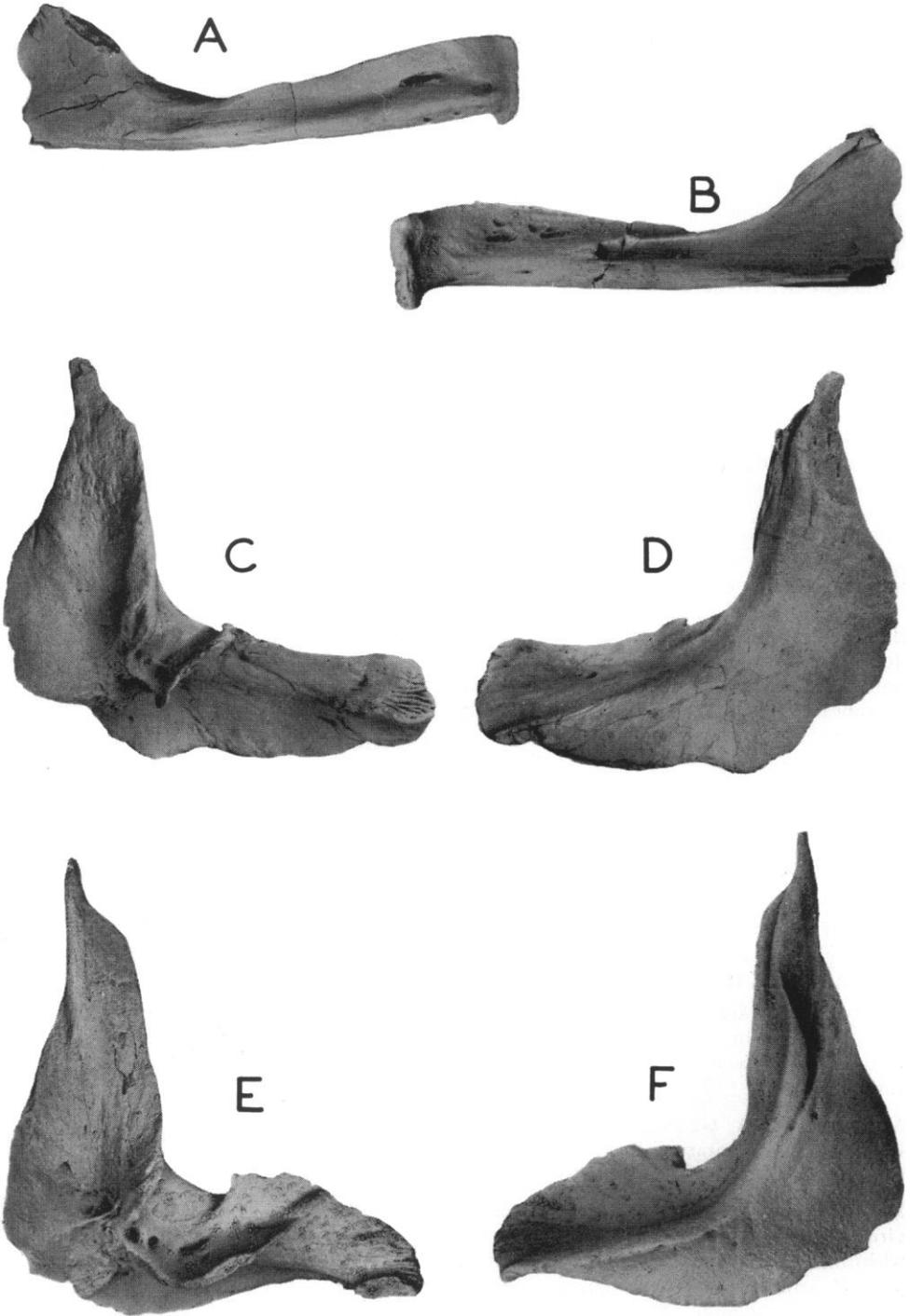


Fig. 3. Lateral view (A) and mesial view (B) of right dentary, holotype of *Ptychocheilus pre-lucius*, MNA G2.7819. Mesial view (C) and lateral view (D) of left cleithrum, holotype of *Evomus navaho*, UMMP 45502. Mesial view (E) and lateral view (F) of left cleithrum, holotype of ?*Gila cristifera*, MNA G2.7704.

Bones referred to *Ptychocheilus preluicius*.—In addition to the dentaries, the only bones designated as types, other remains (from Roberts Mesa, except as noted) are obviously of the genus *Ptychocheilus* and are apparently referable to the new species. These constitute: 2 left hyomandibulars, 1 left ceratohyal, 1 right epihyal, 1 complete left symplectic, the anterior part of the second left branchiostegal, and 1 fragment of a parasphenoid (MNA G2.7820); 1 right quadrate and 1 left parietal (MNA G2.7821); 1 left and 1 right anterior part of dentaries (MNA G2.7822, White Cone); 1 left and 2 right quadrates, 1 left epihyal, a fragment of a parasphenoid, and 6 vertebrae (MNA G2.7823, White Cone); and 1 left and 4 right hyomandibulars (UMMP 45501b). The hyomandibular shows the distinctive feature of *Ptychocheilus*—a strongly developed lateral ridge (Fig. 4), which separates and provides for a greater area of origin for the 3 neighboring muscles: the *dilatator operculi* which is attached to the area dorsal to this ridge, and the *levator arcus palatini* and the *mandibularis* of the *adductor mandibulae* which

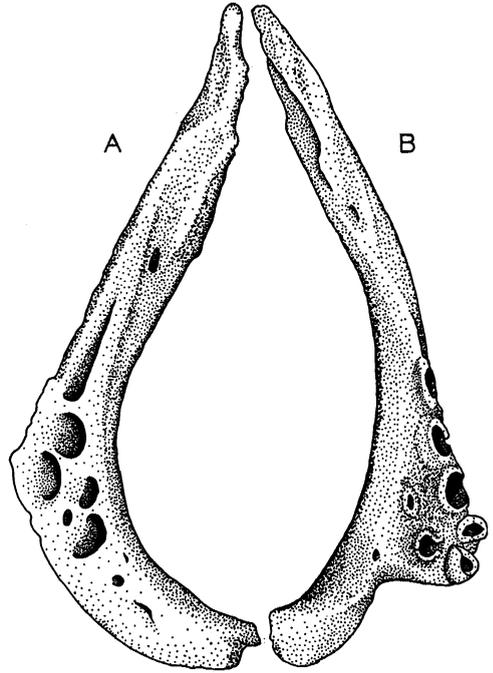


Fig. 5. Left pharyngeal of *Ptychocheilus preluicius*?, UMMP 45523c. A, pitted surface, and B, dentigerous surface.

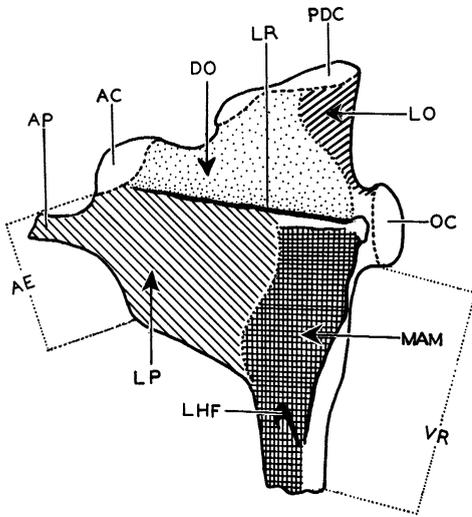


Fig. 4. Schematic drawing of lateral view of left hyomandibular of *Ptychocheilus lucius*. AC, anterior condyle; AE, length of anterior edge; AP, anterior projection; DO, area of attachment of *dilatator operculi*; LHF, lateral hyomandibular foramen; LO, area of attachment of *levator operculi*; LP, area of attachment of *levator arcus palatini*; LR, lateral ridge; MAM, area of attachment of *mandibularis* of *abductor mandibulae*; OC, opercular condyle; PDC, posterodorsal condyle; VR, length of ventral ramus.

are attached to the area ventral to this ridge. In addition, we refer 5 pharyngeals (MNA G2.7836, 1, and UMMP 45523c, 4), 2 nearly complete, to the genus *Ptychocheilus* and, tentatively, to *P. preluicius*, because of the notably long anterior edentulous process (Fig. 5A–B). Although these bones differ considerably from the extremely attenuate pharyngeals of *P. lucius*, the available evidence indicates that *P. preluicius* was less extreme than the Recent species in other features; hence, these pharyngeals may well represent the fossil precursor. The dental formula was 2,5 on the 4 left pharyngeals; the teeth, intact on one, are long, slender, pointed, and hooked at the tips; the fifth, a fragmentary right arch, appears also to have had a formula of 2,5. *P. lucius* and the other two living species of the genus *Ptychocheilus*¹ have the dental formula 2,5–4,2.

Comparison with P. lucius.—The dentary of *P. preluicius* differs from that of the Recent species in the following characters: (1) The

¹ It has recently been suggested (Bond 1961:27) that *Ptychocheilus umpquae* Snyder probably should be recognized only as a subspecies of *P. oregonensis*.

TABLE 1. NUMBER OF SENSORY PORES ON DENTARIES OF THE SPECIES OF *Ptychocheilus*.
The pores were counted on both dentaries of the living species.

Species	Number of Pores													No.	Avg.	
	10	11	12	13	14	15	16	17	18	19	20	21	22			23
<i>P. oregonensis</i>	11	12	12	5	—	—	—	—	—	—	—	—	—	—	40	11.3
<i>P. grandis</i>	3	9	7	7	8	—	—	—	—	—	—	—	—	—	34	12.2
<i>P. lucius</i>	—	—	—	—	1	1	2	2	2	4	1	1	1	1	16	18.3
<i>P. preluclus</i>	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	15

number of sensory pores is near the lower limit of known variation for *P. lucius* but is greater than in either *P. oregonensis* or *P. grandis* (Table 1). (2) The ventral surface of the dentary is much broader than in the living species and forms a right angle with the dorsal process, rather than being tilted obliquely outward. (3) The sensory pores are aligned along the outer edge of the ventral surface in *P. preluclus*, *P. oregonensis*, and *P. grandis*, but in *P. lucius* the alignment tends to be rather straight, not curving along the outer edge. (4) Since the ramus of the dentary is notably more elevated anteriorly than posteriorly, the dorsal edge is not parallel with the ventral surface, as it is in the living forms. The general outline of the dentary (Fig. 3A–B) indicates that *P. preluclus* had a shorter, more curved, and broader anterior shaft than is usual in *P. lucius*.

Evomus, new genus

Type-species.—*Evomus navaho*, new species.

Diagnosis.—The diagnosis of this minnow is based solely on the cleithrum, the structure of which differs strikingly from that of known fossil or living cyprinids. The mesial wing (Fig. 3C) is deflected posteriorly to form a prominent, high ridge that is obliquely oriented at an angle of about 45° with the horizontal ramus (in other American minnows the mesial wing is directed anteriorly, approximately parallel with the ventral surface of the cleithrum). This ridge, which sutures with the coracoid, reaches the dorsal edge of the cleithrum at a point at least twice as close to the ridge that sutures with the mesocoracoid as to the anteromesial corner. The anterior-facing surface of the vertical ramus and the dorsal surface of the horizontal ramus are smoothly continuous with the lateral surface of the cleithrum, and the anterior part of the lateral surface is thickened and expanded. The lateral ridge

of the cleithrum is absent except for incipient development at the dorsal and anterior ends (Fig. 3D).

Etymology.—The generic name is from the Greek *εὖ* plus *ἄμος*, meaning good or well-developed shoulder, in reference to the distinctive features of the cleithrum. The gender is masculine.

Evomus navaho, new species (Figs. 3C–D and 6A–B)

Holotype.—UMMP 45502, 1 complete left cleithrum, collected by R. R. Miller and party on 17 July 1961. Same type locality as for *Ptychocheilus preluclus*.

Paratypes.—UMMP 45503, 1 left and 2 right complete or almost complete cleithra and an anterior fragment of 1 right cleithrum; and MNA G2.7824, 1 left and 5 right incomplete cleithra. The paratypes were taken by the same party in 1960 and 1961.

Nontypes.—MNA G2.7825, 2 fragments of the right cleithrum from White Cone Peak; MNA G2.7342, an incomplete fish from the Coliseum Diatrema (Fig. 6A).

Description of holotype.—The holotype (Fig. 3C–D) is a complete left cleithrum that has weathered whitish. The anterior surface is tilted anterolaterally and is smoothly continuous with the lateral surface. The anterior edge is truncate and perpendicular to the body axis. There is a distinct notch at the posteroventral corner. The ventral edge just anterior to this notch is weakly notched. The anteromesial angle bears a process that is well developed and has longitudinal grooves on its anterior half. The length of the greatest dimension, from the tip of the dorsal process to the anterolateral angle, is 49 mm; the vertical ramus is 34 mm long and its widest part is 17 mm; the greatest horizontal length is 41 mm; the horizontal ramus is 32 mm long, and its widest part is 18 mm; the

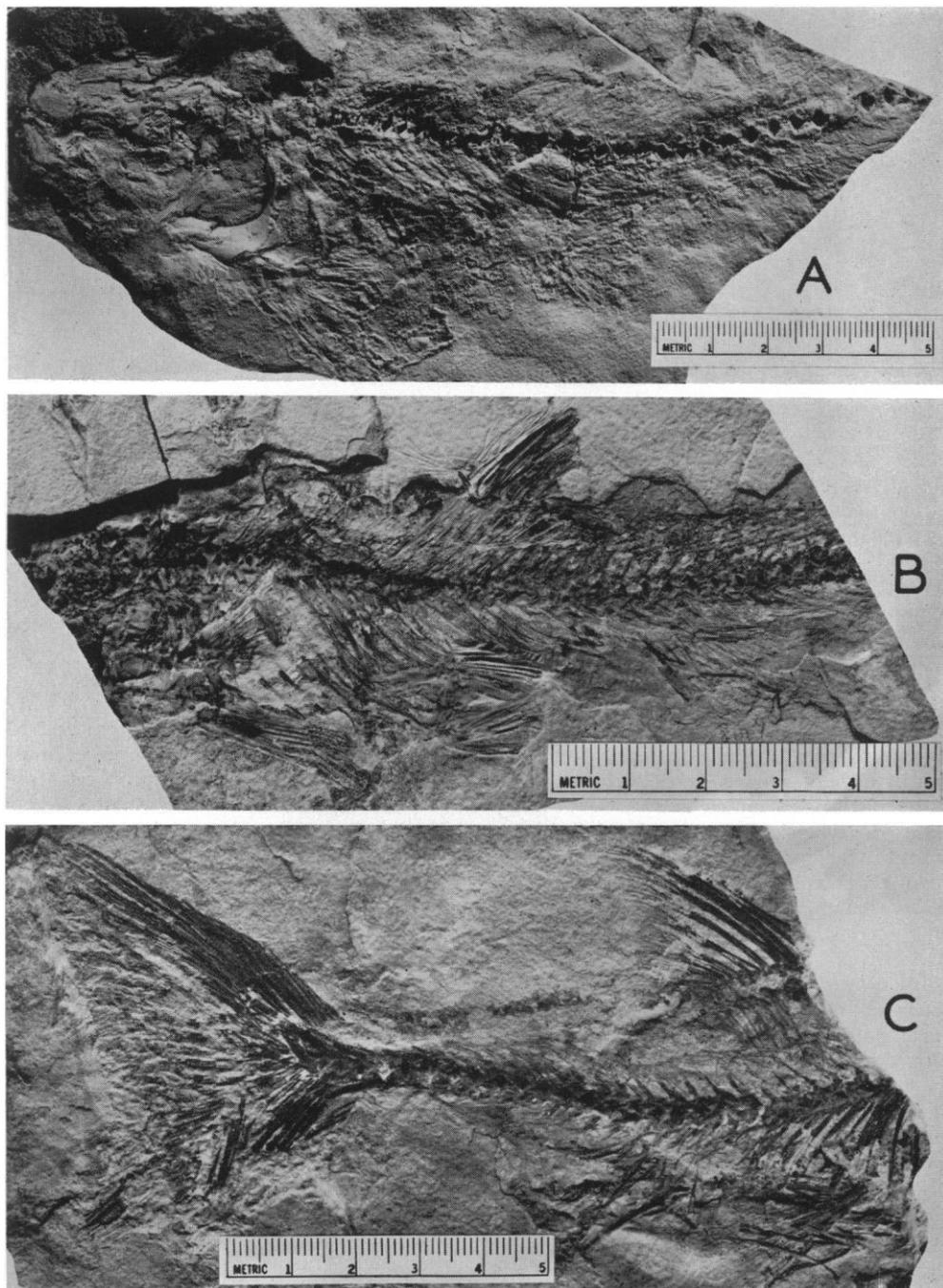


Fig. 6. Lateral views of two species of fossil cyprinids from the Coliseum Diatreme locality. A, *Evomus navaho*, MNA G2.7342; B, *E. navaho?*, RV-58.9:1 (Univ. N. Dak. 10746); and C, *Gila* cf. *G. robusta*, MNA G2.7355.

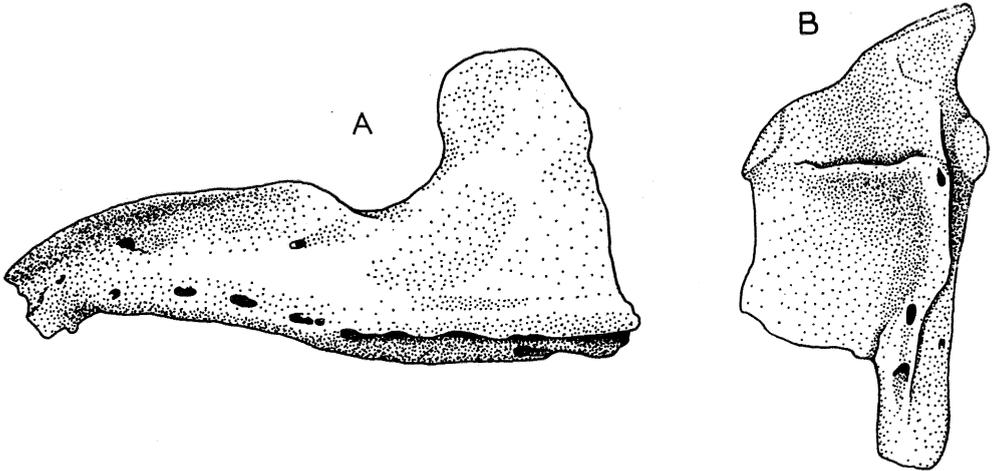


Fig. 7. Lateral views of (A) left dentary, UMMP 45504, and (B) left hyomandibular, UMMP 45515, of *Evomus navaho*? from Roberts Mesa.

length of the mesial wing is 11 mm; and the distance between the anteromesial angle and the anterior end of the mesial wing is about 20 mm.

The paratypes agree so closely with the holotype that there is no need to describe them.

Coliseum Diatrema nontype material.—Of the 2 species of cyprinids that seem to be represented by the available material from this locality, one is referred to *E. navaho*. (The other is discussed under *Gila* cf. *G. robusta*.) This identification seems to be definite for a large, incomplete fossil (MNA G2.7342) having a complete cleithrum characteristic of *Evomus*. Other specimens that may represent this species are: MNA G2.7365, and RV-58.9: 1, 2, 8, 10, 12, and 13 (= USNM 23088-91, in part). This material provides data on meristic characters, general body form, and relative positions of fins not available from the type material. In RV-58.9: 1 (Univ. N. Dak. 10746) the fins are sufficiently preserved to give the following approximate counts: dorsal, 9 or 10; anal, 8 or 9; pectoral, 12; pelvics, about 10 or 11. The origin of the dorsal fin was about over the insertion of the pelvics and the anal fin commenced behind the end of the dorsal fin base. The head was large and the body appears to have been heavy set, but lacking the marked contrasts in depth that characterize such cyprinids as *Gila robusta elegans* and *G. cypha*.

Etymology.—The specific name is that of the Indian tribe on whose land the fossils were obtained. The spelling *navaho* is used in preference to *navajo* in agreement with the spelling adopted by anthropologists and others.

Bones Possibly Referable to *Evomus navaho*

In addition to the readily recognized remains of *Ptychocheilus*, bones representing 3 or 4 different forms occur at Roberts Mesa. Since among these several different kinds of bones the most abundant cleithra belong to *Evomus navaho*, it is reasonable to assume that some of the most abundant remains of other bones also belong to that species. The following isolated bones are tentatively assigned to *Evomus*.

One complete and 2 incomplete left *dentaries* and 1 incomplete right dentary, UMMP 45504 (Fig. 7A). Three left dentaries and 1 right dentary (MNA G2.7826). The complete specimen has 9 sensory pores. The length of the largest (complete) specimen is 29 mm; the height at the dorsal process is 14 mm; and the greatest height of the anterior ramus is 7 mm. The dorsal part of this ramus is considerably deflected laterally. The dorsal process is slightly inclined anteriorly. The mental foramen lies much closer to the anterior end of the dentary than to the origin of the dorsal process.

A complete left *preopercle*, UMMP 45505. There are about 17 sensory pores.

The ventral edge is slightly rounded, but is almost perpendicular to the posterior edge. There is almost no medial expansion (often a pronounced feature in the genus *Gila*). A prominent ridge on the mesial side extends obliquely from the middle part of the vertical ramus to the dorsal edge of the horizontal ramus.

One almost complete and 1 partial left *hyomandibular*, UMMP 45515 (Fig. 7B). Four-fifths of a right *hyomandibular* (MNA G2.7827). The *hyomandibular* of this species has a moderately developed lateral ridge, which is well developed among North American cyprinids only in species of *Ptychocheilus*; the structure is moderately developed in *Acrocheilus*, and some species of *Gila* have it weakly developed. The anterior wing is broad and thin.

One left and 3 right *pharyngeals*, of which 2 are nearly complete, UMMP 45507. All lack teeth. Although these remains are quite fragmentary, we tentatively assign them to this species on the basis of their relatively large size among the pharyngeal remains. The tooth formula, as represented by alveoli on the 4 arches, is 2,5-4,2. The dentigerous surface is not elevated, and the pitted surface extends anteriorly and posteriorly to the middle of the edentulous processes. The anterior angle is distinct, but the posterior one is obscure (for terminology, see Uyeno 1961: Fig. 1).

?*Gila cristifera*, new species

(Fig. 3E-F)

Holotype.—MNA G2.7704, a complete left cleithrum collected by J. F. Lance, presumably in 1953. Middle Pliocene, Bidahochi formation, at White Cone, Navajo Co., Arizona.

Nontypes.—The following specimens of this species, all incomplete, were collected from the type locality (WC) and from Roberts Mesa: MNA G2.7828 (WC), 2 left and 1 right cleithra; MNA G2.7829, 2 left and 3 right cleithra; UMMP 45508, 6 left and 3 right cleithra; UMMP 45509, 3 left and 1 right cleithra; and UMMP 45510, 4 left cleithra.

Description of holotype.—The dorsal surface of the horizontal ramus of the cleithrum is broad and almost horizontal and its anterior edge is slightly oblique. The anterior-facing surface of the vertical ramus is broad, about two-thirds the width of the anterior edge. The

lateral ridge (see Fig. 2A) and groove are weakly developed, and the groove is lacking on the middle part of the lateral surface (Fig. 3F). The mesial wing reaches the dorsal edge of the cleithrum at a point closer to the anteromesial angle than to the ridge that sutures with the mesocoracoid (Fig. 3E).

A diagnostic feature of the cleithrum of this species is the moderately developed free ridge that occupies the space between the mesial wing and the ridge with which the mesocoracoid contacts. This free ridge is wanting in all species of North American cyprinids examined by us, except for the development of a very weak knob at the dorsal edge of the cleithrum in a few species. In the Catostomidae, however, this free ridge is always well developed. A study of the muscle attachments on the shoulder girdle reveals that the free ridge separates a large muscle, which is a modified part of the *musculus lateralis profundis* (of the great *lateralis* muscle) that runs between the expanded transverse plate of the Weberian complex (Nelson 1948:230) and the posterior part of the cleithrum dorsal to the free ridge. This muscle is weakly developed in cyprinid fishes and is attached to the cleithrum along a short segment of the dorsal edge and to a small part of the coracoid.

The following measurements are in millimeters: length of greatest dimension, 41; length of vertical ramus, 31; greatest horizontal length, 30; length of horizontal ramus, 25; length of anterior edge, 11.5; and width of anterior surface, 7.

Since the dorsal and anterior surfaces of the cleithrum of this species are comparatively broad for a minnow, but not nearly as expanded as in the suckers, this suggests that the fossil species had a rather flat ventral surface and was a bottom feeder.

Certain variations appear among the numerous cleithra. In some, the dorsal surface is more strongly tilted outward; in others, the dorsal edge is perpendicular to the dorsal surface. The width of the anterior surface of the vertical ramus varies from about half to two-thirds that of the anterior edge.

Generic allocation.—Although this species, as represented by the cleithrum, is quite distinct from other American minnows, generic allocation was decided on the following basis. The cleithrum bears a general resemblance to that of *Pogonichthys*, *Acrocheilus*, and *Gila* (especially *G. coerulea*). In *Pogonichthys*,



Fig. 8. Lateral view of *Gila* cf. *G. robusta*, UMMP 47116, from Steamboat Wash (see text); the matrix has been masked out (retouched by Suzanne Runyan).

both the anterior and dorsal surfaces are comparatively broad, the anterior edge is nearly truncate, and there is a very weak knob on the dorsal edge of the horizontal ramus. *Acrocheilus* has a broad dorsal surface, but the anterior surface is much narrower; the anterior edge is nearly truncate, and there is a moderately developed knob on the dorsal edge of the horizontal ramus. In *Gila coerulea*, the anterior surface is narrow (and the vertical ramus much elongated), although the dorsal surface is about as broad as in *Acrocheilus* and *Pogonichthys*; the anterior edge is broadly notched, and there is a weak knob along the dorsal edge of the horizontal ramus. Since none of the fossil dentaries from this formation resembles *Acrocheilus*, this genus was not considered further. *Pogonichthys*, which is currently regarded as monotypic and is as now confined to the Sacramento River system of California, is unique among North American minnows in having unequal upper and lower lobes of the caudal fin and, unlike any living species of *Gila*, it has a maxillary barbel. The skeleton of *P. macrolepidotus* is, however, very similar to that of *Gila* and, furthermore, the caudal fin is not asymmetrical in young specimens. This suggests that *Pogonichthys* was possibly derived from *Gila* or a *Gila*-like ancestor. Some of the fossil dentaries resemble those of *Pogonichthys* or *Gila*, as well as some other cyprinids. Until more complete material becomes available we prefer to refer this new species tentatively to *Gila* rather

than to erect a new genus for it. One reason for so doing is our conclusion that *Gila* now includes the most generalized species among the genera considered.

Etymology.—The specific name, of Latin origin, means bearing a crest, in reference to the diagnostic free ridge on the mesial surface of the cleithrum.

Gila cf. *G. robusta* Baird and Girard

Steamboat Wash specimen.—A nearly complete fossil fish (UMMP 47116; Fig. 8), preserved with remarkably little distortion in semiconsolidated conglomerate of very fine gravel, was collected by Frederick W. Forbush (of Stewart, Nevada) in 1954. Mr. Forbush turned the fossil over to Donald B. Sayner (University of Arizona), who gave it to John F. Lance. Charles A. Repenning (pers. comm.) reported that although the exact locality is unknown, the fossil came from Steamboat Wash, and, according to Sayner, from near the intersection of latitude 35°45' and the Navajo–Apache county line. This would place it approximately 15 miles in a direct line northeast of White Cone Peak. The locality is reported to be from the "middle of the Bidahochi," which Mr. Repenning interprets as from the middle of the exposed part of the Bidahochi formation, as in this area only the upper member should be present. In that event, the age is Middle Pliocene.

The rather well-preserved specimen is ap-

proximately 97 mm in standard length and 115 mm in total length and, except for the missing dorsal fin, is nearly complete. The total number of vertebrae (including the urostylar vertebra and 4 in the Weberian apparatus) is 43 or 44, which is within the known range of variation for *Gila robusta robusta* (43–49) and *G. r. intermedia* (38–45), but is too few for *G. r. elegans* (47–50) or *G. cypha* (46–48).² An accurate count of the fin rays is not possible, but the anal fin had at least 9 rays, the caudal more than 18 rays, and the right pelvic fin had more than 8 rays. Only 12 rays are countable in the right pectoral fin. The roof of the skull is rather strongly concave as in *Gila robusta elegans* and *G. cypha*, as well as in some of the frontals from Roberts Mesa. The postero-dorsal corner of the opercle bears an angular projection, as in some specimens from Roberts Mesa and as in *Gila atraria* (Girard). The general form and shape closely resemble that of *Gila robusta elegans*, but the outline of the opercle differs (there is no angular projection in *elegans*) and the vertebrae are larger and less compressed posteriorly. Since this specimen seems to combine certain features found in the various forms of *Gila robusta* that inhabit the Colorado River basin today, we tentatively refer it to that species.

That this fossil and the cleithra referred to ?*Gila cristifera* might represent the same species was explored by exposing most of the left shoulder girdle; this was painstakingly accomplished for us by William G. Melton, Jr., using an air abrasive (dental) unit. The dorsal segment of the vertical ramus of the cleithrum of the Steamboat Wash minnow is not nearly broad enough to identify it with *cristifera*, and the dorsal part of the horizontal ramus, although crushed and somewhat distorted, does not appear to have had the distinctive shape characteristic of that species. Unfortunately, it was not possible to expose the mesial surface of either shoulder girdle without destroying segments of the fossil deemed important in its identification. Nevertheless, we are confident that the bones referred to ?*Gila cristifera* and the specimen here under discussion do not represent the same species.

Coliseum Diatreme material.—The second cyprinid from this locality is represented only

by posterior parts of the body (Fig. 6C). In general appearance these remains bear a striking resemblance to *Gila cypha*, a species living in the Colorado River and its major tributaries: the caudal peduncle was narrow, with depressed neural and hemal spines, and the caudal fin was much expanded; the posterior part of the base of the dorsal fin extended posterior to the origin of the anal fin; both the dorsal and anal fins were large, broad, and falcate; and the body was notably deeper near its middle than in the region of the caudal peduncle. Additional material that represents the anterior end of this fish is needed before confident allocation to genus can be made; for the present, we refer it to *Gila* cf. *G. robusta*.

Bones Unidentifiable to Species

The following descriptions are of isolated bones that may belong to the species described in this paper. Confident matching of bones with these species can only be accomplished when articulated remains are found, but we suggest certain possible identifications. Evidently, a fifth species is represented among the pharyngeals.

Dentary.—There are two types of dentaries. In one type, comprising 2 left and 3 right fragments (UMMP 45511), the anterior part of the dorsal edge is deflected outward, the sensory pores number about 6, and the mental foramen lies closer to the anterior end than to the origin of the dorsal process. In the second type, comprising an almost complete right dentary and the anterior two-thirds of another (UMMP 45512), there is no deflection along the anterodorsal edge, the sensory pores number about 10, and the dorsal process is narrower and is slightly tilted forward; the mental foramen is located about as in the first type.

Opercle.—One complete and 5 incomplete right opercles, 3 left opercles, and 16 fragments (UMMP 45513). In the complete specimen, the posterodorsal corner is extended dorsally to form a sharp angle, the posterior edge is rounded and expanded, the ventral edge is very slightly curved, and the anterior edge is essentially straight over most of its length.

Preopercle.—The 5 right and 5 left preopercles (UMMP 45514, MNA G2.7830) appear to represent 2 species, but the specimens are incomplete and the differences in shape

² Based on original counts of UMMZ material by the authors.

and proportions are rather small. Since the sensory canal is broken in most of the specimens, especially along the vertical ramus, the total pore number cannot be determined. The number of pores along the horizontal ramus is about 5. A ridge is moderately developed along the mesial surface (such a ridge is weak or lacking in *Gila*).

Hyomandibular.—The hyomandibulars represent at least 2 species. One type is represented by 3 complete and 1 incomplete left hyomandibulars (UMMP 45515), all of which have a moderately developed lateral ridge, which runs from the base of the anterior condyle to the base of the opercular condyle. This ridge is rarely observed in North American cyprinids except in *Ptychocheilus*, *Acrocheilus*, and some species of *Gila* (e.g., *G. robusta*). The anterior wing is broad, and the anteroventral corner closely approaches a right angle. The length of the anterior edge is more than half the length of the ventral ramus (below the opercular condyle). The second type is represented by 1 left and 2 right hyomandibulars (UMMP 45516), which lack the lateral ridge, but in its place there is a slightly elevated line that curves ventrally between the opercular condyle and the anterior condyle. The anterior edge is less than half as long as the ventral ramus. Possibly the first type belongs to *Evomus* and the second type to ?*Gila cristifera*.

Frontal.—It appears that there are 2 forms of the frontal, but it is difficult to distinguish them (UMMP 45517, MNA G2.7831). In one extreme, the frontal is strongly concave, as in that of *Gila robusta elegans* and *G. cypha*. The other extreme shows a flat surface. Some specimens, however, are more or less intermediate. The countable specimens have about 9 or 10 sensory pores. Perhaps the concave form represents either *Gila* cf. *G. robusta* (see p. 39) or ?*Gila cristifera*; the flat one could represent *Evomus* or *Ptychocheilus*.

DISCUSSION AND CONCLUSIONS

Our studies of Bidahochi fishes provide clues to the evolutionary history and zoogeography of the Colorado River fish fauna. By Middle Pliocene time, the species of *Ptychocheilus* in the middle Colorado basin was already well advanced toward the highly specialized form, *P. lucius*, that now inhabits

the drainage. The representative of some 4 million years ago is judged to be sufficiently different from the living species to be recognized as a distinct species, *P. prelucius*. Although differing from *P. lucius* in some of the same characters that now separate that species from *P. oregonensis*, of the Columbia River system, other characters of *P. prelucius* definitely suggest that it is ancestral to *lucius*. Another minnow resembles the rather variable living species *Gila robusta*, which is intimately related to *G. cypha*, suggesting that the Colorado River then provided the swift-river habitat to which these modern species are so marvelously adapted (see Miller 1959:193). Such an ecological picture for the Colorado River at that time is in harmony with recent geological studies on its evolutionary history (Repenning *et al.* MS).

In addition to these close relatives of recent species, the middle Colorado also contained a very distinctive and now extinct genus of minnows (*Evomus*), which was evidently sucker-like in its feeding habits, and another well-marked, extinct minnow, ?*Gila cristifera*. The Colorado then had a richer cyprinid fauna, perhaps associated with greater diversity of ecological niches in the large lake of the Bidahochi formation. The disappearance of this lake (through downcutting and drainage), before the close of the Pliocene, and generally increasing aridity were perhaps responsible for the extinction of these species.

The absence of remains of the family Catostomidae from the Bidahochi formation is surprising. There is paleontological evidence that suckers appeared in North America well before minnows. Bones of the living flannelmouth sucker, *Catostomus latipinnis* Baird and Girard, have been recorded from early Pleistocene deposits in the Little Colorado River basin (Uyeno and Miller 1963:8), the same region which earlier supported the Bidahochi fauna. *Catostomus* appears to be, however, a genus of rather recent origin (the earliest known fossil record is late Pliocene), whereas the early evolutionary line of the suckers (*Amyzon*) represented elsewhere in the West is not known to have survived the Miocene. The ancestral line containing *Catostomus* and its relatives may not have reached the area until after the Bidahochi formation was deposited, or suckers may have failed to become preserved in these beds.

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The Systematic Status of *Haemulon boschmae*, A Grunt Fish from Shore Waters of Northeastern South America¹

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The pomadasiid fish *Pristipoma boschmae* Metzelaar and its synonym, *Isaciops facis* Miles, are placed in the genus *Haemulon*. This species is the fourteenth species of this genus known from the Atlantic Ocean, and it occurs along the northeastern coast of South America where it overlaps the range of its closest relative, *H. striatum* (Linnaeus). *H. boschmae* is distinguished from *striatum* primarily by the orientation of the scale rows below the lateral line; in *boschmae* the rows are parallel to the long axis of the body and not oblique as in *striatum*.

AMONG the many interesting fishes collected off Surinam and the Guianas in recent years by the Bureau of Commercial Fisheries vessels COQUETTE and OREGON, and along the Venezuelan coast by William A. Lund, Jr., is a species of pomadasiid fish closely related to *Haemulon striatum* (Linnaeus) and heretofore known from only 4

specimens. This species was first described by Metzelaar (1919:83-84, Fig. 27) as *Pristipoma boschmae*, type locality probably Curaçao. Miles (1953) described the same species from 3 specimens trawled in the Colombian Caribbean Sea as a new genus and species, *Isaciops facis*.

The generic characters of *Haemulon* were discussed by Jordan and Evermann (1898: 1291-1292). Courtenay (1961) treated the

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