FISHES OF THE PLIOCENE GLENNS FERRY FORMATION, SOUTHWEST IDAHO

Gerald R. Smith

FISHES OF THE MIOCENE-PLIOCENE DEER BUTTE FORMATION, SOUTHEAST OREGON

Peter G. Kimmel

1975

Claude W. Hibbard Memorial Volume 5

CLAUDE W. HIBBARD MEMORIAL VOLUMES (1-5)

Index and Bibliography of Late Cenozoic Freshwater Mollusca of Western North America
Dwight W. Taylor

The Fossil Catfishes of North America
John G. Lundberg

Studies on Cenozoic Paleontology and Stratigraphy
(Papers Presented at Hibbard Memorial Symposium, May, 1974, in Ann Arbor)

Geology and Paleontology of the Early Pleistocene (Late Blancan) White Rock Fauna from North-Central Kansas
Ralph E. Eshelman

Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho
Gerald R. Smith
and
Fishes of the Miocene-Pliocene Deer Butte Formation, Southeast Oregon
Peter G. Kimmel

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48104

FISHES OF THE PLIOCENE GLENNS FERRY FORMATION, SOUTHWEST IDAHO

Gerald R. Smith

University of Michigan
Museum of Paleontology
and
Division of Fishes, Museum of Zoology

FISHES OF THE MIOCENE-PLIOCENE DEER BUTTE FORMATION, SOUTHEAST OREGON

Peter G. Kimmel

University of Michigan
Museum of Paleontology

PAPERS ON PALEONTOLOGY NO. 14

1975

Claude W. Hibbard Memorial Volume 5

Claude W. Hibbard Memorial Volume 5
Papers on Paleontology No. 14
The Museum of Paleontology
University of Michigan
Ann Arbor, Michigan 48104
Gerald R. Smith, Director

Edited by N.E. Friedland

APPRECIATION AND ACKNOWLEDGMENT IS EXPRESSED TO THE 1962 CLASS OF THE UNIVERSITY OF MICHIGAN FOR ESTABLISHING AN INSTITUTE OF SCIENCE AND TECHNOLOGY PUBLISHING FUND. THIS FUND AND A CONTRIBUTION BY DWIGHT W. TAYLOR HAVE AIDED IN THE PUBLICATION OF THIS WORK.

December 1, 1975

CONTENTS

Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho: GERALD R. SMITH

Fishes of the Miocene-Pliocene Deer Butte Formation, Southeast Oregon: PETER G. KIMMEL

ABSTRACT

The fish fauna of the Glenns Ferry Formation comprises about 30 species of freshwater fishes represented by disarticulated fossils that occur in lacustrine and fluviatile sediments along the Snake River Plain between Hagerman and the Oregon border in southwest Idaho. The Glenns Ferry is one of several sedimentary and volcanic formations along the western Snake River Plain that contain the characteristic Lake Idaho fish fauna (see Kimmel's description of the Deer Butte fishes in this volume). Most of the Glenns Ferry Formation is Pliocene in age; a younger section, containing a different vertebrate fauna, is middle Pleistocene.

Lake Idaho refers to a series of more or less continuous lacustrine habitats that existed during late Miocene and Pliocene time in the area, probably under structural control of the system of volcanic activity and caldera collapse now centered in the Yellowstone region. The fauna has been regarded as representative of the Blancan North American land mammal age, but associated K-Ar dates of 4.4-6.2 m.y. in the Glenns Ferry Formation near Hagerman indicate that a reevaluation is necessary.

The fishes include representatives of six families: Salmonidae (trouts, whitefish), Catostomidae (suckers), Cyprinidae (minnows), Ictaluridae (catfish), Centrarchidae (sunfish), and Cottidae (sculpins). The salmonids in the fauna include a large extinct trout, *Rhabdofario*; a landlocked, planktivorous salmon, *Oncorhynchus*; two or three species of uncertain affinities; and a large whitefish in the genus *Prosopium*. Catostomids are abundantly represented by at least one species of *Chasmistes* and about five species of *Catostomus*. Cyprinids show the greatest diversity in the system, with 10 species in eight genera, including a large predator in *Ptychocheilus*, two large molluscivores in *Mylocheilus*, two large herbivores in *Acrocheilus* and *Orthodon*, medium and small predators in *Gila* and *Richardsonius*, and unusual small herbivores or molluscivores in the new genus, *Idadon*. Catfishes are represented by one species of *Ictalurus*, and sunfishes by *Archoplites taylori*. A small species flock of sculpins existed, including three species of spiny sculpins in the new genus *Kerocottus*, two species in the arctic and north temperate genus *Myoxocephalus*, and one Pleistocene representative of *Cottus*.

The fauna shows primary zoogeographic affinities to the modern Snake-Columbia river system, the Sacramento-San Joaquin system, the Klamath system, and to Taylor's western North American aquatic fishhook distributional pattern. The sculpins indicate northern affinities; the catfish represents an eastern North American family. The history of Lake Idaho probably involved a former outlet through northwest Nevada to the Sacramento system in California, and early Pleistocene capture by the Columbia through Hells Canyon. At about the time of capture the lacustrine habitat in the area was apparently eliminated by basin filling. The change in ecology at this time probably involved the collapse of the diverse lacustrine trophic system, loss of the selective regime favoring diverse specializations, and elimination of all but a remnant fluvial habitat. The result was extinction of many of the diverse lines and evolution of the remainder from specialized to generalized forms.

FISHES OF THE PLIOCENE GLENNS FERRY FORMATION, SOUTHWEST IDAHO

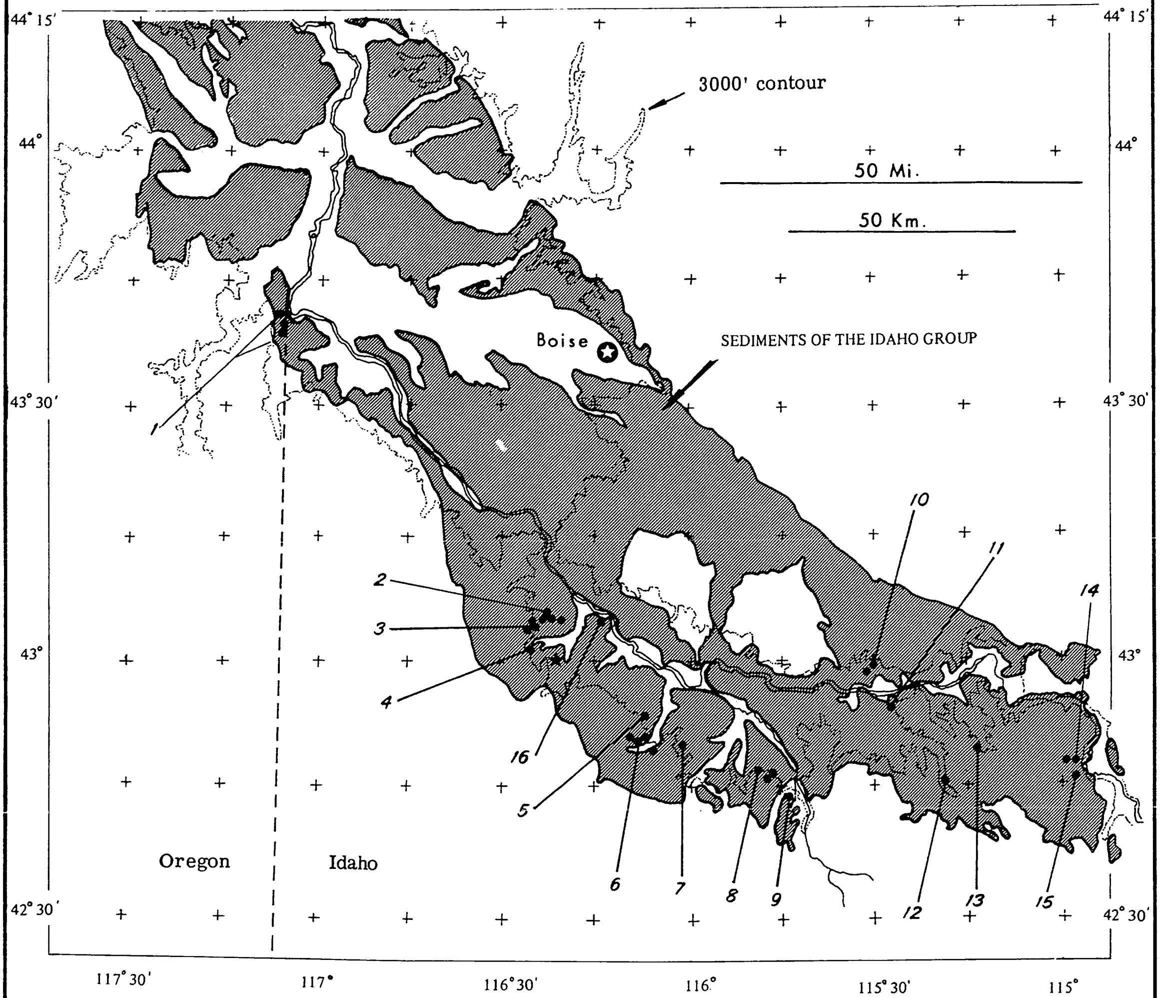
Gerald R. Smith

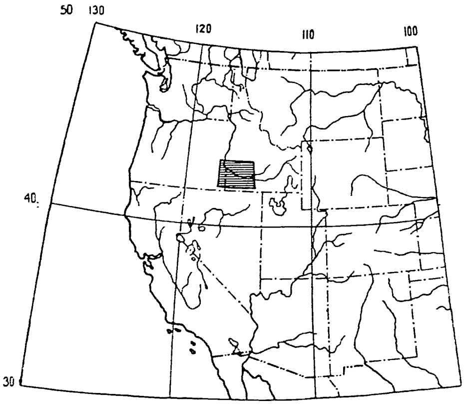
THE FIRST FISHES known from the Glenns Ferry Formation were recorded and placed in zoological, ecological, and geological context in J.S. Newberry's "Ancient lakes of western America, their deposits and drainage" in 1870 and 1871. Newberry recognized the American cyprinid genera *Mylopharodon* and *Mylocheilus* in the fauna, but until the present paper, all paleoichthyologists except Uyeno, 1961 (in part), have consistently misidentified the elements of the fauna that Newberry recognized. Newberry had studied some bones sent to him by Prof. Thomas Condon of Eugene, Oregon, who first discovered and explored the fossiliferous areas in SE Oregon and SW Idaho (Cope, 1883).

Clarence King's geological survey of the 40th parallel west of the Mississippi River reached Idaho in 1869, and within a few months material sent back to the Smithsonian Institution had been described by E.D. Cope (1870), including 10 new species of fishes. At about the same time, Joseph Leidy came into possession of some fossils and named a new genus and species of minnow and a supposed freshwater ray from the same deposits. The minnow was that correctly identified by Newberry as *Mylocheilus*; the ray has not been seen since, but does not represent a ray from the Glenns Ferry Formation (Uyeno and Miller, 1963:11). Cope (1870) noted that much of the King material remained to be studied, which he somehow found time to do – summarizing it in his report (1883), "On the fishes of Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake," which he finished at about the same time he finished his "Tertiary Vertebrata." (The supposed cobitid Weberian apparatus, described in 1871 from the same collection, is now unknown and has not been duplicated (Uyeno and Miller, 1963:16).)

Notwithstanding a few scattered references in the interim (Lucas, 1901; Leidy, 1873; Russell, 1902; Lindgren and Drake, 1904), no new studies were carried out until Uyeno (1961) reported on Glenns Ferry cyprinids that had been collected by Dwight Taylor, Claude Hibbard, and their associates in the U.S. Geological Survey and the University of Michigan. Uyeno also reviewed the status of all other fossil cyprinids in the Lake Idaho fauna, thus initiating the critical review that was continued by Uyeno and Miller (1963). Robert R. Miller intensified his interest in American fossil fishes at this time and, at the suggestion of Dwight Taylor, began systematic collections at the Fossil Creek roadcuts in Owyhee County as a part of larger paleoichthyological expeditions accompanied by his family and students. At the same time, Dwight Taylor's observations had stimulated Claude Hibbard to spend several field seasons collecting in the Hagerman area, as well as at Sand Point, Bennett Creek RR grade, and other localities in the Glenns Ferry Formation. The Miller and Hibbard collections led to the description of seven new species and a review of the fish fauna by Miller and Smith (1967). Continuing collections by R.R. Miller, R.J. Zakrzewski, and P.R. Bjork of the University of Michigan and by the author and his family and associates while at the University of Utah, University of Kansas, and University of Michigan have led to the present report. Occasional collections by paleontologists at the University of California at Berkeley and the U.S. National Museum have also contributed to this report. An active program of research on Glenns Ferry fishes is also being carried out by Allan D. Linder and his students at Idaho State University (Linder, 1969; Linder and Koslucher, 1974).

As presently understood, the Glenns Ferry fish fauna includes about 30 species: one species of whitefish, four or five species of salmon or trout, six species of suckers, 10 species of minnows, two catfish, one sunfish, and seven species of sculpins. However, one sucker, one catfish, and one species of sculpin, though technically found in Glenns Ferry sediments, may not be part of the Lake Idaho fish fauna. The floodplain facies at Jackass Butte (Grandview local fauna), though not yet distinguished from the Glenns Ferry Formation lithologically, are obviously a part of a much later (middle Pleistocene)





LOCALITY	COUNTY	QUADRANGLE
Oregon		
1 TUNNEL EXIT	MALHEUR	ADRIAN
Idaho		
2 CRAYFISH HILL	OWYHEE	OREANA
3 HWY 78 ROADCUT	"	"
4 PICKET CREEK	"	"
5 SAND PIT	"	GRAND VIEW
6 SHOOFLY	"	CHALK HILLS
7 JACKS CREEK	"	"
8 HORSE HILL	"	SUGAR VALLEY
9 HOT SPRING	"	HOT SPRING
10 OLD RR GRADE	ELMORE	INDIAN COVE
11 SAND POINT	OWYHEE	HAMMETT
12 DOVE SPRING	ELMORE	GRINDSTONE BUTTE
13 ROSEVEAR	ELMORE	TWENTYMILE BUTTE
14 USGS 19217	TWIN FALLS	HAGERMAN
15 USGS 20765	" "	"
16 JACKASS BUTTE	OWYHEE	JACKASS BUTTE

depositional system on the basis of the contained fishes (Recent species) and mammalian fauna (Irvingtonian, Taylor, 1966). This system is closer to the Bruneau Formation in time, and the fauna should probably be referred to the Bruneau Lake system (Miller and Smith, 1967).

Cope (1883a, b) first used the name "Idaho Lake." This terminology is still useful to denote the more or less continuous bodies of water and their evolving fauna through part of Miocene and Pliocene time, even though the lake system probably migrated as it opened from west to east and then closed, perhaps from east to west, leaving a record that comprises at least four formations, especially the Glenns Ferry Formation (but as noted above, possibly not all of the Glenns Ferry Formation).

An early stage of the Lake Idaho fish fauna is represented in the Deer Butte (or Chalk Butte) Formation in SE Oregon, as described by Kimmel (1975, this volume). The Chalk Hills and Poison Creek formations in Idaho are similar in time, but their faunas are not well enough known to add to the discussion.

This paper is based on a middle or later stage of Lake Idaho, as represented in the Pliocene Glenns Ferry Formation. Current knowledge of the structure and stratigraphy of the Glenns Ferry Formation is based on the work of Malde and Powers (1962), Malde (1972), and Armstrong, Leeman, and Malde (1975). The tectonic framework for the entire system may eventually be understood in terms of the cycle of volcanic activity and caldera collapse outlined by Eaton et al. (1975). In this system "Lake Idaho" might represent early stages in the western Snake River Plain of a system of volcanic foci that migrated along the trace of the Snake River Plain to its present position as the Yellowstone volcanic field, with the analogous present aquatic habitat being represented by Yellowstone Lake.

The Glenns Ferry fauna generally has been taken to represent the Blancan North American land-mammal age (Taylor, 1966; Zakrzewski, 1969; Bjork, 1970; Malde, 1972). However, potassium-argon dates of 4.4-6.2 m.y. for Glenns Ferry basalts (Armstrong et al., 1975) indicate that the fauna is much too old to fit into the Blancan land-mammal age as currently understood. The Mount Blanco fossils occur in the lower Matuyama (reversed) magnetic interval, 1.4-2.4 m.y. in age (Lindsay et al., 1975). The early Blancan time spans the Gauss (normal) magnetic interval and may be interpreted as beginning late in the Gilbert (reversed) interval, about 3.5 million years ago. The Glenns Ferry fauna (generally associated with reversely magnetized rocks, Armstrong et al., 1975) apparently contains the earliest record of many Blancan mammals and requires a redefinition of the Blancan-Hemphillian age boundary or recognition of time-transgression of the Blancan fauna (Armstrong et al., 1975).

The fish fauna of the Glenns Ferry Formation is too restricted geographically to be useful in broad correlations at this time. Some faunal changes of local stratigraphic usefulness will be outlined in this paper and the accompanying one by Kimmel.

Localities that have yielded most of the material on which this report is based are listed here and mapped very generally in Figure 1. The eastern localities near Hagerman (14, 15) and the localities near Hammett were collected extensively by C.W. Hibbard and students, especially R.J. Zakrzewski and P.R. Bjork in the 1960s. All localities were collected by the author and field parties in the field seasons of 1968, 71, 72, 74, and 75. R.R. Miller and his field parties collected at locality 3 and elsewhere. Peter Kimmel collected extensively in 1974 and 75 in the cluster of localities designated 1.

1) Oregon, Malheur County, Deer Butte Formation: T. 22 S, R. 46 E, Secs. 7, 16, 22, and T. 23 S, R. 46 E, Sec. 2; elevations 2540-3200 ft (775-975 m). These localities and the fossils recovered from them are discussed by Kimmel in the companion paper of this volume.

Localities 2-15 are in the upper Pliocene Glenns Ferry Formation of Idaho. The names applied are not formal, but may assist the discussion.

2) Crayfish Hill, Owyhee County: T. 4 S, R. 1 W, SW¼, Sec. 1. Twenty-two units generally rich in volcanic ash and fossil fish fragments, ranging from about 2800-2900 ft (853-884 m). Several distributary channels are preserved in the section. Lake sediments are extensively burrowed. Few fish are preserved relatively intact. In the upper part of the section concentrations of disarticulated bone are preserved in granule sand containing clay-ball clasts.

2a) In the western part of Sec. 7, T. 4 S, R. 1 E, elevation 2900 ft (884 m), is a fine-grained lacustrine unit just below lake sediments of the Bruneau Formation and above and to the west of the typical pale yellow Glenns Ferry silts. Fossils in this unit are preserved in unusually delicate detail, frequently in articulated condition. The presence of a representative of a deep-water and arctic sculpin add evidence for deep lacustrine origin of the unit.

3) Highway 78 (45) roadcuts at Fossil Creek, Owyhee County: T. 4 S, R. 1 W, S Sec. 11 and N Sec. 14, elevation 3000 ft (914 m). Disarticulated fish fossils occur in several units of burrowed lacustrine sediments, predominantly very fine sands and silts with mica and some oolites. There is little evident crossbedding.

Figure 1. Western Snake River Plain showing distribution of sediments of the Idaho Group (after Malde and Powers, 1962) and collecting localities yielding fossil fishes reported here.

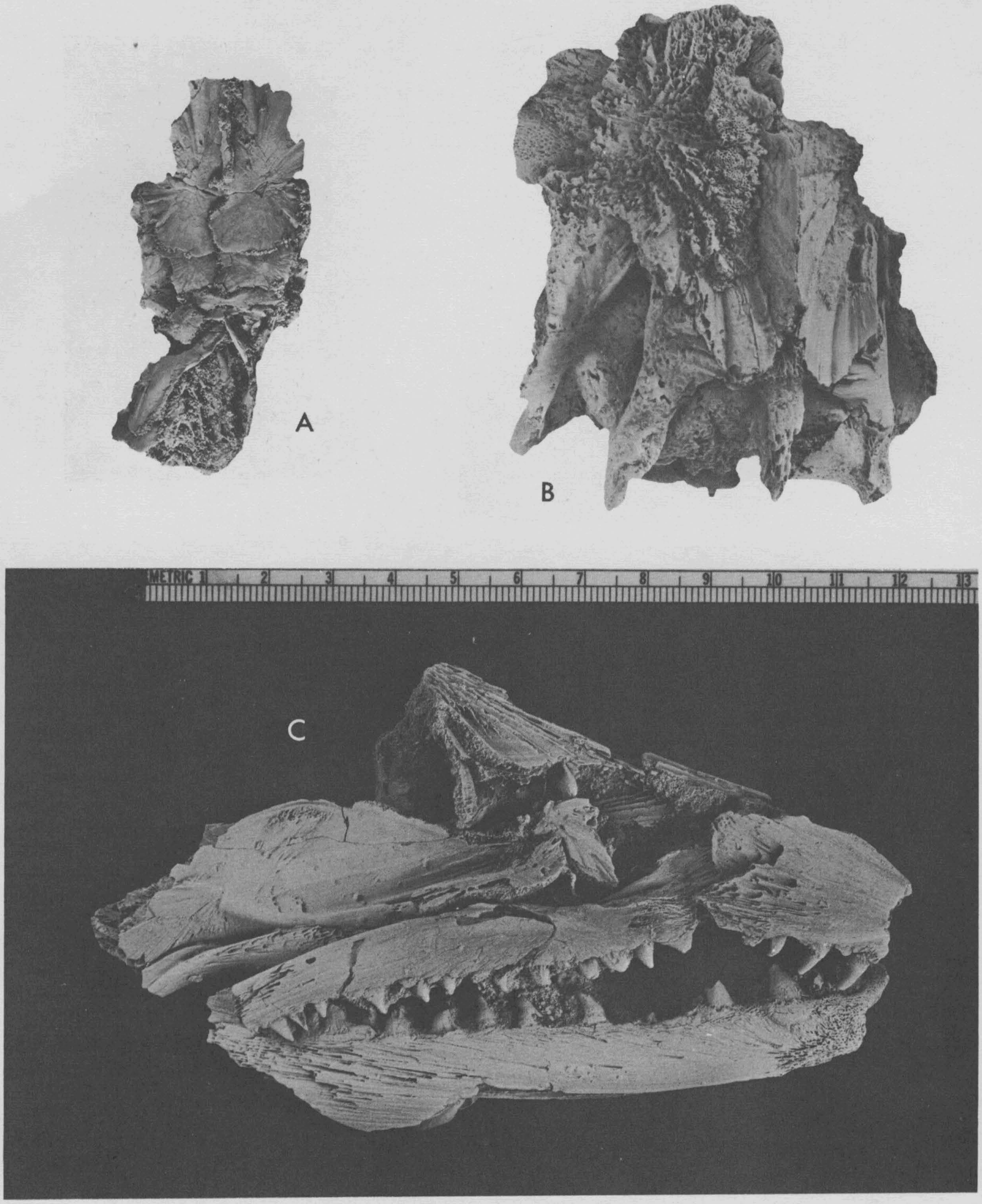


Figure 2. (A) Posterior part of cranium of *Prosopium prolixus*, UMMP 53715. (B) Posterior part of cranium of *Rhabdofario lacustris*, UMMP 62091. (C) Holotype of *Rhabdofario lacustris*, USNM 16352. All specimens actual size.

4) Picket Creek, or Catherine Creek, Owyhee County: T. 4 S, R. 1 W, NW¼, Sec. 24, elevation 2950-2975 ft (900-907 m). Very fine sands and silts contain disarticulated fish bone.

5) Sand Pits, Owyhee County: T. 6 S, R. 3 E, SW¼, Sec. 21, elevation 2850-2875 ft (869-876 m). Iron-oxide stained granule sands and disarticulated fish bones occur in a thick, extensive unit.

6) Shoofly, Owyhee County: T. 7 S, R. 3 E, Sec. 4, elevation 3025-3060 ft (922-933 m). Disarticulated, iron-oxide stained fish bones occur in granule sands above and below a thick, crossbedded oolite unit. Volcanic ash rich units below the oolite contain some fish.

6a) Poison Creek, Owyhee County: T. 7 S, R. 3 E, W Sec. 5, elevation 3150-3225 ft (960-983 m). Disarticulated fossil fish occur in generally fine-grained, ashy lacustrine units with moderate lateral extent.

7) Jacks Creek, Owyhee County: T. 7 S, R. 3 E, NE¼, Sec. 25, elevation 3150 ft (960 m). Disarticulated, abraded, iron-stained fossils occur in relatively coarse sediments.

8) Horse Hill, Owyhee County: T. 7 S, R. 5 E, NW¼, Sec. 36, elevation 3050 ft (930 m). Disarticulated fossils occur in an iron-oxide stained sand unit resting on an indurated, heterogeneous quartzite cobble unit of considerable lateral extent.

9) Hot Springs, Owyhee County: T. 8 S, R. 6 E, NE¼, Sec. 10, elevation 3070 ft (936 m). Disarticulated and abraded fossil fish bones occur in iron-oxide stained granule sands above the limestone reef.

10) Bennett Creek abandoned railroad grade, Elmore County: T. 5 S, R. 8 E, SW¼, Sec. 16, elevation 2725 ft (831 m). Disarticulated but finely preserved fish bones occur in pale, fine sands and silts, and in associated concretions.

11) Sand Point (Shell Mountain), Owyhee County: T. 6 S, R. 8 E, S½, SW¼, Sec. 1, elevation 2600-2690 ft (794-819 m). Fossil fish, mollusks, and mammals (Taylor, 1966) occur in poorly sorted, heterogeneous sediments said to be fluviatile in origin (Malde, 1972).

12) Dove Spring, Elmore County: T. 7 S, R. 10 E, NE corner, Sec. 31, elevation 3100 ft (945 m). Disarticulated, abraded, and iron-oxide stained fossils occur in a brownish-gray sandstone with abundant fossil wood.

13) Rosevear Gulch, Elmore County: T. 7 S, R. 10 E, W boundary, SW¼, Sec. 12, elevation 2975 ft (907 m). Disarticulated fossils are in concretion-bearing massive gray sands and very fine, pale gray, unstructured sands with abundant ostracods.

14) USGS Cen. loc. 19217 (DWT 432), Twin Falls County: T. 7 S, R. 13 E, NE¼, Sec. 20, elevation 3115 ft (949 m). Disarticulated fossils in very fine sand and silt of floodplain facies. See Bjork (1970) and Zakrzewski (1969) for associated localities and fauna.

15) USGS Cen. Loc. 20765 (DWT 540), Twin Falls County: T. 7 S, R. 13 E, SW¼, Sec. 28, elevation 3025 ft (922 m). Disarticulated fossils in very fine sand and silt of floodplain facies. See Bjork (1970) and Zakrzewski (1969) for associated localities and fauna.

16) Jackass Butte (Grandview local fauna), Owyhee County: T. 4 S, R. 2 E, NE¼, Sec. 15, elevation 2500 ft (762 m). Disarticulated fossils occur in floodplain facies not differentiable from Glenns Ferry sediments but bearing fossil elements indicating a middle Pleistocene (Irvingtonian) age (Taylor, 1966:72).

SPECIES ACCOUNTS

The following accounts provide taxonomic background, descriptions, diagnoses, and remarks concerning abundance, size, and ecology of members of the fauna. The diagnoses are exclusively osteological and oriented to characteristics preserved in the fossils, even though the living genera represented often have some useful external characteristics of the soft anatomy that customarily have formed the basis of classifications by workers on Recent fishes.

Family **Salmonidae**

The family Salmonidae includes three subfamilies: Salmoninae (trouts, salmons, and chars), Coregoninae (whitefishes and ciscoes), and Thymalinae (graylings). No chars or grayling have yet been found in the Glenns Ferry Formation, although they are each a part of the Recent fauna of western North America. The family is represented in the fauna by a large salmon (*Rhabdofario lacustris*), a new planktivorous salmon in the genus *Oncorhynchus*, a large trout of uncertain affinities but similar to the Eurasian *Hucho*, a possible species of *Salmo*, and a large whitefish (*Prosopium*).

Subfamily SALMONINAE

Genus *Rhabdofario* Cope

Diagnosis.– A salmonid with very large, well-socketed teeth on the premaxillae, maxillae, dentaries, vomer, palatines, glossohyal, and pharyngeal bones. The jaws and teeth are not modified in breeding specimens. The dentaries are deep, convex anteroventrally, and marked by rugose exostosis on the anterolateral face. The vomerine teeth are in a longitudinal alternating file of ca. 6-8 teeth. The middle sections of the maxillae are round or even dorsoventrally compressed in cross section. The premaxillary process is not strongly divergent from the maxilla and is not toothed. The premaxillae are deltoid, rounded anteriorly, and slightly emarginate posteriorly. The frontals have extensive, rugose exostosis. The parietals are divided. The posttemporal fossae are very deep but


A
B
C
D
E
F
59265
G

closed. The intercalar does not fully separate the pterotic and the exoccipital and does not contact the prootic.

Rhabdofario lacustris Cope

(Figs. 2C, 3)

Rhabdofario lacustris Cope 1870:545 (type, USNM 16352, skull). Cope, 1883:161. Cavender and Miller, 1972: 40-41.

Rhabdofario sp., Russell, 1902.

Salmo copei Uyeno and Miller 1963:12. Taylor, 1966:74, Miller and Smith, 1967:22.

Taxonomy.— Cope erected the genus and species *Rhabdofario lacustris* based on Idaho material collected by Capt. Clarence King. The type skull was compared with *Salmo* (apparently *Salmo salar*) and the original description clearly and accurately distinguished *R. lacustris* from *Salmo* on the basis of the cylindrical rather than flattened maxilla. Uyeno and Miller (1963) concluded from their studies that *R. lacustris* should be classified as a species of *Salmo* and applied the new specific name, *copei*, because the name *lacustris* was preoccupied in *Salmo*. Cavender and Miller (1972) stated that *Rhabdofario* is distinct from *Salmo* and *Oncorhynchus.*

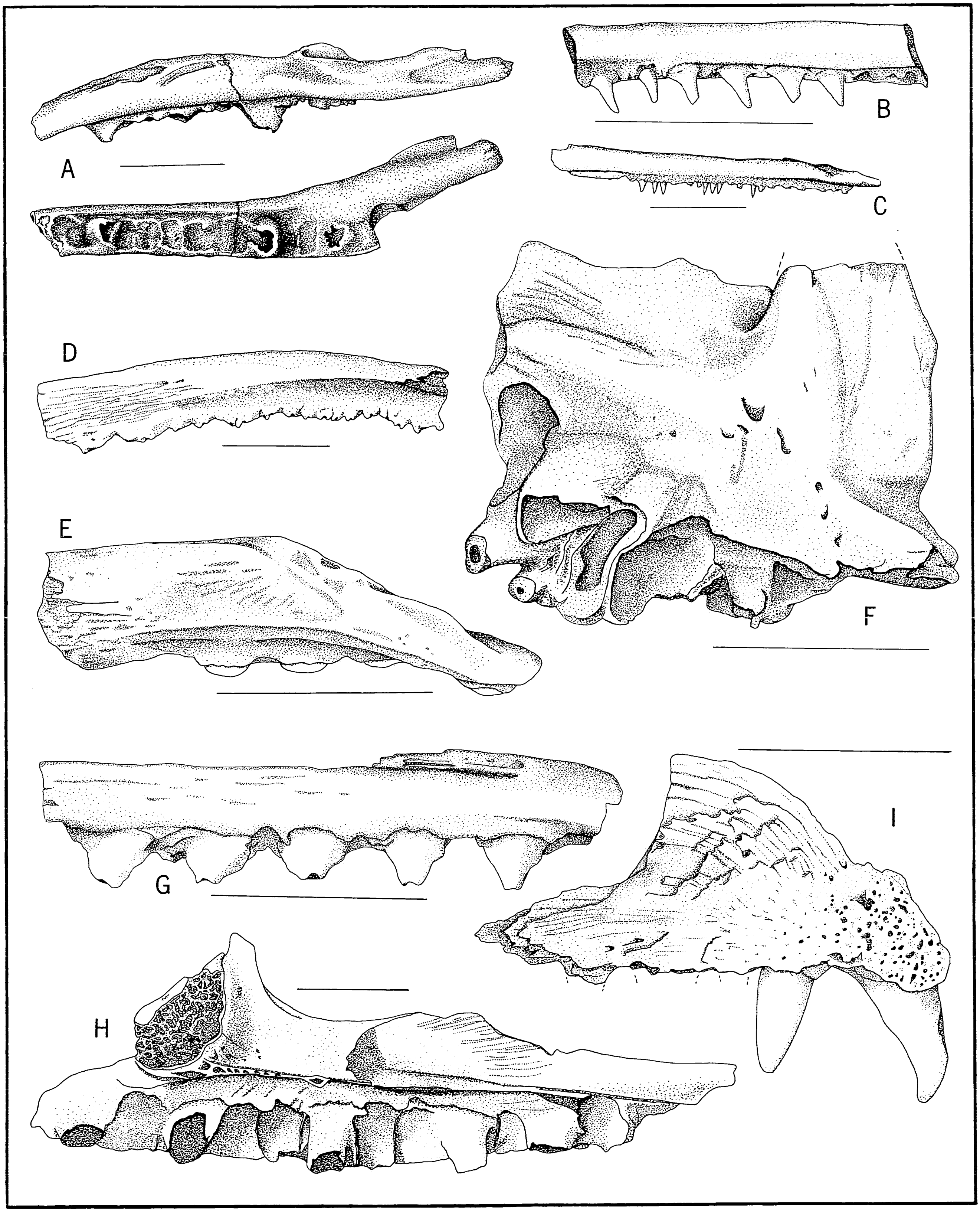
It is possible that several species of *Rhabdofario* occur in the "Lake Idaho" sequence. The type species, *Rhabdofario lacustris* Cope, was described from Castle Creek, Owyhee County, Idaho. Two similar forms occur in the Deer Butte Formation in Oregon. The common *Rhabdofario* in lake sediments in the Glenns Ferry Formation is similar to the type of *R. lacustris*. New material enables an expansion of the description and diagnosis of the species.

Redescription.— UMMP V59265 consists of associated parts of one skeleton including two maxillae, two dentaries, two articular-angulars, a partial vomer, a partial parasphenoid, a partial palatine, a pterotic, a posttemporal, a partial urohyal, 30 vertebrae, and miscellaneous fragments. It was collected in very fine micaceous sand of a lacustrine facies of the Glenns Ferry Formation in the NW¼, Sec. 12, T. 4 S, R. 1 W (Oreana Quadrangle), Owyhee County, Idaho, at an elevation of 2940 ft (905 m). The left maxilla is complete, 99.8 mm in length, with a tooth row 76.2 mm long, containing eight teeth in 19 spaces. The anterior 48 mm of the tooth row contains spaces for 10 large teeth; the posterior 28.2 mm is deflected laterally and spans spaces for 9 small teeth. The large teeth are 4.8-6.5 mm in maximum width at their bases; the small teeth are 2.7-3.3 mm wide at their bases. The teeth are set in rather deep sockets directly in the shaft of the bone, with little development of a platform. A sulcus extends longitudinally along the base of the tooth row on the median side, expanding to a shelf about 3 mm wide at the point of deflection of the posterior row of smaller teeth. The depth profile of the bone, excluding teeth, is 10.5 mm at the second tooth space and the edge of the palatine cotyla, 10.2 mm at the 5th tooth space, 8.8 mm at the 8th space, 6.2 mm at the 10th space, 5.2 mm at the 15th space, and 7.3 mm at the end of the last space. The maximum width at the same points is 8.5, 8.1, 7.6, 8.0, 8.0, and 3.5 mm. The palatine cotyla is directly above the second and third teeth and is the high point on the bone. Posteromediad to it is a deep fossa; above the fossa is a dorsal ridged surface. The premaxillary process extends forward at an angle 10 degrees lower than a line through the bases of the anterior teeth, viewed in the lateral aspect. It diverges mediad at an angle of about 20 degrees from the axis of the anterior part of the tooth row. A broad system of grooves marks its anterodorsal surface and a distinct longitudinal median-ventral groove separates a median ala from the central part of the process. The median surface is ornamented with fine, longitudinal grooves and ridges, the dorsal three-fourths of which cross over to the dorsal surface of the bone in the area above the end of the large anterior tooth row.

The dentaries are 95 and 94 mm long from the anterior tip to the end of the dorsal, tooth-bearing ala; each has spaces for about 15 well-socketed teeth in a row 85 mm long. The anterolateral 25 mm of each dentary is extensively ornamented with cancellous, fibrous-textured bone. The tooth sockets are about 5.5 mm wide and occupy all but 2 or 3 mm of the tooth-bearing platform over the anterior half of the row. There is no indication of breeding teeth; the anterior nine tooth sockets are about equal in diameter. The sockets remain in alignment inside the outer edge of the dentary throughout the row. The ventral edge of the dentary is keeled over the anterior 25 mm but smoothly rounded posteriorly.

The articular-angulars are 67 and 87 mm long, the latter (left) lacking about 10% of the anterior tip. The angle of the coronoid process is about 40 degrees from the axis of the anteroventral margin. The posterior process of the angular is vertical above the retroarticular, marked laterally by numerous striations that curve under the articular fossa, and perforated by a large foramen of the acoustico-lateralis canal. It is posterior to the lateral half of the articular fossa. The vomer consists of an anterior ramus 13 mm long and an incomplete tooth row 12 mm long with

Figure 3. *Rhabdofario lacustris*, UMMP 59262. (A) Left maxilla. (B) Anterior part of vomer. (C) Posterior part of vomer, UMMP 59393. (D) Lateral view of left pterotic, UMMP 59262, anterior up. (E) Mesial view, left premaxilla. (F) Lateral and mesial views of right dentary. (G) Lateral view of articular-angular and quadrate, and mesial view of ectopterygoid (displaced), epihyal, and ceratohyal, UMMP 62091. Actual size.


A
B
C
D
E
F
G
H
I

spaces for 5 teeth alternating on either side of the midline and increasing in size posteriorly. The fifth tooth is 4.3 mm long and 3.6 mm in maximum diameter. The fragment of the palatine is 8 mm wide (intact) with the tooth sockets 4.2-4.9 mm in diameter. The median fragment of parasphenoid is flat on its anterior palatal surface but distinctly keeled posteriorly. The pair of large, anterior foramina are 7.8 mm apart. The left pterotic is 41 mm in maximum (incomplete) length. It is similar to that of *Oncorhynchus keta* and *O. rhodurus* in the possession of a flattened dorsolateral keel, which is up to 4.3 mm wide, rounded on the median edge, and sharp on the lateral edge, with considerable lateral overhang. It possesses at least five acoustico-lateralis canal pores. The posttemporal is 35.5 mm long (incomplete) and is like that of *Salvelinus* and *Salmo trutta*, with a wide anterodorsal ramus. The vertebrae are 12-13 mm in diameter, with fine sculpturing as in similar-sized *Oncorhynchus.*

Diagnosis.– *Rhabdofario lacustris* is a salmonid with the maxilla somewhat rod shaped in cross section, tending to be dorsoventrally flattened in the third quartile of its length, and laterally compressed only at its extreme distal one-sixth. The lateral border of the premaxillary process extends directly forward with little or no angle of departure from the prominent median longitudinal sulcus at the base of the tooth row but extends about 10 degrees ventral to a line through the bases of the anterior teeth. The posterior two-thirds of the maxilla is deflected laterally. The teeth anterior to the point of lateral deflection form a primary row with spaces for only 10-14 enlarged teeth, followed by a secondary, deflected, row with spaces for about 9-11 teeth.

The maxillae of the other forms of *Rhabdofario* have a less distinct median longitudinal sulcus at the base of the tooth row, a less distinct or absent median sulcus on the premaxillary process, a strong divergence and discontinuity of the median striation pattern from the longitudinal axis in the area of deflection, and smaller, more numerous teeth on a moderately deep platform. *Oncorhynchus* differs from *Rhabdofario* in having less prominent development of tooth sockets, anteroventral deflection of the premaxillary process (in the American species), and extension of the tooth row onto the premaxillary process of the maxilla. In *Salmo* the maxilla is laterally compressed over at least its posterior one-half and has a more dorsally deflected premaxillary process. Among Recent species, large *Salmo gairdneri* share more characteristics of the maxilla with *Rhabdofario lacustris*. The maxilla of *Salmo gairdneri* differs in being more compressed laterally, having smaller, more numerous teeth, and having the palatine cotyla in a more anterior and ventral position.

Additional Material and Comparisons.– The posterior part of a large neurocranium with an associated part of a left hyomandibular (UMMP 62091) from the same locality as the above material and probably conspecific with it shows many *Oncorhynchus*like characteristics. The fossil is 43 mm between the tips of the epiotics and 45 mm from the midline of the supraoccipital to the tip of the pterotic. The pterotic is slightly more indented dorsally and ventrally than *R. lacustris* and appears to have an acute rather than a flattened dorsolateral crest; however, the difference might be due to abrasion. The intercalars are limited and do not contact the prootics. The epiotics have much enlarged posterior processes. The supraoccipital has a large, prominent posteromedian process that emanates from a dorsal platform between the ends of the frontals. The posterolateral surfaces of the supraoccipital are separated from the dorsal platform by deep, lateral grooves and are in contact with the parietals. The contact between each parietal and the dorsal platform of the supraoccipital is covered by the posterior tip of the frontal. Most of the dorsal surface of each frontal, except posteriorly, is covered by a rather thick mass of finely textured, cancellous bone, as in *Oncorhynchus*. The sphenotic is most like that of *Oncorhynchus* but is more extreme in the development of a broad, prominent dorsolateral shelf. The hyomandibular shows a dorsally placed median foramen and a prominent ridge abutting the metapterygoid.

An associated but unconnected part of 62091 is a left articular-angular with the quadrate, ectopterygoid, symplectic, ceratohyal, epihyal, and parts of the preopercle and interopercle of a specimen somewhat larger than the type. The articular-angular is identical to those of UMMP V59265. The quadrate is like that of *Oncorhynchus*. The postventral surface is somewhat deflected laterally. The postventral process is not greatly divergent from the fan-shaped anterior part of the bone, which is somewhat concave laterally.

The ceratohyal might be diagnostic. It is 52 mm in maximum length (anterodorsal to posteroventral), 25 mm in maximum depth (posteriorly), 14.6 mm in minimum depth (medially), and 17.2 mm deep at the anterior edge. Its dorsolateral groove is pronounced and parallels the dorsal edge under a ridge 2 mm wide. Its plane is not greatly distorted. The surfaces are deeply scored by nutrient grooves and foramina. The anterior and posterior

Figure 4. *Rhabdofario lacustris*: (A) Anterior of left maxilla, UMMP 58029, lateral and ventral views. (H) Right palatine, UMMP 62080, mesial view. *?Oncorhynchus* sp.: (B) Right maxilla, UMMP 62016, mesial view. (C) Left maxilla, UMMP 62112, mesial view. (E) Anterior of left maxilla, UMMP 58428, mesial view. (G) Left maxilla, UMMP 62105, mesial view. (I) Right premaxilla, UMMP 62107, anterior view. *?Salmo* sp.: (D) Left maxilla, UMMP 62108, mesial view. Genus and species of salmonine described by Kimmel (this volume): (F) Left premaxilla, UMMP 62005, posterior view. All scales equal 1 cm.

Figure 5. Holotype, *Oncorhynchus salax* new species, UMMP 62100. Scale in cm.

margins are subparallel to each other. The posterodorsal corner has an angle of 85 degrees. In *Salmo* the plane of the bone tends to be more deflected or distorted; in *Salvelinus* the proportions are similar but the angles of the sides are less perpendicular; American *Oncorhynchus* are shorter and deeper; *Oncorhynchus rhodurus* of Japan is very similar to the fossil in every way. The epihyal of the fossil is 34 mm long and 19 mm in maximum width, with gradual curvature of the ventral border. It has a single, broad (9.5 mm) facet at the posterodorsal corner. Like the ceratohyal, it is similar to *Oncorhynchus rhodurus*, unlike American *Oncorhynchus*, and only moderately similar to other American salmonids. The interopercle is remarkable in the possession, at its anterior end, of a cancellous, rugose layer of bony tissue similar to that on the frontals and anterior corner of the supraoccipital (as well as on chondral bones). This characteristic also occurs in *Oncorhynchus*.

Several bones in the additional material contribute more diagnostic characteristics to the description of *Rhabdofario*. A vomer (UMMP 59393) has a double alternating tooth row 15.5 mm long with 8 teeth, the anterior four or five of which were over 5 mm long. The premaxillae (UMMP 59393) are flat, elongate deltoid, with a longitudinal lateral depression and a slight posterior notch, as in *Salmo*. In 18 measurable articular-angulars the coronoid angle exceeds 40 degrees and ranges as high as 52 degrees.

A right palatine (UMMP 62080, Fig. 4H) is similar to that of the type specimen of *R. lacustris* except for the broader lateral shelf, which bears the teeth. The anterodorsal facet of the dorsal process lies at an angle of 30 degrees above the axis of the tooth row, as viewed in the lateral aspect. In *Oncorhynchus* and *Salmo* the process has a more prominent dorsal extension and the angle is nearer 60 degrees and may appear to be near 90 degrees. The posterior articulating surfaces of the dorsal process are widely separated from the anterior facets in *Rhabdofario*. The fossil is 65 mm long and has 12 large teeth. The bone is heavier and more compact than in Recent *Oncorhynchus.*

Smaller dentaries are common in the fine, micaceous sands exposed by the roadcuts southeast of fossil Butte (UMMP 59311, 62099). They represent young fish, and I am unable to confidently assign them to genus. The collection contains maxillae of both *Rhabdofario* and *Oncorhynchus* (see following section). The collection from Horse Hill contains remains of more mature fish; three kinds of dentaries are recognizable: *Rhabdofario, Oncorhynchus,* and an unidentified genus.

Remarks.— Identifiable specimens of *Rhabdofario* have been collected from all of the well-worked localities in the Glenns Ferry Formation. The many localities along Fossil Creek, the Shoofly section, Poison Creek, Picket Creek, and Horse Hill have produced much material. Poorer, less identifiable material has been found at most of the other localities. *Rhabdofario lacustris* is the common salmonid in the finer sediments; *Oncorhynchus* is prominent in coarser sediments. The most abundant and largest specimens are from Crayfish Hill and the beds across Fossil Creek (59265, 59393, 59423, 59438, 59434, 59588, 62080, and 62091). Most of the bones of the skull are represented among the several hundred bones from the collections, which include mostly remains of large fishes. It is significant that no specimens of breeding teeth or other bones identifiable as *Oncorhynchus* occur among this material, including the samples from coarser sands.

The largest salmonid specimen is a distal end of a left dentary, which is about 40-50% larger in its proportions than the corresponding parts of a 28 pound king salmon (UMMZ 186299) that was 980 mm in total length. Various vertebrae and jaw bones are 30-35% larger than parts of the same salmon. The most commonly represented size class averages slightly larger than a salmon about 1 meter in total length.

Genus *Oncorhynchus* Suckley

Specimens of *Oncorhynchus* from the Glenns Ferry Formation were first reported by Cavender and Miller (1972) in connection with their description of *Smilodonichthys rastrosus* from the Pliocene of Oregon and California. Although breeding teeth referable to *Oncorhynchus* have been known from the Glenns Ferry Formation for many years, a specimen sufficiently complete for description was not collected until 1974. Specimens are known from the Hagerman local fauna, from the Sand Pits near Hammett, and from the Shoofly and Horse Hill areas. The species is assigned to the genus *Oncorhynchus* on the basis of the small, poorly socketed teeth, numerous gill rakers, low coronoid process, intercalar contacting the prootic, divided parietals, and enlarged breeding teeth (in specimens other than the holotype). It is most similar to *O. nerka kennerlyi*, a landlocked form (Kokanee) of the Sockeye salmon of the Columbia drainage. The fossil differs in the possession of longer, more numerous gill rakers. The species name is selected with reference to this branchial sieve.

Oncorhynchus salax new species

(Fig. 5)

Holotype.— UMMP 62100, an incomplete skull collected in the Glenns Ferry Formation, 1000 ft S and 2200 ft E of the NW corner, Sec. 4, T. 7 S, R. 3 E (Chalk Hills Quadrangle), Owyhee County, Idaho, at an elevation of 3025 ft (922 m), by Beverly Smith, June 18, 1974. The specimen was in a fine-grained concretion.

Description.— The head is that of a fish that was 6±1 years old (well-developed annuli are apparent in the opercle). The length of the head in life was about 140 mm, but the anterior part of the dentaries, maxillae, premaxillae and ethmoid region are missing. The maxillae are represented by fragments adhering to the lateral surface of the dentaries. They are more compressed than the maxillae of *Rhabdofario* and possessed relatively minute teeth — a tooth 0.8 mm long is present 18 mm from the posterior end of the left maxilla. The supramaxillae were more than 7 mm deep and apparently extensively covered the maxillae posteriorly. The dentaries possessed small, poorly socketed teeth, as in *Oncorhynchus* and unlike the large teeth with well-developed sockets in *Rhabdofario.* The right dentary has a tooth 1.1 mm long, about 11 mm ahead of the posterior end of the tooth-bearing ramus. The articular-angular is long, with a low coronoid process. The coronoid angle (as measured by Cavender and Miller, 1972, as the angle between the dorsal border of the coronoid and a line through the articulation and the axis of the mandible) is 22 degrees. The angle of the posterodorsal process of the angular is about 105 degrees.

The quadrate and symplectic are similar to those in *Oncorhynchus nerka* (Walbaum). The ectopterygoid, however, is nearly straight by comparison. Otherwise the pterygoid series is similar to that of *O. nerka* in its diagnostic characteristics. The hyomandibular has a well-developed lateral (adductor) crest. The opercular series is like that of *O. nerka*. The opercle is rhomboid, with a well-developed posterodorsal corner. The subopercle is deep and rounded. The interopercle is only moderately extended posterodorsally. The opercular

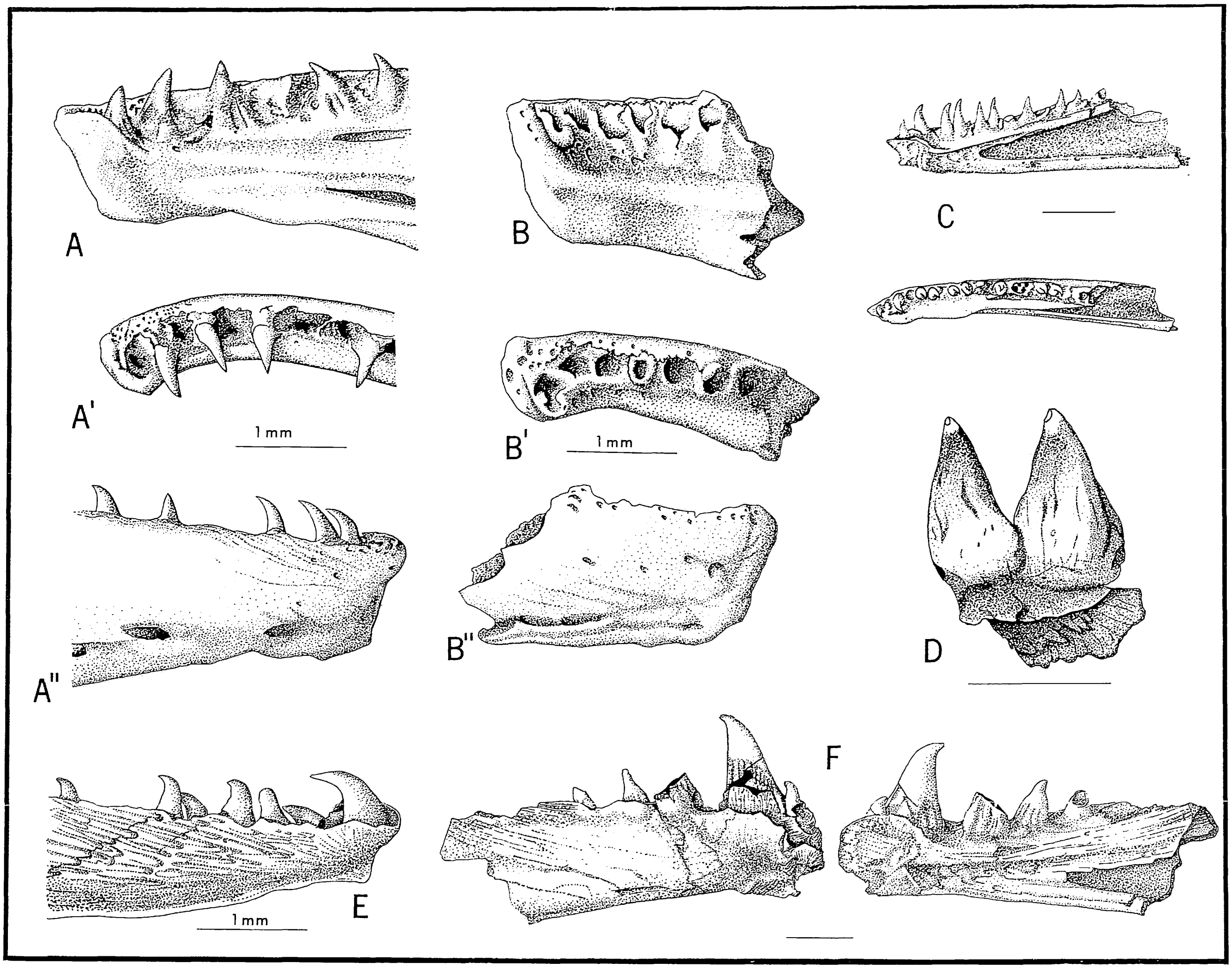


Figure 6. (A) *Hucho perryi* (R., Japan, UMMZ 187612), right dentary, mesial, dorsal, and lateral views. (B) cf. *Hucho* sp. (Horse Hill, UMMP 62109), right dentary, mesial, dorsal, and lateral views. (C) *Rhabdofario lacustris*, UMMP 62094, mesial and dorsal views. (D) *Oncorhynchus* sp., dentary breeding teeth, UMMP 62113, mesial view. (E) *Oncorhynchus nerka* (R., Colorado, UMMZ 186230), right dentary, lateral view. (F) *Oncorhynchus* sp., Horse Hill, UMMP 62104, right dentary, lateral and mesial views. Scales (except A,B,E) equal 1 cm.

bones do not show rugose or cancellous bony tissue, as in *Oncorhynchus*; the preopercle shows more extensive bony covering of the acoustico-lateralis canals. A tubular suprapreopercle is present. Five branchiostegals occur under the opercular series (four were probably attached to the epihyal and six appear under the dentaries). The ceratohyal shows space for about five missing branchiostegals. The length of the urohyal exceeded 32 mm. The glossohyal is 8.2 mm wide at its anterior end and more than 22 mm long. There are about eight teeth in each lateral row. They are small, about 1.3 mm long, at the lateral margin of the bone, and each is at the end of a ridge radiating from the midline of the bone.

The gill rakers of the first branchial arch on the right side are little displaced or distorted and have been revealed by air-abraded cuts made in the quadrate and pterygoid series. The median rakers are more than 18 mm long; the lower rakers are elongated as well. There are 11 or 13 on the upper half of the arch and at least 37, perhaps more than 40, on the lower part of the arch. In length, shape, and spacing, the rakers are similar to those of a large *Coregonus artedii* Lesueur. No denticles appear on any of the rakers. Rakers on the second or third arch are about 7 mm long, pointed, about 2 mm wide at the base, and are very closely spaced.

Although incomplete, the bones of the neurocranium are similar to those of *O. nerka kennerlyi*. The frontals are rugose and cancellous only over the sensory canals.

They extend posteriorly over the anterior end of the well-keeled supraoccipital. The parietals are well separated. The pterotics have a sharp dorsolateral keel along the line of emergence of the acoustico-lateralis pores. The posttemporal fossa is moderate or shallow compared to *Rhabdofario.* The intercalar extends along the dorsal border of the exoccipital to contact the prootic. The postorbital bones are well developed, with entire margins. The dermosphenotic and the fifth and sixth infraorbitals are well preserved and equal in length. The fourth infraorbital is at the posteroventral angle of the series.

The cleithrum of the fossil is unusual for a salmonid. A sharp keel separates the anterior or branchial concavity from the lateral face of the bone. This keel forms a prominent edge in both the lateral and perpendicular planes.

Diagnosis.– An *Oncorhynchus* with more than 48 gill rakers, which apparently lack denticles and are longer than the maximum height of the mandible at the coronoid process; small, poorly socketed teeth (except, presumably, in breeding specimens); a nonangular ectopterygoid; rugose, cancellous bony tissue not extensively developed on frontals and apparently lacking on other bones; a low coronoid angle on the articular-angular; intercalar contacting the prootic, pterotic with a sharp rather than a rounded dorsolateral process; glossohyal with two lateral rows of minute teeth; and cleithrum with a prominent lateral ridge at the angle or edge of the anterior (branchial) concavity.

Additional Material.– Additional maxillae and dentaries, possibly referable to *Oncorhynchus*, occur in most other localities in the Glenns Ferry Formation. The maxillae are more compressed laterally, with a more ventrally directed premaxillary process and with smaller teeth, which usually extend farther onto the premaxillary process, than in *Rhabdofario.* The dentaries differ little from those of *Rhabdofario* but seem to have smaller teeth with poorly developed sockets (except for several large teeth on the anterior end of the mandible), a narrower anterior end, a less convex anteroventral border, a lower coronoid angle, a more prominent median extension of the tooth platform, and more anterior extension of the anterior flange at the base of the first tooth. All of these characters vary and overlap with those of *Rhabdofario* except, possibly, the presence of breeding teeth. Nevertheless, it may be that the differences in the mandible recorded here are sexual, and that the above characters describe small males of *Rhabdofario.* The pattern of distribution and co-occurrence suggests a separate species of fish more similar to *Oncorhynchus*, however.

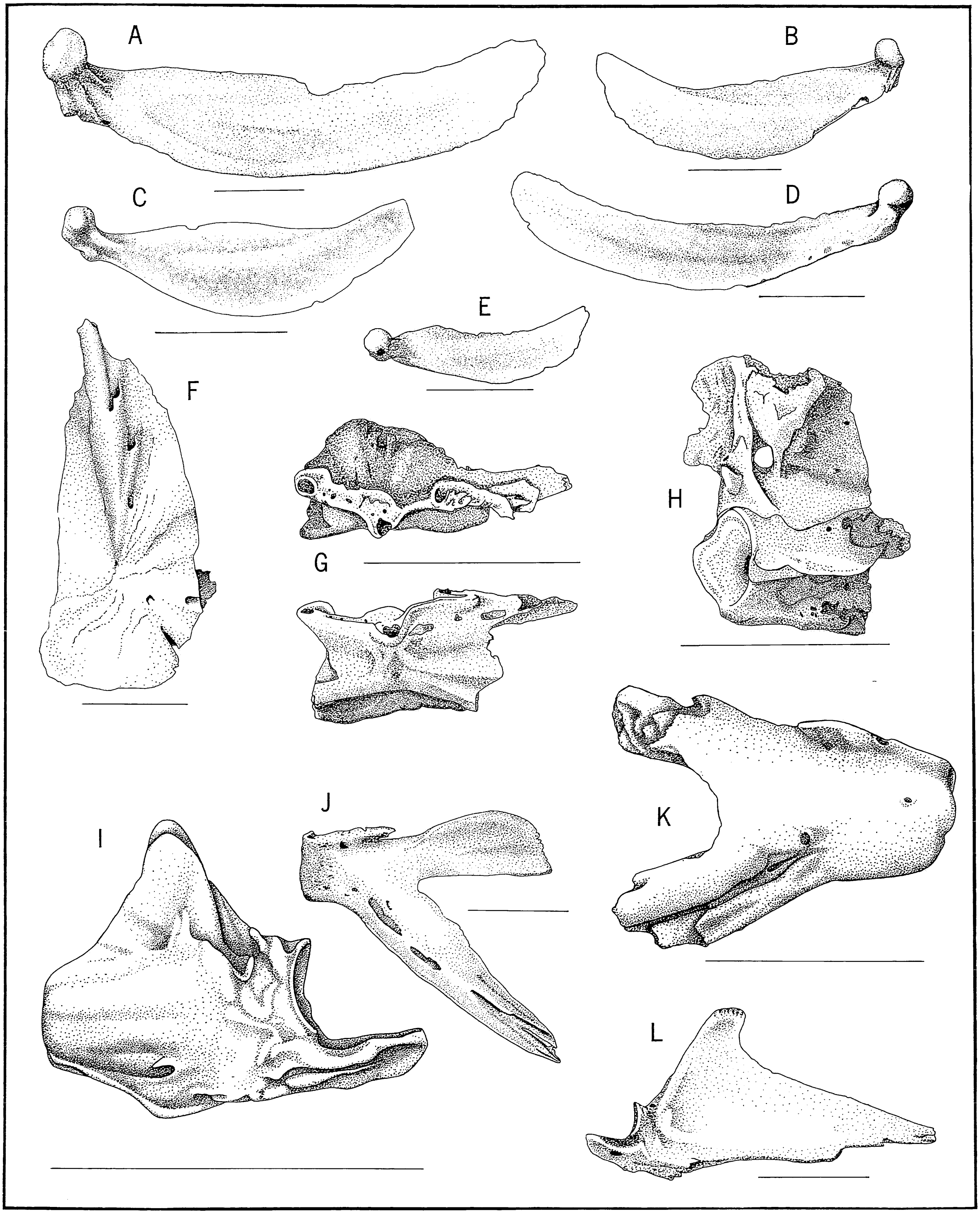
The most obvious specimen of *Oncorhynchus* is a dentary (UMMP 59669) 74 mm long, with weak tooth sockets and without development of breeding teeth, that is essentially identical to specimens of *Oncorhynchus nerka kennerlyi* of the same size. The bone is narrow and elongate anteriorly, is slightly convex anteroventrally, has a prominent shelf extending medially from the tooth platform, and has a prominent anterior flange at the base of the first tooth. An additional dentary and a pair of large, swollen mandibular breeding teeth (Fig. 6D) were collected at the same locality, the Sand Pits 12 mi S of Grandview. Two fragments of maxillae (UMMP 58002) were taken from the same locality. The most complete differs from *Rhabdofario* in the lower angle of the premaxillary process, the smaller teeth, which extend farther forward onto the maxillary process, and the lack of a sharp longitudinal groove along the median edge of the tooth row. It differs from *Oncorhynchus* in that the axis of the premaxillary process becomes more nearly vertical distally.

A number of small dentaries from Horse Hill show various stages of development of the *Oncorhynchus* characters mentioned above and two show well-developed breeding teeth on the dentary (Fig. 6F). Most of the maxillae from Horse Hill are readily identifiable as *Rhabdofario*, but several (Fig. 4B,C,G) seem to be *Oncorhynchus* on the basis of distal compression, somewhat smaller teeth, and the absence of a median longitudinal groove at the base of the tooth row. A maxilla and a dentary of a third species of salmon or trout have been collected from Horse Hill, as noted below.

A right premaxilla (Fig. 4I, UMMP 62107) with two anterior teeth and spaces for three additional teeth was collected from the Horse Hill locality. It is unlike the *Rhabdofario* form of premaxilla, which is similar to *Salmo gairdneri* Richardson or *S. clarki* Richardson. It is not very similar to the premaxillae of *Oncorhynchus* except that it is robust, lacks a sharp posteromedian crest, and has a similar dorsal crest. The bone is provisionally placed with the *Oncorhynchus* material because of the above characters and because it is clearly not *Salmo, Salvelinus, Hucho,* or *Rhabdofario*, and the external texture of the bone is similar to the external texture of the anterior end of the *Oncorhynchus* dentaries from Horse Hill.

At the Hot Springs locality, material of *Oncorhynchus* seems to be exclusively or at least dominantly represented. Five sets of swollen breeding teeth have been collected and several fragments of maxillae, a basioccipital, and an articular-angular are more similar to *Oncorhynchus* than to *Rhabdofario.* A premaxilla is rather flat, deltoid, and slightly notched posteriorly. It is similar to UMMP 62107 from Horse Hill.

Two distinct kinds of maxillae are present in the fine, micaceous sands and silts in Fossil Creek, southeast of Fossil Butte. The bones represent small, one- or two-year-old fishes. The *Rhabdofario* maxilla is represented by bones that agree in all respects, except the miniature size


A
B
C
D
E
F
G
H
I
J
K
L

and the relatively smaller teeth, with the description given for *R. lacustris.* In addition are several rather straight, distally compressed, small-toothed maxillae with a low premaxillary process. These maxillae are also marked by a long, smoothly rounded, edentulous distal extension (Fig. 4C). It is tentatively concluded that they represent *Oncorhynchus*.

Although salmonid bones are rare in the floodplain deposits from which the Hagerman local fauna has been collected, two dentaries were collected by C.W. Hibbard and his field parties in 1962 (UMMP 45232) and 1965 (UMMP 52792). These dentaries agree in most respects with the *Oncorhynchus* characters given above, but the anterior teeth are only moderately enlarged and the posterior teeth are rather large and well socketed.

Remarks.– There is good evidence that the genus *Oncorhynchus* is represented as at least one of the four or more kinds of trout and salmon in the Glenns Ferry Formation. Salmon are best represented in the localities with the most extensive bodies of coarse sands – the Sand Pits, Hot Springs, and Horse Hill localities. Furthermore, these localities are dominated by breeding specimens. The only other locality with breeding specimens is the floodplain deposits at Hagerman. Evidence of young specimens occurs in the fine sands at Fossil Creek. The type specimen of *Oncorhynchus salax* represents a single known occurrence in a concretion in the tuffaceous lower part of the Shoofly section. The occurrence of the breeding specimen over the coarsest substrate suggests that spawning occurs in tributary streams or on beach areas. The presence of young and intermediate-sized fishes in the lake indicates that the fishes were probably iteroparous and did not migrate to the sea. The age, 6±1 years, of the type specimen of *Oncorhynchus salax*, plus its small size and morphological similarity to landlocked salmon, suggests a long life history in the lake without migration to the sea. *Oncorhynchus salax* was a planktivore, as indicated by the numerous, long gill rakers and the small jaw teeth. These observations do not rule out the possibility that the larger *Oncorhynchus* jaws belong to other, possibly sea-run, species of salmon. The definitive comparison cannot be made until additional associated salmon material becomes available for study.

Subfamily COREGONINAE

Several hundred fossils representing whitefish of the genus *Prosopium* have been collected from nearly all well-collected localities in the Glenns Ferry Formation. The specimens represent a size range of fishes from 100 mm to over 800 mm in length, based on extrapolation from representative bones. The size and massive structure of the jaws are reminiscent of the genus *Stenodus*, but the lower jaws of the fossil *Prosopium* are not as well adapted to predaceous habits as *Stenodus.* One incomplete skull is known; individual skull and jaw bones comprise the remainder of the specimen. The occurrence in the Glenns Ferry Formation was first mentioned by Miller and Smith (1967:22).

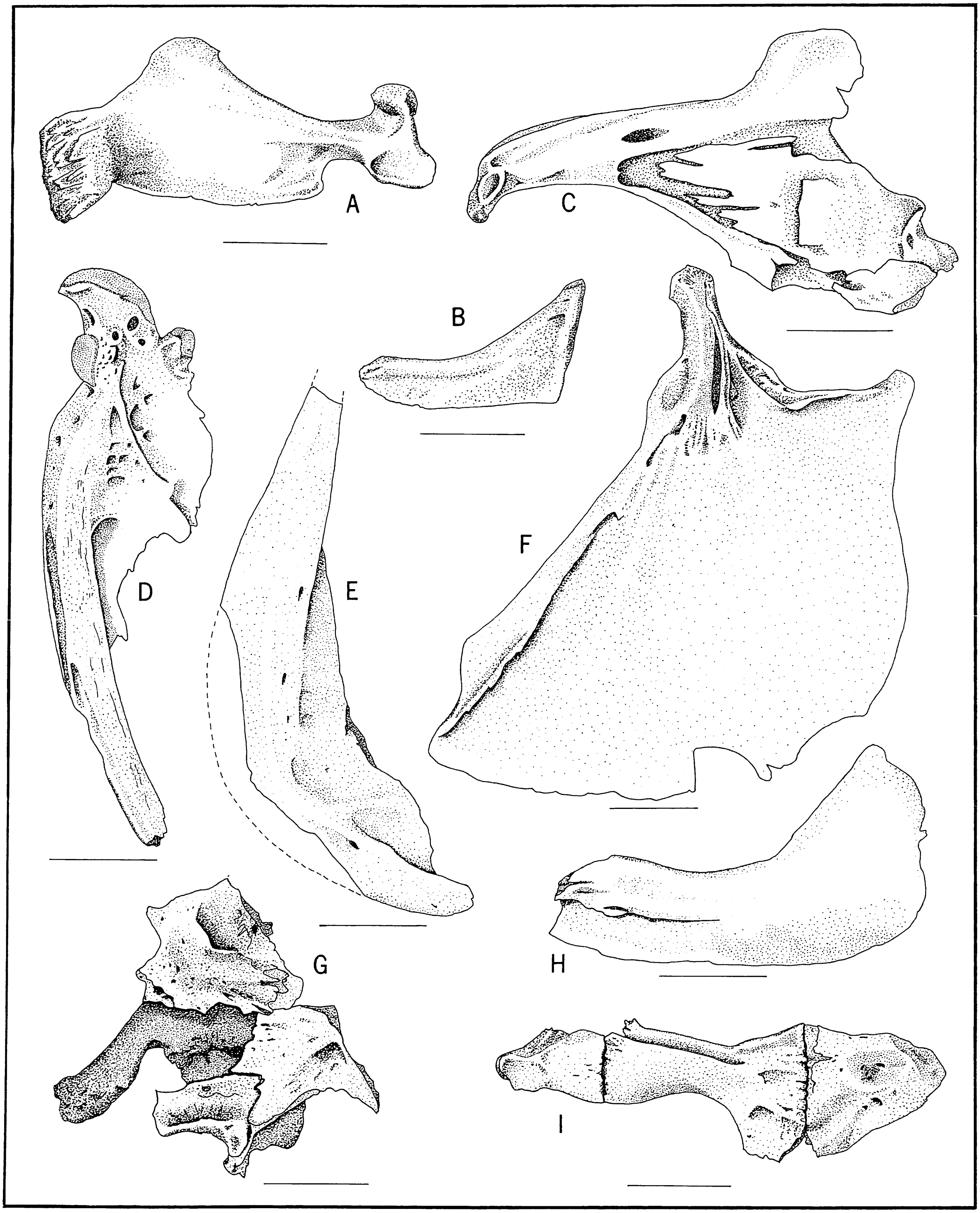
The fossils are readily identified as coregonines by the toothless maxillae and dentaries, the globose dorsal process of the maxillae, the high coronoid process and the horizontal posterior process of the articular-angular, the complete contact of the left and right parietals, the postparietal bridge, the relatively smooth, anteriorly pointed frontals with radiating acoustico-lateralis canals, the perforate ceratohyal, the extreme development of the adductor ridge on the hyomandibular, the intercalar not contacting the prootic, and the relatively unmodified first vertebra.

Although the maxillae are slender and elongate, as in ciscoes of the genus *Coregonus*, the fossils can be identified as *Prosopium* on the basis of the well-developed posttemporal fossa, the strong ridge at the posterolateral edge of the exoccipital, the relatively straight parasphenoid, the shorter and more truncate anterior (gnathal) edge of the dentary, the less expanded posterior part of the coronoid process of the dentary, the high coronoid angle of the articular-angular (50-60 degrees), and the more dorsal and less median direction of the dorsal process of the maxilla.

Within the genus *Prosopium* there are six species, four with short, deep, lunate maxillae and two with elongate maxillae. The Glenns Ferry fossils are variable, but all maxillae are at least as long and slender as the extreme living species, *P. gemmiferum* (Snyder) and *P. coulteri* (Eigenmann and Eigenmann). The four species with short maxillae [*P. cylindraceum* (Snyder), *P. williamsoni* (Girard), *P. spilonotus* (Snyder), and *P. abyssicola* (Snyder)] also have distinctly higher coronoid processes on the articular-angular, similar to that in the fossils. The fossils have a long, slender coronoid process on the dentary, as in *P. gemmiferum* and *P. coulteri*, but more extreme. The hyomandibular possesses a large, arcuate adductor ridge. The angle of the anterior border relative to the dorsal articulating border of the hyomandibular is less than 120 degrees in the fossils and the two long-jawed species, and greater than 120 degrees in the other four species.

Although the dentaries, the articular-angulars, and

Figure 7. *Prosopium prolixus*: (A-E) Variability in maxillae (UMMP 59535, 62068, 57990, 58432, 62068), mesial views. (F) Right frontal, UMMP 58279. (G) Right pterotic, UMMP 62068, dorsal and lateral views. (H) Basioccipital and right exoccipital, UMMP 62068, ventrolateral view. (I) Left articular-angular, part, UMMP 55041, lateral view. (J) Left dentary, UMMP 59300, lateral view. (K) Right dentary, part, UMMP 50385, lateral view. (L) Right articular-angular, UMMP 62068, lateral view. Scales equal 1 cm.


A
C
B
D
E
F
G
H
I

especially the maxillae show variations that might represent several species, the different phenotypes are limited to a range similar to that shown within the two subgroups mentioned above. Larger samples of complete maxillae will be necessary to establish a basis for identifying more than one species; therefore only one new name is proposed at this time. If new species are to be recognized later, the maxillae will probably be the most diagnostic bones; therefore a maxilla serves as the basis for identifying this species. The name refers to the elongation of the maxilla.

Prosopium prolixus new species

(Figs. 2A, 7)

Diagnosis.– A species of *Prosopium* with the maxilla four to five times longer than its maximum depth; the dentary truncate anteriorly and with a long, slender coronoid process; a high coronoid process with its posterodorsal border forming an angle of 50-60 degrees with the longitudinal axis of the bone; and the dorsal (articulating) and anterior borders of the hyomandibular forming an angle of less than 120 degrees.

Description of the Holotype.– The holotype is a complete left maxilla collected from fine sands of the Glenns Ferry Formation in NW¼, Sec. 12, T. 4 S, R. 1 W (Oreana Quadrangle), Owyhee County, Idaho, at an elevation of 2900 ft (884 m), by G.R. Smith et al., June 5, 1974. The bone is 33.2 mm in length, 8.0 mm in maximum depth, 12.7 mm in maximum standing depth (from the ventral margin to a line between anterior and posterior dorsal tips of the bone), 3.6 mm in minimum depth at the neck of the bone posterior to the dorsal process, and 4.6 mm in maximum width of the dorsal process. Viewed dorsally, the dorsal process forms an angle of 100 degrees with the axis of the neck of the bone; its shape is a spheroid, elongated mesially. Viewed laterally, it extends anterodorsally at an angle of 120-130 degrees from the axis of the neck of the bone. The maximum thickness is 1.0 mm near the center and 2.0 mm at the neck. The dorsal border is concave over a distance of 19 mm anterior to the posterior tip. The concavity probably conforms approximately to the shape and size of the supramaxilla. In the area of attachment of the premaxilla there is a well-developed premaxillary cotyla postventral to the two-lobed, anteroventral, premaxillary process. An emargination of the ventral contour extends 8 mm posteriorly from the premaxillary cotyla. A distinct ridge appears on the mesial edge of this margin. A strong, low-profile ridge arches (concave up) from just behind the premaxillary cotyla to the posterodorsal point of the bone.

Additional Material.– The Glenns Ferry material includes 43 additional maxillae, nine of which are complete, ranging in length from 13-54 mm (UMMP 58271, 58275, 58277, 58278, 58428, 58434, 58816, 58991, 59383, 59424, 59535, 59537, 62030, 62068). They resemble the holotype except for variations in the curvature of the margins, the length of areas for association with the supramaxillae and premaxillae, the angle of the dorsal process, and proportional details of the premaxillary cotyla and premaxillary process. UMMP 59537 from a sand horizon in the Glenns Ferry Formation at Crayfish Hill, SW¼, Sec. 1, T. 4 S, R. 1 W (Oreana Quadrangle), Owyhee County, Idaho, is similar enough to the holotype to be designated a paratype. It is 31.9 mm in maximum length, 6.7 mm in maximum depth, and 11.0 mm in maximum standing depth.

More than 200 dentaries, 18 of them complete, have been collected. They show less variation than the maxillae and less indication of multiple species. The largest complete dentary (59424) is 42 mm long through the coronoid axis and 56 mm long through the ventral axis. The gnathal ridge is 12.2 mm long. The anterior end is 7.4 mm deep and truncate. The coronoid process is 24 mm long from the inner fork, 4.2 mm in minimal depth (midway along its length), and 6.9 mm in maximal depth (posterior end). The acoustico-lateralis system is represented by four or five pores along the lateral and mesial faces of the ventral ala; the lateral pores may appear as elongate grooves. A mental foramen appears mesial to the gnathal ridge and externally under the posterior part of the gnathal ridge. Large specimens are numerous, the largest dentaries being 10-12 mm deep anteriorly. These specimens are at least 60% larger than those of a *Stenodus* 700 mm in total length, indicating not only large jaws and probably predaceous habits, but also exceptionally large size for coregonines in general.

More than 50 articular-angulars have been collected from the same localities as the holotype, paratype, and other material. The most distinctive feature of these bones is the high coronoid angle, 60-65 degrees above the horizontal axis of the bone. Like the other bone, the largest specimens are at least 60% larger than a *Stenodus* more than 700 mm in total length.

Other disarticulated bones include skull bones (Fig. 7), urohyals (which are long and slender), opercles (which are rather quadrate in form), ceratohyals (which are pierced by a dorsal foramen), and parasphenoids (which are longitudinally and transversely rounded ventrally).

Figure 8. *Chasmistes spatulifer* associated specimen, UMMP 59581. (A-C) Mesial views of jaw bones: (A) Left maxilla. (B) Left premaxilla. (C) Right dentary. (D) Left hyomandibular, posterior view. (E,F,H) Lateral views of opercular bones: (E) Right preopercle. (F) Left opercle. (H) Left interopercle. (G) Left posterior corner of cranium: pterotic, epiotic, and fragment of parietal. (I) Left hyoid series (basihyal, ceratohyal, epihyal), lateral view. Scales equal 1 cm.

An incomplete skull and associated parts (UMMP 53715) from the Glenns Ferry Formation at the Hagerman locality, NE¼, Sec. 32, T. 7 S, R. 13 E, Twin Falls County, Idaho, was collected by C.W. Hibbard et al., in June, 1965. The specimen includes the skull roofing bones and otic bones of the neurocranium. The frontals are each about 15 mm wide posteriorly, the parietals about 11 mm wide anteriorly, the postparietal bridge was 17-20 mm wide. The five anterior vertebrae are 16-16.5 mm in transverse diameter. Although the specimen is distorted, the characters of *Prosopium* are clear, as mentioned above. Comparison of the measurements with those of Recent specimens of *Prosopium williamsoni* indicates that the specimen was about 430-440 mm in total length. If these assumptions of proportions are correct, then the largest frontals in the collection are from fish about 700 mm long. This may be a closer estimate of maximum size than those based on jaw bones because it is likely that the species had disproportionately large jaws, but not as likely that it had a disproportionate skull roof. The largest frontals are the same size as those of a *Stenodus* 700 mm long. There are only about 50 frontals in the sample, however.

The size of the fish and the proportional size of its jaws are interesting from the paleoecological viewpoint. It may be that *Prosopium prolixus* was the largest, most predaceous, known coregonine – it was certainly the largest, most predaceous, known *Prosopium*. It is especially interesting that this species was sympatric with, and probably more common than, a planktivorous species of *Oncorhynchus*.

Unidentified Salmonines

Additional troutlike fishes are represented in the fauna at the Horse Hill locality by an incomplete maxilla (UMMP 62108, Fig. 4D), a dentary (UMMP 62109, Fig. 6B), and a group of associated bones including a premaxilla (UMMP 62005, Fig. 4F). The maxilla from the left side is 38.2 mm long, with 19 sockets for very small teeth, only 0.7-1.0 mm in diameter. It is too laterally compressed to be that of an *Oncorhynchus* or a *Rhabdofario.* The bone is 6.5-7.0 mm deep throughout its length (the anterior part of the bone is missing), the tooth-bearing edge is 1.5 mm thick, and the maximum thickness of the bone at the last tooth is 1.5 mm. The median keel is triangular in cross section and well developed, giving the bone a maximum thickness of 3.6 mm. The depth, width, proportions of the tooth-bearing and median ridges, and the pattern of striations on the bone are similar to maxillae of *Salmo clarki* from the Middle Fork of the Boise River (UMMZ 191615). The primary difference is the small size of the teeth. In addition, the lateral surface of the fossil is convex ventrally and concave dorsally, in transverse section, with a slight tendency for the dorsal edge to be tilted into a sharp dorsolateral keel except anteriorly and posteriorly. Because the anterior end is missing, the bone does not provide an adequate basis for the description of a new species or for confident placement in a known species or genus.

The dentary is not only unlike any others in the fauna, it is unlike that of any other North American salmonid. It is the anterior end of a right dentary, 14.7 mm long, about 9 mm in maximum depth, 6.7 mm in depth at the anterior end, 3.3 mm in maximum width, with seven tooth sockets 2.0 mm in maximum diameter. The outline of the bone is truncate in lateral aspect – the dorsal, ventral, and anterior margins are relatively straight. The lateral surface is smoother than in *Oncorhynchus, Rhabdofario,* or *Salmo*, with the acoustico-lateralis canal along the ventral margin and with four pores about one-third of the depth below the dorsal edge. The dorsal edge of the bone contains numerous pores anterior and lateral to the tooth sockets. The tooth sockets are well below the dorsolateral edge of the bone yet attached to it well above the median platform. The median platform is connected to the ventral edge of the bone by a smooth, convex or flat surface lacking the midventral groove, which is the anterior extension of the Meckelian fossa. In all other American salmonids, this surface is concave in cross section – the groove below the edge of the platform leaves it standing as a longitudinal median ridge. The dentary is remarkably similar in all of the above features to a specimen (UMMZ 187613) of *Hucho perryi* from Japan. The similarity suggests the occurrence of *Hucho* in the Pliocene of North America, but it is possible that the above characters were shared by Pliocene members of the *Salmo* or *Salvelinus* lineage.

The third sample bearing on this problem consists of a group of associated articular-angulars, dentary, premaxilla, posttemporal, epiotic, exoccipital, preopercle, hyomandibular, quadrate, and other fragments (UMMP 62005). The specimen was about one m long. The bones represent a distinct species characterized by a distinctive premaxilla (Fig. 4F), a high (ca. 50 degrees) coronoid angle on the articular-angulars, a horizontal keel on the hyomandibular, and other characteristics. The species is better represented by material collected by Peter Kimmel and G.R. Smith from the Deer Butte Formation in Oregon, and is described in a separate paper (this volume). Characters of *Hucho, Salvelinus,* and *Salmo* are shared by the fossil.

It appears possible that the three sets of material mentioned here belong to the same taxon. The diverse size of the specimens and the fragmentary nature of the material does not allow a confident conclusion. In any case there was an unusual diversity of salmonids in the habitat that is represented by the Glenns Ferry sands at Horse Hill. The fauna includes *Rhabdofario*, the unassigned species sharing *Hucho* characters, and at least one species each of *Oncorhynchus* and *Prosopium.* Channel gravels associated with the fossil-bearing sands and the proximity of a nearby limestone algae reef suggest the possibility of diverse habitat.

Family **Catostomidae**

The suckers of the cypriniform family Catostomidae are the most abundant fishes in the Glenns Ferry Formation. They are the second most diverse family, with six or more species. In 1883 Cope named two species of *Catostomus* from "Pleistocene" beds of Lake Idaho in southwest Idaho, *C. cristatus* and *C. shoshonensis*, on the basis of incomplete neurocrania. In 1967 Miller and Smith recognized two species of suckers apparently related to *Catostomus (Deltistes) luxatus*, on the basis of maxillae, and named them *D. owyhee* and *D. ellipticus.* Evidence will be cited below for recognizing *Catostomus shoshonensis, C. cristatus,* and *C. owyhee* as separate species, although they are difficult to diagnose completely. *Catostomus ellipticus* is synonymized with *C. shoshonensis.* Miller and Smith (1967) also named *Chasmistes spatulifer*, a long-jawed, terminal-mouthed, pelagic planktivore, and *Catostomus (Pantosteus) arenatus*, a presumed fluviatile species.

Diagnosis of the two genera of catostomids in the fauna is relatively straightforward. They are members of the subfamily Catostominae on the basis of the restricted posttemporal openings, expanded frontals, and the absence of supraorbital bones. They are members of the tribe Catostomini on the basis of the combination of the broad dorsal laminae of the pterotics and epiotics with posterior processes, in the dermal part of the skull roof. *Chasmistes* is recognizable by the elongate, slender jaw bones and short, wide skull. The pterotics have extensive anterior and posterior dermal roofing laminae over the adjacent portions of the temporal and posttemporal fossae.

Catostomus may be diagnosed from *Chasmistes* as follows: The maxillae are shorter and deeper with more posteriad direction of the premaxillary processes. The gnathal rami of the dentaries are shorter and broader with a more horizontal symphysis. There are several arrangements of the labial grooves, but their position is usually at the outer edge of the gnathal rami in *Catostomus* and dorsal in *Chasmistes.* The premaxillae are at least as high as they are wide. The skulls are longer and narrower. The dermethmoid varies from subquadrate to longer than wide. In the Glenns Ferry *Catostomus*, the pterotics have less extensive development of horizontal roofing laminae over the anterior part of the posttemporal fossae.

Genus *Chasmistes* Jordan

Chasmistes spatulifer Miller and Smith

(Figs. 8, 9B)

Chasmistes, Miller, 1965:576. Taylor, 1966:74.

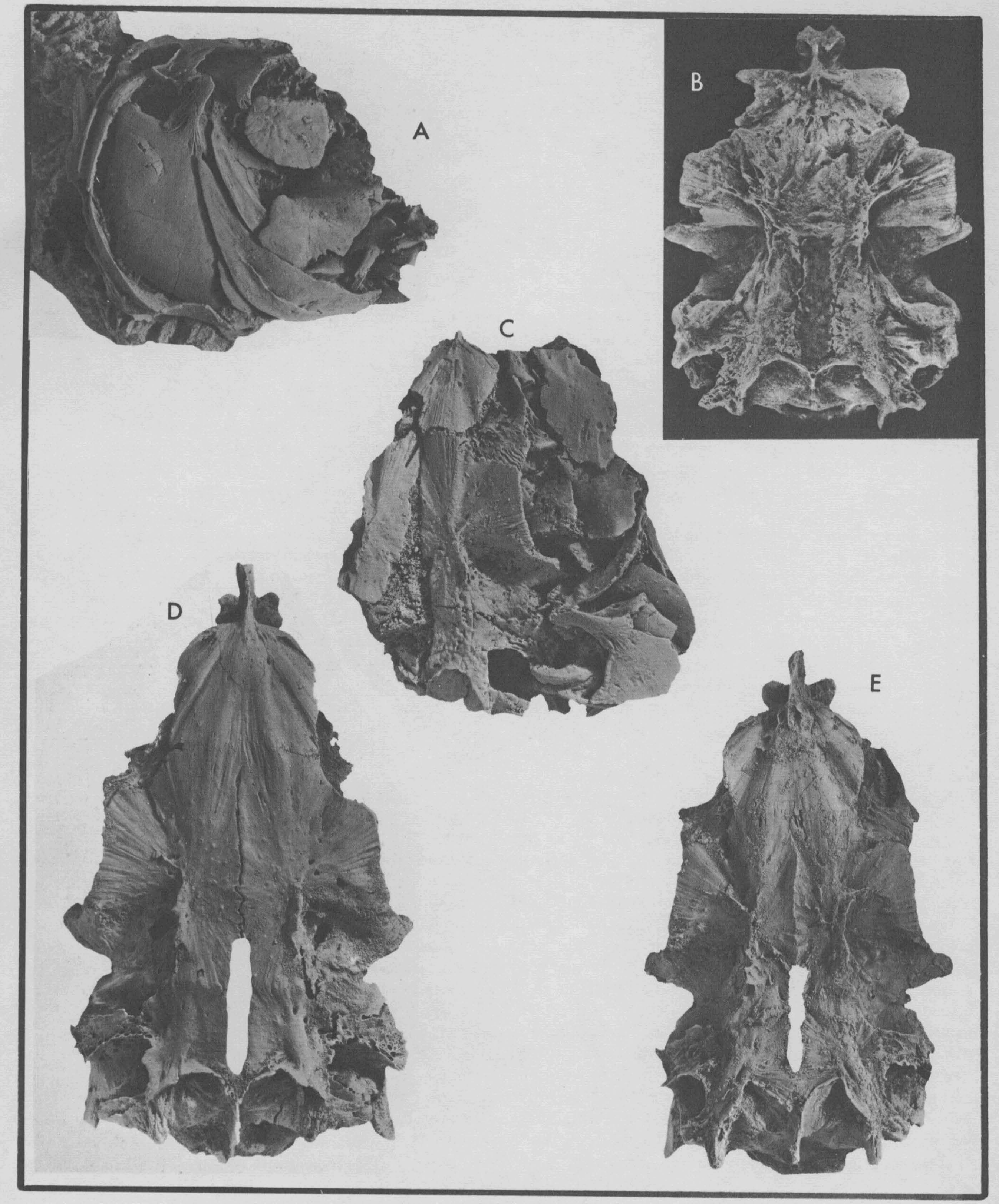
Chasmistes spatulifer Miller and Smith 1967:11, Fig. 4 (type, UMMP 55556, right maxilla).

Taxonomy.– *Chasmistes spatulifer* is a common and easily recognized member of the fauna. Discovery of associated skull bones and inference from recent characters of the genus have enabled identification of skull elements of this species, originally known only from the maxilla. A broad range of variation exists in this material. It is treated here as one variable species but may later prove to be a common, large-jawed species and a less common, short-jawed species similar to *Chasmistes batrachops* Cope.

Diagnosis.– A catostomid assigned to *Chasmistes* on the basis of the wide, short skull, with dermethmoid distinctly broader than long; premaxilla wider than high; the premaxillary process of the maxilla extending at an acute anteroventral angle from the primary plane of the bone; and the dentary with characters indicative of a terminal mouth (a long, slender gnathic ramus bearing a relatively long dorsolateral groove for the labial cartilage and a relatively vertical symphysis). The species is distinct from other *Chasmistes* in the extreme nature of some of the above characters: the dermethmoid is at least twice as broad as long (excluding the anterior process); the maxilla has a long, slender neck; the premaxillary process extends at an angle of no more than 60 degrees from the anterior axis of the maxilla; length of the gnathal ramus is more than three times the depth of the symphysis, which is nearly normal to the axis of the gnathal ramus.

Description.– The type specimen is a right maxilla, 25.6 mm in maximum length, 9.5 mm in depth, with a least depth of 2.6 mm through the neck, and with characteristics as given in the diagnosis. The premaxillary process is spatulate and extends anteroventrally from a long neck. The ventral keel is low but anteriorly abrupt; the dorsal keel is posterior with a gradual anterior slope. The crest for the palatine ligament is elongate and gradually curves upward from the axis of the neck onto the anterodorsal process (compare Fig. 8A). The dentary process is variable.

Based on other material, the premaxilla has a short ascending process and a long lateral (labial) process up to twice the length of the ascending process (Fig. 8B). The dentary is elongate, with a slender gnathal ramus, which is not abruptly deflected ventrally (Fig. 8C). The species clearly had a large terminal mouth. The symphysis, in contrast to that in other catostomines, is nearly vertical (normal to the axis of the gnathal ramus) in correlation


A
B
C
D
E

with the lack of ventral deflection and the terminal mouth. The labial groove is dorsolateral and extends to the base of the coronoid process. The coronoid process is much closer to the articulation of the mandible with the quadrate than to the symphysis of the dentaries.

The hyomandibular is long, slender, and relatively straight (Fig. 8D). There is a prominent boss just anterior to the opercular condyle on the posteromesial side and a posterior groove below the opercular condyle. The preopercle is long and slender, especially dorsally (Fig. 8E). The opercle is deep but relatively short between the dorsal processes (Fig. 8F). The interopercle is short, deep, and expanded posterodorsally (Fig. 8H). It has a long, deep anterolateral groove. The hyomandibular and opercular series indicate a short-headed, deep-bodied shape.

The skull is short, broad, and dorsally flat. UMMP 58210 (Fig. 9B) is 57.3 mm long from the tip of the anterior process of the dermethmoid to the base of the posterior process of the supraoccipital. The dermethmoid is 30.5 mm wide but only 11-12 mm long (excluding the anterior process). The frontals are 27 mm long and 25 mm wide. The frontal (temporal) crests are 17 mm apart at the anterior end of the frontoparietal fontanelle, which is 21 mm long and 6 mm wide. Between the outer edges of the sphenotics the maximum width is 55 mm; the minimum width is 37.6 mm. The parietals are 18.5 mm long (maximum) and 12-14 mm wide from the fontanelle to the pterotic border. The pterotics have an extensive dorsal horizontal lamina, 10-11 mm long (between the temporal and posttemporal fossae) and 10-11 mm wide from the parietal to the dorsolateral edge. The epiotic has prominent lateral and posterior processes.

The temporal, posttemporal, and subtemporal fossae are deep. The skull is deep; the depth from the dorsal surface to the ventral point on the parasphenoid is 28 mm. The anterior part of the parasphenoid and the adjacent vomer are not arched or concave ventrally, though the anterior processes of the vomer are ventrally deflected. They are anteroventral to the anterior process of the dermethmoid.

The hyoid series is typical for catostomines (Fig. 8I). The urohyal is more elongate than in *Catostomus* or other *Chasmistes.*

In the characteristics that differentiate the Recent species of *Chasmistes* from *Catostomus* – those of the jaws and skull roof – *Chasmistes spatulifer* is the most specialized and advanced. It is approached in the degree of specialization only by *Chasmistes cujus* of the Lahontan Basin.

Genus *Catostomus* Lesueur

Two or three subgenera of *Catostomus* may be represented in the Glenns Ferry Formation. The subgenus *Pantosteus* may be recognized by the extremely short gnathic ramus of the dentary, the short, robust maxillae with extreme development of crests for origin of the palatine ligament and the maxillaris dorsalis muscle, and the extreme posteriad direction of the premaxillary process (Smith, 1965). It is represented only by the relatively rare *Catostomus arenatus.*

The subgenus *Deltistes* is characterized by dentaries broad at the symphysis, maxillae with deep ventral crests for attachment of the maxillaris dorsalis muscle, and the metapterygoid with a ventrally directed symplectic process and a prominent dorsolateral crest. Included in the group are *C. owyhee* and (apparently) *C. shoshonensis* from the Glenns Ferry Formation and *C. luxatus* from the Recent fauna of Klamath Lake (Figs. 9, 11). As indicated below, however, the constancy of characters and allocation of species in this group are still uncertain.

The subgenus *Catostomus* (Fig. 10) is represented by fossils of *Catostomus macrocheilus* in the Pleistocene Grandview local fauna at Jackass Butte and by maxillae and associated bones of *Catostomus cristatus* from the Pliocene Glenns Ferry deposits. The Idaho species may be characterized by narrow symphyseal ends of the dentaries, shallow (low-angled) ventral crests on the maxillae, and metapterygoids with the symplectic processes directed anteroventrally (more or less parallel to the limbs of the hyomandibulars) and with weak dorsolateral crests. Skull proportions are intermediate between *Chasmistes* and *Deltistes*, although much closer to *Deltistes.* The relationships of the subgenus *Catostomus* are discussed in Smith and Koehn (1969).

The identifications and taxonomic conclusion presented here are based on the study of variations of maxillae, dentaries, neurocrania, and other skull bones. Statistical analyses of morphological variation have been used to supplement sorting of bones into categories. Correlation analysis of frequency distributions of the "species" of maxillae and dentaries, in addition to the rare co-occurrence of associated skull bones of relatively nontransported fossils, have aided in the partial matching of the maxillae, dentaries, neurocrania, and other bones. This has been the most difficult part of the study, and the conclusions are incomplete. An unusual amount of variation is seen in some of the recognized taxa. Some of this can be sorted into stratigraphically meaningful trends. Some, however, might be due to the presence of taxa still not recognized.

Figure 9. Skulls and neurocrania of Glenns Ferry Catostomidae. (A,C,E): *Catostomus shoshonensis* (UMMP 59190, 59606, 59605). (B) *Chasmistes spatulifer*, UMMP 58210. (D) *Catostomus cristatus?*, UMMP 62400. Actual size.


A
B
C
D
F
G
E

The following discussion will outline the morphological relationships found among the neurocrania, including the type specimens of the two *Catostomus* described by Cope (1883). Following the discussion of the neurocrania, the maxillae and dentaries will be discussed in relation to the nomenclature based on other bones. Tentative species accounts conclude the section.

Catostomus cristatus and *C. shoshonensis* were described by Cope (1883) on the basis of two fragments of neurocrania that display different arrangements of the contact between the parietal, frontal, and pterotic in the area of origin of the temporal muscles (*m. dilator operculi*). In *C. shoshonensis* (holotype, AMNH 2761) the posterolateral corner of the frontal is extended posterolaterally to reach the pterotic, thereby excluding the parietal from the origin of the *m. dilator operculi* (e.g., Fig. 9A,C,E). The type of *C. cristatus* (AMNH 2740), though only a fragment, shows an incomplete contact between the frontal and pterotic. Rather, the parietal extends farther forward to contact the sphenotic, thus separating the frontal and pterotic. The frontal is expanded anteriorly, not posterolaterally, and forms a relatively vertical temporal wall with the parietal for the origin of the *m. dilator operculi* (e.g., Fig. 9D, 10). Most of the skulls collected so far fall readily into one or the other of these two skull types. Several skulls are so similar to one of the types that they can be regarded as clearly conspecific and can be used to augment the species description. However, it is also apparent, on the basis of additional characters, that more than two taxa are represented in the sample.

The third species in this complex is represented by UMMP 57984, a neurocranium and associated bones (Fig. 11D-F) with more extreme involvement of the parietal in the origin of the *m. dilator operculi.* The parietal broadly separates the frontal and pterotic. The skull is remarkably elongate, especially anteriorly. The dermethmoid is considerably longer than wide. The frontals are elongate anteriorly. The above combination of characters is represented in several neurocrania and associated bones from the Glenns Ferry Formation. In particular, UMMP 58192 (Fig. 11B,C) shows the elongate dermethmoid and an associated dentary with a wide, flat, gnathal ramus, which is concave ventrally. This distinctive dentary type has been collected in association with maxillae referable to *C. owyhee* (UMMP 62200). UMMP 57984 and several other specimens (UMMP 58204, 58209, 58211) share additional important taxonomic characters, especially small openings for the tripus in the Weberian apparatus (Fig. 11F,G) and an anteriorly curved hyomandibular (Fig. 10E) (resulting in a more convex lateral border of the bone).

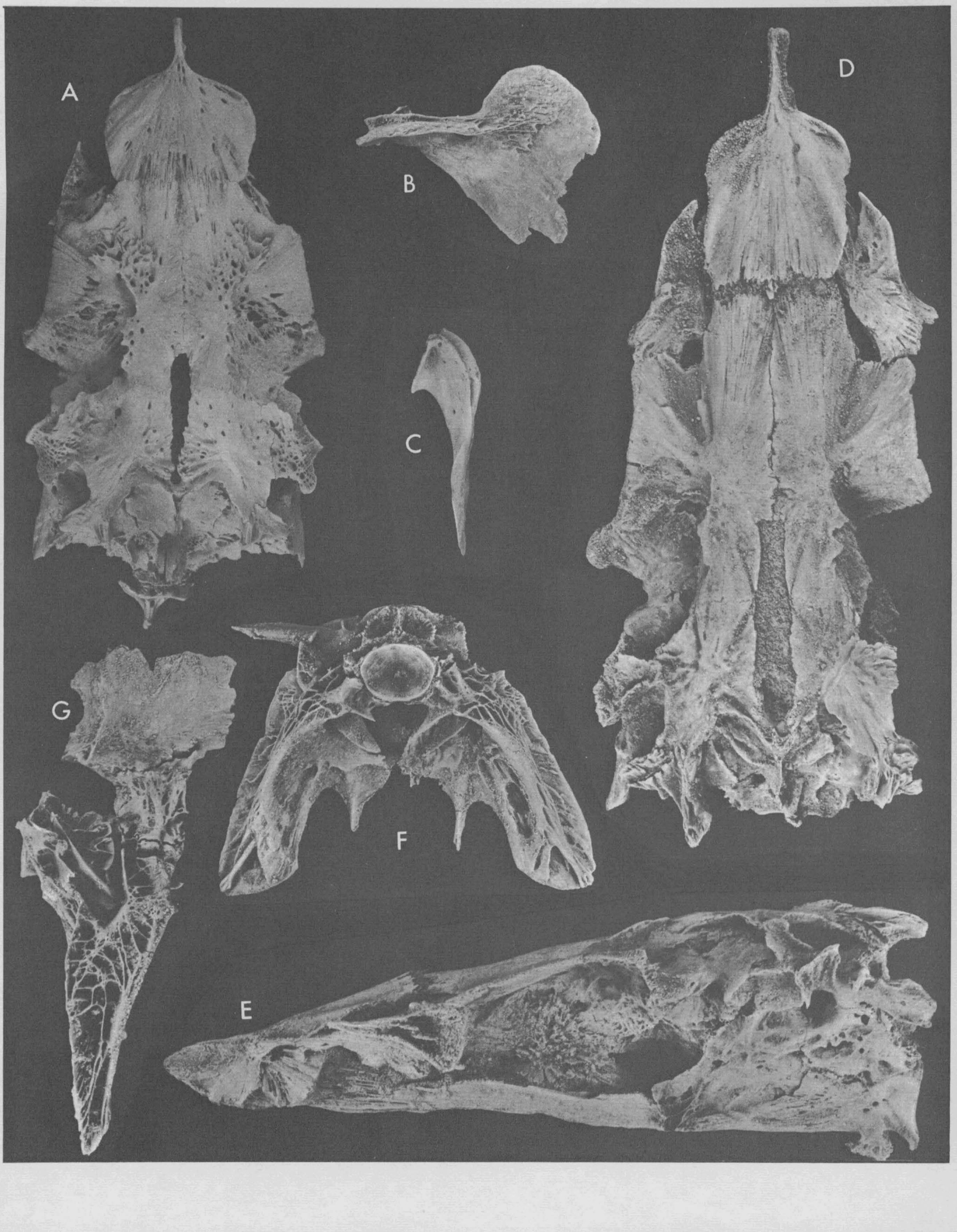
The above observations indicate that if the frontal-parietal-pterotic characters are taxonomically consistent, then *C. shoshonensis* and *C. owyhee* are very distinct species, while *C. cristatus* is intermediate, at least in the characters of the temporal region. Further information on *C. cristatus* is available through UMMP 55202, a skull and associated bones (Fig. 10A-D), which show similarity to the type of *C. cristatus* in the arrangement of the frontal, parietal, and pterotic bones. Additional characteristics of 55202 include large openings for the tripus in the Weberian apparatus, a relatively straight hyomandibular (Fig. 10D), and a distinctive metapterygoid in which the symplectic process is directed anteroventrally, more parallel to the axis of the stem of the hyomandibular compared to the more ventrally directed symplectic process on the metapterygoid of *C. owyhee.* An anterior fragment of a maxilla on 55202 (Fig. 10C) is essentially like that of *C. ellipticus.* It is definitely not *C. owyhee*, but it lacks sufficient characters to confidently distinguish it from the other forms of *C. ellipticus-C. shoshonensis* maxillae. (See below).

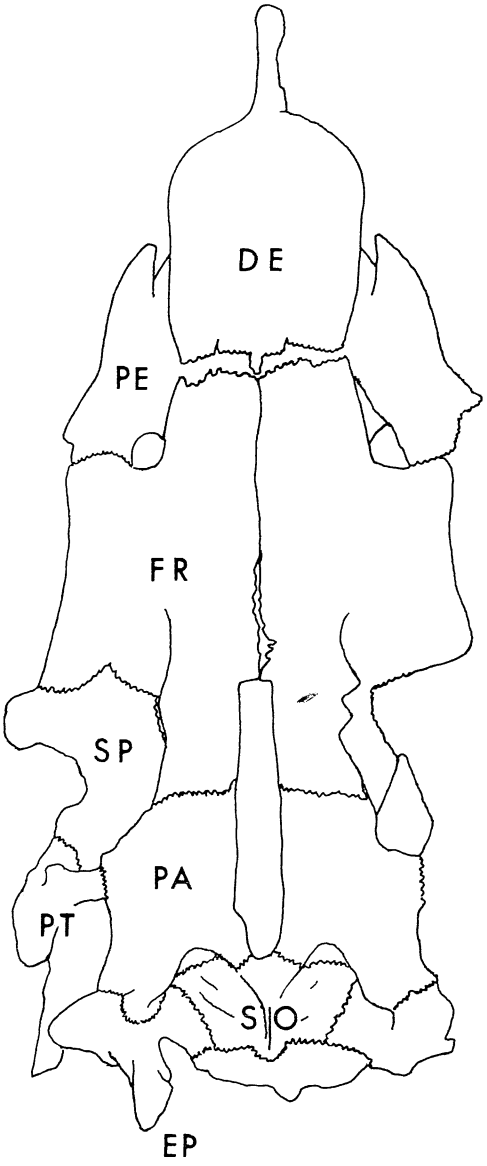
If UMMP 55202 represents *C. cristatus* Cope and UMMP 57984 represents *C. owyhee* (Miller and Smith) as indicated above, it is probable that these species are quite distinct (compare Fig. 10 with Fig. 11). The characteristics described above hold true for rather small sample sizes so far studied in the fragmentary material that is available at this time.

Most of the skulls available in the fauna are similar to the type specimen of *C. shoshonensis.* A partial skull (UMMP 59606, Fig. 9C) from Crayfish Hill is identical to the type of *C. shoshonensis* and shows several additional important characteristics. The specimen has a deep pharyngeal arch, like those found in the sucker genera *Ictiobus* and *Carpiodes* and unlike the pharyngeals in any other known catostomine sucker. (The pharyngeals of *C. owyhee* and *C. cristatus* are unknown, but "normal" catostomine pharyngeals are common in the fauna.) The specimen also shows a dermethmoid just slightly longer than wide and an arched hyomandibular.

The above interpretations are based on good but limited material, but several problems remain unsolved and suggest that parts of the interpretation may be faulty. The first problem is a small skull (UMMP 59190, Fig. 9A), which shows the typical *shoshonensis* characters of the posterior part of the neurocranium but has an intermediate catostomine pharyngeal arch (not deep), a rather straight hyomandibular, and relatively large openings for the tripus in the Weberian apparatus. The simplest

Figure 10. (A-D) *Catostomus cristatus*, UMMP 55202, lateral and dorsal views of cranium, anterior of left maxilla, and posterior view of left hyomandibular. (E) Left hyomandibular of *Catostomus owyhee*, UMMP 57984, of Fig. 11. (F,G) Right maxilla and neurocranium of *Catostomus macrocheilus* (R., Cultus L., British Columbia, UMMZ 181694). Actual size.


A
B
C
D
G
F
E



Neurocranium of *Catostomus owyhee*, Fig. 11, facing page: DE - dermethmoid, PE - parethmoid, FR - frontal, SP - sphenotic, PA - parietal, PT - pterotic, EP - epiotic, SO - supraoccipital.

explanation is that the specimen is a young *shoshonensis* and the discrepancies are ontogenetic. It is possible, however, that the temporal characters of this skull are subject to ontogenetic or other variation, and that *cristatus* and *shoshonensis* are not different species. UMMP 62400 (Fig. 9D) is also intermediate. If there are three species, as suggested above, there is still no incontrovertable evidence to enable complete discrimination of the skulls or maxillae of *cristatus* and *shoshonensis* and the allocation of *ellipticus* to the synonomy of one or the other. A detailed study of the maxillae therefore follows.

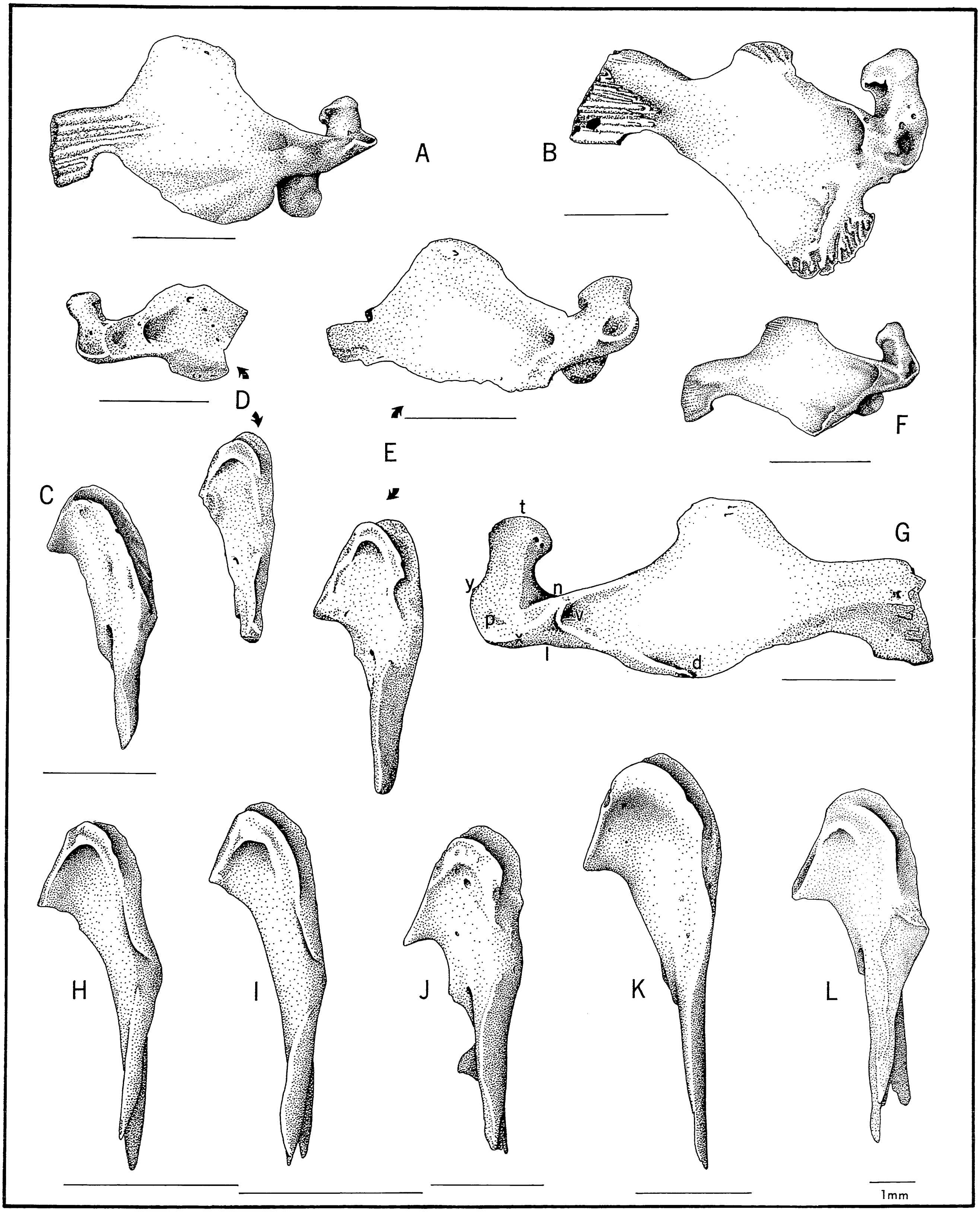
Miller and Smith (1967) found that catostomid maxillae are diagnostic to species, in addition to being abundant as fossils. They therefore used maxillae as holotypes. Since that time more than 1000 *Catostomus* maxillae have been collected from Glenns Ferry sediments. The sample shows a number of diverse trends in variation among species, among localities, and within populations. Four species plus intermediates appear to be present.

Principal components analysis (Sneath and Sokal, 1973) was employed as a technique for sorting out trends in variation. The method is a multivariate statistical tool for resolving the patterns of correlation among the characters of a sample of specimens into a smaller number of reference variables. These reference variables become axes for scatter diagrams and summarize the major trends in variation among the specimens. This method has been especially useful for identifying clusters, patterns of variation, and individual specimens in size-graded samples of fishes of uncertain identification (Smith, 1973).

Ten characters were chosen to describe geometrically the positions of diagnostic anatomical features on the anterior lateral face of the maxillae. A sample of 141 specimens was measured. The measurements are in similar units and dimensions, so the principal components were extracted from the between-character covariance matrix. (Programs of the Statistical Research Laboratory were used at the University of Michigan Computing Center.)

A scatter diagram of the 141 maxillae, according to their scores on the first two principal components, reveals two imperfectly distinct clusters (Fig. 13). The specimens identifiable as *Catostomus owyhee* form an elongate cluster that overlaps slightly with the other taxa. Five specimens of *Catostomus arenatus* are among the extremes of the remaining large cluster (the characters that best discriminate this species were not included in this data set). The remaining specimens, *Catostomus shoshonensis* and *C. cristatus*, are not differentiated in this set of axes. The important characters for the first axis are measurements D-P, D-V, V-Y, and V-P (see Fig. 12) in that order. The first axis accounts for 83% of the variance in the covariance matrix. Component II, which accounts for 8%

Figure 11. (A) Neurocranium of *Catostomus luxatus* (R., Klamath L., Oregon, UMMZ 179364). (B,C) Lateral view of left dentary and dorsal view of right dentary of *Catostomus owyhee*, UMMP 58192. (D,E) Dorsal and lateral views of neurocranium of *Catostomus owyhee*, UMMP 57984. (F) Same specimen, posterior view of Weberian apparatus. (G) Lateral view of Weberian apparatus of *Catostomus owyhee*, UMMP 58209. Actual size.


A
B
D
E
F
C
t
y
n
p
v
l
d
G
H
I
J
K
L
1mm

of the variance in the matrix, is most heavily influenced by D-V, V-P, and V-Y. These characters all involve the orientation and positions of the ridges for insertion of the dorsal and ventral maxillaris muscles and the palatine ligament. Other characters contribute to subsequent axes, which were not taxonomically useful.

The cluster of *C. owyhee* is shaped normally for a size-graded sample of measurements of a species of fish (Smith, 1973). The relative integrity of the cluster suggests that a separate species is represented by these maxillae, but that the differentiation in this bone is not quite complete and that some misidentification of juvenile specimens might have occurred. The holotype of *C. owyhee* (UMMP 55549) is the specimen represented at the extreme right of the scatter diagram; small specimens of all species are at the lower left (Fig. 13). The maxillae of *owyhee* are recognizable (Fig. 12) by the dorsal position of the fossa for insertion of the ventral maxillary muscle and the axis of the crest for insertion of the palatine ligament, which is at right angles to the axis of the body of the bone.

The remainder of the points in Figure 13 do not form a normal single-species cluster, nor does the pattern suggest several discrete or modal phenotypes. Nevertheless the breadth of the cluster, plus prior knowledge of the different shapes of maxillae represented, suggests the possibility of more than one species in the complex. Therefore, the 77 specimens believed to represent the *shoshonensis-cristatus* complex were analyzed separately to see if there is an objective basis for recognition of more than one species in the sample. Figure 14 shows the plot of 77 specimens on the new principal components. The specimens thought to represent two species, *C. shoshonensis* and *C. cristatus*, sort into overlapping and rather poorly shaped clusters. The *shoshonensis*-type maxillae are unusually variable. Component I accounts for 76% of the variation but shows no discrimination between the two phenotypes. The observed variance is especially correlated with character D-P, the distance between the insertion of the dorsal maxillary muscle and the crest for the palatine ligament. Characters with lower but significant loadings are those involving the position of insertion of the ventral maxillary muscle. Component II accounts for only 9% of the variance and reflects some discrimination of the two phenotypes, based primarily on two characters that describe the orientation and position of the crest for attachment of the palatine ligament. The two phenotypes being separated in this analysis are illustrated in Fig. 12. It is not known if this division is separating maxillae of two species, but that seems to be the most supportable conclusion at this stage. It is possible that even if two species are represented, many of the intermediate specimens may be misidentified.

The specimens in Fig. 14 have been labelled according to locality to see how much of the variability can be attributed to between-locality (possibly time) differences. The resulting pattern, especially on Component I, is suggestive but not conclusive. Specimens from some of the localities are clustered more or less together, not randomly through the scatter diagram. This suggests differentiation between samples and contains stratigraphic information even in the absence of a firm species interpretation (see species account for *C. shoshonensis*).

The maxillae described as *C. ellipticus* are referred to here as *C. shoshonensis*. They are distinguished by the axis of the crest for insertion of the palatine ligament, which is posteriorly nearly parallel to the axis of the main body of the maxilla and nearly at right angles to the axis of the head of the bone except anteriorly. The dorsal and ventral keels are prominent, giving the body of the bone an elliptical shape in lateral aspect. The fossa for insertion of the ventral maxillary muscle is usually intermediate between the dorsal and ventral borders of the neck. The head of the bone is offset dorsomesiad to the plane of the body of the bone and the dorsal and ventral keels. There is much variability in the shape and pattern of the crest for attachment of the palatine ligament – in extreme forms it is nearly as high as the dorsal edge of the neck (Fig. 12).

The maxillae referred to as *C. cristatus* differ in the axis of the crest for attachment of the palatine ligament. The crest is curved and anteriorly nearly parallel to the anterior edge of the head of this bone; it is never as high on the neck of the bone as in extreme *shoshonensis*. The head is less offset from the plane of the body of the bone. The ventral keel is less developed, and its ridge for insertion of the dorsal maxillary muscle forms a low angle with the axis of the body of the bone. A long-necked, slender maxilla, often with a high head, is the resulting shape. These maxillae appear to attain a much larger maximum

Figure 12. Lateral views of maxillae and dorsal views of dentaries of *Catostomus* from the Glenns Ferry Formation (except H). (A) Maxilla of *C. shoshonensis* ("*ellipticus*" phenotype, UMMP 58124). (B) *C. owyhee*, UMMP 58669. (C) Dentary of *C. cristatus?*, UMMP 58617. (D) Associated maxilla and dentary of *C. shoshonensis?*, UMMP 59589. (E) Associated maxilla and dentary of *C. shoshonensis*, UMMP 62581. (F) *C. owyhee* (juvenile, UMMP 58804). (G) *C. cristatus?*, UMMP 58823. (H) *C. macrocheilus* (R., Cultus L., B.C., UMMZ 181694). (I) *C.* cf. *macrocheilus*, UMMP 58650. (J) *C. shoshonensis*, UMMP 58523. (K) *C. owyhee*, UMMP 58760. (L) *C. arenatus*, UMMP 62028. Scales (except L) equal 1 cm. Letters on (G) indicate measurement points for analysis of maxillae (see text). (d) insertion of dorsal maxillary muscle, (v) insertion of ventral maxillary muscle (names refer to d-v position at origin), (n-l) "neck," (xpy) ridge for insertion of palatine ligament. Ten measurements used to describe sample are: v-p, v-n, v-l, d-p, x-n, y-t, x-y, d-v, v-y, and v-x. Compare pattern of these triangulations on A, B, F, and G.

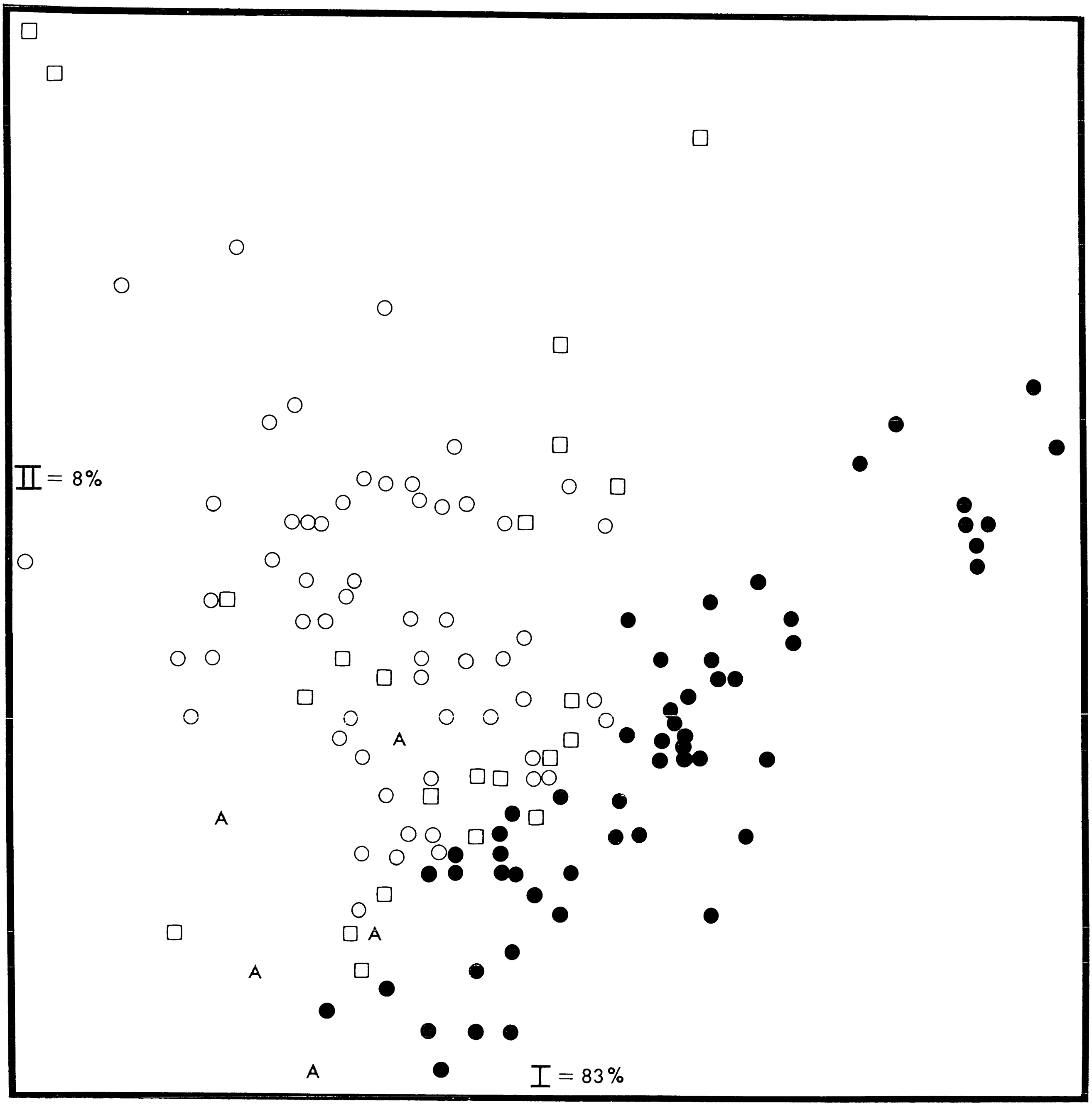


Figure 13. Scatter diagram of principal components scores for 141 specimens of *Catostomus* maxillae. Axes are components I and II, which explain 83+8% of the total variance in an analysis of 10 characters. (●) *C. owyhee*, (○) *C. cristatus?*, (□) *C. shoshonensis*, (A) *C. arenatus.*

size than do those of *C. shoshonensis*. At several localities, including Horse Hill, Dove Springs, and Bennett RR grade, there occur relatively rare maxillae and dentaries of very large size (double the size of maximum *shoshonensis*). The dentaries are characterized by long, straight, dorsal ridges for the labial cartilages (Fig. 12C) and the maxillae fit the description given above for *C. cristatus* (Fig. 12G). This observation and its correlated observation among the skulls is one of the reasons for assigning *C. ellipticus* to the synonymy of *C. shoshonensis*. The data are not strong, however, and the assignment is tentative, subject to test by collection of associated skulls and jaw bones.

There are four or five kinds of dentaries in the fauna that can be assigned to the genus *Catostomus* (Fig. 12C,I, J,K,L). Only one of these (*owyhee*) has been collected in direct association with a skull and maxilla, allowing confident identification. *Catostomus arenatus* is represented by short, angular dentaries. *Catostomus cristatus* (Fig. 12C) grades into a form similar to *C. macrocheilus* (Fig. 12I) at eastern localities and Jackass Butte. This variability in dentaries, taken with evidence for two kinds of skulls and possibly two kinds of maxillae in addition to *C. owyhee*, further suggests that *C. cristatus* and *C. shoshonensis* differ and that one of them is a synonym of *C. ellipticus.* The association of maxillae and dentaries shown in Fig. 12D,E establishes the basis for part of the interpretation. Three sets of associated bones from Poison Creek and two from Fossil Creek support the match of the dentaries characterized by a sigmoid groove for the labial cartilage with maxillae assignable to *C. shoshonensis.* The maxillae are variable and indicate occasional overlap in some of the individual characters separating *cristatus* and *shoshonensis.*

In summary, four species of *Catostomus* may be tentatively recognized, but the correct association of bones and the species limits of the *cristatus-shoshonensis-(ellipticus)* group needs more research. The solution to this problem has stratigraphic and evolutionary implications. The species accounts that follow are not definitive, but provide the basis for further work.

Catostomus shoshonensis Cope

(Figs. 9A,C,E; 12A,D,E,J)

Catostomus shoshonensis Cope 1883:159 (type, AMNH 2761, neurocranium). Uyeno and Miller, 1963:8. Taylor, 1966:74. Miller and Smith, 1967:22.

Catostomus reddingi, Cope 1883:160. (*Nomen nudum* erroneously used for *Catostomus shoshonensis* in the description of *Catostomus cristatus.*) Hussakof, 1908: 66 and Fig. 34).

Deltistes, Miller, 1965:574, 576. Taylor, 1966:74.

Deltistes ellipticus Miller and Smith 1967:10, Fig. 4 (type, UMMP 55554, right maxilla).

Taxonomy.— In 1883 Cope described the first catostomids from the Glenns Ferry Formation. Some confusion in the literature originated when he apparently substituted the name *shoshonensis* for material he had intended to name *C. reddingi.* In so doing he neglected to change the museum label or the reference to the specimen in the description of *C. cristatus* (on the next page – Cope, 1883:160). Thus, Hussakof (1908:66 and Fig. 34) refers to the "undescribed" "*C. reddingi,*" while the type of *C. shoshonensis* was supposedly unknown. However, the description and measurements of *C. shoshonensis* (Cope 1883:159, 160) clearly refer to AMNH 2761, a neurocranium 75 mm long, labelled as the type of "*Catostomus reddingi* Cope."

On the basis of numerous points of similarity, some possibly involving derived characters, this species is considered close to *C. luxatus*, type species of the subgenus *Deltistes.*

Diagnosis.— A *Catostomus* with the frontal and pterotic usually in contact; parietal quadrate in shape (not extended anteriorly), without temporal crests or area for origin of temporal muscles; fontanelle narrow; parasphenoid strongly arched. Based on bones other than the type specimen, the diagnosis may be expanded as follows: ventral limb of hyomandibular strongly curved anteriorly; metapterygoid with a ventrally directed symplectic process; pharyngeal arch deeper than in any other catostomine; maxilla with strong dorsal and ventral keels, ridge for palatine ligament high on the neck of the bone and parallel to the axis of the bone, and fossa for insertion of ventral maxillary muscle not high on the neck of the bone; dentary with sigmoid groove for labial cartilage.

Description.— The holotype (AMNH 2761) is 69 mm long from the tip of the dermethmoid to the supraoccipital. The dermethmoid is 18.5 mm long excluding the spine; the maximum width is 17.2 mm. The frontals are 31 mm long and 11.5 mm between the crests at the anterior end of the fontanelle, which is 20 mm long. The side of the frontal has a steep, deep wall below the crests for attachment of temporal muscles. This wall extends posteriorly to the anterior margin of the parietal and wraps around the anterolateral corner of that bone to contact the anteromesial corner of the pterotic. The posttemporal fossa is deep; its anterior wall is vertical, but the roofing bone of the pterotic is broken off and may not have been vertical. The parietals are not extended anteriorly; their dorsal surfaces are marked by prominent pores. The parietal measurements are 9.3 (left) and 9.0 mm (right) from the posterior notch to the anterior extreme, 12.0 and 12.1 mm from the fontanelle to the posttemporal border, and 18.7 mm (both) in maximum diagonal length. The parietal extends posteriorly in association with a strong epiotic process. The fontanelle is 1.5-2 mm wide (except for broken edges). The subtemporal fossa is deep. The parasphenoid is arched, with a strong ventral deflection of the vomer.

Based on additional material (UMMP 59605, 59606, and 62061), the description can be augmented as follows. The dermethmoid is about as broad as long (not including the anterior process), narrowing somewhat posteriorly. Three grooves radiate posteriorly and posterolaterally from the anterior center of the bone. The width of each frontal (at the orbital rim) is about 55-58% of its length. They are not elongated anteriorly much beyond the

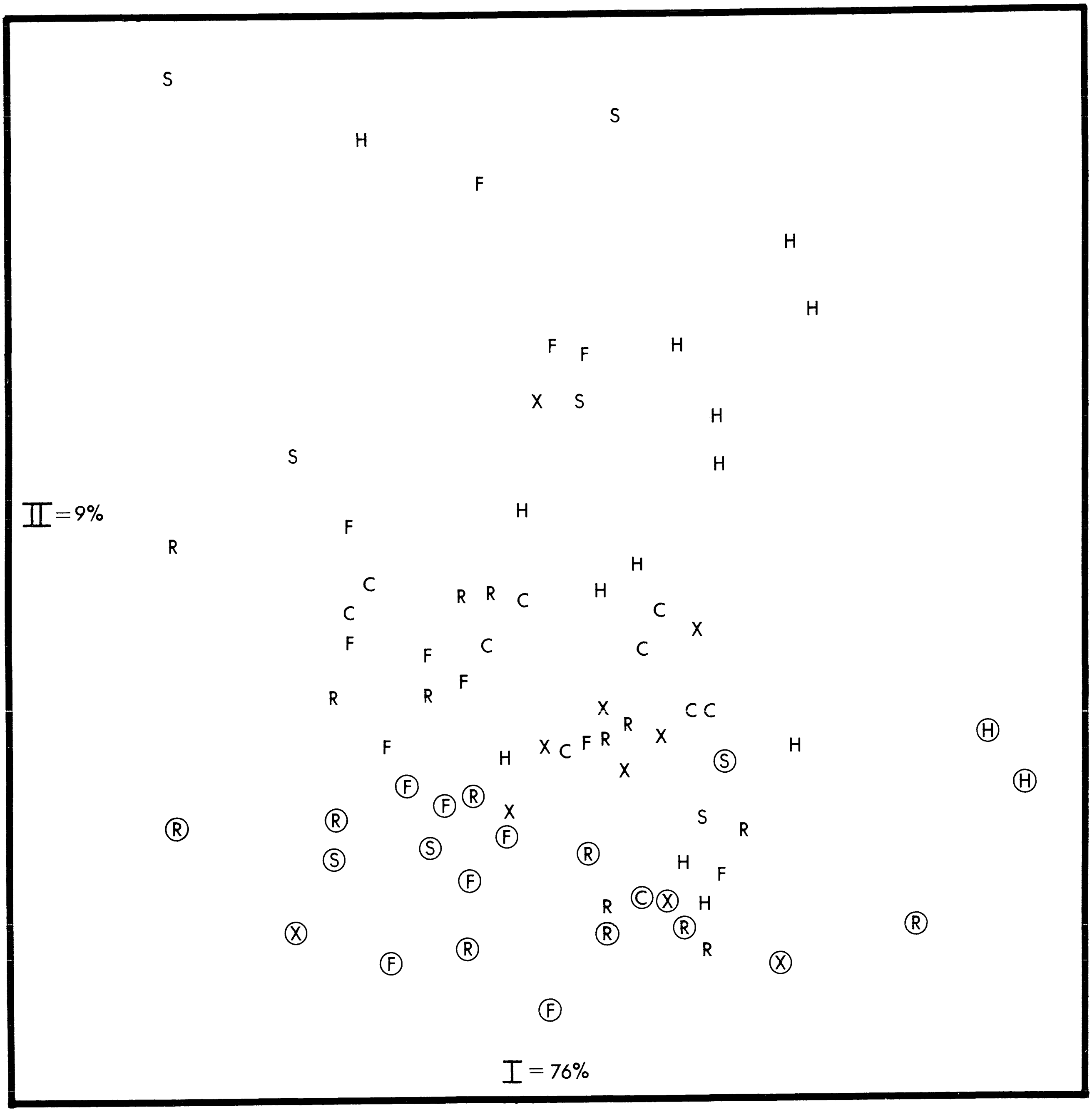


Figure 14. Scatter diagram of principal components scores of 77 specimens of *Catostomus* maxillae. Axes are components I and II. Circled letters – *C. cristatus?*; uncircled letters – *C. shoshonensis*. Letters designate localities from which specimens were collected: (F) Fossil Creek, (H) Horse Hill, (C) Crayfish Hill, (R) Bennett Creek RR grade, (X) Hagerman and Sand Point, (S) Shoofly and Poison Creek. See localities, Fig. 1.

orbital rim. Posterodorsally, the frontals are marked by prominent longitudinal temporal crests; these do not extend onto the parietals. The frontoparietal fontanelle is open. The dermal roofing bone of the pterotic slants posteriorly over the posttemporal fontanelle at an angle of about 70 degrees from the horizontal. The frontals and parietals are in contact, separating the sphenotics and parietals. The posterior processes of the epiotics are prominent. The subtemporal fossae are deeper than in modern catostomines. The parasphenoid and vomer are strongly arched. The metapterygoid has a strong lateral crest and a ventrally–directed symplectic process. The hyomandibular is strongly arched. The pharyngeal arch is deep, as in ictiobine suckers, with numerous, small teeth (59606).

The maxillae (Fig. 12) are presumed here to be the "*ellipticus*" form (see above), characterized by prominent dorsal and ventral keels, the ventral forming an abrupt angle at its anterior contact with the neck of the bone. The scar for the ventral maxillary muscle is in an intermediate position on the neck of the bone (not dorsal), usually with a similar depression anterior to it. The crest for the palatine ligament tends to be mainly horizontal (nearly parallel to the axis of the maxilla) and often has its posterior end near the dorsal part of the neck of the maxilla.

The dentaries (Fig. 12) associated with the above maxillae are characterized by a sigmoid flexure in the groove for the labial cartilage. A line through the coronoid process passes near the anterior tip of the gnathal ramus (as viewed from above). The symphysis is broad and forms an obtuse angle with the line through the coronoid axis. The ventral surface of the gnathal ramus tends to be mainly convex.

Catostomus cristatus Cope

(Figs. 9D; 10A-D; 12C,G)

Catostomus cristatus Cope 1883:160 (type, AMNH 2740, neurocranium). Hussakof, 1908:65, Fig. 33. Uyeno and Miller, 1963:8. Taylor, 1966:74. Miller and Smith, 1967:22.

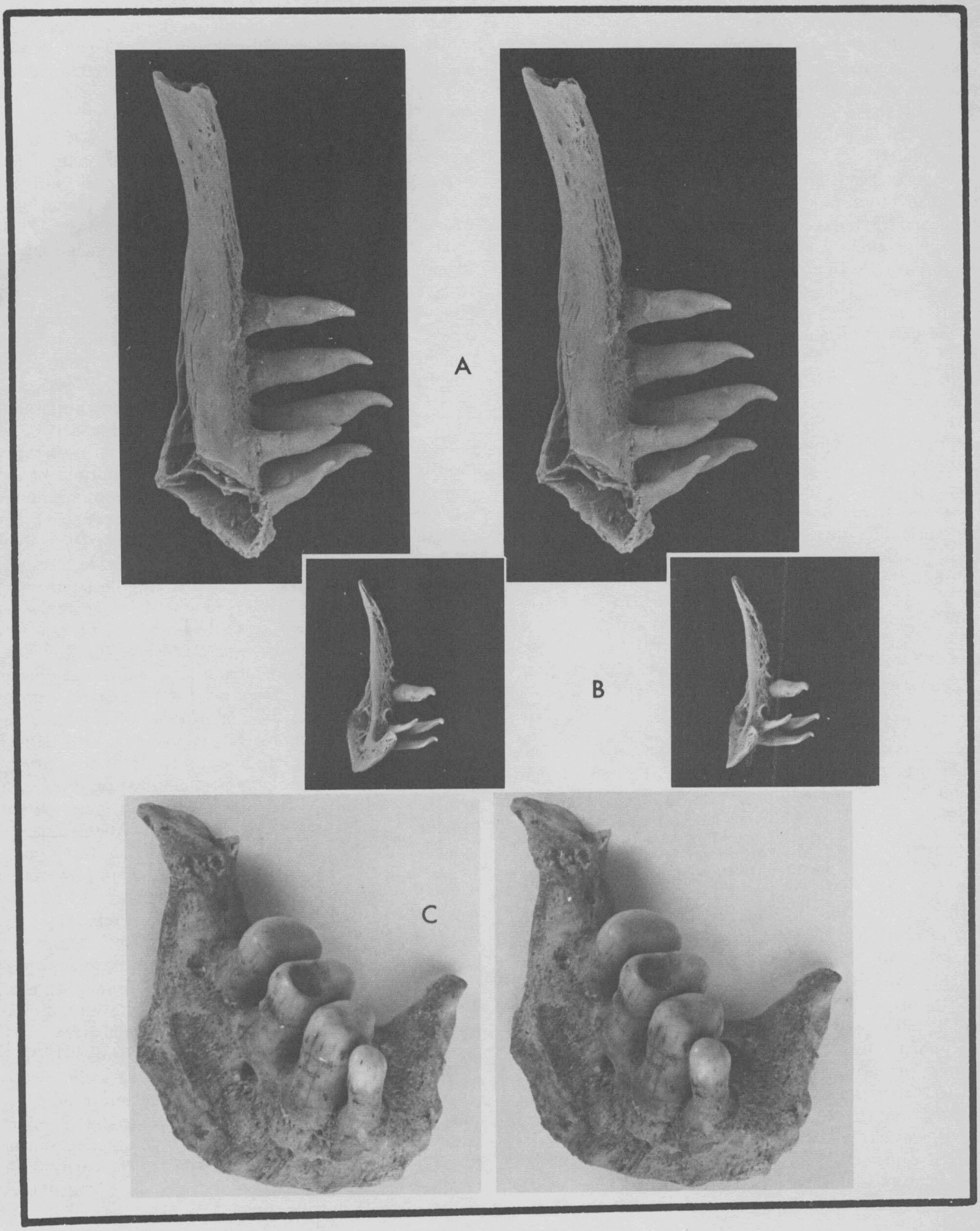
Taxonomy.— The neurocranium (AMNH 2740) on which this name is based, though fragmentary, is distinct from that of *C. shoshonensis* and that associated with *C. owyhee*, as described in the preceding section. On the basis of characters of a comparable skull and associated bones (UMMP 55202), the species is assigned to the subgenus *Catostomus.*

Diagnosis.— A *Catostomus* with reduced or slight frontal-pterotic contact; parietal extended anteriorly, longer than broad, with temporal crests continuing from frontals and with some area for origin of temporal muscles; frontoparietal fontanelle moderately wide; parasphenoid not strongly arched (?); hyomandibular deep, not strongly arched; metapterygoid with anteroventrally directed symplectic process; pharyngeal arch not deep; canal for tripus of Weberian apparatus large; maxilla with shallow ventral keel and long neck with a less dorsal and less parallel ridge for the palatine ligament than in *C. shoshonensis*; dentary with relatively long and slender gnathic ramus, strongly convex ventrally in cross section and with a strong, relatively anterior and dorsal groove for the labial cartilage.

Description.— The holotype (AMNH 2740) is an incomplete posterior fragment of a neurocranium, 30.5 mm from the anterior end of the rather broad frontoparietal fontanelle to the posterior end of the supraoccipital (excluding the posterior process). The frontals have high crests capping nearly vertical walls for origin of the temporal muscles. The width of the frontals from crest to crest across the anterior end of the fontanelle is 14.6 mm. The parietals are elongate anteriorly and posterolaterally. The measurements of the right parietal are 11.6 mm from the posterior notch to the anterior point, 10.3 mm from the fontanelle to the posttemporal fossa, and 20.9 mm from the anteromesial corner to the posterolateral corner. The parietal has well-developed sensory canal pores. The posttemporal and subtemporal fossae are deep. The transverse, horizontal roofing portion of the pterotic (broken) was thin at its base; its posterior edge was probably nearly vertical; anteriorly it contacted the frontal slightly or not at all. The parietal-sphenotic border is prominent and both bones show surfaces for origin of the temporal muscles. The anterior (sphenotic) cotyla for the articulation of the hyomandibular is distinctly ventral to the axis of the dorsal articulation.

Based on additional material (UMMP 55202, Fig. 10), which has the same parietal and temporal characteristics as the holotype, the description of *C. cristatus* can be augmented as follows. The dermethmoid (excluding the anterior process) is almost as wide as long. The dermal roofing bone of the pterotic extends nearly horizontally over the anterior part of the posttemporal fossa (at least in large specimens). The parasphenoid and vomer are not as strongly arched as in *C. shoshonensis.* The hyomandibular is long and relatively straight – lacking strong anterior curvature of the ventral limb. The Weberian apparatus has large openings around the tripus; the bridge formed by the dorsal part of the fourth pleural rib is relatively long and slender. The metapterygoid has a weak horizontal crest at the juncture of its dorsomesial and lateral planes; the symplectic process is directed anteroventrally, approaching an orientation parallel to that of the ventral limb of the hyomandibular. The pharyngeal arch is probably not as deep as in *shoshonensis* (based on UMMP 59190).

The maxilla of 55202 is represented only by an anterior fragment (Fig. 10) with incomplete characters, compatible with either *shoshonensis* or *cristatus.* The size suggests *cristatus*, however. The phenotype presumed to belong to *cristatus* is described in the analysis of maxillae and summarized in the diagnosis. The dentaries are described in the diagnosis.


A
B
C

Catostomus owyhee (Miller and Smith)

(Figs. 10E; 11B-G; 12B,F,K)

Deltistes, Miller, 1965:574, 576. Taylor, 1966:74.
Deltistes owyhee Miller and Smith 1967:5, Figs. 3,4 (type, UMMP 55549, right maxilla.)

Taxonomy.– *Catostomus owhyee* was described in the genus *Deltistes* on the basis of the maxilla and a partial neurocranium. The subsequent discovery of several sets of associated maxillae and dentaries and of a number of skulls, one with associated dentaries, allows a relatively complete description and diagnosis of this species to be given. The predominance of presumably derived characters is shared with the *Deltistes* group.

Diagnosis.– A *Catostomus* with the dermethmoid much longer than broad; frontals and pterotics broadly separated by parietal-sphenotic contact; parietals elongated anteriorly and with extensive temporal crest area for attachment of temporal muscles; fontanelle wide; parasphenoid not strongly arched; hyomandibular relatively straight; metapterygoid with ventrally directed symplectic process and strong lateral crest; passage and openings for tripus of Weberian apparatus small; maxillae with reduced dorsal keel, strong, anteriorly abrupt ventral keel, fossa for insertion of ventral maxillary muscle high on neck of bone, and axis of ridge for attachment of palatine ligament normal to axis of bone; dentary with gnathal ramus expanded, wide at the symphysis, and concave ventrally.

Description.– The holotype (UMMP 55549) is a maxilla characterized as above. (The augmented species description is based on UMMP 57984, 58192, 58204, 58209, 58211, 62200, and individually catalogued bones too numerous to list.) The skull is elongated (Fig. 11B-G); the dermethmoid is much longer than wide, with a long anterior process. The frontals are extended anteriorly. The parietals are prolonged anteriorly and possess a prominent continuation of the temporal crest of the frontals, with extensive area for origin of the temporal (*dilator operculi*) muscles; they contact the sphenotic and broadly separate the frontals from the pterotics. The posterior pterotic wall is vertical, with no horizontal roofing lamina. The epiotics have well-developed posterior processes. The parasphenoid and vomer are relatively straight, not as strongly arched as in *C. shoshonensis.* The ventral surfaces of the lateral ethmoids bear prominent cotylae for articulation with the mesopterygoids. The subtemporal fossae are deep. The anterior hyomandibular cotyla of the sphenotic is not as ventral as in *C. cristatus* or *C. shoshonensis.* The dorsal part of the fourth pleural rib of the Weberian apparatus is relatively short and broad, forming a short bridge over the rather restricted canal for the tripus. The metapterygoid has a strong, horizontal keel at the juncture of the dorsomesial and lateral planes of the bone; its symplectic process is ventrally directed, forming an angle with the lower limb of the hyomandibular. The pharyngeal arch is probably relatively shallow as in Recent catostomines. The dentaries have wide, mesially deflected, and ventrally concave gnathic rami with expanded symphyses. They are readily identified by a rugose anterolateral expansion of the edge that ventrally constricts the groove for the labial cartilage.

Catostomus arenatus Miller and Smith

(Fig. 12L)

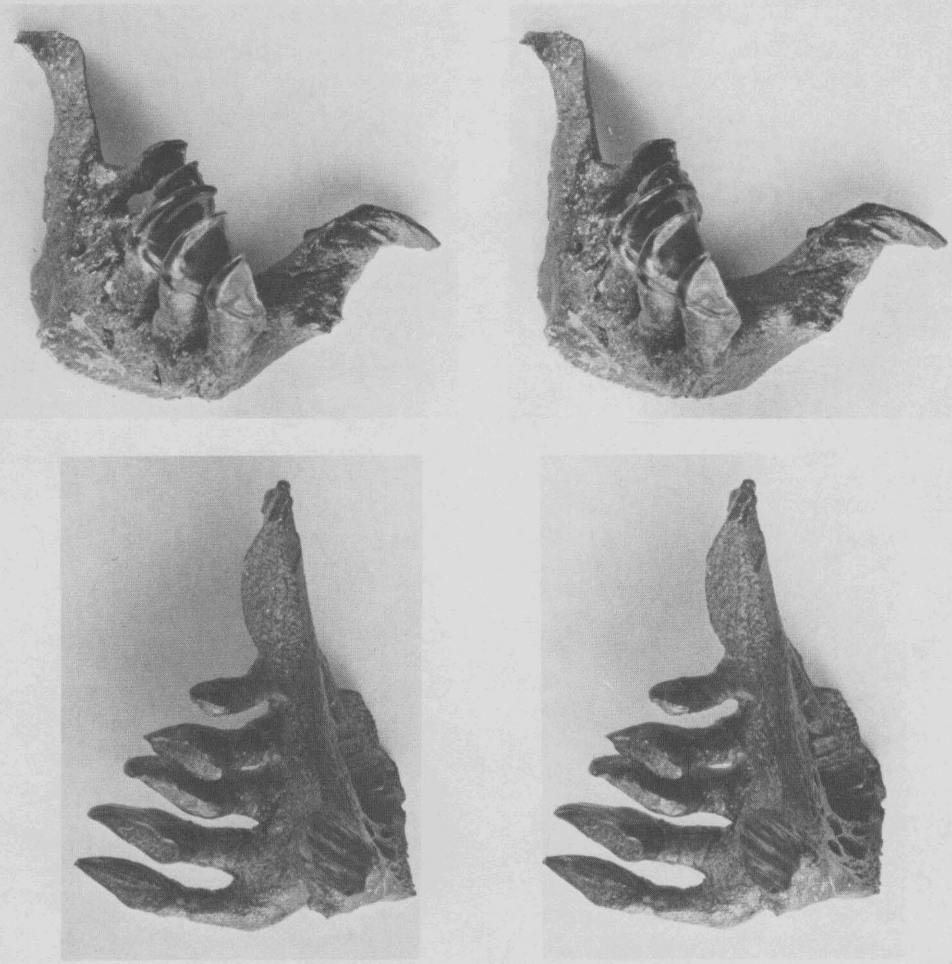
Pantosteus, Miller, 1965:574.
Catostomus (Pantosteus), Taylor, 1966:74; Smith 1966: 114.
Catostomus arenatus Miller and Smith 1967:12, Fig. 5 (type, UMMP 55560, right maxilla).

Taxonomy.– *Catostomus (Pantosteus) arenatus* was described on the basis of one maxilla and one dentary. Material is still rare in collections, and known variation in other species is much closer to *arenatus* than originally recognized. The status and classification of the species is somewhat doubtful.

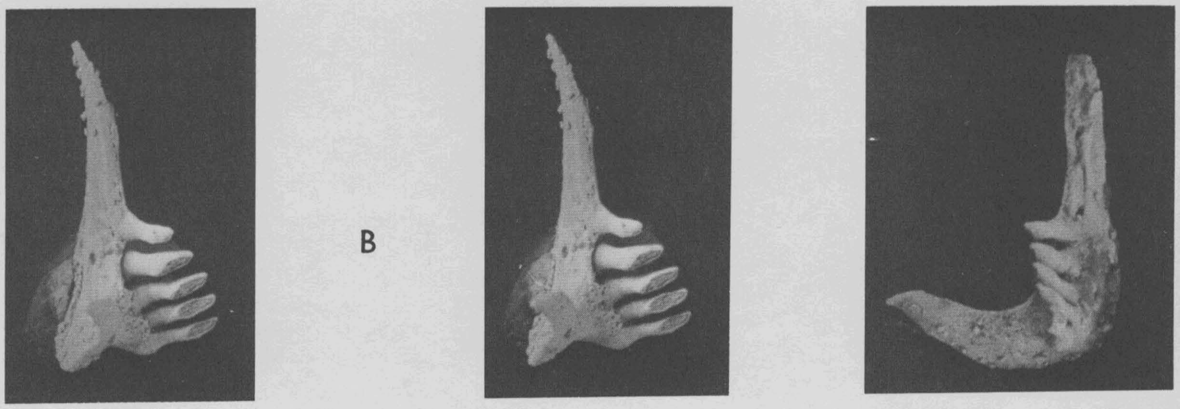
Diagnosis.– Maxilla heavy and robust, with a reduced dorsal keel and a strong ventral keel, as in other members of the subgenus *Pantosteus.* It differs from other species in the subgenus in the large, truncate area for attachment of the palatine ligament and the more abrupt anterior margin of the ventral keel. The depth of the maxilla is greater, relative to its length, than in *C. columbianus.*

Description.– The maxilla bears the above characters. Other maxillae, collected subsequently, have higher dorsal keels and are questionably referred to this species. The available dentaries are not certainly known to be associated with the maxillae. However, in the collection there are rare dentaries that possess some of the characters expected of a *Pantosteus* (e.g., short gnathal ramus deflected ventrally and mesially more than in other *Catostomus*). These dentaries have a large, relatively anterodorsal groove for the labial cartilage. A hyomandibular collected at the type locality in 1975 has the extreme anterior deflection of the ventral limb expected in a member of this group. A skull (59570) from Fossil Creek has the frontoparietal fontanelle reduced and partly closed, as in *Pantosteus*, but shows few other characters expected in this group. Until more material is collected, this species must remain poorly known.

Figure 15. Stereograms of: (A) *Ptychocheilus arciferus*, UMMP 58127, left pharyngeal teeth and part of arch. (B) *Gila milleri*, holotype, UMMP 59460, left pharyngeal. (C) *Mylocheilus robustus*, UMMP 58136, right pharyngeal. All figures times 2.



A



B

Family **Cyprinidae**

Genus *Ptychocheilus* Agassiz

Ptychocheilus arciferus (Cope)

(Figs. 15A, 18A, 21B)

Oligobelis arciferus Cope 1870:541. (Four right and one left pharyngeal bones obtained by Capt. C. King at Catherine Cr. [near Oreana, Owyhee County], Idaho. USNM 9782, 9791, specimens not examined.) Uyeno, 1961:342. (USNM 2115, referred to under this name, is a specimen of *Mylocyprinus [=Mylocheilus] robustus* that "does not seem to agree with original description," Uyeno [1961:340] notes that the catalogue numbers given by Cope have been changed subsequently. The type specimens may be lost or misplaced.) Uyeno and Miller, 1963:15.

Oligobelis laminatus Cope 1870:541. Uyeno, 1961:342 (type? "too fragmentary" for confident identification). Uyeno and Miller, 1963:14 ("synonym of *Ptychocheilus oregonensis*).

Semotilus posticus Cope 1870:541. Uyeno, 1961:342 (type?=*Ptychocheilus* sp.). Uyeno and Miller, 1963: 15 (synonym of *Ptychocheilus oregonensis*).

Semotilus bairdii Cope 1870:542. Uyeno, 1961:342. Uyeno and Miller 1963:15 (synonym of *Ptychocheilus oregonensis*").

Squalius arciferus, Cope, 1883:157, 158. (*Squalius* Bonap. here intended to include *Ptychocheilus* Agassiz, *Clinostomus* Girard, and *Oligobelis* Cope.)

Squalius posticus, Cope, 1883:157.

Squalius laminatus, Cope, 1883:157.

Squalius reddingi Cope 1883:157. Uyeno, 1961:342 (type=*Ptychocheilus* cf. *oregonensis*). Uyeno and Miller, 1963:15 (synonym of *Ptychocheilus oregonensis*).

Squalius bairdi, Cope, 1883:157, 158.

Leuciscus reddingi, Hussakof, 1908:80, Pl. V.

Ptychocheilus cf. *oregonensis*, Uyeno, 1961:342. Miller, 1965:577. Miller and Smith, 1967:22.

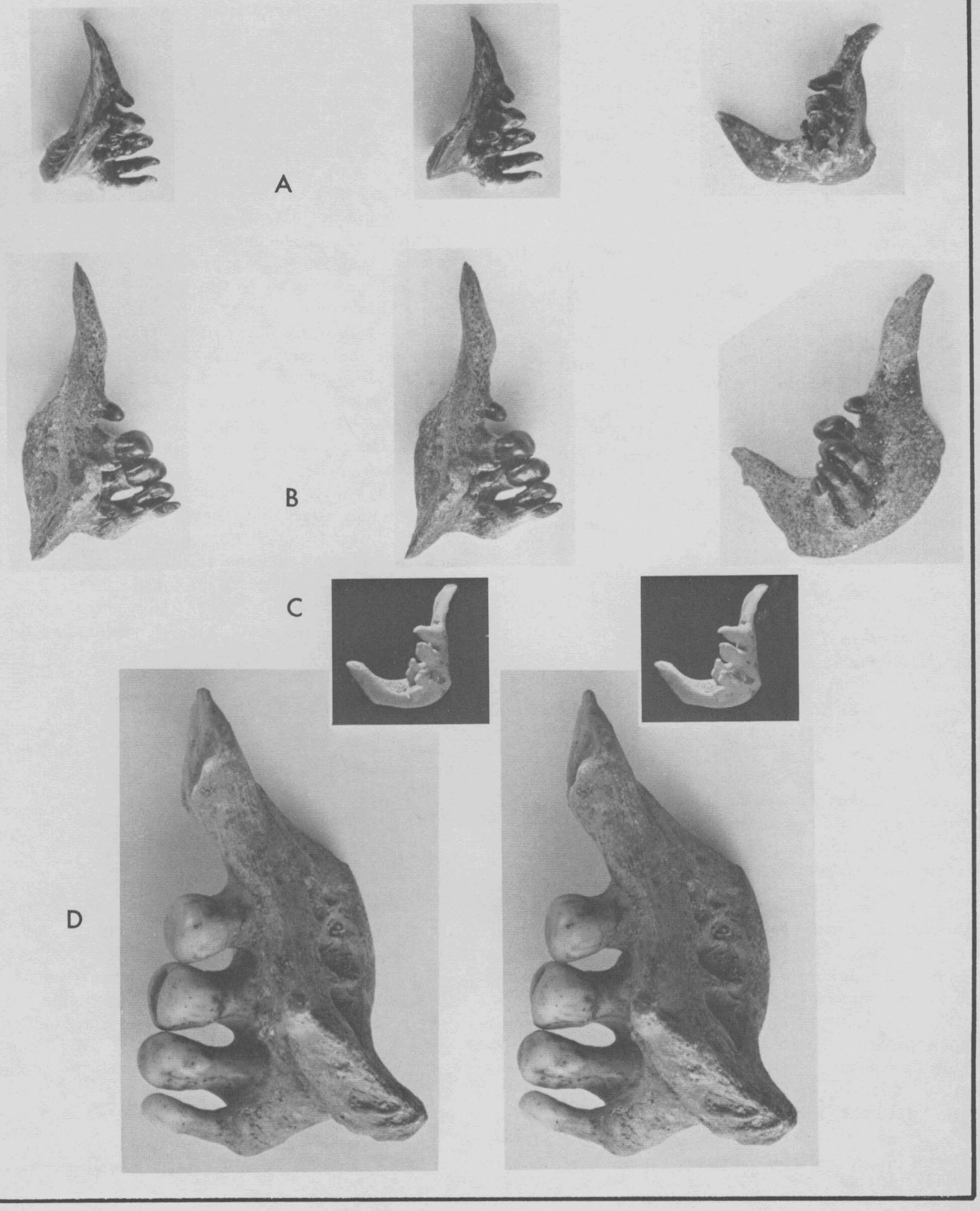
Ptychocheilus oregonensis, Uyeno and Miller, 1963:7.

Taxonomy.— Cope apparently described *Ptychocheilus arciferus* under five different species names and referred them to three different genera. Uyeno and Miller synonomized all but *arciferus* with the Recent genus and species *Ptychocheilus oregonensis* (Richardson). The fossils are distinguished from the living species below. Cope's description of *Oligobelis arciferus* mentions the following characters that clearly apply to *Ptychocheilus*, but no other cyprinids, in the Glenns Ferry fauna: pharyngeal bones with long (to 40 mm), slender anterior limbs, no external ala, bases of teeth rounded and widely separated, and tooth formula 2,3(4?) with small teeth opposite their counterparts in the major row. Despite the fact that numerous subsequent descriptions are based on materials of this species, there is no evidence that more than one species is involved. It is a large, abundant, and often spectacular carnivorous minnow. Ontogenetic variation is responsible for most of the synonyms. The generic assignment of the species, as known from the original description as well as abundant material now in collections, is not in doubt, even though the types of *O. arciferus* are not extant — Cope's characters (above) are a sufficient, though incomplete, diagnosis of *Ptychocheilus*, at least among American cyprinids.

Diagnosis.— Among North American minnows, *Ptychocheilus* is distinct in having long gnathal bones adapted for carnivorous feeding, with a sharp, vertical gnathal ridge on the rather straight dentary (Fig. 18A). The pharyngeal bones are long, the anterior limb longer than the tooth row, which is not elevated. The dorsal limb is angular, slender, and laterally flat. Teeth usually 2,5-4,2, widely spaced, caniniform or slightly hooked, and long (Figs. 18A, 21B). The hyomandibular is long relative to its depth, with widely separated dorsal condyles. Adult size uniquely large; body length to 1.2 m or more. The species differs from all congeners except *lucius* in having a longer anterior limb on the pharyngeal arch, usually more sensory canal pores on the dentary (12-16) and preopercle (9-12 on the lower limb), and the margin of the pterygoid lamina of the hyomandibular rounded rather than acute. *Ptychocheilus arciferus* differs from *P. lucius* in the higher dorsal limb of the preopercle and the well-developed anterodorsal (endopterygoid) lamina of the metapterygoid.

Description.— Similar to *Ptychocheilus oregonensis* in the elongate neurocranium and, especially, jaw bones. UMMP 59664 has the dermethmoid 17 mm long from the notch of the anterior process. The left frontal is 57 mm long and 21 mm in maximum width behind the orbit. The parietals are about 15 mm long from the frontal suture to the sensory canal. From the anterior notch of the dermethmoid to the base of the supraoccipital spine the skull is 87 mm long. The frontals are apparently broadly concave laterally, suggesting a large supraorbital bone as in *P. oregonensis* and *P. grandis* (Ayres), rather than minute as in *lucius*. The jaws are extremely large — the dentary is 22.7 mm high at the coronoid process (measured from the ventrolateral angle) and 10 mm wide across the ventral surface below the end of the gnathal ridge. The maxilla is 14 mm high at the postdorsal process. The articular-angular is short but robust, with

Figure 16. (A) Mesial and dorsal views (times 2) of right pharyngeal of *Acrocheilus latus*, UMMP 59295. (B) Dorsal and mesial views (times 4) of left pharyngeal of *Idadon hibbardi*, holotype, UMMP 59230.


A
B
C
D

three sensory pores in the angular. Preopercle not angular but lunate, with a substantial dorsal limb. Pterygoid series as in *P. oregonensis* and *grandis*, as mentioned above.

The following characteristics are based on disarticulated specimens. The dentary is notably long and straight. The coronoid process is vertical or angled slightly anteriorly, in contrast to most other minnows. The gnathal ridge and the symphysis stand relatively parallel to the plane of the coronoid process; the ventral, pore-bearing surface is at an angle of 90-115 degrees from that plane. The length of the gnathal ramus, measured from the coronoid process, is more than two times ($\bar{x}$=2.2) the height of that process (measured from the ventrolateral angle of the dentary). The mental foramen is in the anterior one-third ($\bar{x}$=.29, SD=.02, N=10) of the gnathal ramus. The dentary has 12-16 ($\bar{x}$=13.5, SD=1.3, N=16) sensory-canal pores (counted from beneath the coronoid process because of the usual position of breakage). Premaxilla and maxilla as in *P. grandis* and *oregonensis.* Preopercle not angular; anterodorsal margin moderately concave; numerous sensory canal pores in sub-marginal row (9-12 on lower limb); dorsal limb longer than ventral. Hyomandibular with strong dorsal and posterior adductor ridges; anterior lamina rounded, not angular; dorsal condyles widely separated by a notch.

The pharyngeal arches and teeth are as described in the diagnosis, with the anterior limb longer than the major tooth row (and minimally as slender as the larger teeth). The external ala of the arch is reduced or absent. The ratio of the height of the dorsal limb to the length of the anterior limb is as in *P. grandis* and *oregonensis*, indicating moderate body depth relative to length.

The species reached a large size. The collection includes a vertebra 26 mm in diameter, a maxilla at least 108 mm long, a dentary 19 mm deep at the symphysis and another 77 mm long to the coronoid process, a hyomandibular well over 75 mm deep, and a preopercle well over 100 mm high. These proportions indicate fish 1.2-1.4 m in total length. The longest tooth is 17.5 mm long.

Genus *Acrocheilus* Agassiz

Acrocheilus latus (Cope)

(Figs. 16A; 20B,D,F,H; 22E,G-K)

Anchybopsis latus Cope 1870:543 (types, USNM 2120, two pharyngeals). Uyeno, 1961:341. Uyeno and Miller, 1963:13.

Diastichus macrodon Cope 1870:539. Cope, 1883:158. Uyeno, 1961:341. Uyeno and Miller, 1963:6. Taylor, 1966:74. Miller and Smith, 1967:10. Linder and Koslucher, 1974:180.

Leucus latus, Cope, 1883:156.

Diastichus parvidens Cope 1870:540. Cope, 1883:158. Uyeno, 1961:341. Taylor, 1966:74. Miller and Smith, 1967:22. Linder and Koslucher, 1974:181.

Diastichus strangulatus Cope 1883:158 (AMNH 2764). Hussakof, 1908:70, Pl. V.

Sigmopharyngodon idahoensis Uyeno 1961:336, Fig. 2, and p. 342 (as *Sigmopharyngodon hagermanensis*, a *lapsus*). Uyeno and Miller, 1963:7. Taylor, 1966:74. Miller and Smith, 1967:22.

Diastichus [two spp.], Miller 1965:571.

Sigmopharyngodon, Miller 1965:571.

Acrocheilus, Taylor, 1966:74.

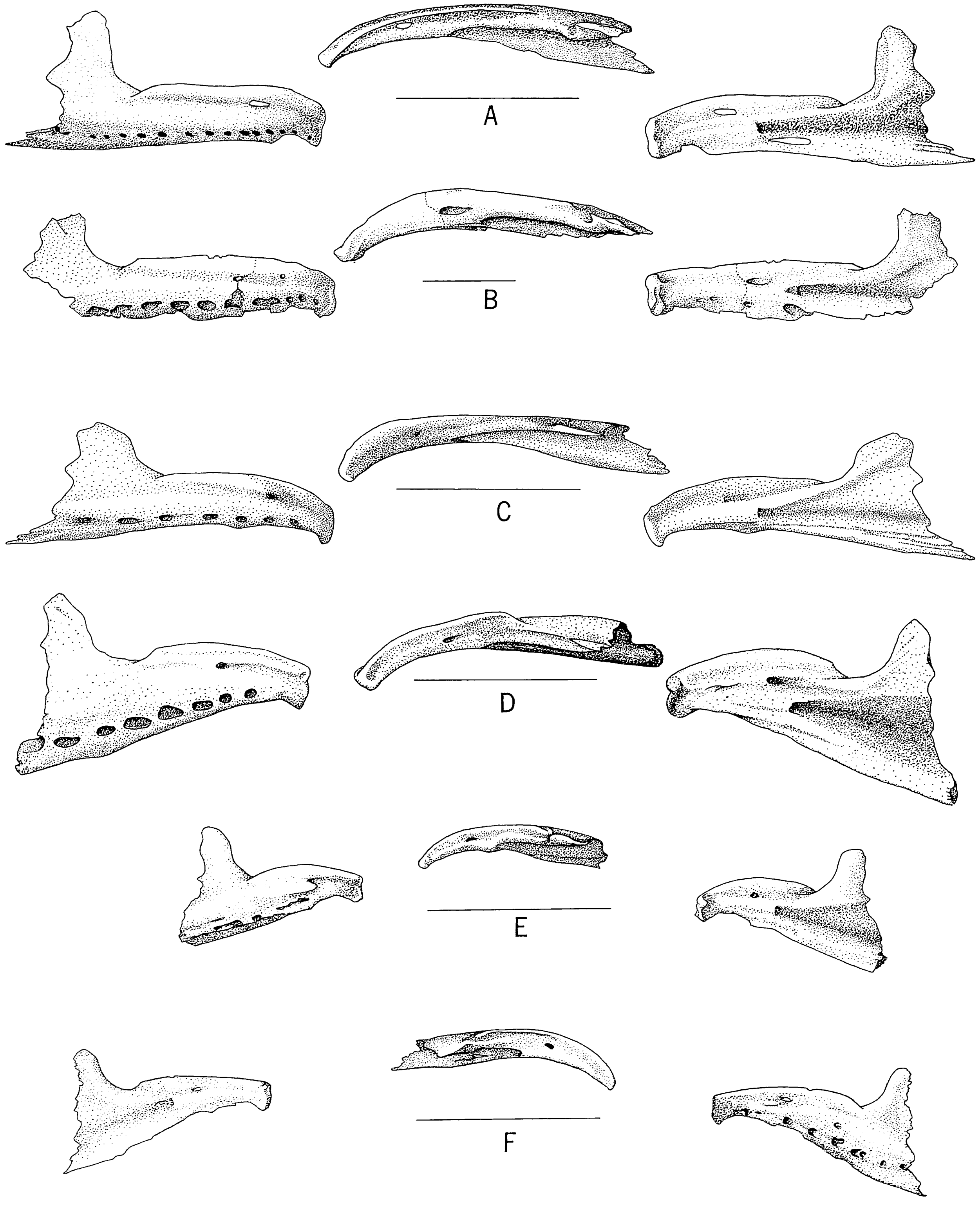
Acrocheilus xestes Miller and Smith, 1967:3, Fig. 2.

Taxonomy.– It appears that Cope described pharyngeals of this form under four species names and referred them to three genera. Uyeno (1961) described a very small pharyngeal arch as still another genus and species. Miller and Smith (1967) first recognized *Acrocheilus* in the fauna on the basis of a distinctive dentary, but their new species is also a synonym of most if not all of the names applied to pharyngeals that are now recognized as bones of *Acrocheilus.*

The name *latus* of Cope (1870:543) is selected as the valid name because of the unambiguous identity of the types (USNM 2120, Fig. 22I). Two synonyms of the same date have page precedence but are not as clearly identified. The original descriptions are most difficult to interpret because the stout distal (dorsal) limb of the pharyngeal arch in this form led Cope to mistake it for the proximal limb and describe the bones backwards in 1870. (Cope corrected his error in 1883. Compare the last sentence under *Diastichus*, 1883:158, with the last paragraph under *D. parvidens*, 1870:540. Historians may note Cope's rather sarcastic attribution [1870:54] of the same error to Leidy later in the same paper – the irony of which is magnified in light of the nearly contemporaneous reversals of *Cimoliasaurus* and *Elasmosaurus*, and the attendant controversy.)

It is still possible that some of the type material referred to in the above synonymy could be a part of the species that has contributed the dentaries and other bones referred to the genus *Orthodon* in this paper. The pharyngeals of *A. latus* are probably too robust to be associated with an *Orthodon*, but one or more of the others might eventually be allied with this genus and bear the valid species name for its Glenns Ferry representative. The type of *Diastichus strangulatus* (AMNH 2764, Fig. 22H) is conspecific with *A. latus* (Fig. 22I). I have not examined the types of *Diastichus parvidens* or *D. macro-*

Figure 17. (A) Left pharyngeal of *Mylopharodon hagermanensis*, UMMP 59461. (B) *Mylocheilus robustus*, UMMP 58144. (C) *Richardsonius durranti*, holotype, UMMP 62580, left pharyngeal. (D) *Mylocheilus robustus*, UMMP 58136. All figures times 2.


A
B
C
D
E
F

don, but the original description and the notes by Uyeno (1961) seem consistent with the above taxonomic arrangement.

Diagnosis.— A cyprinid with the dentary short and robust, the gnathal ramus deflected sharply mesiad at an angle of 90 degrees from the sagital plane, with a truncate anterior gnathal ridge. In *Acrocheilus latus* the coronoid process is more anterior and mesial, in relation to the gnathal ramus, than in *A. alutaceus* Agassiz and Pickering. The pharyngeal arches are strongly angular; the dorsal limb is relatively straight and stout, longer than the toothless part of the anterior limb, and forms an angle of 60-75 degrees with it. The pharyngeal teeth are in two rows of five teeth each and bear strong grinding surfaces on the dorsomesial angle of the dentine crown, which is on a relatively slender pedicel of moderate length. The teeth are borne on an elevated platform. The platform is more elevated (Fig. 22G) than in *A. alutaceus* (Fig. 22F), which also has less robust arches, a tendency to develop terminal hooks on the teeth, and teeth reduced to four on the right arch.

Description.— The gnathal ramus of the dentary (Fig. 21B) is vertically less angular than in *A. alutaceus*; its ventral margin is more nearly ventral to the coronoid process. There are four or five pores in the sensory canal. The maxilla resembles that of *A. alutaceus* in having an anterolateral lamina.

The pharyngeals are as described above. In addition, the anterior limb is short – distinctly shorter than the tooth row. The dorsal process is longer than the tooth row and bears a terminal twist. The lateral face is distinctly striated. Figure 22E illustrates a specimen similar in size and characteristics to *Sigmopharyngodon idahoensis* Uyeno (1961:Fig. 2).

A partially articulated specimen has been described by Linder and Koslucher (1974), who figure the pharyngeals, basioccipital, opercle, subopercle, hyomandibular, cleithrum, postcleithrum, and frontal. All of the bones are similar to *Acrocheilus* except the hyomandibular, which has a deep, angular anterior lamina similar to that of *Orthodon*, and the basioccipital, which has a more extensive grinding platform than in *A. alutaceus.*

Genus *Orthodon* Girard

Diagnosis.— North American cyprinids with a mesially laminar pharyngeal arch bearing five or six long, slender, and compressed teeth in one row; dorsal limb of arch strongly curved anteromesiad; and ala strongly oriented to the transverse plane. Pharyngeal process of basioccipital long, the masticatory platform truncate, faviform, oriented posteroventrally, and bearing an anterior process as well as a long posteriorly curved posterior process. Dentary with long, posteriorly expanded, and relatively flat (dorsally) gnathal ramus; coronoid process posteriorly inclined.

Orthodon hadrognathus new species

(Figs. 19D; 20A,G; 22B,C,D)

Holotype.— UMMP 57728, a complete left dentary from the Glenns Ferry Formation, excavation pits along Bennett Creek RR grade, SW¼, Sec. 16, T. 5 S, R. 8 E, Elmore County, Idaho, elevation 2730 ft (collected by C.W. Hibbard et al., July 5,6, 1965). (See Fig. 4E, p. 78)

Paratypes.— UMMP 59657, three specimens with gnathal edges 7.8, 9.6, and 10.9 mm, from the same locality and horizon as the holotype.

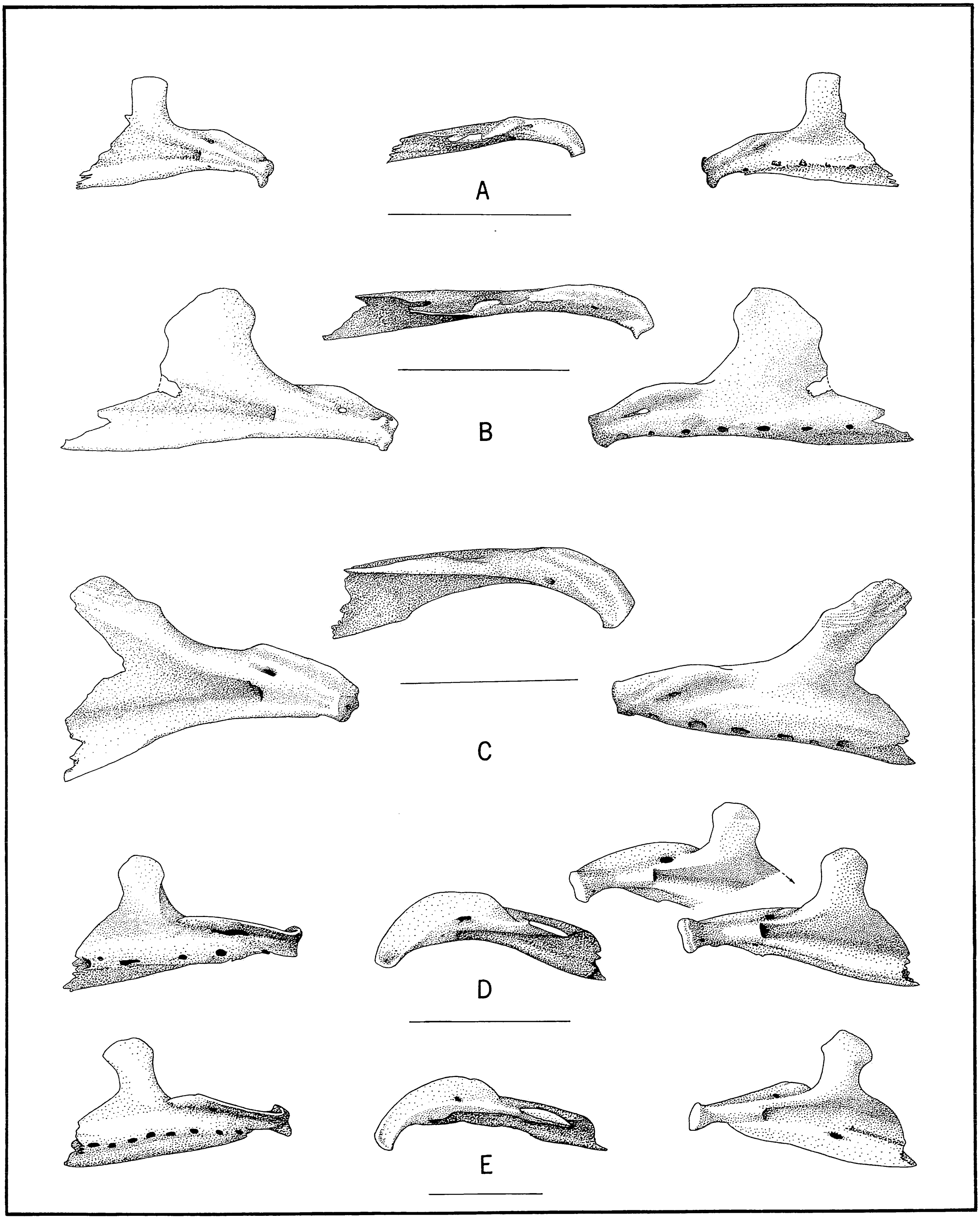
Diagnosis.— An *Orthodon* with a robust dentary, its gnathal edge flatter and broader laterally than in *O. macrolepidotus*, and the median ventral lamina less extensive posteriorly.

If elements presumed to be associated with this species are correctly allocated, the diagnosis also includes: pharyngeals with less laminar arch, especially dorsally; pharyngeal process more posteriorly inclined than in *O. microlepidotus.*

Description.— The holotype is 19 mm long from the postventral tip to the anterior tip, 15.1 mm from the top of the coronoid process to the anterior tip, 13.5 mm from the base of the coronoid process to the anterior tip, and 10 mm from the posterolateral end of the gnathal surface to the anterior tip. The bone is 12.5 mm deep from the top of the coronoid process to the posterior tip. The gnathal surface is 3.9 mm wide at its widest point, near the base of the coronoid process, and tapers anteriorly to 1.3 mm wide, 1 mm behind the symphysis. The gnathal edge flares sharply laterally in cross section, extending 1.7 mm dorsolateral to the external opening of the mental foramen. The symphysis is 3.1 mm deep, 5.5 mm from the Meckelian groove, 6.7 mm from the internal (dorsal) opening of the mental foramen, and 6.2 mm from the external opening of the mental foramen. There are 6 pores in the sensory canal; the fourth and fifth are below the coronoid process. The median-ventral lamina is absent below the first pore, flares out below the second and third, is recessed beneath the fourth, and finally expands beneath the fifth and sixth.

Variability exists in the width and robustness of the gnathal edge of the dentary. In general, the eastern samples seem to be less robust than the western samples, but this comparison has not been quantified.

Figure 18. Dorsal, lateral, and mesial views of dentaries. (A) *Ptychocheilus arciferus*, UMMP 58319. (B) *Mylocheilus robustus*, UMMP 57722. (C) *Mylopharodon conocephalus*, UMMZ 179598. (D) *Mylopharodon hagermanensis*, UMMP 54763, Hagerman. (E) *Richardsonius durranti*, UMMP 62446, Sand Point. (F) *Gila milleri*, UMMP 62415, Fossil Creek. Scales equal 1 cm.


A
B
C
D
E

The pharyngeals that are assumed to represent this species are basically extremes of the *Acrocheilus latus* form. *Orthodon* is most likely represented by those pharyngeals that have a mesial lamina or keel on the anterior limb, compressed teeth, and an expanded lateral ala, especially beneath the anterior teeth (Fig. 22B,C,D). Pharyngeals fitting this description are known from Sand Point, Sand Pits, and the Fossil Creek roadcuts. The dorsal limb in these specimens, where known, is like that of *Acrocheilus latus.*

Remarks.– The dentaries of this form are never common. They are present in modest numbers from Sand Point, Bennett Creek RR grade, and Fossil Creek, and are rare from Shoofly, Picket Creek, Hagerman, and Horse Hill. The ecology is not clear. If the dentaries and pharyngeals are representative of relationships, this form indicates that *Acrocheilus* and *Orthodon* are sister groups.

The species name is from the Greek *hadros*, strong, and *gnathus* (m.), jaw.

Genus *Mylocheilus* Agassiz

Diagnosis.– American cyprinid fishes with molariform pharyngeal teeth that have predominantly flat grinding surfaces except in very young specimens; the grinding surfaces function in opposition to each other (except in *M. inflexus*). Pharyngeal arches robust, the anterior limb shorter than the tooth row and deflected at the symphyseal surface.

Mylocheilus robustus (Leidy)

(Figs. 15C; 17C,E; 18B; 21E,I)

Milocheilus, Newberry 1870a; 1870b:365; 1871:647.

Mylocyprinus robustus Leidy 1870:70 ("said to have been brought from the Rocky Mountains").

Mylocyprinus robustus, Cope, 1870:543. Leidy, 1873: 262, Pl. XVII, Figs. 11-17. Cope, 1883:155. Hussakof, 1908:82, Pl. V. Uyeno, 1961:342. Uyeno and Miller, 1963:7, 14 (synonymy). Taylor, 1966:74. Miller and Smith, 1967:22.

Mylocyprinus kingii Cope 1870:544. Cope, 1883:155 (reduced to subspecies of *M. robustus*). Uyeno, 1961: 341.

Mylocyprinus longidens Cope 1870:545. Cope, 1883:155 (reduced to subspecies of *M. robustus*). Uyeno, 1961: 342.

Mylocyprinus, Miller, 1965:571.

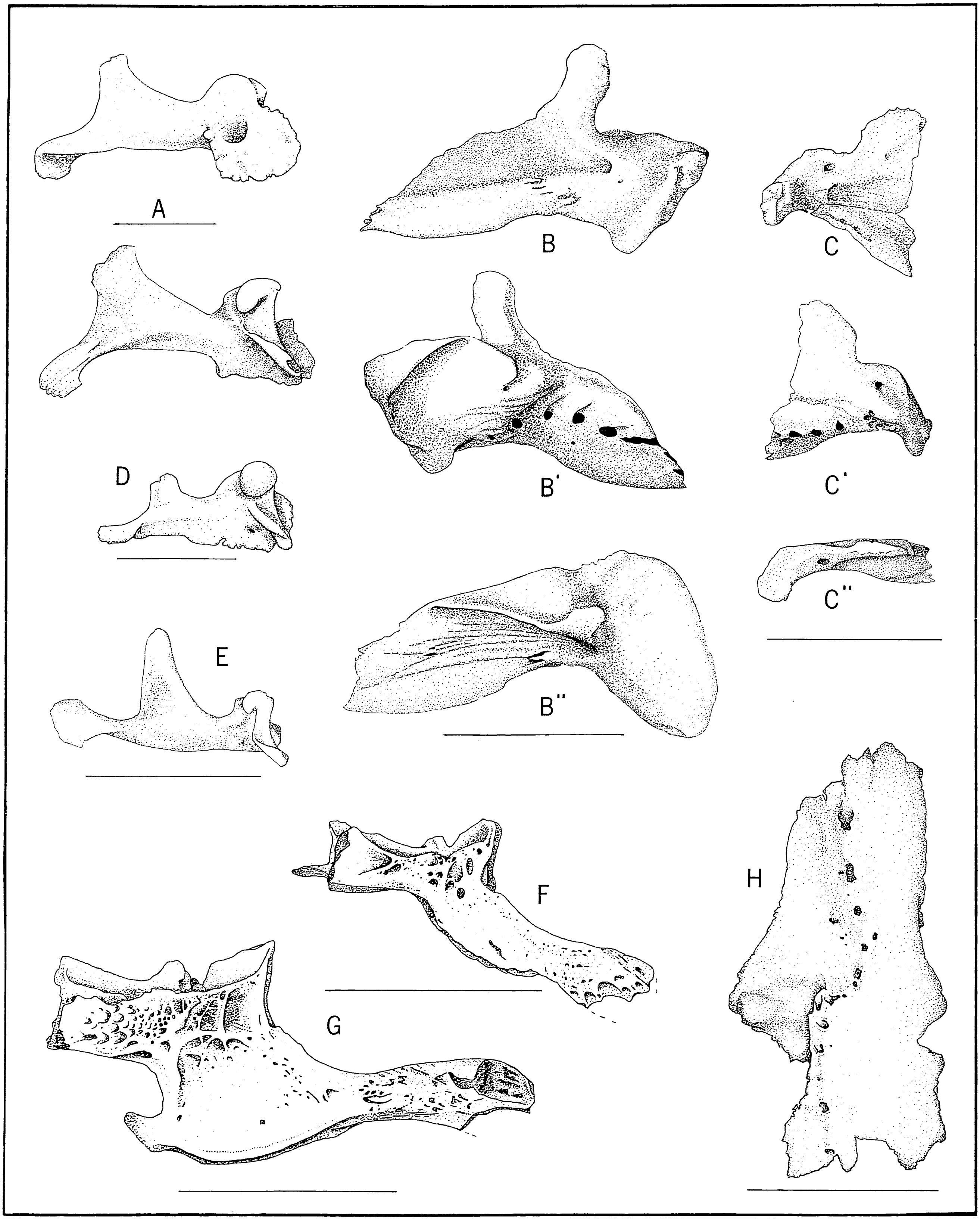
Taxonomy.– In 1870 these large pharyngeals with their unusual molariform teeth were the object of some attention as part of a small collection of fossils from "the Rocky Mountains." Before 20 members of the Academy of Natural Sciences of Philadelphia, Prof. Joseph Leidy described a supposed ray (disposition now unknown) and eight cyprinid pharyngeals with teeth from the collection. The pharyngeals of this species had already been correctly identified as *Mylocheilus* by Dr. J.S. Newberry (1870a,b; 1871). Leidy, however, confused the proximal and distal rami of the arches (see Cope, 1870:544; Leidy, 1870:70; 1873:262) and erected the new generic name *Mylocyprinus*, species *robustus*, under which they have been known until now. Cope (1870, 1883) understood the orientation of the arches in this case but left them in the genus *Mylocyprinus*, to which he added several fossil species and a living Asian species (*Mylopharyngodon aethiops*, compared below). In 1883 Cope considered most of his fossil species of *Mylocyprinus* to be only subspecies of *robustus*. It is perhaps the most conspicuous vertebrate fossil in the formation, except at Hagerman. *Mylocyprinus inflexus* Cope, 1883, is a separate species (see below).

Diagnosis.– A cyprinid with massive pharyngeal arches and teeth. Arch with both edentulous limbs shorter than the tooth row – the anterior has a large symphyseal surface; the dorsal is abruptly attenuate. There is a distinct postventral emargination in the lateral face (Figs. 17D; 21E,I). Four molariform teeth are present in the major row on each arch; their grinding surfaces are in the symphyseal (sagital) plane. Minor teeth (2) are rudimentary or absent, especially in adults.

Description.– The pharyngeal teeth and arches may be further characterized as follows: The teeth have heavy, enamel caps, which are frequently found as separate fossils. The grinding surfaces are smooth except when worn. The posterior two teeth are elevated on a strong platform, bringing their grinding surfaces into the common plane of contact – these are among the few cyprinids known to have the grinding surfaces of the left and right tooth sets in opposition. The arches have relatively fewer and smaller lateral lacunae and more laminae of bone, especially posteriorly and ventrally, than in other cyprinids.

Neurocrania associated with pharyngeals (Univeristy of California F. 1577) are similar to *M. caurinus.* The skull is deep, with the neurocranium strongly tapered anteriorly. It is 67.2 mm long from the notch of the dermethmoid to the base of the supraoccipital process. The dermethmoid is 9.6 mm long from the notch and 11.6 mm wide

Figure 19. Mesial, dorsal, and lateral views of cyprinid dentaries. (A) *Mylocheilus caurinus*, UMMZ 192603. (B) *Idadon hibbardi*, UMMP 57724. (C) *Mylopharyngodon aethiops*, UMMZ 187624. (D) *Orthodon hadrognathus*, UMMP 62414. (E) *Orthodon microlepidotus*, UMMZ 179936. Scales equal 1 cm.


A
B
C
B'
C'
D
C''
E
B''
F
H
G

(estim.). The frontals are 40-44 mm long and 31.5 mm wide (combined) at the postorbital process and 29.3 mm in maximum combined width at the dermosphenotics. The parietals are 12.5-16 mm long in the midline and 30.0 mm wide (combined) posteriorly. The left pterotic is 29 mm long. The supraorbitals are large. The preopercle is 43.5 mm in maximum diagonal length and 37.2 mm in depth; the limbs are at right angles and the lower one has about 9 pores. The opercle is 39 mm high (excluding the dilator process) and 39 mm long (from the anteroventral corner). The pharyngeal process of the basioccipital is large and well developed. The masticatory platform is surprisingly well developed, despite the opposition of the teeth. It might have played a role as a third force vector in the masticatory process. The pharyngeals are large relative to the skull; those associated with the measurements above have a tooth row about 17 mm long and an arch about 25 mm high from the dorsolateral to ventrolateral angles. The adductor ridges of the hyomandibular are weakly developed; the dorsal condyles are separated by a small, shallow notch.

Jaw bones have not yet been found in association with pharyngeals of *Mylocheilus robustus.* Dentaries similar to those of *Mylocheilus caurinus* (Fig. 19A) and *Mylopharyngodon aethiops* (Fig. 19C) are abundant in the formation, but these are nearly always small and are associated circumstantially with pharyngeals of *Idadon* spp. (Fig. 19B). At this time it appears that the dentaries most likely to belong to *Mylocheilus robustus*, on the basis of size and circumstantial association, have an elongate, somewhat spatulate form shown in Fig. 18B. (They are the only cyprinid dentaries in the fauna other than those of *Ptychocheilus* to reach large size, and their frequency among localities is similar to that of the pharyngeals of *M. robustus.* This interpretation is contradicted, however, by the resemblance of these dentaries to those of *Mylopharodon conocephalus* (Fig. 18C) of the Recent fish fauna of the Sacramento drainage, and the resemblance, discussed below, of dentaries of the Pliocene *Idadon* spp. to the Recent *Mylocheilus caurinus.*) The dentaries (Fig. 18B) are elongate – the gnathal ramus is usually about 1.6-1.8 times as long (from the front of the coronoid process) as the height at the coronoid process (from the anterolateral angle). The gnathic ramus is gradually curved mesially; its edge is flared out, especially above the mental foramen, giving a more spatulate appearance than in *Ptychocheilus arciferus* (Fig. 18A). The mental foramen is usually just posterior to the one-third point on the length of the gnathic ramus ($\bar{x}$=.35, SD=.03, N=13). There are 10-16 sensory-canal pores on the ventral surface ($\bar{x}$=12.6, SD=1.6, N=16) counted anteriorly from beneath the center of the coronoid process. In cross section, the ventral surface forms an angle of 100-110 degrees with the coronoid process. The symphysis is angled slightly posteroventrally and is not as deep as in *Ptychocheilus arciferus.*

Mylocheilus inflexus (Cope)

(Fig. 21G)

Mylocyprinus inflexus Cope 1883:154 (type, AMNH 2741, Sinker Creek, Idaho, two pharyngeals). Hussakof, 1908:82, Pl. V. Uyeno, 1961:341 (type examined and found not to be congeneric with *Mylocyprinus [=Mylocheilus] robustus*). Uyeno and Miller, 1963:14.

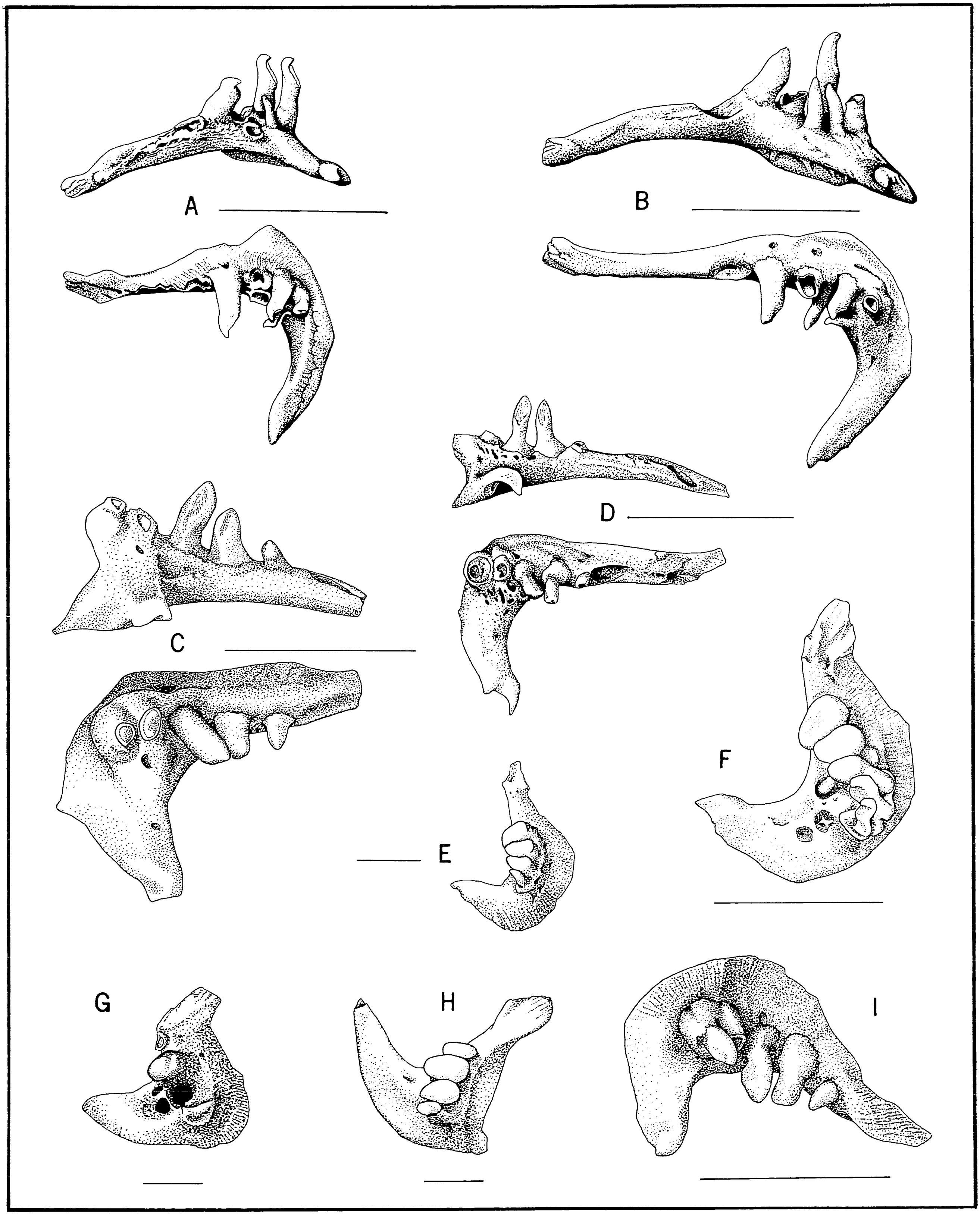
Taxonomy.– These peculiar pharyngeals are known from several specimens and from several localities in the Glenns Ferry Formation. The generic placement of the species is questionable. Its similarities are with *Mylopharodon, Mylocheilus,* and *Mylopharyngodon.*

Diagnosis.– A cyprinid with robust molariform teeth, 5 on the left arch and 4 on the right, with flat crushing surfaces oriented in opposition to the pharyngeal process. Anterior limb of arch short and deflected sharply ventrad from the anterior tooth; dorsal limb extremely elongate and straight, with an open foramen at its base communicating with the lateral lacuna.

Description.– The posterior pharyngeal teeth are smaller, more compressed, and more extremely elevated than the anterior teeth. The anterior teeth have blunt crushing surfaces oblique to the axis of the teeth, in contrast to teeth of *Mylocheilus robustus.* The anterior limb of the arch is shorter than the tooth row and extends ventrad at an angle of about 100 degrees from it. The dorsal limb is unlike that of any other American cyprinid in its height, straightness, and acute angle to the tooth row. There is a single lateral lacuna. The alar angle ventrolateral to the posterior tooth is sharp, with a posterolateral alar extension. In most respects, the arch is similar to that of *Mylopharyngodon aethiops* of Asia (Fig. 21H).

Remarks.– Only two pharyngeals of this distinctive form occur in the collections from the Glenns Ferry Formation, one from Horse Hill and one from Shoofly. The species is far more common in the Deer Butte Formation of Oregon. The similarity of this species to *Mylopharyngodon aethiops* (see Cope, 1883) is here tentatively explained as a parallel evolution because of the lack of other bones similar to that distinctive species in

Figure 20. (A) Lateral view of right and mesial view of left maxillae of *?Orthodon hadrognathus*, UMMP 59572. (B) *Acrocheilus latus*, left dentary, mesial, lateral, and dorsal views, UMMP 57822. (C) Unidentified (?hybrid, *Acrocheilus* times *Orthodon*) cyprinid right dentary, UMMP 62416, views as in B. (D) *?Acrocheilus latus*, left maxilla, mesial view, UMMP 59332. (E) *Idadon hibbardi*, left maxilla, mesial view, UMMP 57734. (F) *Acrocheilus latus*, basioccipital, UMMP 57782. (G) *Orthodon hadrognathus*, basioccipital, UMMP 58892. (H) *Acrocheilus latus*, left frontal, UMMP 62417. Scales equal 1 cm.


A
B
C
D
E
F
G
H
I

the fossil collections. The characteristics of the arch, though extreme, suggest similarity to *Mylopharodon*. The dentaries were probably similar to those of *Mylopharyngodon* (Fig. 19C), *Mylopharodon*, or *Mylocheilus* species (but see description of dentaries described below under Cyprinidae *incertae sedis*). The species was clearly a molluscivore. It was apparently approaching extinction in Lake Idaho.

Genus *Mylopharodon* Ayres

Diagnosis.— American cyprinid fishes with short, high pharyngeal arches, the posterior limb as long or longer than the anterior limb; teeth conic-molariform, formula 2,5-4,2, and arranged with crushing surfaces opposing the pharyngeal process of the basioccipital. The elongate dorsal limb is angular.

Mylopharodon hagermanensis Uyeno

(Figs. 17A; 18D)

Mylopharodon, J.S. Newberry, 1871:647.

Mylopharodon hagermanensis Uyeno 1961:338 (type, UMMP 40582, from T. 7 S, R. 13 E, Sec. 28, elevation 3025 ft, Hagerman Quadrangle, Twin Falls County, Idaho).

Mylopharodon, Miller, 1965:576.

Taxonomy.— Uyeno (1961) recognized that *Mylopharodon* was abundantly represented in the Glenns Ferry fish fauna and described *Mylopharodon hagermanensis*, to which he assigned the majority of his specimens. He examined the very poorly preserved and fragmentary type material of *Leucus condonianus* Cope, 1883, and tentatively referred it to the genus *Mylopharodon* as well. That type material is complex, representing *Mylocheilus* and a previously undescribed genus (see *Idadon condonianus*: Taxonomy). Since none of the type material of *Leucus condonianus* is referable to the genus *Mylopharodon*, Uyeno's name, *hagermanensis*, is valid.

Diagnosis.— A species of *Mylopharodon* with 2,5-4,2 pharyngeal teeth, which are conic-molariform with rudimentary terminal hooks; teeth more strongly molariform in old individuals. Pharyngeal arches with long anterodorsally angled dorsal limb, which is longer than tooth row or anterior limb, and short anterior limb with symphysis sharply deflected from axis of tooth row. The arch is especially similar to *Mylopharodon conocephalus* in shape but has a higher dorsal limb and a shorter, more deflected anterior limb. The dentary (Fig. 18D) is apparently shorter than in *M. conocephalus* (Fig. 18C).

Description.— The species is known only from the pharyngeals, which have the characters given above. The posterior pharyngeal teeth are more compressed, hooked, and bladelike than the anterior, and are elevated on a platform. The anterior tooth is usually conic. The minor teeth are posterior in position. The anterior symphysis of the arch is deflected ventrad and the alar margin is broadly rounded.

The common cyprinid dentaries (Fig. 18D) found in collections with *M. hagermanensis*, which is represented as the most common pharyngeal where it occurs, are similar to the usual form in *Gila*. They are moderately long, mesially curved, and have a relatively broad gnathic edge. There are about six ventral sensory pores anterior to the midbase of the coronoid process.

Remarks.— This species is abundant in Hagerman collections, uncommon at Sand Point, and rare at the Bennett Springs RR grade. Rare specimens of pharyngeals intermediate between *Mylopharodon hagermanensis* and *Idadon hibbardi* (see below) have been collected at Horse Hill. These specimens have conic-molariform teeth with traces of rugose grinding surfaces and intermediate, angular dorsal pharyngeal limbs. One rather intermediate specimen (UMMP 59417) is also known from the upper part of the section at Crayfish Hill at an elevation of 2850 ft. The relationship between these two forms is a puzzle requiring more stratigraphic information. The relationship between *M. hagermanensis* and *M. conocephalus* is phenetically assured and zoogeographically significant. The fossil distribution suggests that the habitat of *M. hagermanensis* was fluvial.

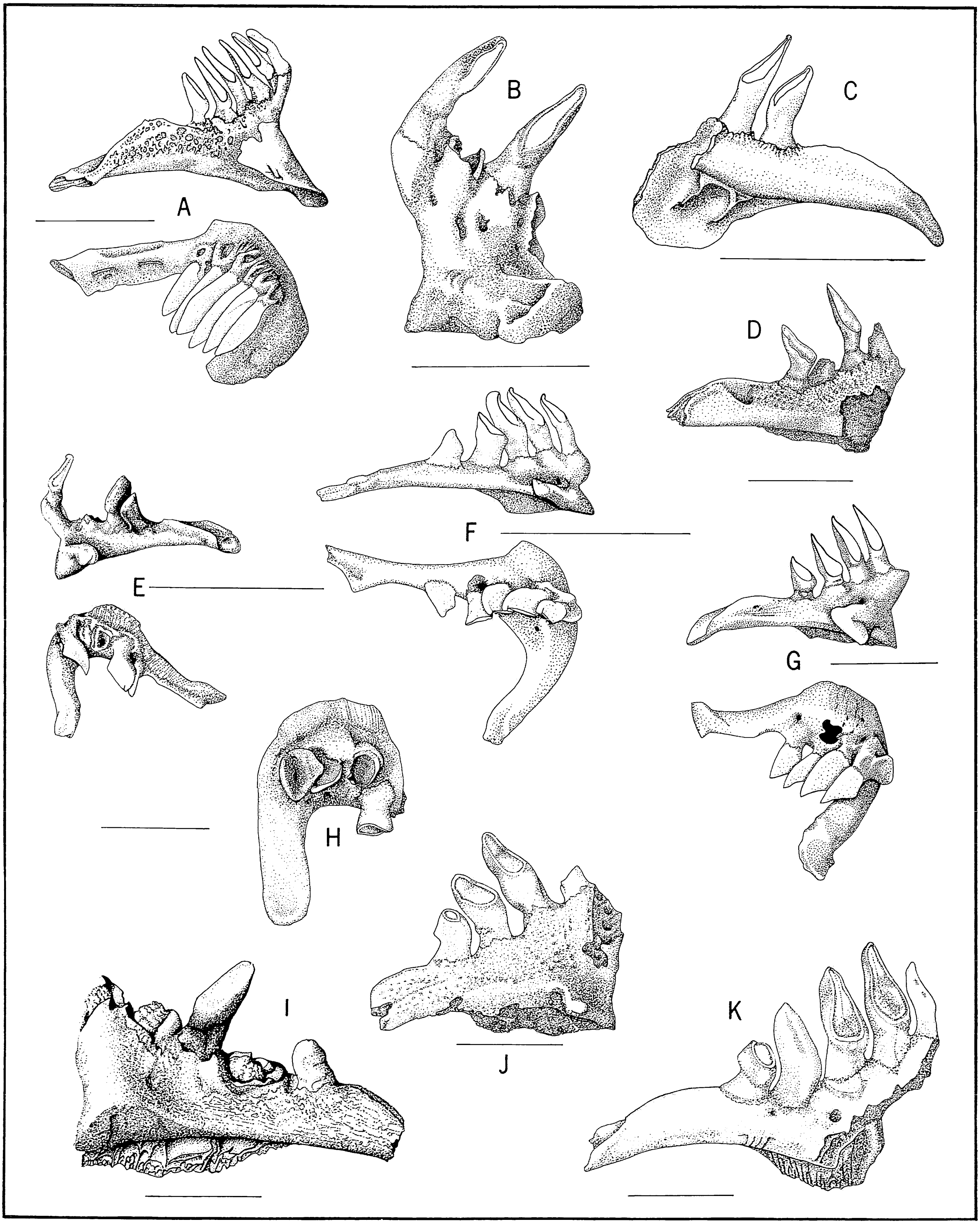
Idadon new genus

Diagnosis.— Cyprinid fishes with at least some of the pharyngeal teeth bearing grinding surfaces marked by wavy-ridged rugosity. Tooth formula 2(1),5-5,2(1). Arch with a moderate to elongate anterior limb, smoothly rounded alar (posterior) margin, and short dorsal limb with lunate terminal hook; its lateral face with extensive lacunae. Teeth subconic to compressed and pointed; the posterior teeth elevated on a platform.

Type Species.— *Idadon condonianus* (Cope).

Etymology.— *Ida*, for Idaho, and *don*, from the Greek *odontos* (m.), tooth.

Figure 21. Comparison of Lake Idaho and other cyprinid pharyngeal arches and teeth. (A) *Gila milleri*, holotype, dorsal and mesial (inverted) views, UMMP 59460. (B) *Ptychocheilus arciferus*, UMMP 58338. (C) Holotype (Lectotype), *Leucas condonianus* Cope, AMNH 2756. (D) *Idadon hibbardi*, UMMP 62418. (E) *Mylocheilus robustus*, UMMP 58166. (F) *Mylocheilus caurinus*, UMMZ 192603. (G) Holotype, *Mylocyprinus inflexus* Cope, AMNH 2741. (H) *Mylopharyngodon aethiops*, UMMZ 187624. (I) "Type" *Leucas condonianus* Cope, AMNH 2762=*Mylocyprinus robustus*, see text. Scales equal 1 cm.


A
B
C
D
E
F
G
H
I
J
K

Idadon condonianus (Cope)

(Fig. 21C)

Leucus condonianus Cope 1883:156 (type, AMNH 2756, pharyngeal arch – see below). Uyeno, 1961:341.
Rutilus condonianus, Hussakof, 1908:96, Pl. V.
?Mylopharodon condonianus, Uyeno, 1961:339, 342. Uyeno and Miller, 1963:7, 13. Miller, 1965:572.

Taxonomy.– The type series includes four pharyngeals, belonging to two species. One specimen (AMNH 2756) is here designated the lectotype of *Leucus condonianus*, which becomes the type species of *Idadon*. AMNH 2756 is labeled "*Richardsonius condonianus* (Cope); one pharyngeal with teeth. Pleistocene; "Equus beds," S.E. Oregon; Wortman," but has an interior tag bearing "*Leucus condonianus*" in Cope's handwriting and a subsequent indication in another hand: "No. 2756 *Richardsonius condonianus* (Cope) Cotype," and the generic name "*Rutilus*" crossed out. The specimen, a right pharyngeal arch with the tooth row 11 mm in length and bearing three anterior teeth and two posterior alveoli in the same row, is not a *Richardsonius, Mylopharodon, Gila, Mylocheilus, Acrocheilus, Ptychocheilus,* or any other known North American cyprinid. Neither does the specimen fit the description nor the measurements given in Cope (1883, length of tooth row, 7 mm), although it could have been one of the four specimens in the type series. The teeth are somewhat widely spaced, and the second and third teeth have elliptical grinding surfaces with rugose ridges, as in *Idadon hibbardi*, described below. Uyeno (1961:341) reports examining the specimen and concluding that the general form was somewhat similar to *Mylopharodon*, but that the specimen was too incomplete to be compared in detail.

AMNH 2762 consists of two specimens: (1) a complete right arch, 17 mm long in the axis of the tooth row, and (2) a small left arch (broken dorsally), 12 mm maximum length. They are associated with a tag in Cope's handwriting saying "*Leucus condonianus* types." The tag bears the number 2562 but has been emended to 2762, with the indicated locality Silver Lake, Oregon, in pencil. An additional tag gives J.L. Wortman as the collector. The original description (Cope, 1883) gives no locality or collector.

The larger of the two specimens does not have the same measurements as given in Cope (1883:156) and is a juvenile *Mylocheilus robustus* on the basis of the short superior limb of the arch, the median inflection of the external alar border opposite the fourth (from anterior) tooth, and the expanded alar margin dorsolateral to the most posterior tooth.

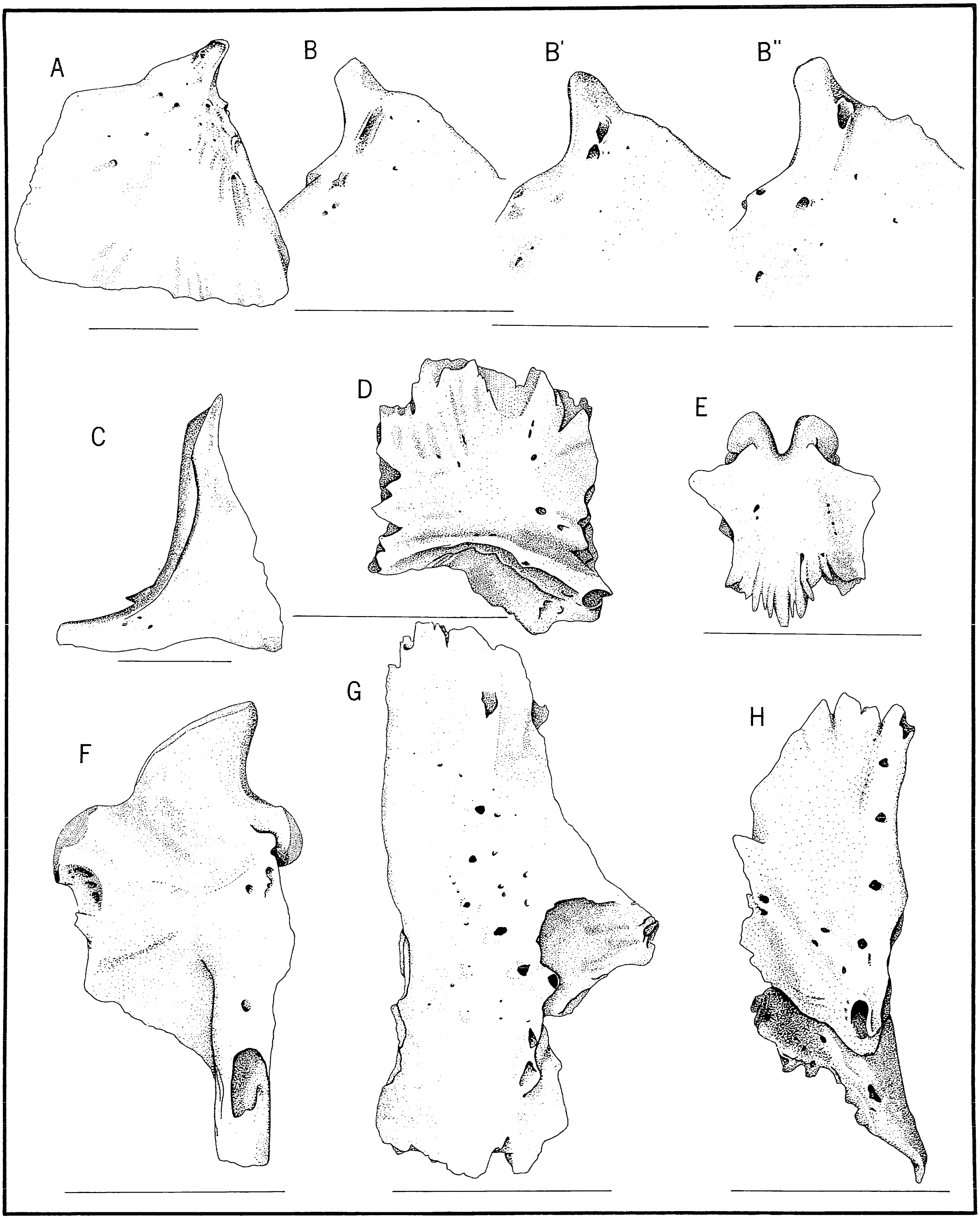
The smaller specimen is too small to be represented by the measurements in the type description and is here assigned to *Idadon condonianus* on the basis of the small size, rounded alar margin, short anterior limb, and trace of a grinding surface on the third tooth. The first tooth is short and peglike. The other teeth are subconical.

The fourth pharyngeal arch mentioned in the original description has not been seen. It is probably the specimen whose measurements are given on p. 156 (Cope, 1883). The mention of "but little grinding surface, and . . . swollen subconic crowns" is a probable description of the species as here restricted. The type specimens were probably collected from the Glenns Ferry or Deer Butte formations, not from Fossil Lake, Oregon.

Diagnosis.– An *Idadon* with the anterior tooth peglike, the second conic-molariform, and the subsequent teeth in the major row successively compressed, smaller, more pointed, and more likely to bear the grinding surface that characterizes the genus. Teeth in the inner row minute or rudimentary. Length of anterior limb of pharyngeal subequal to length of the tooth row. Differs from *Idadon hibbardi* in the possession of conic-molariform teeth and a shorter anterior limb. Differs from young *Mylocheilus robustus*, to which the pharyngeals are most similar, in the more conic teeth (not flat, terminally), the rugose grinding surface on one or more of the posterior teeth, and the absence of the posterolateral inflection of the alar margin. Differs from species of *Mylopharodon* in the grinding surface and the short, rounded, and terminally hooked dorsal limb, as opposed to the high, angular dorsal limb of that genus.

Description.– The species is known only from the pharyngeal arches and teeth. In addition to the characteristics given above, the following may be noted: the symphyseal surface occupies most or all of the anterior limb, which is not otherwise sharply deflected from the axis of the tooth row. In old adults, the anterior tooth, as well as teeth in the minor row, occasionally become conic-molariform, and the grinding surfaces are occasionally rudimentary, requiring careful microscopic examination for verification. The alar margin is not as extensively expanded posterodorsally or ventrally as in *Mylocheilus robustus.*

Figure 22. Pharyngeal arches and teeth of Lake Idaho cyprinids and their relatives. (A) *Orthodon microlepidotus*, UMMZ 179936. (B) *?Orthodon hadrognathus*, UMMP 62413. (C) *?Orthodon hadrognathus*, UMMP 62412. (D) *?Orthodon hadrognathus*, UMMP 62411. (E) *Acrocheilus latus*, UMMP 45187. (F) *Acrocheilus alutaceus*, UMMZ 179596. (G) *Acrocheilus latus*, UMMP 55042. (H) Type, *Diastichus strangulatus* Cope, AMNH 2764. (I) Holotype, *Anchybopsis latus* Cope, AMNH 2120. (J) *?Acrocheilus latus*, UMMP 62409. (K) *Acrocheilus latus*, UMMP 62410. Scales equal 1 cm.


A
B
B'
B''
C
D
E
F
G
H

Idadon hibbardi new species

(Figs. 16B; 19B; 20E; 21D; 23A-H)

Holotype.– UMMP 59230, a left pharyngeal arch from the upper Pliocene Glenns Ferry Formation, 400 m N of Picket (Catherine) Creek, 1 mi NW Oreana, NW¼, Sec. 24, T. 4 S, R. 1 W, Owyhee County, Idaho. The arch has five teeth in the major row, each with a rugose grinding surface. The minor teeth are missing. Each tooth consists of an enamel cap on a slender, bony pedicel. The posterior teeth are borne on an elevated platform. The teeth are relatively uniform, except that the first and last are smaller. The anterior limb of the arch is 5.7 mm long (possibly incomplete); the tooth row is 4.8 mm long at the base and 3.4 mm between the tips of the first and last teeth. It has a characteristic median longitudinal groove. The tip of the dorsal limb is 10.7 mm from the tip of the anterior limb and 6.2 mm from the base of the middle tooth; it is recurved posterolaterally. The posterior alar margin is smoothly rounded. The distinctive grinding surface of the teeth consists of an ovoid depression containing wavy ridges with long axes parallel to that of the tooth. The teeth are pointed.

Named for Dr. Claude W. Hibbard, vertebrate paleontologist, who initiated and encouraged my interest in paleontology.

Diagnosis.– A species of *Idadon* with rugose grinding surfaces on all or nearly all of the pharyngeal teeth, which are also non-molariform, more uniform, sharper, and more compressed than those of *I. condonianus*. The anterior limb of the pharyngeal arch is longer than the tooth row.

Description.– The type pharyngeal is described above. The remainder of the description is based on a series, designated paratypes (UMMP 62063), found as a concentrated apparent death assemblage in a unit of fine, gray sand in the Glenns Ferry Formation, NW¼, Sec. 12, T. 4 S, R. 1 W (Fossil Creek), Owyhee County, Idaho, elevation 2900 ft.

The pharyngeals (Figs. 16B; 21D) are as described above. In all cases (100) the teeth are pointed, non-molariform, and usually bear rugose grinding surfaces on all teeth (often rudimentary on the anterior tooth), even in the large (arch length 23 mm) individuals. Only 10-20 % of these arches have a tooth in the minor row. The median groove in the anterior limb of the arch is always well developed.

The maxilla is distinguished by a high middorsal process originating behind the middle of the bone (Fig. 20E). The depth at this process is more than one-half the length. The anteromesial (premaxillary) process extends anteroventrally at an angle of 90-100 degrees from the axis of the maxilla. The posterior (dentary) process is large and flares out from a slender pedicel. The ventral margin of the maxilla is relatively straight; the anterolateral face is not greatly expanded. The maxilla is similar only to that of *Mylocheilus* among western North American minnows.

The dentary (Fig. 19B) is short and relatively straight, with a short gnathic edge, which is separated from the coronoid process by a distinct gap and deflected outward near the symphysis. It is similar to dentaries of *Mylocheilus caurinus* (Fig. 19A) and *Mylopharyngodon aethiops* (Fig. 19C).

The hyomandibular (Fig. 23F) is long relative to its depth, with a rather acute angle between the ventral limb and the dorsal condyles. The posterior adductor ridge is strong; the dorsal is weak.

The preopercle is lunate, slightly higher than long, with divergence of the limbs approaching right angles. There are 13 or 14 pores, 7-9 on the lower limb.

The roofing bones of the skull are more like those of *Pogonichthys macrolepidotus* than any other western American cyprinids. The dermethmoid (Fig. 23E) is just about as long as broad. The alae are prominently flared from the anterior processes, which are separated by a deep notch. The supraorbital margins of the frontals are broadly concave (Fig. 23G). The anterior end is truncate, not strongly tapered, and nearly flat. There are 9-13 sensory-canal pores. The parietal (Fig. 23D) is quadrate, with a posteriorly concave sensory canal with 4-6 pores and an anterolateral canal deflected at nearly right angles from the frontal branch with 2 or 3 pores, to the pterotic branch with 2 pores. The sensory canal branch from the parietal crosses the pterotic (Fig. 23H) posterolaterally to join the lateral canal of the pterotic at pore 4 or 5 in a line of 6.

The opercle (Fig. 23A) is more like those of *Gila* or *Mylopharodon* in the length and lack of a prominent posterodorsal corner. The sensory canal is variably covered or open between two pores near the base of the dilator process (Fig. 23B).

The fragments of the pleural ribs of the Weberian apparatus are generalized as in *Gila*. Other elements, such as the parasphenoid, urohyal, articular-angular, and cleithrum (Fig. 23C), show similarities to *Pogonichthys, Gila,* and *Mylocheilus.*

Figure 23. Skull bones of *Idadon hibbardi*, UMMP 62063. (A-B) Series of opercles showing variation in opercular sensory canal. (C) Left cleithrum. (D) Right parietal. (E) Dermethmoid. (F) Left hyomandibular. (G) Right frontal. (H) Right pterotic. Scales equal 1 cm.

Genus *Gila* Baird and Girard

Subgenus *Gila* Baird and Girard

Diagnosis.—Moderate to large North American cyprinids with moderately hooked pharyngeal teeth, usually with the formula 2,5-4,2 (minor teeth occasionally 1; major teeth 4 or 5) on arch with relatively long anterior limb; supraethmoid about as wide as long; no anterior projection on masticatory platform of basioccipital; anterior division of urohyal shallow; intercalarium without bar at tip of lateral ramus; hyomandibular with strong, angular anterior ala, but lacking dorsolateral (horizontal) adductor ridge (Uyeno, 1960). Dentary with moderately long gnathic ramus and vertical coronoid process.

Gila milleri new species

(Figs. 15B; 18F; 21A)

Holotype.— UMMP 59460, a left pharyngeal arch with teeth, from the Glenns Ferry Formation, NE¼, Sec. 32, T. 7 S, R. 13 E, Twin Falls County, Idaho, elevation 3260 ft (collected by C.W. Hibbard and party, 1966).

Diagnosis.— A species of the subgenus *Gila* with 2,5-4(or 5),2 pharyngeal teeth, and long, slender, relatively attenuate anterior and dorsal limbs of the pharyngeal arch. All other species in the subgenus have shorter, more robust and recurved anterior and dorsal limbs, and usually shorter, more robust teeth. The teeth in the major row are more crowded than in *Ptychocheilus.*

Description.— The holotype is a left pharyngeal arch, complete except for the absence of 3 teeth, measuring 15.9 mm from the tip of the anterior limb to the tip of the dorsal limb, 7.3 mm from the base of the first tooth (socket) to the tip of the anterior limb, 8.4 mm from the base of the last (posterior) tooth to the tip of the dorsal limb, 7.8 mm between the bases of the first and fifth teeth (inclusive), 5.1 mm over the full length of the symphysis, 2.3 mm over the anterior face of the symphysis, 12.8 mm from the anterior tip to the angle of the external alar expansion (below the third tooth), and 12.9 mm from the latter point to the dorsal tip. Tooth lengths as follows: In the major row, the first (anterior) is missing, second (4.4 mm), third (missing), fourth (4.2 mm), fifth (4.1 mm), second minor (2.8 mm), first minor (missing). The teeth are all terminally hooked and have bladelike posterodorsal grinding surfaces. The anterior limb is 1.35 mm wide (minimum) at its midlength; the dorsal limb is 3.1 mm wide (maximum) at its midlength angle.

Remarks.— *Gila milleri* is rare in the Glenns Ferry Formation, except at the Hagerman localities, where it is uncommon. Specimens are known from Hagerman, Sand Point, Bennett Springs RR grade, Fossil Creek, (?)Sand Pits, and (?)Jackass Butte.

Variation exists in the number of teeth (4 or 5) in the major row of the right arch. The left arch apparently has 5 teeth in the major row consistently.

The species is most similar to *Gila coerulea* (Girard) of Klamath Lake and its tributaries and the Klamath River system. The holotype is nearly identical, except in the diagnostic characters, to a *Gila coerulea* 232 mm in standard length from Copco Lake, Siskiyou County, California (UMMZ 176740).

The distribution in the formation suggests that the species occurred in tributaries and perhaps tributary mouths in the lake.

The species is named for my teacher and colleague, Robert R. Miller, in recognition of his leadership in the study of western North American freshwater fishes.

Genus *Richardsonius* Girard

Diagnosis.— Small North American cyprinid fishes with moderately hooked pharyngeal teeth usually with the formula 2,5-4,2; orbitosphenoid Y-shaped in transverse section; autosphenotic usually between frontal and posttemporal at dorsolateral edge of cranium roof; metapterygoid much smaller than endopterygoid; coronoid process of dentary inclined posteriorly (Uyeno, 1960). Anterior limb of pharyngeal short, with symphysis reaching to base of anterior tooth.

Richardsonius durranti new species

(Fig. 17E)

Holotype.— UMMP 62550, left pharyngeal with teeth, from the Glenns Ferry Formation, Sec. 1, T. 6 S, R. 8 E, Owyhee County, Idaho (collected by C.W. Hibbard and party, June 29, 1965).

Diagnosis.— A species of *Richardsonius* with a short anterior limb and a round rather than angular anteroventral alar expansion on the pharyngeal arch. The anterior limb is less expanded under the anterior teeth, and the ala and posterior limbs are shorter, wider, and often more angular than in its most similar congener, *R. balteatus* (Richardson). The teeth are more robust than in *Richardsonius (Clinostomus) elongatus* (Kirtland).

Description.— The holotype is a left pharyngeal arch, complete except for the absence of one tooth, measuring 5.5 mm from the tip of the anterior limb to the tip of the posterior limb, 2.05 mm from the base of the first tooth to the tip of the anterior limb, 2.7 mm from the base of the last (posterior) tooth to the tip of the dorsal limb, 3.2 mm between the bases of the first and fifth teeth (inclusive), 2.0 mm over the full length of the symphysis, 3.75 mm from the anterior tip to the angle of the alar expansion (below the third tooth), and 4.35 mm from the latter point to the dorsal tip. Tooth lengths are as follows: in the major row, first (1.35 mm), second (1.7

mm), third (missing), fourth (1.6 mm), fifth (1.3 mm); in the minor row, first (0.7 mm), second (0.85 mm, broken). The teeth are all rather robust (especially the anterior), terminally hooked, and flattened in a grinding surface posterodorsally below the terminal hook. The dorsal limb of the arch is wider and more angular than usual in *Richardsonius.*

Dentaries probably representing this species in the fauna are similar to those of *Mylopharodon* and *Gila* but have shorter, more curved and broader gnathic rami, similar to those of living western *Richardsonius.*

Remarks.– The species is uncommon at Hagerman and rare in collections from Sand Point, Bennett RR grade, Rosevear Gulch, and Jackass Butte. It is probably underrepresented in collections because of its small size. Its most similar counterpart in the Recent fauna is *Richardsonius balteatus.*

Richardsonius durranti is named for Stephen D. Durrant, evolutionary biologist and comparative anatomist at the University of Utah. Steve Durrant is the finest teacher that Claude Hibbard and I, and many others, ever had the privilege of listening to.

Cyprinidae *incertae sedis*

The collection includes 25 dentaries of variable and unusual form not assignable to any species, although there is a remote chance that they represent *Mylocheilus inflexus.*

They are usually large dentaries, distinct in the sharp ventral deflection of the gnathic ramus (Fig. 20C). The ramus is short, heavy, blunt, and moderately deflected mesiad. They are variable in shape, angles, and texture but are more similar to each other than to any other known dentaries, Recent or fossil. They are intermediate between dentaries of *Acrocheilus* and *Orthodon* in a way suggestive of hybrids.

The collection also contains several large pharyngeals with heavy molariform teeth marked by oblique grinding surfaces, and an arch with a combination of the unique characteristics of *Acrocheilus latus* and *Mylocheilus robustus.* The pharyngeals clearly represent hybrids between those species. The dentaries described above probably represent hybrids between *Acrocheilus latus* and either *Mylocheilus* or *Orthodon.*

Family **Ictaluridae**

Genus *Ictalurus* Rafinesque

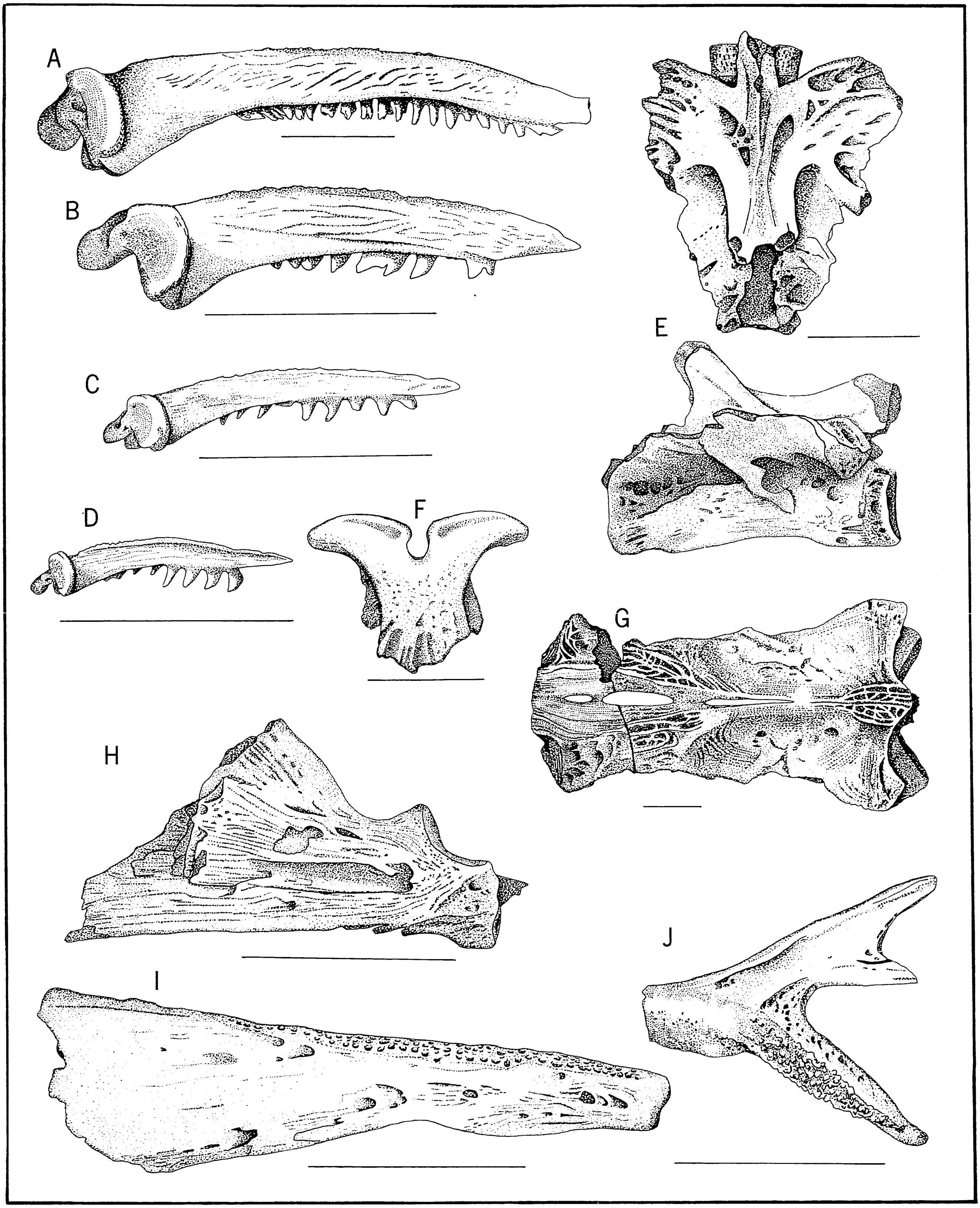
Ictalurus vespertinus Miller and Smith

(Fig. 24)

Ictalurus vespertinus Miller and Smith 1967:15, Figs. 6, 7 (holotype, UMMP 55561, right mandible, Owyhee County, Idaho). Lundberg, 1970, 1975:41, Fig. 5, Pls. VII-IX (diagnosis, list of material, classification).
Amiurus sp., Cope, 1883a:161.
Ictalurus, Miller, 1959:194.
Ictalurus [?], Uyeno and Miller, 1962:340. Uyeno and Miller, 1963:16.
Ictalurus sp., Miller 1965:573, 576, 577. Taylor, 1966:74.

Diagnosis.– (After Lundberg, 1970, 1975; Miller and Smith, 1967.) The species is a member of the subgenus *Amiurus* on the basis of the enlarged and elongate anteroventral crest of the dentary, the steep inclination of the posterodorsal margin of the coronoid process of the articular-angular, and the erect proximal posterior dentations on the dorsal half of the pectoral spine shaft. It is distinguished from other members of the subgenus by the combination of the relatively long posterior process and the high mesially appressed longitudinal crests of the basioccipital; the restricted posterior fontanelle; the broad supraethmoid with mesial processes on the cornua; the large dentary with a broad tooth band, moderately prominent anteroventral crest, and first sensory pore remote from symphysis; the long, slender posterior process of the cleithrum, ornamented basally and ventrally with prominent reticulae and tubercles; and the pectoral spine with strong, relatively even posterior dentations, relatively strong anterior dentations, and weak or absent anterior distal serrae.

Description.– *Ictalurus vespertinus* was thoroughly described by Lundberg (1970, 1975). Subsequently, additional material has been collected. The most important descriptive characters are mentioned in the diagnosis. In addition, the following features bear on the identification and relationships of the species. The supraethmoid is broad across the posterior section as well as across the cornua, and there are lateral fossae posterior to the cornua. The anterior fontanelle may be divided by a bridge; the posterior is constricted posteriorly by appression of the mesial crests, which are high but narrow anteriorly in old specimens. The posterior process of the supraoccipital is long; the transverse processes are concave posteriorly and slightly inclined posteriorly as in *I. catus* and *I. serracanthus* rather than *I. nebulosus.* The lateral process (wing) of the lateral ethmoid is long and ventrally curved as in *I. catus* and *I. serracanthus.* The dentary is long, with a long, broad tooth patch. The articular-angular has a high coronoid process; its mesial shelf is high, as in *I. nebulosus.* The premaxillae are three times as wide as long. The palatine is long, as in *I. catus* and *I. serracanthus.* The hyomandibular has an arrangement of A3 crests like that of *I. nebulosus.* The Weberian apparatus has high neural spine processes as in most other bullheads; the fourth neural spine is broad, the pattern of fossae anterior to its base, and


A
B
C
D
E
F
G
H
I
J

the relatively flat ventral profile of the first and second centra are like *I. catus* and *I. serracanthus*, not *I. nebulosus* or *I. natalis*.

The posterior process of the cleithrum is long and tapered; its tuberculation is extensive, usually regular, and semireticulate. In these features it seems to me to resemble the advanced form in *I. catus* more than any other bullhead. The corocoid is relatively broad, with at least seven or eight sutures, as in *I. serracanthus*. The ventral keel extends more than half the corocoid width, as in *I. catus*. The pectoral spines show an ontogenetic progression (Fig. 24A-D), becoming more robust and losing the anterior distal serrae with advanced size; the teeth tend to become relatively smaller, less retrorse and regular, and more bifid.

Remarks.– *Ictalurus vespertinus* is most similar in nearly all features to *I. catus* and *I. serracanthus*. Much of this similarity can be interpreted as the sharing of primitive character states. Lundberg (1970, 1975) interpreted shared advanced character states as indicating that *I. vespertinus* was more closely related to the *I. natalis* species group (including *I. nebulosus*) than to the *catus* group. The characters on which this conclusion was based included a short lateral ethmoid wing, short palatine, vertical transverse crests on the supraoccipital, and deep pits on the supraoccipital process. On the basis of new material, the first three of these characters are here reinterpreted in *vespertinus* and are seen to possess the character states typical of the *catus*, not the *natalis*, species group. As noted by Lundberg (1970) the supraoccipital process of *vespertinus* is marked by deep pits, unlike species in the *catus* group. The characters of the *catus* group said to be lacking in *I. vespertinus* – a broadened premaxilla, extensive and uniform development of tubercles on the posterior process of the cleithrum, and an increased number of corocoid sutures – are all found as well developed in *vespertinus* as in *serracanthus*, on the basis of collections now available. Therefore, *I. vespertinus* is here regarded as a sister species to *I. serracanthus* and *I. catus*. Lundberg (1970, 1975) notes that *I. serracanthus* retains more primitive features than any other living bullhead. Its similarity to the geographically remote *I. vespertinus* of 5 million years ago suggests a chronological and geographic perspective for the dispersal of primitive bullheads and the subsequent evolution and specialization of several lines in the Mississippi Basin and southeastern coastal plain of North America.

Ictalurus vespertinus is present at all localities in the Glenns Ferry Formation. Its abundance is positively correlated with sediment size. It seems to be rather uncommon in lake facies and common to abundant in fluvial and floodplain facies, especially at the Hagerman localities. The species grew to substantial size. Large elements in the collection are at least 10% larger than counterparts from *I. catus* that are 355 mm in standard length.

Ictaluridae *incertae sedis*

Lundberg (1975:Fig. 6D) illustrates the presence of a *Noturus*like Weberian apparatus (UMMP 58002) from the middle Pleistocene Grandview local fauna (Jackass Butte). The structure is definitely more depressed than that of *I. vespertinus* (compare Fig. 24E), but other characters for definitely assigning this fossil are not available. Pectoral spines distinctive of *Noturus* have not been found at Jackass Butte. *Ictalurus vespertinus* is present, however.

Family **Centrarchidae**

Genus *Archoplites* Gill

Archoplites taylori Miller and Smith

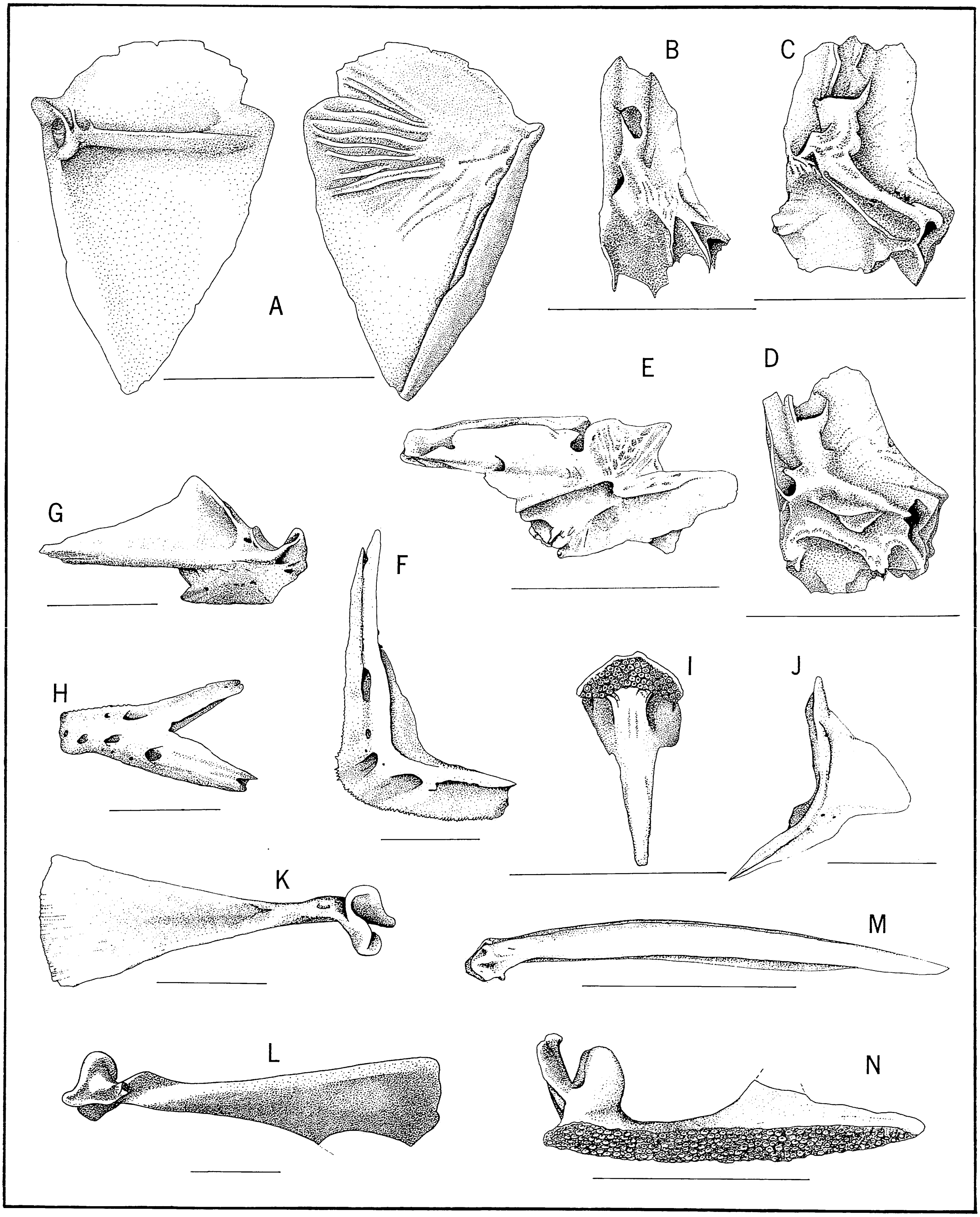
(Fig. 25)

Archoplites taylori Miller and Smith 1967:18, Fig. 8 (holotype UMMP 55562, left dentary, Owyhee County, Idaho).
Percidae, Cope, 1883a:164.
Lepomis, Miller, 1959:194.
?Lepomis, Uyeno and Miller, 1963:18.
Archoplites sp., Miller, 1965:575, 576, 577. Taylor, 1966:74.

Diagnosis.– The genus consists of Pliocene to Recent centrarchid fishes distinguishable by the combination of the presence of well-developed teeth on the endopterygoid, ectopterygoid, and posterior basibranchial; vomerine teeth small, in more than 8 by 20 rows in adults; maxilla with short ascending process; dentary truncate anteriorly, with expanded tooth patch anteriorly; teeth small; preopercle angular, normally with six distinct pores, a deep adductor groove, strong serrae ventrally and weak serrae posteriorly; lachrymal serrate and rounded postventrally; sphenotic with a deep anterior fossa.

The species differs from *A. interruptus* (Girard) in the less abrupt posterior constriction of the dentary tooth patch, longer dorsal process of the dentary, more prominently serrate preopercle, broader at its angle, and the striate opercle.

Figure 24. *Ictalurus vespertinus*. (A-D) Right pectoral spines, showing ontogenetic variation (A, UMMP 59676; B,C,D, UMMP 58994). (E) Weberian apparatus, dorsal and right lateral views, UMMP 62667. (F) Dermethmoid, UMMP 62047. (G) Neurocranium, UMMP 62089. (H) Articular-angular, UMMP 58004. (I) Right dentary, UMMP 58004. (J) Left cleithrum, UMMP 58127. Scales equal 1 cm.


A
B
C
E
D
G
F
H
I
J
K
M
L
N

Description.— Thousands of elements of this species are now in the collection. The characteristics are those given in the diagnosis and, except where noted, are like those of *A. interruptus.* No articulated specimens are known, but a posterior section of a skull (UMMP 62090) has been collected. Variation exists in the pattern of sensory canals and pores on the frontal (Fig. 25B-D), and small vomer have fewer, relatively larger teeth, but no evidence has been found among other elements for more than one species in the formation. The most noteworthy character is the pattern of thick ridges on the opercle (Fig. 25A). These are not found in *A. interruptus* or other Recent centrarchids. The ridges are analogous to those of Pleistocene (and to a lesser extent, Recent) *Perca flavescens* (Mitchill) of North America (Smith, 1963). The function of these ridges is not known.

Remarks.— This species is commonly represented at all fish localities. No decided habitat preference is evident. Specimens were commonly 150-200 mm in standard length, as in the Recent species. Large specimens existed, however; UMMP 57997 contains a maxilla 52 mm long that probably came from a fish more than 350 mm in standard length. *Archoplites interruptus* reaches a maximum length of about 600 mm (Jordan and Evermann, 1896).

This sunfish represents the clearest faunal example of the evidence for a former connection between the Sacramento system and the upper Snake River.

Family **Cottidae**

An unusual diversity of sculpins existed in Lake Idaho, as recorded in the Glenns Ferry Formation and associated rocks. Three genera and at least seven species are known, though not all coexisted at the same time. The two genera characteristic of the North American Recent freshwater fauna, *Cottus* and *Myoxocephalus*, are present but not common. The dominant sculpins in the Glenns Ferry Formation are three species described by Cope (1883) and tentatively placed in *Cottus.* They are here reevaluated and elevated to generic rank.

Kerocottus new genus

Type Species.— Cottus divaricatus Cope 1883.

Diagnosis.— Cottid fishes with four prominent preopercular spines, a posterior pair oriented in the usual plane and an anterior pair projecting more or less anterolaterally; angle of anterior and dorsal arms of preopercle 70-90 degrees; suborbital bones with prominent spines — lachrymal usually with three anterior, four or five lateral, and one to three postventral spines surrounding sensory-canal pores; second suborbital with two or three spines; third suborbital with one spine on preopercular stay; frontal with one prominent, simple supraorbital spine and one postcumbent posterior spine; parietal with one spine between posterior canal pores; dentary and articular-angular with medium-large sensory-canal pores; teeth on premaxilla, dentary, vomer, palatine, and pharyngeals; notch between hypurals shallow.

Remarks.— The genus contains three known species, restricted to the Pliocene Glenns Ferry Formation: *K. divaricatus, pontifex,* and *hypoceras.* The name (m.) is after the Greek Goddess Ker, with reference to the armament as well as the extinction of these fishes; and *cottus*, sculpin.

Kerocottus divaricatus (Cope)

(Figs. 26; 27A; 28)

Cottus divaricatus Cope 1883:162 (types AMNH 2779, two preopercles, Willow Creek, Oregon). Hussakof, 1908:68, Fig. 36. Uyeno and Miller, 1963:10, 20. Taylor, 1966:74. Linder, 1970:755.

Cottus cryptotremus Cope 1883:163. Hussakof, 1908:68, Fig. 36 (placed in synonymy of *Cottus divaricatus*). Uyeno and Miller, 1963:10.

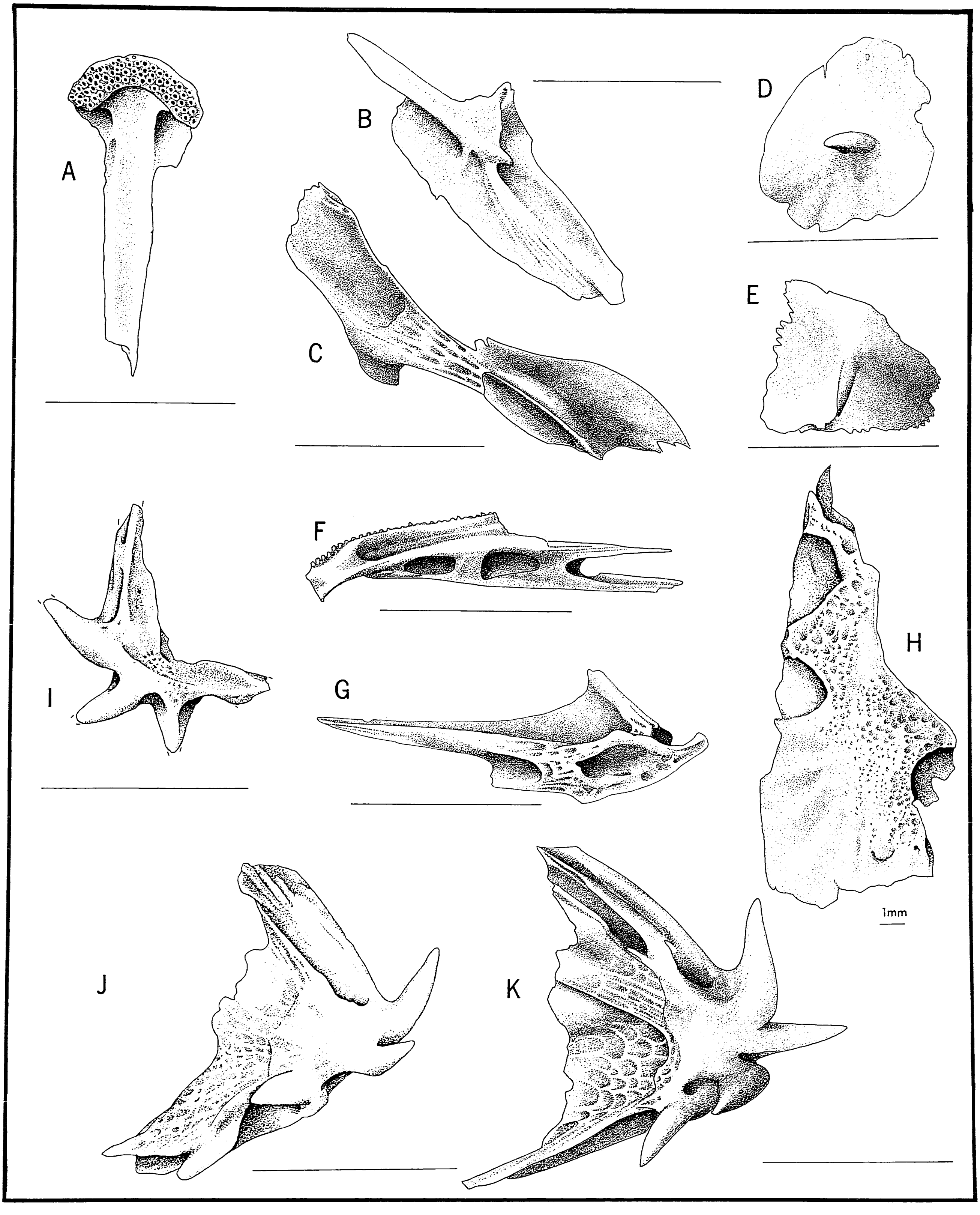
"Cottus," Miller, 1965:574, 575 ("unnamed genus").

"Cottus" divaricatus, Miller and Smith, 1967:23.

Taxonomy.— The types of all of Cope's sculpins from the Glenns Ferry Formation have been examined. *Cottus cryptotremus* is the same species as *divaricatus*, as noted by Hussakof (1908). The original descriptions are confused because Cope confused the mesial and lateral sides of the bones.

Diagnosis.— A sculpin distinguishable from all others by the position and angle of projection of the ventral (anterior) pair of preopercular spines. The first (anterior) spine extends anterolateral in the horizontal plane; the

Figure 25. *Archoplites taylori* and compared bones. (A) Mesial and lateral views of right opercle, UMMP 45232. (B) *Archoplites interruptus*, right frontal, UMMZ 179918. (C,D) *A. taylori*, right frontals, UMMP 53436, 55491. (E) Left pterotic, lateral view, UMMP 59241. (F) Right preopercle, UMMP 59297. (G) Left articular-angular, UMMP 62668. (H) Left dentary, UMMP 62071. (I) Vomer, UMMP 59146. (J) Left cleithrum, UMMP 62669. (K) Left maxilla, mesial view, UMMP 62071. (L) Left maxilla, lateral view, UMMP 57990. (M) Dorsal spine, UMMP 62071. (N) Right premaxilla, UMMP 59297. Scales equal 1 cm.


A
B
C
D
E
F
G
H
I
J
K
1mm

second extends nearly perpendicular to the plane of the preopercle or slightly anterior; the bases of the first and second spines are usually connected, though a small pore of the sensory canal opens laterally between them; the second and third (angular) spines are separated by a moderate-sized sensory-canal pore with a diameter smaller than that of adjacent spine bases (unlike *K. pontifex*); the third and fourth spines project posterodorsally from connected bases separated only by a small posterior pore; adductor fossae are divided but not separated from the spine-bearing face by a sharp lateral ridge (unlike *K. hypoceras*).

Description.– The generic diagnosis is based primarily on material of this species. In addition to characters described in the diagnosis, the following are given, although some mixed characters may occur because identities of other sculpin bones are not known from definite associations with preopercles but are assumed on the basis of relative abundance.

The premaxilla is long and low, with low, posterolaterally inclined ascending processes; tooth band wide, with sharp process at its mesoposterior corner (at base of mesial ascending process); teeth small; dorsolateral process long and low, and may be separated from ascending processes by a flat area in large specimens. Maxilla long, slender, evenly tapered, not sharply curved, and relatively flat dorsally behind head; shares characteristics with *Cottus* and *Myoxocephalus.* Dentary long, with long, wide tooth band; teeth small; sensory-canal pores four, larger than interspaces as in *M. q. quadricornis* (except possibly in very large specimens); a sharp ridge extends from the ventral projection of the symphysis, past the first pore and dorsal to the second, separating them from the adductor muscle scar, which usually reaches anteriorly to a position above the posterior border of the first pore. Articular-angular with large sensory-canal pores, their interspace about equal to their length; angle between axis of bone and postarticular process about 140 degrees; coronoid process long, as in *Cottus*, with a small accessory process at its base, posterior to an extensive fossa for muscle attachment. Palatine with strong band of more than 5 by 20 rows of teeth, shape as in *Cottus*, not *Myoxocephalus.* Vomer with broad, shallow, arcuate tooth patch of about 4 by 20 rows of small teeth; tooth platform moderately elevated.

The hyomandibular is shaped like that of *Myoxocephalus*, not *Cottus.* The pterygoid wing extends the full length of the bone; the horizontal adductor ridge is prominent but usually lacks an anterior process; the horizontal adductor ridge is lacking. The preopercle and suborbital series are as described in the diagnosis.

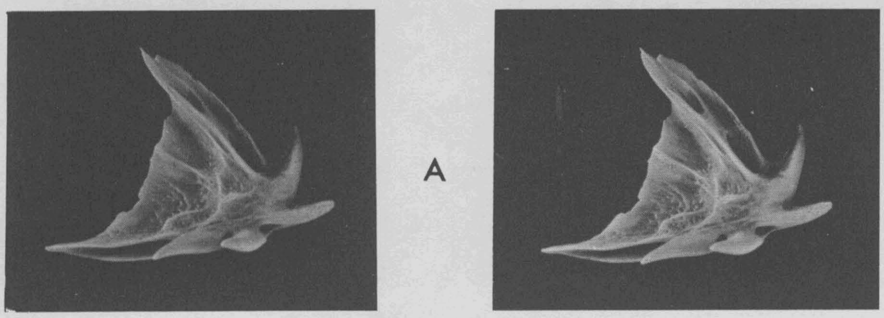
The frontal is similar to that of *Myoxocephalus q. quadricornis* (L.) in shape and canal pores, except that the spine is simple and is followed by two parallel ridges, the mesial of which may end in a postcumbent spine; the orbital rim is more strongly deflected dorsally and has a small radius, indicating small, dorsal eyes. The parietal has ridges following those of the frontals; they converge at the posterior spine, which is flanked by small sensory-canal pores. The basioccipital and parasphenoid are wider and flatter ventrally than in *Cottus* or *Myoxocephalus.* The atlas vertebra may be fused to the basioccipital and is ornate and highly modified, as in *Myoxocephalus q. quadrocornis*. It is also fused to the exoccipital, which is distinct in the 90-degree angle between the posterior process and lateral wing (*Myoxocephalus* and *Cottus* have obtuse angles).

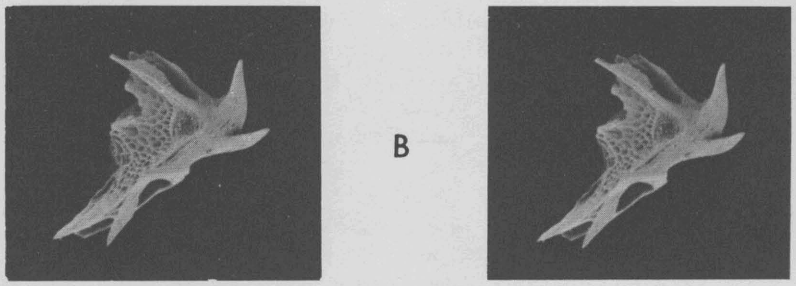
The cleithrum is elongate anteroventrally, with proportions, angles, and lamina as in *Cottus*, except that the lateral edge is confluent with that of the posterior dorsal process, as in *Myoxocephalus,* rather than ending between the dorsal processes; the basal groove is prominent. Pelvic spines, apparently belonging to this species or the next, are robust and twisted, with spiral striations. The hypural plate is completely fused except for a shallow posterior notch.

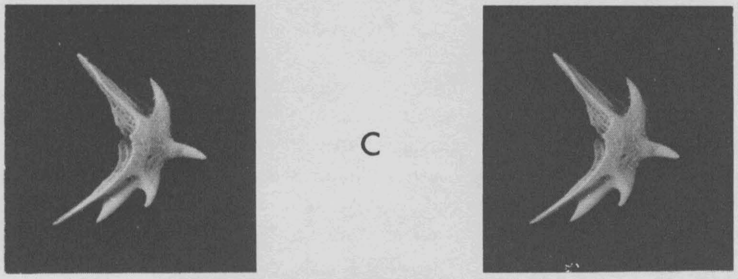
This species and presumably the others in the genus apparently had large prickles somewhere on the body. Numerous round prickles, usually 4-7 mm in diameter and bearing a single long, sharp spine on the median ridge, have been collected. The plates are low∧-shaped in cross section; the spine lies along the ridge at an angle of 30 to nearly 90 degrees. There are no associated canals or pores. The plates are too thin and the spines too long and slender to represent sturgeons.

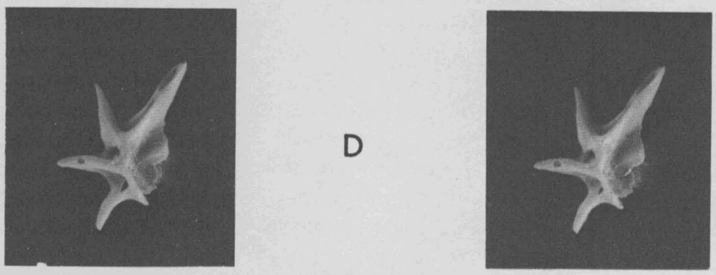
Remarks.– This species is common or abundant at all Glenns Ferry fish localities except those in the Hagerman section and at Jackass Butte, where it is absent. It is the most common sculpin at all localities except at one Poison Creek locality. It is interpreted as a lake inhabitant. Variability exists among local samples, but its interpretation requires a better chronological framework. On the basis of characteristics of this species it appears that *Kerocottus* is intermediate between *Cottus* and *Myoxocephalus.*

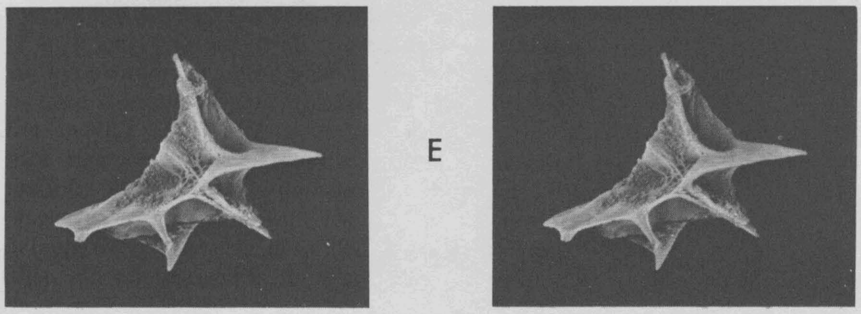
Figure 26. Lake Idaho cottids. (A-H,K) *Kerocottus divaricatus*, UMMP 59031 (not one individual). (A) Vomer. (B) Left third suborbital. (C) Right cleithrum. (D,E) Prickles. (F) Left dentary. (G) Left articular-angular. (H) Right frontal. (K) Left preopercle. (I) *Myoxocephalus antiquus*, right preopercle, UMMP 59087. (J) *Kerocottus pontifex*, left preopercle, UMMP 62051. Scales equal 1 cm.


A


B


C


D


E

Kerocottus pontifex (Cope)

(Figs. 26J; 27B; 28)

Cottus pontifex Cope 1883:163 (type AMNH 2776, right preopercle, Willow Creek, Oregon). Hussakof, 1908:69, Fig. 36. Uyeno and Miller, 1963:20. Linder, 1970:755, Fig. 1.

Taxonomy.– Most authors following Cope have been bewildered by the variation in the *divaricatus* group of cottids in the Glenns Ferry Formation. Dr. Allan D. Linder (1970) of Idaho State University first established the basis for recognizing the validity of Cope's *C. pontifex*.

Diagnosis.– A *Kerocottus* distinguishable from the other species by the enlarged sensory-canal pores of the preopercle and articular-angular; in particular, the pores on either side of the second preopercular spine exceed the diameter of the adjacent spine; ventral margin of the preopercle expanded to accomodate the large pores. The first spine projects more ventrad than in *K. divaricatus* and the third often projects more laterad than in that species.

Description.– As in *K. divaricatus* except for the following possible differences. The adductor muscle scar of the dentary is apparently more posterior – nearer the second sensory-canal pore. The articular-angular has more elongate pores, especially the posterior, which extends anteriorly to beneath the coronoid process. The frontals may be distinctive but are not yet sorted from those of *K. hypoceras*. At the Poison Creek locality, where those species are common, there are frontals with supraorbital spine reduced or absent and unusually large sensory-canal pores, probably representing *K. pontifex*. Lachrymals from the same locality are variable, probably representing three sets of species characteristics, but are not sorted out yet. Specimens with larger pores are distinctly longer anteriorly and probably represent *K. pontifex*.

Remarks.– This is the second most abundant sculpin in the Glenns Ferry Formation. It is common at Poison Creek in a lake horizon at 3200 ft. It is uncommon at Fossil Creek and Catherine Creek localities and rare in other sites except at Hagerman and Jackass Butte, from which it is absent. It is apparently a lake species. Its stratigraphic significance is not yet known.

Kerocottus hypoceras (Cope)

(Figs. 27C; 28)

Cottus hypoceras Cope 1883:164 (type, AMNH 2775, right preopercle, Willow Creek, Oregon). Hussakof, 1908:69, Fig. 36. Uyeno and Miller, 1963:20.

Cottus idahoensis, Hussakof, 1908:69, Fig. 36b (*nomen nudum* for AMNH 2780).

Taxonomy.– Preopercles here called *Kerocottus hypoceras* are similar to those of *K. pontifex* and *divaricatus*. They may be abnormal specimens in which the canals and pores of the acoustico-lateralis system are absent but they differ consistently in other characters as well. They are not uncommon and seem sufficiently distinct to warrant recognition. The types (AMNH 2780) of Cope's intended but unpublished species "*Cottus idahoensis*" (see Hussakof, 1908) have been examined and found to be identical to preopercles of *K. hypoceras*.

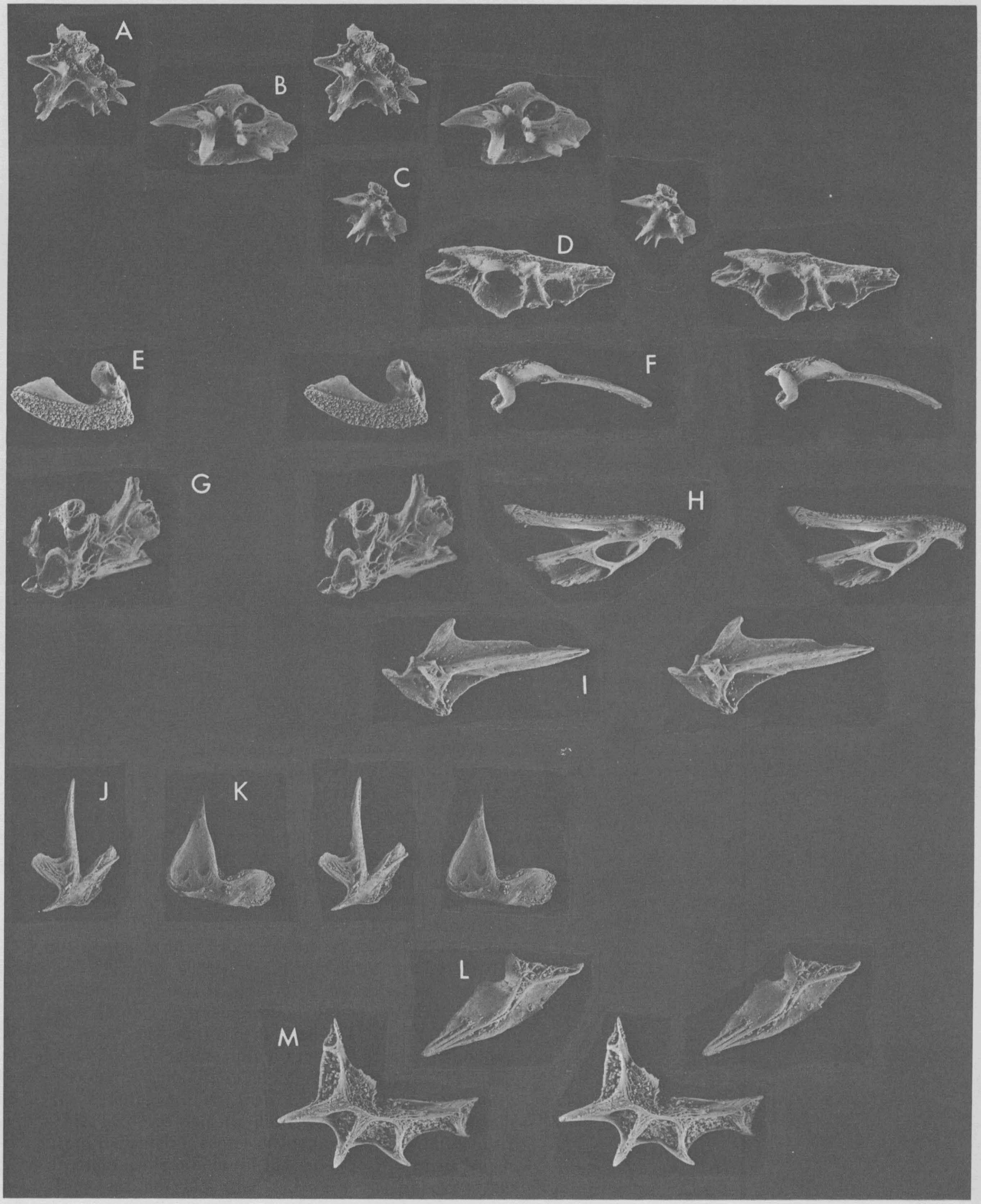
Diagnosis.– Sculpins of the genus *Kerocottus* with the preopercle lacking sensory-canal pores; its anterior spines projecting more ventrad than in *K. divaricatus* or *pontifex*; and with a prominent adductor ridge following the arc of the dorsal and anterior limbs anterodorsal to the bases of the spines.

Description.– This species is known only from its preopercles. However, the sample of lachrymals from Poison Creek, where this species is most abundant, contains one specimen (UMMP 62053, Fig. 28C), with reduced sensory-canal pores, that might belong to *K. hypoceras*. The specimen has two anteroventral spines preceded by a maxillary lamina, four spines (broken) dorsal to the central pore, and four spines (three in the basal lamina) in the postventral cluster.

Remarks.– This species is the rarest of the three *Kerocottus* currently recognized. Thirty-eight specimens have been collected from the Poison Creek locality, 26 from Crayfish Hill, two from Fossil Creek, and two from the Bennett Creek RR grade. It is presumably a lake species.

The preopercle of this species is similar to *Mesocottus haitej* Dubowski and *Cottinella boulengeri* Berg, of Lake Baikal, in the absence of an enclosed sensory canal (Taliev, 1955). If *K. hypoceras* shares the spiny suborbital bones and associated characters of the other *Kerocottus*, the similarity to forms of Lake Baikal is best interpreted as the result of convergence.

Figure 27. Lake Idaho cottid preopercles. (A) *Kerocottus divaricatus*, UMMP 59016, left. (B) *Kerocottus pontifex*, UMMP 59219, left. (C) *Kerocottus hypoceras*, UMMP 59223, left. (D) *Myoxocephalus antiquus*, holotype, UMMP 62580, right. (E) *Myoxocephalus idahoensis*, UMMP 58030, left. (Times 2)


A
B
C
D
E
F
G
H
I
J
K
L
M

Genus *Myoxocephalus* (Steller) Tilesius

Diagnosis.— Cottid fishes with teeth on premaxillae, dentaries, vomer, and pharyngeal bones but not on the palatine; spines on the nasals, preopercle, opercle, subopercle, interopercle, supracleithrum, and posttemporal; spines, cirri, or rugosity at supraocular and occipital crests; preopercular spines usually four, divergent in one plane or slightly mesiad, usually radiating anteroventrally, ventrally, postventrally, and postdorsally. (Freshwater populations often with reduced armature and much enlarged acoustico-lateralis canals and pores.)

Myoxocephalus idahoensis new species

(Figs. 27E; 28)

Holotype.— UMMP 62575, a right preopercle from the Glenns Ferry Formation, Sec. 7, T. 4 S, R. 1 E, Owyhee County, Idaho (collected by G.R. Smith et al., June 1, 1974). The bone has large sensory-canal pores, four short, relatively straight spines emanating from the mesial lamina, a long ventral limb and a short dorsal limb forming an angle of about 90 degrees, and an extensive, wide adductor shelf. The spines are hard pointed and of glassy texture; a grooved bridge extends from the base of each to the median lamina, at the edge of the adductor ridge. Measurements (mm): anterior tip to dorsal tip 14.4; anterior tip to tip of fourth (posterior) spine 17.7; length of spines (to flare of base), 1-0.6, 2-1.0, 3-2.7, 4-4.1 (broken); distance from tip to tip of spines, 1-2—5.9, 2-3—7.3, 3-4—6.3; maximum width of pores (inside distance from mesial lamina to lateral lamina, counted according to the preceding spine), 1-2.8, 2-3.2, 3-2.8, 4-2.1; maximum length of pores (bridge to bridge), 1-5.0, 2-4.0, 3-2.7, 4-4.2; minimum width of bridge, 1-0.4, 2-0.4, 3-0.4, 4-1.0, 5-0.2; maximum width of adductor shelf (above second pore), 2.7.

Paratypes.— UMMP 62576, from the same collections as the holotype: 7 premaxillae, 3 maxillae, ?2 vomers, 16 dentaries, 17 articular-angulars, 4 frontals, 9 suborbitals, and 61 preopercles. The collection also includes (UMMP 62577) 3 opercles, 4 subopercles, 2 interopercles, and 3 pelvic spines, which cannot yet be assigned to this species with certainty.

Diagnosis.— A species of *Myoxocephalus* with large sensory-canal pores in the preopercle, dentary, articular-angular, suborbitals, and frontals, differing from other large-pored forms in the presence of a large pore between preopercular spines 3 and 4; short maxilla, premaxilla, and dentary; expansion of the dentary tooth patch above the first pore; and extremely narrow sensory-canal bridge on the articular-angular.

Description.— The bones are similar to those of *Myoxocephalus quadricornis thompsoni* (Girard) except for the features noted in the diagnosis and the following. The head and palatine ridge of the maxilla occupy one-third of the length of the bone; its shaft is round, not laminar, except for the posterior one-fourth. The premaxilla is short and flat with the tooth patch inside the external lamina rather than on a shelf; the space between the ascending processes and the dorsolateral process is not much wider than the width of the ascending process. The sensory-canal pores of the preopercle, mandible, and suborbitals are always much wider than the bridges between them. The vomerine tooth patch is arcuate, short, and wide, with 3 or 4 by 15 or more rows of teeth. All opercular bones bear the usual strong spine. The suborbital bones do not bear spines. The frontal does not bear crests or spines, but there is a distinct supraorbital rugosity in the crest position. The pelvic spines are long, slender, and slightly twisted.

Remarks.— This species is rare at the Bennett Creek RR grade, Fossil Creek, Crayfish Hill, Sand Point, and Poison Creek localities. It is common in Sec. 7, T. 4 S, R. 1 E, in unique sediments that may be of deep-water origin. The living relatives of this species are generally subarctic in distribution or in deep, cold, north-temperate lakes. They are benthic.

Myoxocephalus antiquus new species

(Figs. 26I; 27D)

Holotype.— UMMP 62580, a right preopercle, from the Glenns Ferry Formation, NE¼, Sec. 14, T. 4 S, R. 1 W, Owyhee County, Idaho, elevation 2975 ft (roadcut) (collected by G.R. Smith et al., June 4, 1968). The bone is a posterior fragment with the dorsal limb and the posterior three spines complete. The three spines are moderately short, relatively straight, and directed postdorsally, posteriorly, and ventrally in the same plane. The sensory-canal pores are moderately developed. Measurements (mm): dorsal tip to tip of second (ventral) spine - 12.5, to third spine - 10.6, to fourth spine - 6.0; spine lengths, tip to base at edge of adductor ridge, second - 3.9, third - 4.7, fourth - 4.9; tip of second to tip of third - 5.2, tip of fourth to tip of third - 5.9;

Figure 28. (A-D,G) *Kerocottus* spp. (A-C) Right lachrymals of three species (?), UMMP 62053. (D) Left second suborbital, UMMP 62300. (G) First vertebra and occipital region of skull, UMMP 59401. (E-F,H-L) *Myoxocephalus idahoensis*, UMMP 62576. (E) Left premaxilla. (F) Right maxilla. (H) Right dentary. (I) Right articular-angular. (J) Left subopercle. (K) Right interopercle. (L) Right third suborbital. (M) Holotype, *Myoxocephalus idahoensis*, right preopercle, UMMP 62575. All figures times 2.

maximum width of pores (numbered according to preceding spine), second - 1.6, third - 0.8, fourth - 1.0, dorsal - 0.7; length of pores (bridge to bridge), second - 1.8, third - 0.7, fourth - 2.8, dorsal - 2.5; depth of adductor ridge, 1.2; the rim of the adductor ridge terminates abruptly at the base of the fourth spine. Angle of fourth spine to dorsal limb about 45 degrees.

Paratype.– UMMP 59087, a right preopercle, from the same horizon and locality as the holotype. Collected by G.R. Smith et al., July 26, 1971. The paratype has the same proportions, spine angles, pore arrangement, and adductor ridge characteristics as the holotype but is slightly more robust. Measurements (mm): dorsal tip to second spine - 11.7, to third spine - 10.3, to fourth spine - 6.2; spine lengths, second - 3.5, third - 4.3, fourth - 4.6; tip of second to third - 4.7, tip of fourth to third - 5.7; width of pores, first - 1.1, second - 1.0, third - 0.6, fourth - 0.6, dorsal - 0.5; length of pores, first - 2.3+, second - 1.0, third - 0.4, fourth - 2.4, dorsal - 1.9; depth of adductor ridge - 1.5. Angle of fourth spine to dorsal limb about 50 degrees.

Diagnosis.– A *Myoxocephalus* with moderately short, straight spines, the fourth much less than twice the length of the second or third; tips of second and fourth spines nearly equidistant from third, direction of third spine posterior and second spine about parallel to the dorsal limb, the pore between the third and fourth spines smaller than the diameters of the bases of the adjacent spines.

Myoxocephalus antiquus is distinguishable from species of *Cottus* in having longer, straighter spines, the second, third, and fourth relatively similar in length and radiating (posteriorly) at 30-45 degree angles from each other.

Remarks.– This species might be placed in the wrong genus. On the basis of the characters known, it is intermediate between *Cottus* and *Myoxocephalus* but most similar to species of the latter, especially *M. sellaris* (Gilbert). It has shorter spines, especially the fourth, than any of the 13 small-pored species of *Myoxocephalus* with which it has been compared. *Myoxocephalus sellaris* of Asia has similar angles of the second, third, and fourth spines, but the second is relatively shorter and the fourth relatively longer. *Myoxocephalus antiquus* is known only from Fossil Creek.

Genus *Cottus* Linnaeus

Cottus bairdi Girard, species group

Diagnosis.– Sculpins with the fourth preopercular spine short, stout, and slightly curved dorsally from an axis about 90 degrees posterior to the dorsal limb; third spine short, ventral, slightly curved anteroventrally; first and second spines sharp, but much reduced, directed anteroventrally.

Remarks.– A species of sculpin of this species group is represented at Jackass Butte (UMMP 59094, articular-angular; 59095, preopercle). The species has not yet been taken from the Pliocene sections of the Glenns Ferry Formation.

Cottidae, *incertae sedis*

A right preopercle from Crayfish Hill (UMMP 59596) is unlike any of the above forms. The short, straight fourth spine projects posteriorly at right angles to the dorsal limb. The third spine is straight, about two-thirds the length of the fourth, and projects posteriorly at an angle of less than 15 degrees from it. The short second spine is much anterior to the third and projects anteroventrally at an angle of about 100 degrees from the second. The second spine is confluent with the ventral lamina as in *Cottus* and *Myoxocephalus quadricornis*. The positions of the spines are similar to the latter species, but the spines are shorter and project in the same plane. The second and fourth pores are large; the third is smaller than the diameter of the adjacent spines. This form is probably another species of *Myoxocephalus*, but more material is needed before a description can be completed.

DISCUSSION

Zoogeography

The Lake Idaho fish fauna of the late Pliocene Glenns Ferry Formation is about twice as diverse as the richest Recent western faunas in North America (Miller and Smith, 1967). Only about one-third of the species in the fauna are represented by closest relatives in the same geographical region today. Approximately one-third are represented by closest relatives in drainages elsewhere in northern and western North America, and about one-third are apparently without known Recent representation (Table 1). This situation contrasts with that in eastern North America, where late Cenozoic fish faunas are all representative of the Recent fauna, with allowances for minor reassortment of distribution patterns during the evolution of late Cenozoic climatic extremes. In this comparison, the fish faunas are similar to molluscan faunas (Henderson, 1931; Taylor, 1966). The more active tectonic history of western America and the relative isolation of the major river basins have contributed to increased endemism, more severe late Cenozoic extinction, and a more complex hydrographic history of the region.

The search for sister groups of Glenns Ferry species has involved the comparison of known Recent and fossil members of the North American and (to a limited extent) Eurasian freshwater fishes for similarity in osteological features. Where a possible phylogenetic context is reasonably evident, primitive and advanced characteristics have been discriminated and the latter (synapomorphic characters) have been given increased weight in evaluating possible sister species. Most-similar populations or species that occupy different time frames in the same drainage basin are assumed to represent ancestor-descendant sequences. The estimated relationships of Lake Idaho species in the Glenns Ferry Formation are summarized (by drainage basin) in Table 1.

The relationships of the fossil fauna are numerically strongest with the Recent fauna occupying the present drainage system of the Glenns Ferry area, the Snake-Columbia system. However, faunas of two other regions show strong phyletic affinities – the Klamath system of Oregon and adjacent California and the Sacramento-San Joaquin system of central California (Table 1). The independence (nonoverlap) of the hypothetical ties or tracks suggests that they are remnants of separate historical connections. These biogeographic-hydrographic ties were discovered and documented by D.W. Taylor (1960, 1966) on the basis of molluscan and fish distributions and were supported by additional fish studies (Miller, 1965; Miller and Smith, 1967).

Taylor (1966) recognized two patterns, a Blancan age "fishhook"-shaped pattern extending from the Bonneville Basin through the upper Snake, across SE Oregon, and thence south through the basins just east of the Sierra Nevada to the Mohave Basin in California (Taylor, 1966: Fig. 7) and a pre-Blancan Idaho Lake–Sacramento-San Joaquin pattern. The relative ages of these patterns were estimated by the ages of the fossils involved and the larger number of species shared by the more recent "fishhook" pattern. The relationship of the Klamath system to the two patterns is undoubted but of uncertain timing.

Three criteria may be applied to estimate the sequence of the above biogeographic tracks: (1) the earliest fossil occurrences of the taxa involved, particularly in the basins of concern, (2) the relative strength of each track in numbers of species, and (3) the relative divergence of the species representing the tracks. Most of the evolutionary lines under consideration here are already present in Lake Idaho at the time of deposition of the Deer Butte Formation (Table 1), perhaps 8 million years ago; several make their appearance late in that episode (Kimmel, this volume).

Table 1. Zoogeographic affinities of fish species in the Glenns Ferry Formation

	Deer Butte Fm.	N,W, North America	Columbia R.	Sacramento R.	Klamath Dr.	"fishhook" pattern	E United States
Prosopium prolixus	U	X	?	-	-	?	-
Oncorhynchus salax	-	X	X	?	?	-	-
Rhabdofario lacustris	X	X	-	-	-	-	-
?Salmo sp.	-	X	?	?	?	?	-
Paleolox larsoni[1]	X	X	-	-	-	-	-
?Hucho sp.	-	-	-	-	-	-	-
Chasmistes spatulifer	U	-	-	-	X	X	-
Catostomus shoshonensis	X	-	-	-	X	-	-
Catostomus cristatus	X	X	X	?	?	X	-
Catostomus owyhee	X	-	-	-	X	-	-
Catostomus arenatus	?	-	X	-	-	X	-
Ptychocheilus arciferus	X	?	X	?	-	-	-
Gila milleri	-	?	?	?	X	?	-
Richardsonius durranti	-	-	X	-	-	X	-
Mylopharodon hagermanensis	-	-	-	X	-	-	-
Idadon condonianus	X	-	-	?	-	-	-
Idadon hibbardi	X	-	-	?	-	-	-
Mylocheilus robustus	X	-	X	-	-	-	-
Mylocheilus inflexus	X	-	-	-	-	-	-
Orthodon hadrognathus	X	-	-	X	-	-	-
Acrocheilus latus	X	-	X	-	-	-	-
Ictalurus vespertinus	X	-	-	-	-	-	X
Archoplites taylori	X	-	-	X	-	-	-
Kerocottus divaricatus	U	?	-	-	-	-	-
Kerocottus pontifex	-	?	-	-	-	-	-
Kerocottus hypoceras	-	?	-	-	-	-	-
Myoxocephalus idahoensis	?	N	-	-	-	-	-
Myoxocephalus antiquus	-	N	-	-	-	-	-

U - Upper Deer Butte Formation only
X - Presence
? - Questionable sister species
N - Northern
[1] See Kimmel, this volume

The Lake Idaho-Sacramento track is thus seen to antedate the Klamath and "fishhook" connections, as pointed out previously by Taylor (1966). The three obvious remnants of that connection among the fishes, the species pairs of *Mylopharodon, Orthodon,* and *Archoplites,* are most distinct. Other possible evidence of this track has diverged sufficiently to make any relationships unclear. The shared fishes of Lake Idaho and the Klamath system were probably shared no earlier than late in the time of deposition of the Deer Butte Formation. The connections between Lake Idaho and the fishhook pattern were probably partly contemporaneous. The time was clearly Blancan in the sense of Taylor (1966). The Lake Idaho fauna shares about the same proportion of elements with the fishhook pattern and the Klamath system, and there is some overlap among the species shared with each. The amount of divergence between taxa shared by Lake Idaho and the

Table 2. Ecological characteristics and occurrences of fish species in the Glenns Ferry Formation.

	Approximate Adult Size (m)			Habitat and Substrate				Trophic Adaptation				
	.2	.5	1	River	Creek	Sand	Silt	Small Carnivore	Large Carnivore	Molluscivore	Planktivore	Herbivore
Prosopium prolixus	-	x	-	?	u	c	c	x	-	-	?	-
Oncorhynchus salax	-	x	?	?	?	?	u	?	?	-	x	-
Rhabdofario lacustris	-	-	x	?	-	c	c	-	x	-	-	-
Salmo sp.	-	x	-	?	?	-	-	x	?	-	-	-
Paleolox larsoni[1]	-	-	x	?	-	-	-	-	x	-	-	-
Chasmistes spatulifer	-	x	-	c	u	c	c	-	-	-	x	-
Catostomus shoshonensis	-	x	-	c	c	c	c	-	-	-	?	?
Catostomus cristatus	-	x	-	c	u	c	c	-	-	-	?	?
Catostomus owyhee	-	x	-	c	-	c	c	-	-	-	?	?
Catostomus arenatus	x	-	-	?	?	-	-	-	-	-	-	x
Ptychocheilus arciferus	-	-	x	c	c	c	c	-	x	-	-	-
Gila milleri	-	x	-	-	u	-	u	x	-	-	-	-
Richardsonius durranti	x	-	-	u	u	-	-	x	-	-	-	-
Mylopharodon hagermanensis	x	?	-	-	c	-	-	x	-	-	-	-
Idadon condonianus	-	x	-	-	-	c	-	x	-	?	-	-
Idadon hibbardi	x	-	-	-	-	-	c	x	-	-	-	?
Mylocheilus robustus	-	x	?	c	-	c	c	-	-	x	-	-
Mylocheilus inflexus	-	x	?	u	-	-	-	-	-	x	-	-
Orthodon hadrognathus	-	x	-	?	?	?	u	-	-	-	-	x
Acrocheilus latus	-	x	-	c	c	c	c	-	-	-	-	x
Ictalurus vespertinus	-	x	-	c	c	u	u	x	?	-	-	-
Archoplites taylori	-	x	-	c	c	c	c	x	?	-	-	-
Kerocottus divaricatus	x	-	-	?	-	c	c	x	-	-	-	-
Kerocottus pontifex	x	-	-	-	-	-	u	x	-	-	-	-
Kerocottus hypoceras	x	-	-	-	-	-	u	x	-	-	-	-
Myoxocephalus idahoensis	x	-	-	-	-	-	u	x	-	-	-	-
Myoxocephalus antiquus	x	-	-	-	-	-	u	x	-	-	-	-

c - Common
u - Uncommon

[1] See Kimmel, this volume

Klamath system (*Chasmistes, Catostomus*) may be slightly greater than among other combinations. On the other hand, until the salmonids are better understood, the data are incomplete. The connection could well be multiple, complex, and in part earlier than 8 million years ago. The general connections to the north, northwest, and east were probably earlier than 8 million years ago.

Geological evidence for the connection between Lake Idaho and the Sacramento system was first presented by H.E. Wheeler and E.F. Cook (1954) in a thorough elucidation of the post-Miocene Snake River history. They suggested that the former "Snake may have had a southwesterly course from western Idaho, through southeastern Oregon via the general route of the lower Owyhee River and Crooked Creek. . .; southward east of the Steens, Pueblo, and Pine Forest Mountains; again southwestward across northwestern Nevada via Black Rock and Snake Creek deserts and eastern Honey Lake Valley; southward immediately west of the California-Nevada boundary to Chilcoot Pass; and thence westward into Feather River."

The fish faunas of the Deer Butte and Glenns Ferry formations indicate a long, relatively continuous existence of a lake fauna (see below), only a limited part of which is represented in the Sacramento-San Joaquin basins today. The connection was probably limited either in time (early) or by habitat barriers to dispersal of lake fishes. The present course of the Snake through Hells Canyon was established in the early Pleistocene (Wheeler and Cook, 1954), and probably marks the end of Lake Idaho and the lacustrine fauna and the beginning of the Snake-Columbia fluviatile fauna.

Ecology

The Lake Idaho fish fauna is regarded as lacustrine (except at Hagerman) for the following reasons: (1) The diversity of 25 or more species is much greater than that expected in a fluviatile fauna near 3000 ft in elevation and 43 degrees N latitude in western North America. (2) The large size attained by nearly all members of the fauna (Table 2), especially by the three predators that grew to about 1 m, indicates a larger volume of habitat than is normally provided by rivers at that elevation. (3) The Glenns Ferry Formation shows a remarkable paucity of coarse clastic material and sedimentary structure. If the fish inhabited a river large enough to support the diversity and size of individuals observed, coarser sediments and more sedimentary structure should be present.

Nevertheless, much evidence exists for fluviatile deposition. The Hagerman section is predominantly floodplain in origin (Malde and Powers, 1962; Zakrzewski, 1969; Bjork, 1970; Malde, 1972), and it completely lacks the characteristic Lake Idaho fishes, such as *Mylocheilus, Idadon,* and the five species of cottids (Table 2). The evidence for fluvial deposition at Sand Point is accompanied by many of the lacustrine fishes, but with a higher than normal incidence of *Ictalurus*, a likely fluviatile indicator. All other localities produce the standard Lake Idaho fauna with sediments ranging from very fine sands and silts to granule sands, and occasional evidence of sedimentary structure. The apparent debris flow, including cobbles, wood, mollusks, and vertebrate fossils, at Horse Hill is a special case. Several kinds of trout unknown from elsewhere in the fauna accompany the lake fishes in this unit. (Further study of this unusual situation is planned.) In general the only distinct correlations between sedimentary environment and fauna not included in the above special cases are the positive correlation between occurrences of *Ictalurus* (catfish) fossils and coarser sediments, and the association of sculpins (Cottidae), especially *Myoxocephalus*, with finer sediments only. The characteristic pale yellow lacustrine silts of the Glenns Ferry Formation have produced no fossil fishes, though mollusks are present (Taylor, 1966).

It is tentatively concluded that the basic fauna inhabited a lake (except at Hagerman) and is preserved in a variety of shore facies that accumulated at various depths. Distributary channels (e.g., Crayfish Hill), offshore bars (e.g., Shoofly), and low discharge tributaries are apparently represented. The pale yellow silts might have been deposited in a soft, oozy, flocculent environment that was not frequented by the diversity of endemic mollusks (Taylor, 1966), other fish-food organisms, or fishes. Assuming that the lake might have had a maximal size similar to that of Lake Ontario, the number of recognized species is slightly smaller than that predicted by Barbour and Brown's (1974) regression of species number on area for world lakes.

Table 2 summarizes the occurrence of the species by habitat. Reference to a river habitat is based primarily on the Horse Hill situation. The "creek" designation refers to my estimation of low-discharge, marshy habitat in the Hagerman area (compare Bjork, 1970; Malde, 1972). The fish distribution requires an environment that totally excluded the basic lacustrine elements. If the barrier was not ecological, then a barrier falls or a post-Lake Idaho time must be hypothesized. *Mylocheilus* spp., *Idadon* spp., and the sculpin species are present only west of Hagerman, from Sand Point and Bennett Creek RR grade to Oregon; *Mylopharodon hagermanensis* is rare west of Hagerman.

The trophic adaptations of Lake Idaho fishes were more diverse than in any other late Cenozoic or Recent freshwater fauna in North America. *Mylocheilus robustus* and *inflexus* are unique in the possession of large molariform mollusk-crushing pharyngeal teeth. *Prosopium prolixus* is unique among known whitefish in the large jaws and large body size. *Oncorhynchus salax* is unique in the high number of plankton-straining gill rakers. *Idadon* spp. and *Acrocheilus latus* are unique in their grinding pharyngeal teeth – the former because of the striate grinding surface, the latter in the extremely large size. The diversity represented by at least five sympatric species of sculpins, some of which approached 1 ft in length is remarkable for North America, but does not approach the 26 species of this family of fishes in Lake Baikal (Taliev, 1955). On the other hand, inspection of the osteological diversity of the Baikal forms as figured by Taliev suggests that five species could well be a gross underestimate of the actual diversity represented by the sculpin bones from Lake Idaho. Many of the sculpins in Lake Baikal are very similar to each other in their osteology.

The sculpins represent the small, benthic predators on crustaceans of Lake Idaho. *Prosopium prolixus* and *Oncorhynchus salax* probably fed on zooplankton also, but the size of the jaws in these salmonids suggests piscivorous predation as well. The other salmonids were piscivores: *Rhabdofario lacustris* was one of the two large, top carnivores in the system; the second was *Ptychocheilus arciferus.* The catostomids were probably benthic, small-particle omnivores, except for *Chasmistes spatulifer,* which is shown by the length, angle, and symphysis of the dentaries to be a midwater planktivore. Among the other minnows, *Orthodon hadrognathus* and *Acrocheilus latus* were herbivores; *Gila milleri* and *Richardsonius durranti* were apparently uncommon, medium and small midwater carnivores; *Mylopharodon* and *Idadon condonianus* were possibly medium to small omnivores that frequently took mollusks; the grinding surfaces on pharyngeal teeth of *Idadon hibbardi* suggest that this small, abundant minnow was an herbivore. *Ictalurus vespertinus* was probably a medium-sized, nocturnal omnivore, scavenger, and carnivore. *Archoplites taylori* was a medium-sized predator.

The most striking climatic indicators in the fauna are the sculpins of the genus *Myoxocephalus*, which are arctic or deep-water, north-temperate lake inhabitants today. By contrast North American catfish and sunfish (e.g., *Ictalurus* and *Archoplites*) are temperate elements whose modern relatives are cold-limited to ranges south of southern Canada. The only place *Myoxocephalus, Ictalurus*, and sunfish are sympatric today is in the Great Lakes, suggesting that Lake Michigan and Lake Huron might be the closest modern analogues to Lake Idaho in North America. Lake Baikal might also be considered an ecological and evolutionary analogue.

Evolution

The most striking evolutionary features of the Lake Idaho fishes center on the diversity and extreme specializations of the species in relation to their counterparts in western North America and in other North American freshwater fish faunas. Despite the antiquity of the fauna and the presence of a variety of primitive features among osteological characters of the species, one totally unexpected generalization emerges from comparison of the forms from Lake Idaho with their known Recent counterparts. In most cases in which the sister species (or in the case of geographic stasis, the probable descendant form) is identifiable, the Lake Idaho species, not the Recent relative possesses the most advanced state of the shared-derived characters that define the relationship of the pair or their group.

This unusual situation must be viewed in the ecological and evolutionary background of the Lake Idaho-Snake River history. The lake apparently had a long, relatively stable history during at least four to ten million years of Pliocene and Miocene time, in which minor species flocks of catostomids, cyprinids, and cottids evolved or at least accumulated through dispersal from other drainages. There is no evidence contrary to the possibility that Lake Idaho was one of the primary centers of evolution of western American fishes during this time. But as the basin filled with sediments and the drainage was captured by the Columbia system, it became a segment of an arid-lands fluviatile system, and the fauna was transformed into a depauperate, rather generalized remnant of the former specialized diversity. This is not an unusual pattern in evolutionary history; it has been observed many times (e.g., Taylor, 1966; Lipps, 1970), but the faunal succession is usually interpreted as the survival of generalized members, which may become the stem forms from which later adaptive radiations diverge. In the case of the history recorded here, it appears that the diversity of specialized forms may have evolved directly to more generalized representatives under common environmental control in 3 to 10 instances and suffered direct extinction in about 10 others. The evidence is as follows:

1) *Oncorhynchus salax* and its Recent sister species (descendant?), *O. nerka*, differ from other members of the genus primarily in the specialized possession of more gill rakers; the fossil species has more gill rakers than the Recent form. In this case, numerous gill rakers is specialized in an ecological sense but could be plesiomorphic in a cladistic sense.

2) *Prosopium prolixus* is the most extreme member of the genus in the possession of specialized elongate maxillae and dentaries (Fig. 7). The present inhabitant of the Snake-Columbia system and other western drainages, *P. williamsoni*, has the standard, short jaw form typical of most members of the genus and most related forms. Two other species of *Prosopium* have elongate jaws, *P. gemmiferum* of Bear Lake (part of the zoogeographic fishhook pattern) and *P. coulteri* of northwestern lakes and streams and Lake Superior. The relationship of *P. prolixus* with these species is uncertain, but it is the most extreme and presumably the most advanced member of the group in jaw morphology.

3) *Chasmistes spatulifer* has elongate, unusually-angled dentaries and anteriorly-directed premaxillary processes of the maxillae as a basis for its terminal-mouthed planktivorous food habits. All other members of the genus are somewhat more similar to the generalized sister genus, *Catostomus*. The fossil form is similarly advanced in the short, broad neurocranium and other features of the skull (Figs. 8, 9B). The Recent species are clearly more plesiomorphic in all of these characters. None is likely to be a descendant of *C. spatulifer*, although several [*C. cujus* (Pyramid Lake), *C. brevirostris* (Klamath system), and an undescribed species in the upper Snake River] are zoogeographically associated (Table 1).

4) *Catostomus owyhee* is probably a sister species to *C. luxatus* of the Klamath system. The fossil species is clearly the more advanced member of the pair, which in turn represents the most advanced section of the genus in the elongation of the skull, especially anteriorly, and specializations in shape and muscle attachments of the jaw bones (Figs. 11; 12B,F,K).

5) *Ptychocheilus arciferus* is very likely the direct ancestor of *P. oregonensis*. They are similar and endemic to an extensive area in common. The only likely alternative would be sister-group status and a history of replacement of *arciferus* by *oregonensis* at about the time of

the capture of the Snake River by the Columbia system – an unnecessarily complicated explanation for which there is no evidence. The differences between the species involve the longer anterior limb of the pharyngeal arch (Figs. 15A; 21B) and the greater number of sensory-canal pores in *P. arciferus*. These are primary characters by which the genus *Ptychocheilus* differs from its less specialized sister genus, *Gila*.

6) *Acrocheilus latus* is probably ancestral to *A. alutaceus* (see map, Miller and Smith, 1967). The fossil species is more extremely specialized in the characters that differentiate the two species from all other American cyprinids: the long sharp grinding surfaces on the pharyngeal teeth and the long, sigmoid dorsal limb of the pharyngeal arch. The Recent species has more generalized teeth with vestiges of the hooks found on teeth of most other western minnows, and an unspecialized dorsal limb of the pharyngeal arch.

7) *Orthodon hadrognathus* may be a sister species to *O. macrolepedotus* (Table 1). *Orthodon* differs from other genera in the flatness of the gnathic edge of the dentary, the angle of the pharyngeal process of the basioccipital, and the shape of the pharyngeal arch. The fossil species is apparently plesiomorphic in the last two characters but is more specialized in the first (see Kimmel, Fig. 4, this volume).

8) *Mylocheilus robustus* is probably the ancestor of *M. caurinus* (Table 1). The fossil species is more specialized than the Recent in the degree of molariform development of the teeth (Figs. 15C; 17D) and associated modifications of the arch – the diagnostic characters of the genus.

9) *Mylopharodon hagermanensis* is the sister species and only congener of *M. conocephalus* (Table 1). The fossil species has a more specialized pharyngeal arch in that the dorsal limb is longer and the anterior limb is shorter and more sharply deflected (Fig. 17A). The arch of the Recent species is more like that of generalized, related genera such as *Gila*.

10) *Myoxocephalus idahoensis* may be a sister group to *M. quadricornis thompsoni*. The two are the only species of freshwater sculpins in North America characterized by greatly enlarged sensory-canal pores. The fossil species is more extreme in this obviously derived character in that all of the pores, including that between spines 3 and 4, are fully expanded.

11) *Idadon* was a specialized cyprinid fish with grinding surfaces on the pharyngeal teeth (Fig. 16B) that are unmatched among other American cyprinids. The evolutionary line is now either extinct or represented by a completely generalized form such as *Pogonichthys*.

12) *Kerocottus* was represented in Lake Idaho by three species with specialized opercular armature unmatched elsewhere in the family (Fig. 27). The group apparently suffered complete extinction with the end of the lacustrine habitat of Lake Idaho.

The above list supports the generalization that the specialized lacustrine fauna of Lake Idaho underwent evolution that resulted in generalized survivors or extinction with the end of the lacustrine habitat. At least three, and probably more, of the above examples involved direct evolution to "less specialized" forms. The examples are based on trophic and defensive specializations in a system initially characterized by greater trophic diversity than any other known late Cenozoic (including Recent) North American lake. Sedimentary filling of the lake, a new, lower drainage outlet, and onset of desert conditions surrounding the resulting large river habitat were sufficient to cause collapse of the spatial diversity, climatic and temporal stability, and trophic system. The result was a selective regime that produced smaller individuals with more generalized feeding adaptations in the few species that survived.

ACKNOWLEDGMENTS

Initiation and completion of this project were made possible by Claude W. Hibbard, Robert R. Miller, and Dwight W. Taylor, who provided the initial stimulus, specimens, and guidance for the work. The illustrations were patiently produced by Krys Butterfield, Debra Bennett, Susann Jacobshagen, and Nancy Neff. Mr. Karoly Kutasi did the photographic work.

To the many people who participated in the field work, I express my gratitude and my fond reminiscence of sunny days and sagebrush campfires: Bob Miller and his family, Ted Uyeno, Dan Sable, Dick and Judy Koehn, Pete Kimmel, Debra Bennett, Jerry Larson, Nancy Neff, Bruce Wilkinson, Joe McGowan, Ruth Elder, Bob Bright, Dwight Taylor, and especially Beverly, Kathy, Cindi, and Keith Smith. Rick Zakrzewski, Phil Bjork, Bill Melton, and others in the legendary Hibbard field parties also collected a tremendous quantity of fossils. Additional specimens were kindly loaned by the American Museum of Natural History, The Museum of Comparative Zoology, The U.S. National Museum, and the Museum of Paleontology, University of California. Colleagues at the University of Utah and the University of Kansas, especially Frank B. Cross and E.R. Hall, provided substantial assistance. Financial support was provided by the University of Michigan Museum of Paleontology under R.V. Kesling and an N.S.F. grant for work with R.K. Koehn.

Pete Kimmel, Nancy Neff, Russ King, Krys Butterfield, Mary Cismar, and Beverly Smith helped with sorting and cataloguing. John Lundberg, Reeve Bailey, Robert Miller, Gerald Larson, Phil Gingerich, and Pete Kimmel made many helpful suggestions in valuable discussions.

Typing was done by Nancy Friedland, Beverly Smith, Ocie Hess, and Gladys Newton. Robert Miller read and improved the manuscript. Nancy Friedland edited and composed this and the other volumes in the Claude W. Hibbard memorial series.

LITERATURE CITED

Armstrong, R.L., W.P. Leeman, and H.E. Malde. 1975. K-Ar dating, Quaternary and Neogene volcanic rocks of the Snake River Plain, Idaho. Amer. J. Sci., 275:225-251.

Barbour, C.D., and J.H. Brown. 1974. Fish species diversity in lakes. Amer. Natur., 108:473-489.

Bjork, P.R. 1970. The Carnivora of the Hagerman local fauna (late Pliocene) of southwestern Idaho. Trans. Amer. Phil. Soc. Philadelphia, 60(pt. 7):3-54.

Cavender, T.M., and R.R. Miller. 1972. *Smilodonichthys rastrosus*, a new Pliocene salmonid fish. Mus. Nat. Hist. Univ. Oregon Bull., 18:1-45.

Cope, E.D. 1870. On the fishes of a fresh water Tertiary in Idaho, discovered by Capt. Clarence King. Proc. Amer. Phil. Soc., 11:538-547.

Cope, E.D. 1883a. On the fishes of the Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake. Proc. Acad. Nat. Sci. Philadelphia, 35:134-167.

Cope, E.D. 1883b. A new Pliocene formation in the Snake River Valley. Amer. Nat., 17:867-868.

Eaton, G.P., et al. 1975. Magma beneath Yellowstone National Park. Science, 188(4190):787-796.

Henderson, J. 1931. Molluscan provinces in the western United States. Colorado Univ. Stud., 18:177-186.

Hussakof, L. 1908. Catalogue of type and figured specimens of fossil vertebrates in the American Museum of Natural History. Part I. Fishes. Bull. Amer. Mus. Nat. Hist., 25:1-103.

Jordan, D.S., and B.W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus., 47.

Kimmel, P.G. 1975. Fishes of the Miocene-Pliocene Deer Butte Formation, southeast Oregon. Univ. Michigan Mus. Paleont. Pap. Paleont., 14:69-87.

Leidy, J. 1870. [Remarks on *Elephas americanus* and *Bison americanus* from Kansas and on new fossil fishes from the Rocky Mountains region.] Proc. Acad. Nat. Sci. Philadelphia, 22:69-71.

Leidy, J. 1873. Contributions to the extinct vertebrate fauna of the western territories. Rep. U.S. Geol. Geogr. Surv. Terr., 1(1):1-358.

Linder, A.D. 1970. Fossil sculpins (Cottidae) from Idaho. Copeia, 1970(4):755-756.

Linder, A.D., and D.G. Koslucher. 1974. A partial *Diastichus* (Cyprinidae) skeleton from Plio-Pleistocene Lake Idaho. NW Sci., 48(3):180-182.

Lindgren, W., and N.F. Drake. 1904. Silver City, Idaho. U.S. Geol. Surv. Geol. Atlas U.S., Folio 104:1-6.

Lindsay, E.H., N.M. Johnson, and N.D. Opdyke. 1975. Preliminary correlation of North American land mammal ages and geomagnetic chronology. Univ. Michigan Mus. Paleont. Pap. Paleont., 12:111-120.

Lipps, J.H. 1970. Plankton evolution. Evolution, 24(1):1-22.

Lucas, F.A. 1901. Vertebrate fossils found in Idaho beds. U.S.G.S. Rept., 20(3):99.

Lundberg, J.G. 1970. The evolutionary history of North American catfishes, family Ictaluridae. Doctoral thesis, Univ. Michigan:1-524.

Lundberg, J.G. 1975. The fossil catfishes of North America. Univ. Michigan Mus. Paleont. Pap. Paleont., 11:1-51.

Malde, H.E. 1972. Stratigraphy of the Glenns Ferry Formation from Hammett to Hagerman, Idaho. U.S.G.S. Bull., 1331-D: 1-19.

Malde, H.E., and H.A. Powers. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. Bull. Geol. Soc. Amer., 73:1197-1220.

Miller, R.R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Amer. Assoc. Adv. Sci. Publ., 51:187-222.

Miller, R.R. 1965. Quaternary freshwater fishes of North America. *In* H.E. Wright, Jr., and D.G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton:569-581.

Miller, R.R., and G.R. Smith. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occ. Pap. Mus. Zool. Univ. Michigan, 654:1-24.

Newberry, J.S. 1870a. The ancient lakes of western America, their deposits and drainage. Proc. New York Lyc. Nat. Hist., 1:25-32.

Newberry, J.S. 1870b. The ancient lakes of western America, their deposits and drainage. Nature, 2:385-387.

Newberry, J.S. 1871a. The ancient lakes of western America, their deposits and drainage. U.S. Geol. Geogr. Surv. Terr. Ann. Rep., 4:329-339.

Newberry, J.S. 1871b. The ancient lakes of western America, their deposits and drainage. Amer. Natur., 4:641-660.

Russell, I.C. 1902. Geology and water resources of the Snake River Plains of Idaho. U.S. Geol. Surv. Bull., 199:1-192.

Smith, G.R. 1963. A late Illinoian fish fauna from southwestern Kansas and its climatic significance. Copeia, 1963(2):278-285.

Smith, G.R. 1965. Distribution and evolution of the North American fishes of the subgenus *Pantosteus*. PhD Dissert. Univ. Michigan:1-359.

Smith, G.R. 1966. Distribution and evolution of the North American catostomid fishes of the subgenus *Pantosteus*, genus *Catostomus*. Misc. Publ. Mus. Zool. Univ. Michigan, 129:1-132.

Smith, G.R. 1973. Analysis of several hybrid cyprinid fishes from western North America. Copeia, 1973(3):395-410.

Smith, G.R., and R.K. Koehn. 1969. Phenetic and cladistic studies of biochemical and morphological characteristics of *Catostomus*. Syst. Zool., 20(3):282-297.

Sneath, P.H.A., and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Company, San Francisco, 573 pp.

Taliev, D.N. 1955. Sculpins of Baikal (Cottoidei). Acad. Sci., USSR, Moscow, 602 pp.

Taylor, D.W. 1960. Distribution of the freshwater clam *Pisidium ultramontanum*; a zoogeographic inquiry. Amer. J. Sci. Bradley vol. 258A:325-334.

Taylor, D.W. 1966. Summary of North American Blancan nonmarine mollusks. Malacologia, 4(1):1-172.

Uyeno, T. 1960. Osteology and phylogeny of the American cyprinid fishes allied to the genus *Gila*. PhD Dissert. Univ. Michigan:1-174.

Uyeno, T. 1961. Late Cenozoic cyprinid fishes from Idaho with notes on other fossil minnows in North America. Pap. Michigan Acad. Sci., 46:329-344.

Uyeno, T., and R.R. Miller. 1962. Late Pleistocene fishes from a Trinity River terrace, Texas. Copeia, 1962(2):338-345.

Uyeno, T., and R.R. Miller. 1963. Summary of late Cenozoic freshwater fish records for North America. Occ. Pap. Mus. Zool. Univ. Michigan, 631:1-34.

Wheeler, H.E., and E.F. Cook. 1954. Structural and stratigraphic significance of the Snake River capture, Idaho-Oregon. J. Geol., 62:525-536.

FISHES OF THE MIOCENE-PLIOCENE DEER BUTTE FORMATION, SOUTHEAST OREGON

Peter G. Kimmel

Abstract.– The fish fauna of the Deer Butte Formation consists of about 24 species represented by disarticulated fossils found in loosely consolidated siltstones, sandstones, and conglomerates. The sediments were probably deposited in a floodbasin or lakeshore environment. There are no radiometric dates associated with these sediments, but they may correlate with the Poison Creek Formation to the south, which is dated at about 11 million years b.p. In other areas the Deer Butte Formation contains mammal faunas of Barstovian age (upper Miocene).

The Blackjack Butte local fauna differs by several species from the rest of the Deer Butte local faunas and is similar to the Glenns Ferry fish fauna. It is above the Blackjack Basalt Member of the Deer Butte Formation. This newly recognized member was first named the Blackjack Basalt (Bryan, 1929) and then synonomized with the Owyhee Basalt (Kittleman et al., 1965). Although lithologically similar to the Owyhee Basalt, this member is contained in Deer Butte sediments and has been mapped separately from the Owyhee Basalt (Bryan, 1929). The local faunas below this member represent a recognizable earlier stage.

Six families are present in this fauna: Salmonidae, Catostomidae, Cyprinidae, Ictaluridae, Centrarchidae, and Cottidae. The salmonids in the fauna include two large carnivores, *Rhabdofario* and the new genus *Paleolox*, a smaller species of uncertain affinities (below the Blackjack Basalt), and a large whitefish of the genus *Prosopium* (above that member). Catostomids are abundantly represented by about five species of *Catostomus*, with one species of *Chasmistes* occurring only in the upper part of the formation. The cyprinids are the most diverse family with about eight species in five genera, including a large predator in *Ptychocheilus*, three large herbivores in *Acrocheilus* and *Orthodon*, two large and abundant molluscivores in *Mylocheilus*, and a rare herbivore and rare molluscivore in *Idadon.* The catfish are represented by one species in *Ictalurus*, and the sunfishes by a species in *Archoplites.* Sculpins include species in *Cottus, Myoxocephalus,* and *Kerocottus.*

The stratigraphically higher Blackjack local fauna may come from a later stage of Lake Idaho like that of the Glenns Ferry Formation. The lower Deer Butte fauna differs from the Glenns Ferry fauna in several species of Salmonidae, Cyprinidae, and Cottidae. The relative lack of midwater carnivores, planktivores, and lacustrine sculpins may reflect the influence of the environment of deposition or the stage of evolution of the fauna.

FOSSIL FISHES in the Deer Butte Formation represent an early stage in the development of the Lake Idaho fauna. Their occurrence is in Miocene and Pliocene rocks at the southwest end of the Snake River Plain. Fishes discussed in this paper were collected from five localities in Malheur County, Oregon, between 1962 and 1975, especially during the summer of 1974. The localities are:

Tunnel Road locality: SE Sec. 16, T. 22 S, R. 46 E, at 2600 ft (792 m).

Tunnel Mountain locality: SW¼, Sec. 22, T. 22 S, R. 46 E, ca. 2600 ft (792 m).

Desert Pavement locality: NW¼, Sec. 16, T. 22 S, R. 46 E, ca. 2750 ft (838 m).

Shenk Ranch locality: NE¼, Sec. 2, T. 23 S, R. 46 E, at 2540 ft (774 m).

Blackjack locality: NE¼, Sec. 7, T. 22 S, R. 46 E, ca. 3200 ft (975 m).

All of the localities are in an area mapped by Kittleman et al. (1967) as Deer Butte Formation, which they regard as upper Miocene to lower Pliocene.

The Tunnel Mountain and Tunnel Road localities are believed to be equivalent in stratigraphic position because of the occurrence at each locality of a white ash marker bed associated with the fossiliferous layer and underlain by a gray ash and a lower yellowish ash. At the Tunnel Mountain locality, the gray ash occurs 56 ft below the white ash, and the yellow-stained ash is 2 ft below the gray ash. Near the Tunnel Road locality, a gray ash occurs about 20 ft below the white ash, and a yellow ash appears 5 ft below the gray ash. At both locations, fossil fish occur in sediments below the white ash. The Desert Pavement locality is stratigraphically only a few hundred feet below these localities. Its horizon can be traced below the Tunnel Road locality. The Shenk Ranch locality is not definitely related to the other localities and appears to be in a faulted valley. Because of its elevation, the presence of a white ash on the opposite side of the valley, and its close proximity to sediments of the Poison Creek Formation, it is probably near the same stratigraphic level as the previous locations. The Blackjack locality, however, seems to be stratigraphically higher than the other localities, and its sediments are separated from the rest of the Deer Butte Formation by a basalt flow on Blackjack Butte.

The geology of the area of these fish localities was first studied in detail by Bryan (1929). He believed the sediments were part of the Payette Formation; this term has since been abandoned. Bryan defined the basalt on Blackjack Butte as a separate formation, the Blackjack Basalt. On the basis of lithologic similarity, Kittleman et al. (1965) synonymized this basalt with the Owyhee Basalt, also defined and mapped by Bryan (1929). However, the stratigraphic relations of the Blackjack Basalt are totally different from the Owyhee Basalt, and thus the Blackjack Basalt should be regarded as a separate unit. The Blackjack Basalt is contained in sediments that have been mapped as Payette Formation (Bryan, 1929), Chalk Butte Formation (Corcoran et al., 1962), and Deer Butte Formation (Kittleman et al., 1967). The Owyhee Basalt unconformably overlies the Sucker Creek Formation and is unconformably overlain by the Deer Butte Formation or formations regarded as its equivalent (Bryan, 1929; Corcoran et al., 1962; Kittleman et al., 1965; Beaulieu, 1972). Because the Blackjack Basalt is completely contained within the Deer Butte Formation or within equivalent formations mapped in that area by other stratigraphers, and because the Deer Butte Formation includes several other basalt members, the Blackjack Basalt should be regarded as a member of the surrounding formation.

The age and formation to which the sediments containing the fish should be assigned is still uncertain. Corcoran et al. (1962) abandoned Bryan's (1929) Payette Formation because of confusion about the type locality and "the impossibility of tracing Miocene stratigraphic units across the Snake River plains into Oregon," and mapped the area as part of the Pliocene Chalk Butte Formation. Kittleman et al. (1967) mapped the area as part of the Miocene-Pliocene Deer Butte Formation. Because this work is the latest and most comprehensive for this area, the Deer Butte Formation is tentatively accepted as the name for these sediments.

No absolute dates or mammalian age determinations have been made for this area. Kittleman et al. (1965) believe that the upper part of the Deer Butte Formation is laterally contiguous with the Poison Creek Formation, which has been dated at approximately 11 m.y. old by Armstrong et al. (1975) on the basis of K-Ar dates of an overlying basalt. Fission-track dating of volcanic ashes associated with the fossil localities may provide verification of the correlation of the Poison Creek and Deer Butte formations and help establish dates for the sediments and fish fauna of this area.

The fish fauna of the Deer Butte Formation includes 15 genera and about 24 species. Its closest affinities are to the younger fish fauna of the Glenns Ferry Formation in adjacent Idaho. In the species accounts that follow, synonomies and taxonomic data are not repeated if they occur in Smith's report on the fish fauna of the Glenns Ferry Formation (this volume).

Family **Salmonidae**

The salmon fauna of the Deer Butte Formation is large and almost completely undescribed. It consists of three genera and three or more species. All of the new species are members of the subfamily Salmoninae, which includes trouts, salmons, and chars. The remaining species is an extinct whitefish, subfamily Coregoninae, represented only be sparse material. Stratigraphy of the area indicates that the whitefish is from younger sediments than the rest of this group.

Subfamily SALMONINAE

Paleolox new genus

The description and diagnosis of the genus is the same as that of the species.

Paleolox larsoni new species

(Figs. 1; 2A)

This species was first collected by G.R. Smith in 1971. Additional specimens, including the holotype, were collected in 1974. This species is found in the Deer Butte Formation of eastern Oregon and the Glenns Ferry Formation of adjacent Idaho and is one of the largest fish in either fauna.

Holotype.– UMMP 62222, an incomplete skull and associated material, collected from the Deer Butte Formation in Malheur County, Oregon, near the Tunnel Mountain locality, in the SW¼, Sec. 21, T. 22 S, R. 46 E, at 2580 ft. The specimen was collected by P.G. Kimmel in a fine-grained sandstone just below a pebble conglomerate. The holotype includes complete ceratohyals and epihyals; a complete right angular, quadrate, basihyal; a complete left epiotic, pterotic, and sphenotic; a partial right dentary, left and right maxillae, parasphenoid, supraoccipital, left frontal, left hyomandibular, left quadrate, left palatine, and opercles, in addition to many other fragmentary associated bones.

Description.– The most diagnostic bone appears to be the maxilla. The length of the maxilla, as reconstructed from the two partial bones, is 150 mm. There are approximately 26 tooth spaces. The premaxillary process is 16.3 mm long and extends from the main axis of the maxilla 30 degrees dorsally and 15 degrees mesially. The end of the process is blunt; it widens from 9 mm near the first tooth socket to 13 mm distally. In most species of Salmoninae the premaxillary process does not extend more than a few degrees above the axis of the whole maxilla. In *Hucho perryi*, which otherwise has a very very similar maxilla, the premaxillary process extends dorsally at 15 degrees and mesially at 20 degrees. A depth profile of the main body of the maxilla is as follows (in mm): at the 3rd tooth (below the palatine cotyla), 14.0; 6th tooth, 16.2; 10th tooth, 15.3; 15th tooth, 16.1; 23rd tooth, 15.3. At its thickest portion near the palatine cotyla, the maxilla is 10.5 mm thick; between the 10th and 15th teeth it is about 6 mm thick. It is deep along its entire length and is flat rather than rodlike. Only two other genera of Salmoninae, *Salmo* and *Hucho*, have similarly deep maxillae. The tooth sockets are well developed and are located below an overhanging mesial shelf. The teeth appear small in comparison to the size of the fish and are more conical than in *Hucho perryi.* The second tooth is 4.15 mm wide at the lower lateral edge of the maxilla and extends 7.2 mm below the edge. At the fourth tooth the base of the overhang is 4 mm above the tooth attachment. This ledge becomes less prominent posteriorly, until it is only a convex surface between the teeth and the dorsal edge of the maxilla. The posterior end is laterally compressed. The position of the palatine cotyla is similar to that in *Hucho perryi.*

Only the posterior 58 mm of the dentary is present. Six tooth spaces (one tooth) are present. The small, conical tooth is similar to the maxillary teeth; it is 4 mm wide and 5.8 mm long. The dentary has a lateral ridge opposite the tooth-bearing shelf and has a distinct groove between this ridge and the top of the dentary.

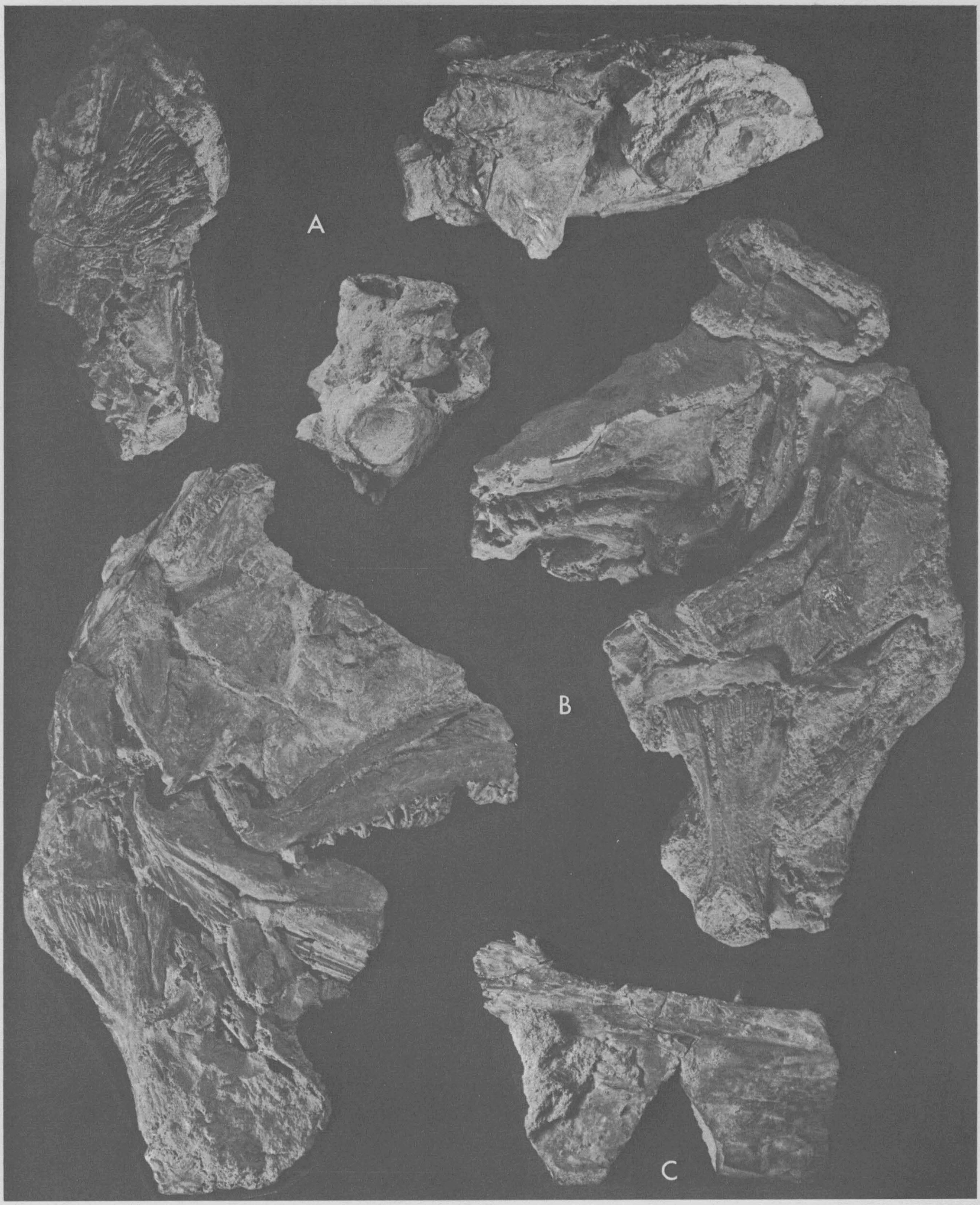
The articular is 93 mm long (tip missing). The ventral posterior wing of the articular is 53 mm long. The coronoid process extends dorsally at 40 degrees from the main axis of the angular. The articulation area in lateral view is more open than in *Rhabdofario.* A groove just below the coronoid process on the mesial surface continues back to the articulation with the quadrate, which terminates the groove.

The ceratohyals are slender in comparison to *Oncorhynchus*, except *Oncorhynchus rhodurus*, resembling those of *Salmo trutta* and *Hucho perryi* in proportion. The holotype has ceratohyals 82.5 mm long, 44 mm wide at the posterior end, and 20.6 mm at the narrowest point.

The sphenotic is also similar to that of *Hucho perryi.* It has a short (11 mm) lateral ridge on the posterolateral surface of the bone extending 35 degrees postventrally from the plane of the dorsal surface of the skull. This ridge begins at the middle of the dorsolateral edge of the sphenotic but does not continue to the ventrolateral edge. The surface that bears this ridge is not as convex as in *H. perryi.*

The posterior surface of the epiotic appears to be flatter than most other genera. There is a distinct ridge on the posterior surface starting from the posterior point and extending 45 degrees ventromesially. The ridge is more prominent than in *Salmo* or *Salvelinus*. The vertical sulcus below the posterior crest is weak.

Paratypes.– The premaxillae are present in two specimens collected by G.R. Smith: UMMP 59400 from the Desert Pavement locality, and UMMP 62005 from the Glenns Ferry Formation, Idaho, Sec. 36, T. 7 S, R. 5 E. The specimen from the Deer Butte consists of a partial left maxilla, which shows the characteristic upward angle of the premaxillary process, a partial left epiotic, a partial left premaxilla, and other associated fragments. The premaxilla resembles that of *Salmo trutta, Hucho perryi,* and *Salvelinus malma.* A ridge on the posterior surface extends horizontally just above the teeth, from the middle of the premaxilla to the posterolateral end. Another strong, well-defined ridge starts near the middle


A
B
C

of the premaxilla and curves dorsally and laterally at an angle of 70 degrees from the first ridge. This ridge is stronger than a similarly placed ridge in *H. perryi.* There is a strong depression between these two ridges, unlike the condition found in *Salvelinus malma.* The dorsomesial edge of the maxilla follows the edge of the upward curving ridge.

The material from the Glenns Ferry Formation consists of two partial articulars, a right epiotic, a partial quadrate, a partial left premaxilla, and other associated material. The specimen is diagnosed as *Paleolox larsoni* by the similarity of the premaxilla to that described above (both have a strong ridge extending dorsolaterally from the center). The premaxilla of UMMP 62005 has more of the mesial portion than the other. A horizontal ridge reappears on the mesial side of the vertical ridge and projects slightly beyond the dorsomesial edge of the premaxilla. The lower portion of this horizontal ridge is broken, but the upper part is straight and robust. The premaxilla probably contained 6-7 tooth sockets. The partial articular also shows the typical characters in the lateral sulcus below the coronoid process and the mesial sulcus extending back to the edge of the articulation with the quadrate. In addition, the epiotic possesses the diagnostic characters of *Paleolox larsoni.*

Diagnosis.– *Paleolox larsoni* can be distinguished from all other salmonine genera by the high dorsal angle of the premaxillary process of the maxilla, 30 degrees from the axis of the maxilla. Only *Hucho perryi* (20 degrees) and *Salmo trutta* (up to 20 degrees) approach this value. The premaxillary process projects only 15 degrees mesially from the axis of the maxilla (less than other salmonines) and is blunter at its anterior end. The maxilla is deep along its entire length and is laterally compressed rather than rodlike, unlike *Salvelinus* and *Rhabdofario.* Only *Salmo* and *Hucho* have similarly deep, compressed maxillae. The teeth are relatively smaller and more obtusely conical than those of *Hucho perryi*, and the tooth sockets are better developed than in most species of *Oncorhynchus.*

The premaxilla has an interrupted ridge on the posterior surface above the tooth row. A near-vertical ridge curves back at 70 degrees from the interruption in the horizontal ridge. The fossa between the vertical ridge and the lateral horizontal ridge is deeper than in *Salvelinus.* The premaxilla is like that of *Hucho perryi* and *Salmo trutta* except that in the latter there is a dorsal projection at the mesial end of the premaxilla, which is lacking in *P. larsoni.* The near-vertical ridge appears to be more distinct in *P. larsoni* and *S. trutta* than in *H. perryi.*

The dentaries have a rounded ridge on the posterolateral surface, separated from the dorsal edge by a shallow groove. This condition is also present but less developed in *H. perryi.* It is absent from other salmonines. The articular is similar to *H. perryi.* It has a strongly developed lateral sulcus below the coronoid process and a mesial sulcus below the coronoid process that extends back to the edge of the articulation with the quadrate. These characters distinguish *P. larsoni* from salmonines other than *H. perryi.*

The epiotic of *P. larsoni* differs from that of other salmonines in the possession of a shallow sulcus on the posteroventral surface. In *Hucho perryi* this sulcus is only slightly deeper than that of *P. larsoni.* Other salmonines, except *Oncorhynchus tshawytscha*, have a deeper sulcus. The sphenotic has a midlateral ridge extending posteroventrally at 35 degrees. It resembles that of *H. perryi* and *Salmo trutta*, but the ridge is shorter. The midlateral ridge extends at a shallower angle than that of *Salmo trutta* and *S. gairdneri*; it is absent in *Oncorhynchus kisutch, O. tshawytscha,* and *O. rhodurus.* The lateral surface bearing the ridge is not as convex as in *Salvelinus malma* or *H. perryi.*

Remarks.– Based on a regression of maxillary length on standard length for a number of salmonines, it is estimated that the standard length of the holotype was probably 1200-1300 mm (length of the maxillae=150 mm). Thus *P. larsoni* is one of the largest known Salmonidae. The maxillae and premaxillae show no indication of development of a kype, and there are associated breeding teeth. It is interesting and perhaps significant that the modern salmonid closest to *P. larsoni* in skeletal characters, *H. perryi*, is also one of the few Salmoninae in which breeding adults lack kypes.

The name *Paleolox* indicates an ancient salmon. The species is named for Gerald P. Larson, whose promising career as a stratigrapher in the Snake River plain ended with an accident in the field in 1974.

Genus *Rhabdofario* Cope

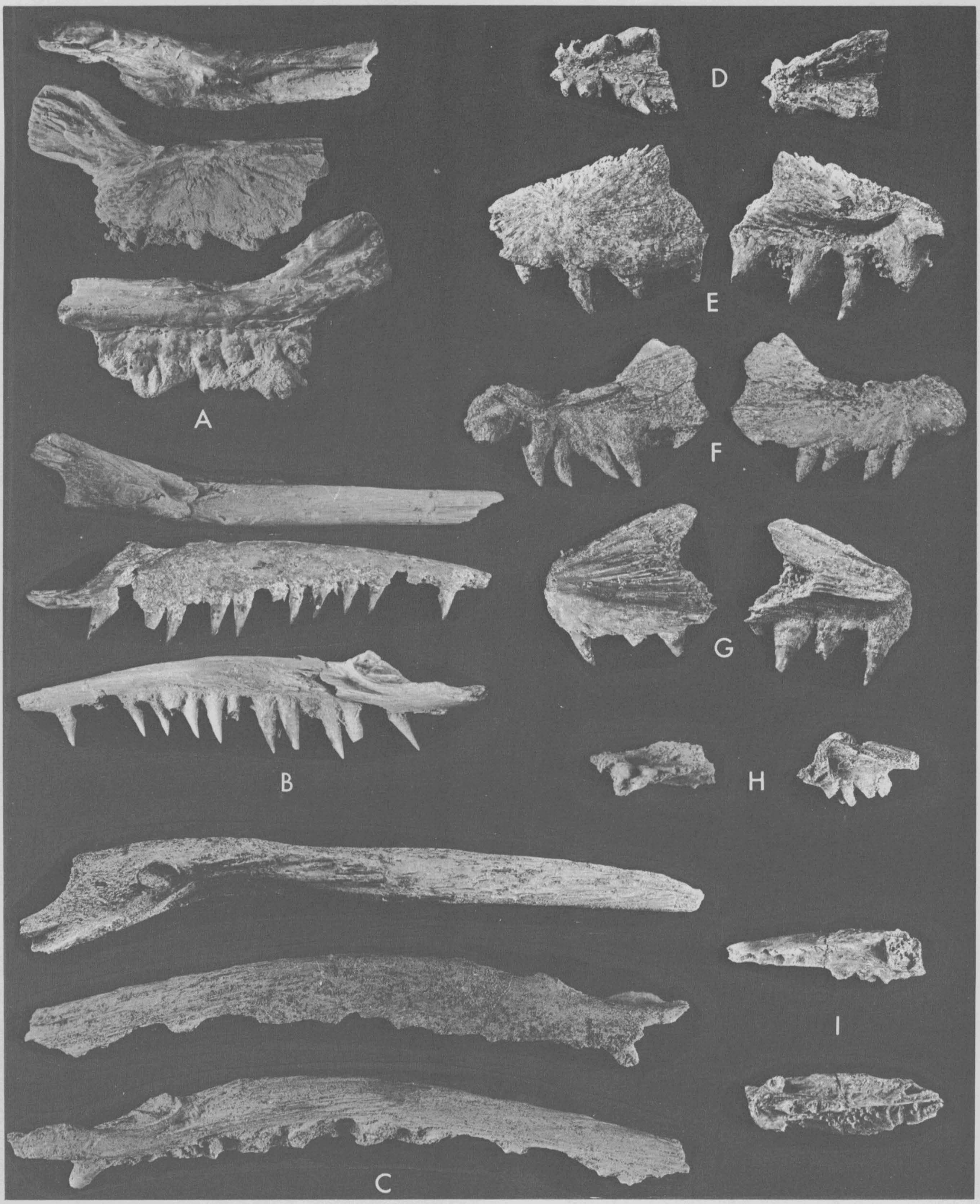
Diagnosis.– See Smith, this volume.

Rhabdofario carinatum new species

(Figs. 2B,F; 3D-H,J)

Holotype.– UMMP 62220, material from one individual, was taken from fine sands of the late Miocene to early Pliocene Deer Butte Formation, below a white ash bed at the Tunnel Mountain locality, Malheur County,

Figure 1. Holotype, *Paleolox larsoni*, UMMP 62222. (A) Posterolateral part of cranium, dorsal, lateral, and posterior views, times one-half. (B) Ceratohyals, articular, maxilla, quadrate, and associated skeletal material, times one-half. (C) Dorsoposterior part of right dentary, lateral view, actual size.


A
B
C
D
E
F
G
H
I

Oregon, at an elevation of 2640 ft. The following complete bones were collected: left articular, basioccipital, left dentary, right preopercle, pterotics, and a left quadrate. Incomplete bones present are: left ceratohyal, right dentary, epihyals, maxillae, parasphenoid, premaxillae, right preopercle, right pterotic, a right quadrate, and unidentified fragments.

Description.– The premaxilla (Fig. 2F) is 40 mm long and has space for 8 teeth. Its tooth row is convex ventrally. A ridge runs along the posterior surface of the premaxilla above the tooth row. It begins at the mesial edge and curves around the first tooth, then dips to the base of the sockets between the second and third teeth before angling dorsally at 10 degrees. The ridge disappears before the lateral edge of the premaxilla. The dorsal edge of the premaxilla curves laterally at an angle of 20 degrees. The general shape is deltoid with an indentation in the dorsolateral edge.

The maxilla (Fig. 2B) has a short premaxillary process and a rodlike, rather than flattened, body. The dorsoventral curve and the thickness of the body give the dorsal surface a keel-like appearance. The length of the premaxillary process (broken) is 8 mm to the first tooth. The middle of the palatine cotyla is 18 mm from the anterior end of the maxilla. The cotyla is oval and projects from the dorsal edge of the maxilla above the third tooth. The maxilla was probably nearly 88 mm long when complete but is now 77 mm long. The teeth range from 2.3-3.5 mm in diameter and from 4.7-7.4 mm long when measured at the lower lateral edge of the maxilla; they gradually decrease in size posteriad, and there is only a small groove at their base. The premaxillary process has a dorsal trough and is truncate. It projects mesially about 23 degrees. There is no ventral groove running under the mesial wing of the premaxillary process.

The articular (Fig. 3D) is 88 mm long. It has a vertical process posterior to the articulation with the quadrate. The mesial groove below the coronoid process does not continue back to the quadrate articulation. The angle of the coronoid process with the main axis of the articular is 30 degrees.

Only the dorsoposterior part of the left hyomandibular (Fig. 3F) is preserved. It has cancellous texture dorsolateral to the adductor ridge. A short (10 mm), vertical ridge extends ventrally from the top of the adductor ridge.

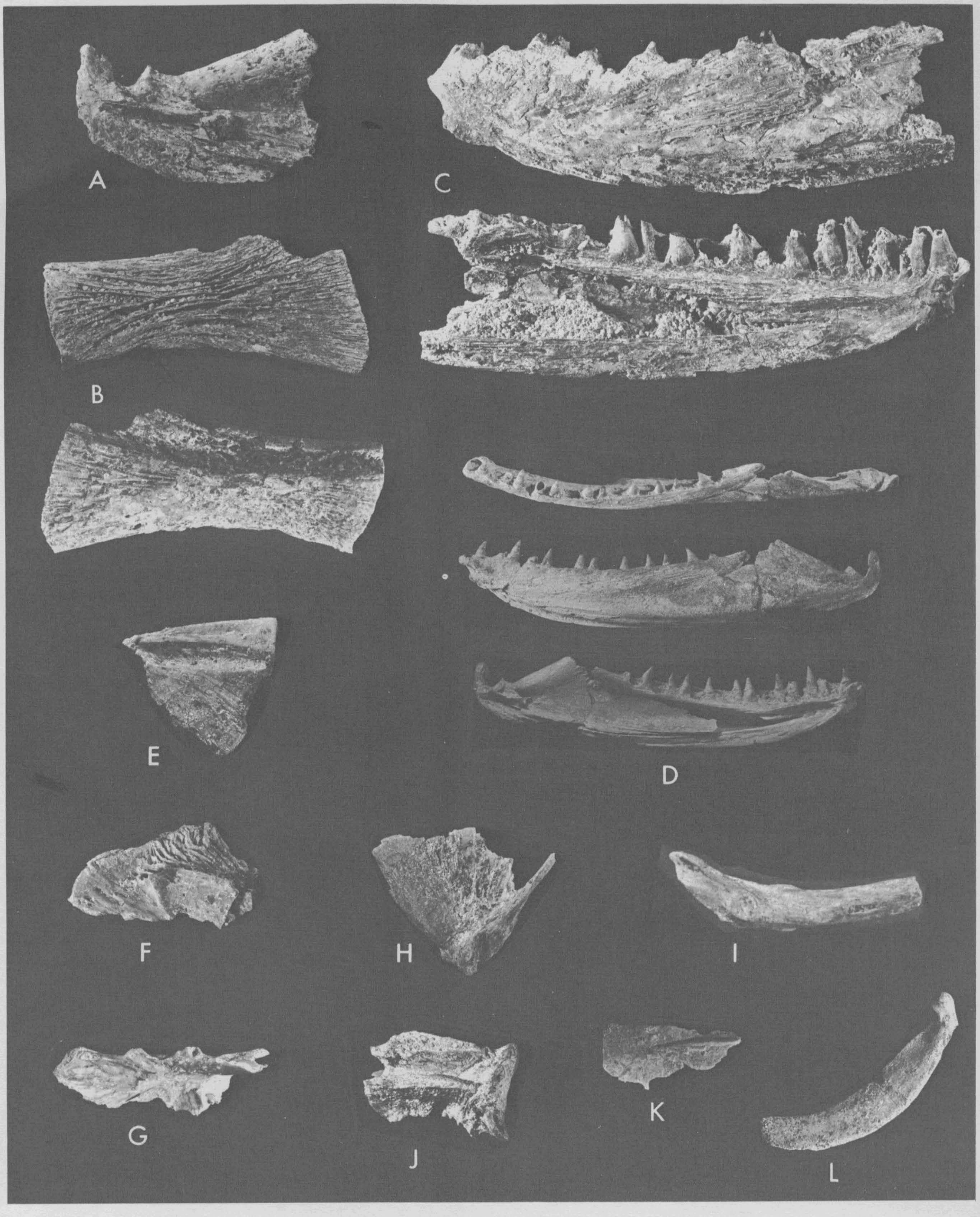
The pterotics (Fig. 3G) of the type specimen of *R. carinatum* are almost identical to the pterotics of *R. lacustris* from the Glenns Ferry Formation, but the dorsolateral edge is not as thick.

Paratypes.– UMMP 62221 (Figs. 2D,E; 3A-C) consists of a left articular, left and right ceratohyals, left dentary, glossohyal, left hyomandibular, right opercle, and left premaxilla. The bones were collected at the Tunnel Mountain locality in 1974. The dentary shows compressed teeth and a slight thickening of the upper lateral edge near the anterior end. The premaxilla has spaces for seven teeth and is 36.4 mm long. The dorsal edge is straight and projects at 25 degrees from the axis of the tooth row. The proximal ledge follows the same pattern as in the holotype but is further from the teeth. The glossohyal is 22 mm long with spaces for at least 11 teeth in the tooth rows. The tooth rows diverge posteriorly, unlike glossohyals in *Salvelinus* and *Hucho.* In *Rhabdofario carinatum* the tooth rows diverge at 24 degrees, more than the 17 degrees maximum found for *Salmo gairdneri.* The glossohyal is indistinguishable from that of *Oncorhynchus kisutch.*

The ceratohyals are 53.3 mm long and 16.3-30 mm high. They have a striated texture on all of the mesial surface. They are thicker and have a deeper texture than fragments of the ceratohyal of the holotype. The other bones in this specimen have characters already reported in the holotype.

UMMP 62551 (Fig. 2C,H) contains two partial dentaries, a complete maxilla, and a vomer. It was collected at the Tunnel Mountain locality in the Deer Butte Formation, June, 1975. The dentaries have compressed teeth but no addition of bone as in the other paratype. The maxilla is rodlike and has no groove on the mesial ventral surface of the premaxillary process. Like the holotype, this specimen has spaces for 26 teeth. Unlike the holotype, the premaxillary process projects mesiad from the tooth axis at 30 degrees. The bone also curves more in a vertical plane than does the maxilla of the holotype. It is 117.7 mm long and the premaxillary process is 13.8 mm long from the tip to the first tooth. The palatine cotyla is 27 mm from the anterior end. The vomer is 33.5 mm long and 9.2 mm wide at the anterior end of the tooth row. Three elevated tooth sockets are present and oriented parallel to the long axis (Fig. 3). The axial tooth row is 11.3 mm long. Another fragment of a salmonid vomer is also present in the fauna. In this specimen (UMMP 62215) almost all of the tooth row is present (12.5 mm), and there

Figure 2. (A) Holotype, *Paleolox larsoni*, UMMP 62222, anterior end of left maxilla – dorsal, lateral, and mesial views. (B-I) *Rhabdofario carinatum*. (B) Holotype, left maxilla – dorsal, lateral, and mesial views – UMMP 62220. (C) Right maxilla – dorsal, lateral, and mesial views, UMMP 62551. (D) Glossohyal – dorsal and ventral views – UMMP 62221. (E) Left premaxilla – anterior and posterior views – UMMP 62221. (F) Holotype, right premaxilla – posterior and anterior views – UMMP 62220. (G) Holotype, left premaxilla – posterior and anterior views – UMMP 62220. (H) Partial vomer – ventral and lateral views – UMMP 62215. (I) Partial vomer – lateral and ventral views – UMMP 62551. All figures actual size.


A
C
B
E
D
F
H
I
G
J
K
L

are spaces for seven teeth. The teeth are in a line posteriorly but double up anteriorly.

Diagnosis.– The premaxilla separates *Rhabdofario carinatum* from other genera and species. The general outline is deltoid with a blunt mesial point and a notch in the dorsolateral edge. The longest side is dorsomesial. This shape differentiates these premaxillae from all others except those of *Salmo gairdneri*, which occasionally have the same outline. The premaxilla differs from that of *S. gairdneri* in the possession of a ridge on the lateral part of the posterior side that projects upward at 10 degrees from the tooth row instead of following the tooth row. The premaxilla of *R. carinatum* is not as elongate nor is the dorsomesial edge parallel to the tooth row as in *R. lacustris.* The posterior ridge above the tooth row of *R. carinatum* curves dorsally around the base of the first tooth and then curves ventrally toward the tooth row before diverging dorsally from it laterally. In *R. lacustris* this ridge is almost straight near the mesial end.

Unlike other genera of Salmoninae, the posterior body of the maxilla is rodlike except near the extreme posterior end (Cope, 1870). *Rhabdofario carinatum* differs from *R. lacustris* in the premaxillary process. In *R. carinatum* the premaxillary process is truncate and has a dorsal trough; in *R. lacustris* the premaxillary process has a groove running under the anteromesial edge, and the premaxillary process is spatulate. Maxillae of *R. carinatum* and *R. lacustris* also differ in tooth pattern. The tooth size in *R. carinatum* decreases gradually near the posterior end of the maxilla. In *R. lacustris* there is usually an abrupt decrease in tooth size, without a corresponding decrease in the width of the tooth platform. The teeth are large compared to other genera and not as obtusely conical as in *P. larsoni.* The palatine cotyla is oval and opens posterodorsal to the third tooth, as in *Salmo gairdneri.*

The vomer has a narrow, elevated patch of teeth extending posteriad for a short distance. *Hucho, Salvelinus,* and *Salmo* have a transverse row of teeth at the anterior end of the tooth patch, which is absent from *R. carinatum. Oncorhynchus* has a similar, but not as elevated, tooth pattern.

The articular has a vertical process posterior to the articulation with the quadrate, unlike *H. perryi, Paleolox larsoni,* and *Salvelinus malma.* The articular resembles those of *Salmo clarki* and *Salmo gairdneri*; the mesial groove below the coronoid process does not extend to the articular facet.

The hyomandibular has a triangular area of cancellous texture on the posterodorsal part of the lateral surface with a 10 mm vertical ridge beginning below the textured surface and ending 5.6 mm below the dorsal edge of the hyomandibular.

Remarks.– The dentaries of *R. carinatum* lack kypes (breeding distortion) in 11 mature individuals collected from the Deer Butte Formation. The smallest of these is about the same size as a mature *Salmo trutta* with a standard length of 419 mm, thus they are probably from mature individuals. The dentaries present in the fauna are variable in many characters, but modern species are similarly variable. In some, the teeth are not regularly spaced, but seem more numerous near the front, and may be compressed, as in UMMP 62221 (Fig. 3C). The anteroventral edge of the dentary of the holotype has a smooth, curved margin up to the anterior tip, but other dentaries in the fauna have an angle at the symphysis. In *R. lacustris* added bony material may increase this angle to almost 90 degrees, but even larger specimens of *R. carinatum* with a thickened, dorsolateral edge near the anterior end do not have added bony material at the symphysis or along the ventral edge. The addition of bony material to the dentaries of the more recent species of *Rhabdofario* may be related to the evolution of a kype in more recent Salmonidae.

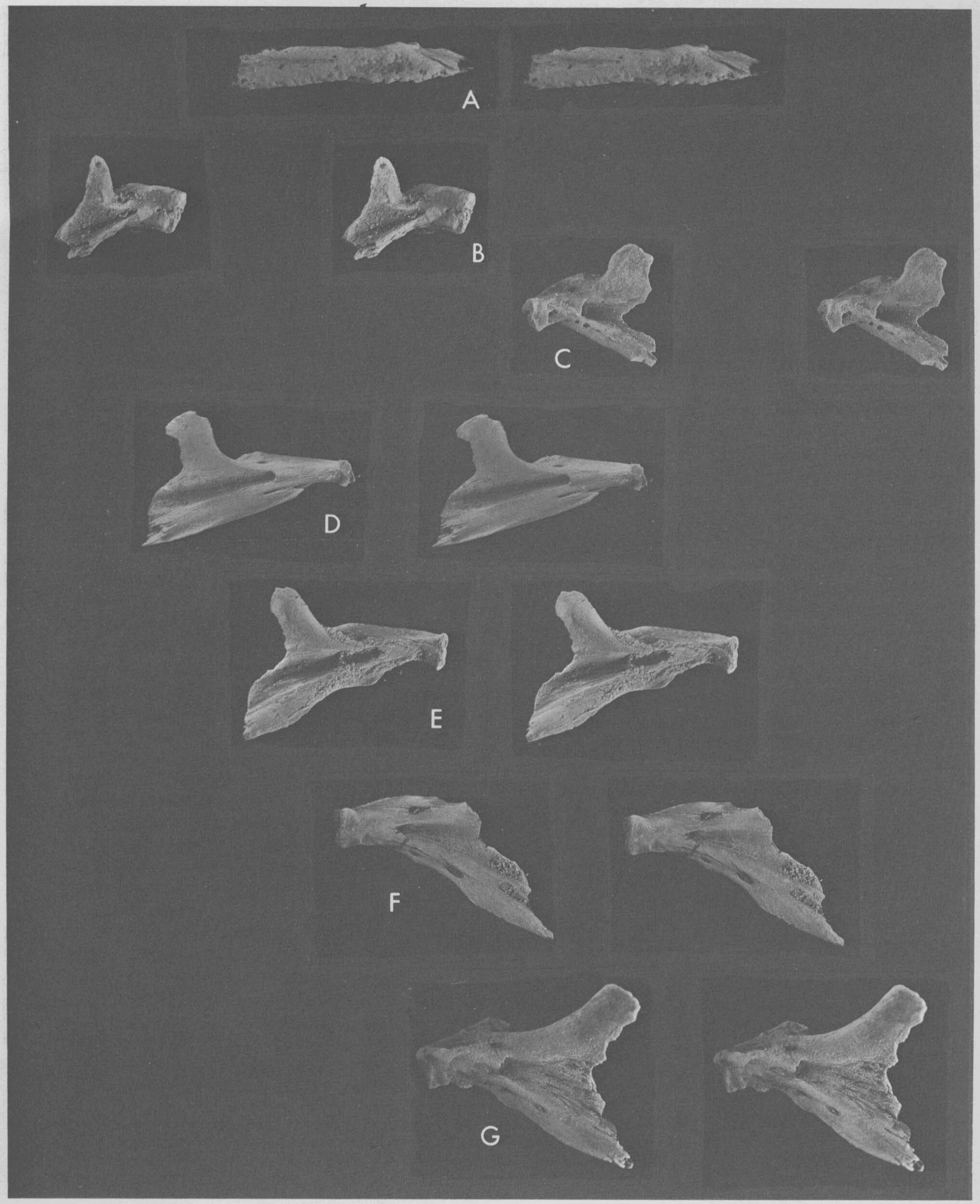
Rhabdofario carinatum was a large salmonid, reaching 900-1000 mm standard length, as inferred from the length of the maxillae. The name *carinatum* refers to the keel-like dorsal surface of the maxillae.

Salmoninae, *incertae sedis*

(Figs. 3I; 4A)

Seven small fragmentary maxillae in the Deer Butte fauna do not seem to belong to any of the genera and species previously discussed. They are usually flattened rather than rodlike and have small teeth. Near the palatine cotyla their cross sectional shape becomes triangular, often with concave dorsal and lateral surfaces. The premaxillary process is long and tapered rather than abrupt. It does not extend dorsally or ventrally from the tooth axis but extends 40 degrees mesiad. The posterior portion of the maxillae is much deeper than other previous genera. Some of these maxillae are concave dorsally (in lateral view). These may represent a separate

Figure 3.(A-H,J)*Rhabdofario carinatum.* (A-C) UMMP 62221. (A) Left articular, mesial view. (B) Right ceratohyal, lateral and mesial views. (C) Left dentary, lateral and mesial views. (D-H,J) Holotype, UMMP 62220. (D) Left dentary and articular – dorsal, lateral, and mesial views. (E) Posterior part of left ceratohyal, lateral view. (F) Dorsal part of left hyomandibular, lateral view. (G) Right pterotic, dorsal view. (H) Left quadrate, lateral view. (J) Basioccipital, dorsolateral view. (I) Salmonidae, *incertae sedis*, UMMP 62238, left maxilla, dorsal view. (K,L) *Prosopium prolixus*, UMMP 62448. (K) Right frontal, dorsal view. (L) Right maxilla, lateral view. All figures actual size except D (times one-half) and I (times 2).


A
B
C
D
E
F
G

species, but no complete or associated bones have been found. These are not juvenile *Rhabdofario carinatum*, and the absence of the characteristic premaxillary process of *Paleolox larsoni* rules out that species.

Several dentaries with sharply curved anterior ends and small teeth are present in the Deer Butte Formation and may belong to the same species as the unusual maxillae, but they may also be variants of the species already discussed.

Subfamily COREGONINAE

Genus *Prosopium* Milner

Prosopium prolixus Smith

(Fig. 3K,L)

Diagnosis.— See Smith, this volume.

Remarks.— *Prosopium prolixus* appears only in the Blackjack local fauna of the Deer Butte Formation, Oregon, and the Glenns Ferry Formation of Idaho. One maxilla and one frontal were collected from the Blackjack local fauna; they are indistinguishable from Glenns Ferry specimens. Since the Blackjack local fauna is stratigraphically higher than the other Deer Butte local faunas, the appearance of *P. prolixus* may prove useful as a stratigraphic marker.

Family **Catostomidae**

The Catostomidae may be the most complex group of fish within the Deer Butte Formation. Except for one species of *Chasmistes*, all of the species of suckers found in the Deer Butte fauna belong to the genus *Catostomus*. A preliminary comparison with the Glenns Ferry sucker fauna indicates that the species diversity is about the same in both faunas and that most of the species are present in both faunas.

Genus *Catostomus* Lesueur

Diagnosis.— See Smith (this volume) for diagnoses of this genus and the species in the Deer Butte and Glenns Ferry formations.

Remarks.— *Catostomus cristatus* Cope, *C. owyhee* Miller and Smith, and *C. shoshonensis* Cope are present in abundance both in this fauna and in the Glenns Ferry fauna, but some of the diagnostic characters of the Glenns Ferry species do not apply to the Deer Butte species. In addition, several dentaries from the Deer Butte appear to be related to *C. arenatus*. They are much larger than the Glenns Ferry representatives but show the shortened gnathal ramus typical of *C. arenatus*. Until a statistical analysis of the character variation in the species is done, positive identifications will not be possible.

Genus *Chasmistes* Jordan

Chasmistes spatulifer Miller and Smith

Diagnosis.— This genus and species are diagnosed in Smith, this volume.

Remarks.— This species is represented by distinctly long and slender dentaries with the symphysis between the dentaries oriented almost vertically. *Chasmistes spatulifer* is present only in the Blackjack local fauna, additional evidence that the section at Blackjack Butte is not equivalent to the rest of the Deer Butte Formation in age or perhaps environment. Like *Prosopium prolixus, Chasmistes spatulifer* is also present in the fish fauna of the Glenns Ferry Formation, Idaho. This genus and species is represented in the Blackjack local fauna by two dentaries, possibly only one individual.

Family **Cyprinidae**

All of the genera and most of the species reported here have been diagnosed by Smith (this volume), and the reader is referred there for this information.

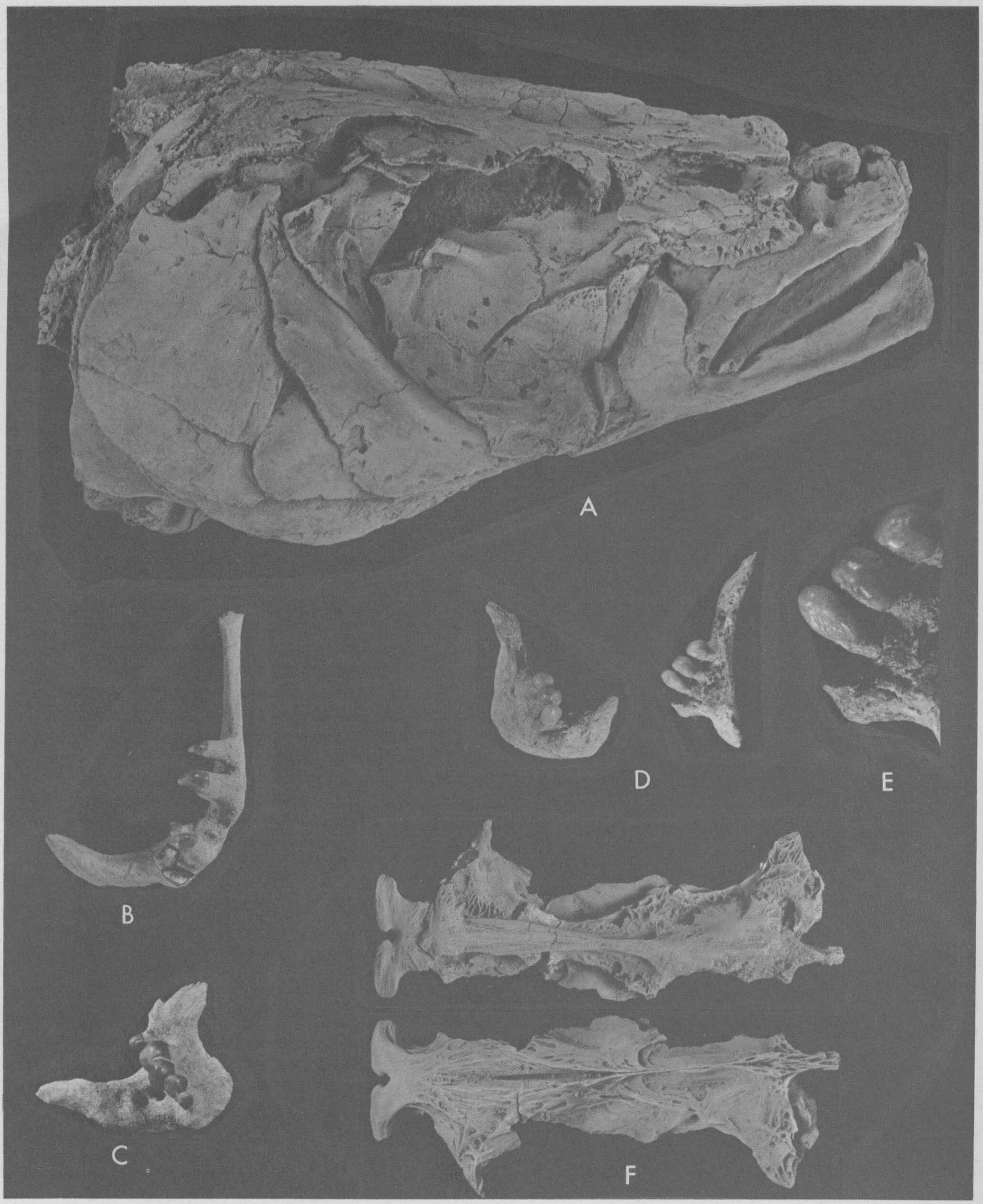
Genus *Acrocheilus* Agassiz

Acrocheilus latus (Cope)

(Fig. 4B)

This species, also present in the Glenns Ferry Formation, closely resembles *Acrocheilus alutaceus*, now present in the Columbia River drainage. The similarity indicates that, like chisel mouth chub, it was probably an algae scraper. It is represented in all the local faunas of the Deer Butte Formation.

Figure 4. Stereograms of: (A) Salmonidae, *incertae sedis*, right maxilla, lateral view, UMMP 62216. (B) *Acrocheilus latus*, left dentary, mesial view, UMMP 62582. (C) Cyprinidae, *incertae sedis*, right dentary, mesial view, UMMP 62588. (D) *Orthodon microlepidotus*, left dentary, mesial view, R., California, UMMZ 179936. (E) Holotype, *Orthodon hadrognathus*, left dentary, mesial view, Glenns Ferry, UMMP 57728. (F) *Orthodon hadrognathus?*, right dentary, mesial view, UMMP 62589. (G) Holotype, *Orthodon onkognathus*, right dentary, mesial view, UMMP 62560. All figures times 2.


A
D
E
B
C
F

Genus *Idadon* Smith

Idadon condonianus (Cope)

(Fig. 5B,E)

Pharyngeals and dentaries of *Idadon condonianus* are present in this fauna as well as in the Glenns Ferry fauna. Although the smaller pharyngeals of this species resemble *Mylocheilus robustus*, larger specimens distinctly lack the flat-topped molariform teeth of that species.

Idadon hibbardi Smith

(Fig. 6B)

Pharyngeal arches of this species are present in the Deer Butte Formation, but only in the Tunnel Mountain local fauna. Six pharyngeals have been found, and none of these has the anteroventral limb. All have the striated or rugose grinding surfaces on the teeth that are typical of this species.

Genus *Mylocheilus* Agassiz

Mylocheilus inflexus (Cope)

(Fig. 5C)

Although this mollusk-eating cyprinid is abundant in the Deer Butte fauna, only two specimens have been collected from the Glenns Ferry Formation. It is absent from the Blackjack local fauna of the Deer Butte Formation. Although the general shape of the pharyngeal arches resembles that of *Mylopharyngodon aethiops*, an Asiatic fish, the angle of the anterior surface on the anterior limb of the pharyngeal and the lack of any other similar skeletal elements in the fauna indicate that the resemblance is probably due to parallel evolution. Dentaries of this species are unknown, but it is possible that they are similar to *Mylocheilus robustus*, since this species is similar and has the most numerous dentaries in this fauna. The dentaries assigned to *Orthodon* (see below) are similar to those of *Mylopharyngodon aethiops* and could belong with *Mylocheilus inflexus.* However, the presence of *Orthodon* in abundance in the Glenns Ferry Formation, where pharyngeals of *Mylocheilus inflexus* are rare, indicates that this is unlikely.

The species is placed in the genus *Mylocheilus* because of its molariform pharyngeal teeth. The pharyngeals have a short, highly deflected, anterior end and an indentation on the lateral ventral edge – characters of the genus *Mylocheilus.* This species differs from others in the genus in the possession of a long dorsal limb similar to that of *Mylopharyngodon aethiops*, and in the orientation of the teeth grinding surfaces as parallel rather than opposed.

Mylocheilus robustus (Leidy)

Mylocheilus robustus is a molluscivore with molariform teeth. It is found at all localities in the Deer Butte Formation and is abundant in the Glenns Ferry Formation. A relative, *M. caurinus*, is found in the Columbia and associated drainages today. *Mylocheilus robustus* has a pharyngeal arch with a shorter and more curved dorsal limb than *M. inflexus*, and the pharyngeal teeth oppose each other more than the basioccipital. The Deer Butte arches seem to have the symphysis at a lower angle to the rest of the anterior limb, longer anterior wings, and occasionally longer dorsal limbs than those from the Glenns Ferry Formation. These differences are not sufficient or consistent enough to justify taxonomic separation, but they probably indicate primitive characters of *M. robustus* and early similarity to *Idadon condonianus*. It is sometimes difficult to separate *M. robustus* and *Idadon condonianus* in this fauna.

Genus *Orthodon* Girard

This genus is represented in the Deer Butte fauna by two types of dentaries, but associated pharyngeals are absent. The modern species of *Orthodon* has very fragile pharyngeal arches and it is possible that the pharyngeals of these fossil species were not preserved. Another possibility is that some of the pharyngeals of *Orthodon* are misidentified as *Acrocheilus latus.* The wide variability in the length of the dorsal limb beyond the tooth row in the *A. latus* pharyngeals supports this possibility. It is unlikely that these dentaries belong with the pharyngeals of *Mylocheilus inflexus*, which has no associated dentaries, since the *Orthodon* jaws are more similar to those of algae scrapers such as *Acrocheilus alutaceus* rather than molluscivores such as *M. caurinus* and *M. inflexus.* The distribution patterns also indicate these dentaries are not associated with *M. inflexus.* One species, *O. hadrognathus*, is present in the Deer Butte sediments and in the Glenns Ferry Formation, where *M. inflexus* is very rare; the other species, *O. onkognathus*, is absent from the Glenns Ferry Formation and most of the Deer Butte local faunas, many of which contain *M. inflexus.*

Figure 5. (A) *Ptychocheilus arciferus*, UMMP 45321. (B) *Ptychocheilus arciferus*, right pharyngeal arch, mesial view, UMMP 62547. (C) *Mylocheilus inflexus*, right pharyngeal arch, mesial view, UMMP 62547. (D-E) *Idadon condonianus*, left pharyngeal arch, UMMP 62455. (D) Mesial and dorsal views. (E) Enlarged view of pharyngeal teeth showing striations. (F) *Ictalurus vespertinus*, dorsal and ventral views, UMMP 62160. All figures actual size except A (times 0.75).

Orthodon hadrognathus Smith

(Fig. 4E,F)

This species is present in all the major local faunas of the Deer Butte Formation, although it is rare in all of them. It has more robust dentaries and may have had more robust pharyngeals than the modern *Orthodon microlepidotus* (Fig. 4D) (Smith, this volume). It is the only species of *Orthodon* present in the Glenns Ferry Formation.

Orthodon onkognathus new species

(Figs. 4G; 6A)

Holotype.– A right dentary, UMMP 62560, collected in June, 1975, from the Tunnel Mountain locality, Deer Butte Formation, Malheur County, eastern Oregon.

Description.– The dentary measures 20.2 mm from the postventral tip (broken) to the anterior tip and 19.2 mm from the anterior tip to the posterior end of the coronoid process. The coronoid process takes up 9.2 mm of the latter distance; the gnathal surface, 8.2 mm. The gnathal surface is 4.4 mm at its widest and does not appear to taper near the anterior or ventral end, unlike *O. microlepidotus* and *O. hadrognathus.* It possesses four sensory pores, with the third and fourth under the coronoid process. The symphysis is 3.8 mm deep, 6 mm from the anterior end of the Meckelian groove, 6.4 mm from the internal dorsal opening, and 5.2 mm from the external dorsal opening of the mental foramen. The medioventral lamina gradually increases posteriorly. The posterolateral edge of the gnathal surface ends in a hooked process, hence the name *onkognathus*, or "hooked jaw."

Diagnosis.– This species is distinguished by its robust and foreshortened dentaries. It differs from other species of *Orthodon* in possessing only four sensory pores (as opposed to six in *Orthodon hadrognathus* and nine in *Orthodon microlepidotus*). The gnathal ramus is short, dorsally flat, and broadly flared laterally.

Remarks.– A low number of sensory pores in the dentary appears to be a primitive character state in the series of *Orthodon* as now understood. Short and robust jaws also appear somewhat primitive, and *O. onkognathus* is so short and robust as to appear somewhat similar to *Acrocheilus latus*, also found in this fauna. These two genera may be more closely related than a comparison of modern dentaries would indicate. This idea lends weight to the idea that the missing pharyngeals of *Orthodon* in this fauna are more robust than the modern *Orthodon* pharyngeals and are to be found among the variants of *Acrocheilus latus. Orthodon onkognathus* is found only in the Tunnel Road and Tunnel Mountain local faunas of the Deer Butte Formation. Fourteen specimens have been collected.

Genus *Ptychocheilus* Agassiz

Ptychocheilus arciferus (Cope)

(Fig. 5A,B)

Ptychocheilus arciferus is an abundant cyprinid in both the Deer Butte and Glenns Ferry faunas. It is carnivorous, as shown by the pointed pharyngeal teeth, and is the largest cyprinid in the fauna, reaching 4 ft in length. A modern relative, probably a descendant, is *P. oregonensis*, which is found in the Columbia River drainage. Other species of *Ptychocheilus* are found in the Sacramento River drainage system and coastal streams of Oregon. Its absence from the Klamath River drainage system is hard to explain (Robbins and Miller, 1957) since this system is between drainage systems in which the genus is found. The discovery of *P. arciferus* in sediments of the Deer Butte Formation may indicate that any connection between Lake Idaho and the Klamath Basin occurred before lower Pliocene and possibly before upper Miocene times.

Cyprinidae *incertae sedis*

(Fig. 4C)

Seven dentaries from this fauna are indistinguishable from a large sample of unidentified specimens from the Glenns Ferry fauna (see Smith, this volume) and are unlike any other known Recent or fossil dentaries. They are distinguished by a short, heavy, and blunt gnathic ramus that has a sharp ventral deflection. They may represent hybrids between *Orthodon* and *Acrocheilus.*

Family **Ictaluridae**

Genus *Ictalurus* Rafinesque

Ictalurus vespertinus Miller and Smith

(Figs. 5F; 6C,D)

This is the only species of catfish found in the Deer Butte Formation. This species was first described from the Glenns Ferry Formation, Idaho, and classified as a bullhead catfish (subgenus *Amiurus*) by Miller and Smith (1967).

A comparison of *I. vespertinus* from the Deer Butte and the Glenns Ferry formations shows no taxonomic differences, although some of the Deer Butte catfish also resemble a Pliocene species of catfish, *I. peregrinus*, described from the upper Juntura Formation, Oregon, by Lundberg (1975). *Ictalurus vespertinus* is said to differ from *I. peregrinus* in having evenly spaced dentations on the posterior edge of the pectoral spines; variations noted below cast doubt on this distinction. It is found in sediments that have been correlated with the Poison Creek Formation (Bowen et al., 1963). The correlation of the Deer Butte Formation with the Poison Creek Formation (Kittleman et al., 1963) indicates that *I. peregrinus* and *I. vespertinus* may be contemporaries, raising the possibility that *I. peregrinus* may be only a local variant of *I. vespertinus*, not of species rank.

The catfish of the Deer Butte Formation are comparatively more abundant and include larger individuals than those of the Glenns Ferry Formation. The Deer Butte catfish show a wider range of variation than is found among Glenns Ferry specimens. Pectoral spines differ in length, curvature, ornamentation, and posterior dentations, as can be seen in Figure 6C. In addition, many examples of deformed spines and even several twinned spines are present in the Tunnel Mountain local fauna (Fig. 6D). Twinned or double spines range from one deformed spine with a knob on one side at its base, to a perfectly formed spine with two shafts, each bearing posterior dentations.

Examination of 54 pectoral spines from the Tunnel Mountain local fauna showed some characteristics of ornamentation and posterior dentation that seem to correlate with size. These variations are probably associated with age and probably do not indicate additional species. The variations are not bimodal but form a continuum. The ornamentation of the spines varies in texture and pattern. For example, striations vary in size and usually run parallel to the spine, although some spines have striations at angles of up to 30 degrees from the main axis of the spine. The dentations on the posterior edge of the spine also vary continuously; they are usually slender, single, and regularly spaced, but some are bifid. The number of bifid teeth and the degree of bifurcation vary. This same pattern is also present in the Glenns Ferry specimens.

Family **Centrarchidae**

Genus *Archoplites* Gill

Archoplites taylori Miller and Smith

(Fig. 6E)

Diagnosis.– See Smith, this volume.

Remarks.– *Archoplites taylori* is the only member of the Centrarchidae present in the Deer Butte fish fauna. It is present in all major collecting localities in the Deer Butte sediments. No differences between specimens in this fauna and those from the Glenns Ferry Formation were observed.

Family **Cottidae**

Sculpins are not as common in the Deer Butte Formation as in the Glenns Ferry Formation. The scarcity of sculpin remains may be the result of several factors. The coarseness of the Deer Butte sediments, the presence of rare terrestrial fossils, fossil wood, and the abundance of catfish indicate that the environment of deposition for these sediments is a flood basin or lake edge rather than an open lacustrine. Sculpins from the Glenns Ferry Formation are most common in fine-grained sediments, indicating a deeper, offshore environment. Cottids might have been more abundant but rarely preserved because of fragility. If this factor is significant, one would expect to find only large adults of fairly robust species. All of the material from the Deer Butte Formation does appear to be from large adults, compared with Recent sculpins and specimens from the Glenns Ferry Formation. Sediments of the Deer Butte are much coarser than those of the Glenns Ferry Formation, and many of the fossils show evidence of wear.

Genus *Cottus* Linnaeus

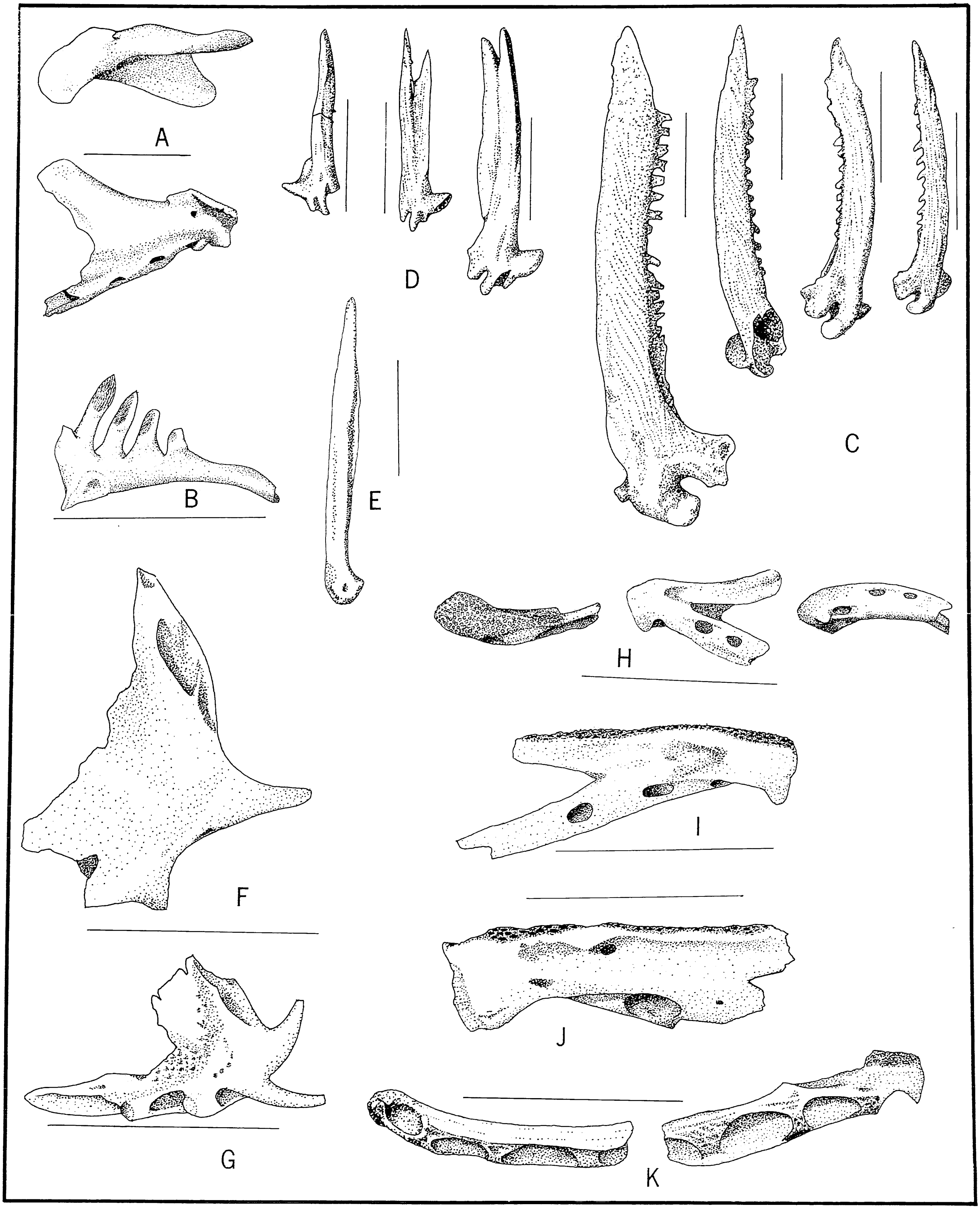
Cottus calcatus new species

(Fig. 6F)

Holotype.– UMMP 62555 is a left preopercle from a large sculpin, found at the Tunnel Mountain locality in the Deer Butte Formation, June, 1975. The posterior two spines and the dorsal limb are preserved.

Description.– The preopercle is broken but retains two posterior spines. The ventral spine is small and laterally compressed. The posterior spine is larger but still flattened. The sensory pores are also laterally compressed and small and are located on the edges of the preopercle rather than on the lateral surface. Measurements for the preopercle are: tip of dorsal limb to posterior spine, 13.0 mm; posterior spine to anterior spine, 8.8 mm; posterior spine, 4.5 mm long, 4.8 by 1.3 mm at its base; anterior spine, 1.3 mm long, 3.1 by 1.0 mm at its base; pore between spines, 3.5 by 2.3 mm (internal dimensions); dorsal limb sensory pore, 5.8 mm long, 1.6 mm wide, ventral 2.2-3.3 mm filled by diagonal bone laminae; adductor ridge, up to 1.5 mm deep.

Diagnosis.– This species is distinguished from other genera and most other species of *Cottus* by its flattened and reduced preopercle armature. Two species of *Cottus* from northwestern America, *Cottus confusus* of the *bairdi* species group and *Cottus pitensis* of the *asper* species group, are very similar to *C. calcatus*. *Cottus confusus* differs from *C. calcatus* in possessing larger and more lateral sensory pores, a broader posterior spine, and a smaller anterior spine. *Cottus pitensis* also has larger and more lateral sensory pores and a smaller


A
D
C
B
E
H
I
F
J
G
K

anterior spine.

Remarks.– The similarity of the fossil and living species may be evidence for the paleodrainage system first theorized by Wheeler and Cook (1954) for this region. *Cottus confusus* is found in parts of the Columbia and Snake River drainages in Oregon, Idaho, and British Columbia and in drainages in Washington; *Cottus pitensis* is found in the Pit and Klamath river systems (Bailey and Bond, 1963). The Pit River is associated with the region through which the Lake Idaho system is thought to have drained before it cut Hells Canyon. At this time, however, no material definitely assignable to the genus *Cottus* has been found in the Pliocene part of the Glenns Ferry Formation.

Genus *Kerocottus* Smith

Kerocottus divaricatus (Cope)

(Fig. 6G)

Diagnosis.– See Smith, this volume.

Remarks.– Preopercles belonging to *K. divaricatus* are present in the Blackjack local fauna of the Deer Butte Formation. Although these preopercles are the earliest record of *K. divaricatus*, the local fauna in which they are found differs by several species and is probably higher stratigraphically than the rest of the Deer Butte fauna.

Genus *Myoxocephalus* (Steller) Tilesius

Myoxocephalus sp.

(Fig. 6K)

Diagnosis.– One of the dentaries found in the Tunnel Mountain locality is unlike other sculpin dentaries. Although broken, enough remains to show that the lower surface of the dentary contains four very large sensory pores. In addition the anteroventral edge of the dentary does not bend down sharply as it does in *Kerocottus* and *Cottus* dentaries. From these characters, this dentary can be assigned to the genus *Myoxocephalus.*

Remarks.– Two species of fossil *Myoxocephalus* are found in the younger Glenns Ferry sediments. These species consist of a large-pored form, *M. idahoensis*, and a small-pored form, *M. antiquus.* The older, Deer Butte *Myoxocephalus* dentary has a pore size that is intermediate and may be ancestral to the two Glenns Ferry species of *Myoxocephalus.* It is more robust than the fossil and Recent species of *Myoxocephalus* and has a rounded rather than elongate pore at the anterior end of the dentary. Because no preopercles of this genus are present and because most fossil sculpins have been defined on the basis of preopercles, a new species is not proposed here.

Cottidae *incertae sedis*

Remarks.– Several cottid dentaries resembling those of *Cottus* or *Kerocottus* are present in the fauna. No sure diagnostic characters are known that separate *Kerocottus* and *Cottus* dentaries. They differ from *Myoxocephalus* dentaries in possessing a stronger ventral extension of the symphysis. The dentaries resemble those of *C. pitensis*, and it is possible that most of them are dentaries of *C. calcatus* (Fig. 6I). Some of the larger dentaries, however, have larger pores and deeper postventral wings than the others and may represent *Kerocottus* (Fig. 6J).

One very unusual cottid dentary (Fig. 6H) is also found in the Tunnel Mountain local fauna. This dentary is extremely short and thick with an anteriorly expanded tooth patch. It is 7.8 mm from the anterior tip to the posterior tip of the coronoid process. The tooth area is 2.0 mm wide and 4.0 mm long. The three sensory pores present are small, equivalent in proportion to those of the small-pored form of the dentaries discussed above. The indentation between the upper and lower posterior wings of the dentary extends anterior to the second sensory pore in the jaw. If the dentary is not deformed, it represents one of the most specialized cottids known.

DISCUSSION

Depositional Environment

Sediments in the area of the fish localities have been regarded as fluvio-lacustrine by Bryan (1929), Corcoran et al. (1962), and Kittleman et al. (1965). The fossiliferous sediments in the lower Deer Butte vary from siltstone to pebble conglomerates, and rounded pieces of petrified wood are often associated with the fossils. The sandstones and siltstones in which most of the fossils are found are massive and interbedded with pure volcanic ash beds.

Figure 6. (A) Holotype, *Orthodon onkognathus*, right dentary, dorsal and lateral views, UMMP 62560. (B) *Idadon hibbardi*, left pharyngeal arch (broken), dorsal view, UMMP 62561. (C-D) *Ictalurus vespertinus* pectoral spines. (C) Ventral views, to show variability, UMMP 62154. (D) Deformed spines, anterior views, UMMP 62162. (E) *Archoplites taylori*, dorsal spine, lateral view, UMMP 62549. (F) Holotype, *Cottus calcatus*, posterior part of left preopercle, lateral view, UMMP 62555. (G) *Kerocottus divaricatus*, left preopercle, lateral view, UMMP 62460. (H) Cottidae (unknown genus), left dentary – dorsal, lateral, and ventral views – UMMP 62556. (I) *Cottus?*, right dentary, lateral view, UMMP 62559. (J) *Kerocottus?*, left dentary, lateral view, UMMP 62559. (K) *Myoxocephalus* sp., right dentary, lateral view, UMMP 62557. Scales equal 1 cm.

This suggests that either deposition was slow, or that it occurred rapidly and that ash falls did not occur during periods of normal deposition, otherwise the ash should contain greater amounts of sand and silt. The presence of articulated fish in the siltstones suggests that deposition was rapid, and the presence of conglomerate beds at the fossil localities indicates that strong currents were involved at some time during deposition. Conglomerate beds increase in number and thickness to the north, until they are the dominant sedimentary rock at Brown Butte near Adrian, Oregon, suggesting a large fluvial system existed in this area. If Wheeler and Cook (1954) were correct in their interpretation of the paleodrainage of this area, Brown Butte is very near the outlet of Lake Idaho.

The above sedimentary evidence and the presence of fish and mammal fossils in the same beds indicates that the environment of deposition in the lower Deer Butte Formation was probably a flood basin or lake edge environment. This is in agreement with Bryan (1929), who considered the depositional environment to be "river floodplain or . . . shallow lakes characteristic of alluvial plains." Although this may have been a shallow nearshore and beach environment, the sedimentary evidence indicates it was not a large, deep lake environment.

Ecology

The fish fauna seems to indicate a lacustrine environment for the Deer Butte Formation as well as for the Glenns Ferry Formation. Its diversity of about 24 species may be higher than expected in a fluviatile system near 3000 ft elevation, located at 43 degrees N latitude in western North America. Individuals in the fauna attain great size; there are three predators approaching 1 meter in length in both the Deer Butte and Glenns Ferry formations. This indicates a large volume of habitat, best explained by a lacustrine habitat.

However, geologic evidence indicates that the Deer Butte Formation may not have been a lacustrine environment. A comparison of the Deer Butte fauna with Glenns Ferry local faunas aids in resolving this conflict. Two localities in the Glenns Ferry Formation are cited by G.R. Smith (this volume) as likely fluviatile environments on the basis of geologic evidence. The Hagerman section, regarded as a floodplain facies, lacks typical lacustrine genera such as *Mylocheilus, Idadon, Kerocottus,* and *Myoxocephalus.* The Sand Point locality, regarded by geologists as fluviatile, does have these lacustrine genera but also has a higher than normal incidence of *Ictalurus*, a likely fluviatile indicator. The Deer Butte fauna contains larger individuals as well as a higher percentage of *Ictalurus.* The lacustrine part of the Deer Butte fauna may have entered a distributary environment as strays or spawning migrants. Alternatively, the fluvial species may have existed in a shallow, higher energy, lake edge environment.

Three top predators are present in the early Lake Idaho fauna. *Rhabdofario carinatum* is very similar and probably ancestral to *Rhabdofario lacustris. Paleolox larsoni* was a larger salmonid and is less common in the Glenns Ferry Formation. The most abundant large predator is *Ptychocheilus arciferus*, a cyprinid. Other trophic categories represented by the cyprinids of the Deer Butte are herbivores (*Acrocheilus latus, Idadon hibbardi, Orthodon hadrognathus,* and *O. onkognathus*), molluscivores (*Mylocheilus inflexus, M. robustus,* and possibly *Idadon condonianus*), and small to medium carnivores (*Idadon condonianus*). The catostomids were probably all benthic, small-particle omnivores. *Ictalurus vespertinus* was probably a medium-sized, nocturnal omnivore, scavenger, and carnivore. The sunfish *Archoplites taylori* was a medium-sized predator. The cottids were probably small, benthic predators on crustaceans and include *Cottus, Kerocottus, Myoxocephalus,* and one unusual, undescribed form. It is interesting that the species found in the Glenns Ferry but not in the lower Deer Butte are all planktivores or midwater carnivores except *Mylopharodon hagermanensis* (from a floodplain environment) and several species of *Kerocottus* (which may have been deep water inhabitants). Table 1 shows that the relationship of trophic adaptations and stratigraphic distribution occurs to a lesser extent within the Deer Butte Formation.

Evolution

Several species in the Deer Butte Formation may have been ancestral to forms in the Glenns Ferry Formation. *Rhabdofario carinatum* is very similar to *R. lacustris* from the Glenns Ferry. An unnamed form of *Catostomus* resembles *Catostomus arenatus* from the Glenns Ferry but is much larger; *Catostomus arenatus* in turn resembles the much smaller, Recent *Catostomus columbianus. Myoxocephalus* sp. from the Deer Butte appears to be intermediate between the two species of *Myoxocephalus* in the Glenns Ferry Formation, indicating that it may have been their common ancestor. Only two Deer Butte species are not represented in the Glenns Ferry Formation by the same species, a sister species, or a possible descendant. One of these, *Cottus calcatus*, is similar to Recent species in the Sacramento, Klamath, and Columbia drainages. The other species is a sculpin represented by a dentary unlike any known form in North America.

Table 1. Distributional and ecological characteristics of fish species of the Deer Butte Formation

	Distribution		Trophic Adaptation				
Species	In Deer Butte	In Glenns Ferry	Large Carnivore	Small Carnivore	Planktivore	Molluscivore	Herbivore
Paleolox larsoni	L	R	R	-	-	-	-
Rhabdofario carinatum	L	S	C	-	-	-	-
Salmoninae (unident.)	L	?	-	R	-	-	-
Prosopium prolixus	U	X	-	R	R	-	-
Catostomus cristatus	B	X	-	-	C	-	-
C. owyhee	B	X	-	-	C	-	-
C. shoshonensis	B	X	-	-	C	-	-
C. sp.	B	S	-	-	-	-	R
Chasmistes spatulifer	U	X	-	-	R	-	-
Acrocheilus latus	B	X	-	-	-	-	R
Idadon condonianus	L	X	-	R	-	R	-
I. hibbardi	L	X	-	-	-	-	R
Mylocheilus inflexus	L	R	-	-	-	C	-
M. robustus	B	X	-	-	-	C	-
Orthodon hadrognathus	B	X	-	-	-	-	R
O. onkognathus	L	S	-	-	-	-	R
Ptychocheilus arciferus	B	X	C	-	-	-	-
Unident. dentary	B	X	-	-	-	-	R
Ictalurus vespertinus	B	X	-	C	-	-	-
Archoplites taylori	B	X	-	C	-	-	-
Cottus calcatus	L	-	-	R	-	-	-
Kerocottus divaricatus	U	X	-	R	-	-	-
Myoxocephalus sp.	L	S	-	R	-	-	-
Cottidae (unident.)	L	?	-	R	-	-	-

L - found in lower Deer Butte Formation only
U - found in upper Deer Butte Formation only
B - found in both upper and lower Deer Butte Formation
X - present
S - closely related species present
R - uncommon in fauna
C - common in fauna

The magnitude of the evolutionary changes between the Deer Butte and Glenns Ferry faunas appears to be less than the changes between the Glenns Ferry and Recent faunas, indicating a shorter time, less ecological disruption, or both between the deposition of the Glenns Ferry and the Deer Butte formations.

ACKNOWLEDGMENTS

This project was inspired, encouraged, and improved by the advice and assistance of Gerald R. Smith. He provided both the initial stimulus and ongoing encouragement in ways too numerous to list. Karoly Kutasi did part of the photography; he advised and aided in the rest.

Collections were made by the R.R. Miller field party, 1962, and the G.R. Smith field parties of 1971, 1972, 1974, and 1975. Leland Crummett donated the *Ptychocheilus* skull UMMP 45321, and Sylvia Chappell collected material in 1975. Leland Crummett, Nina Salomon and Gladys Swigert pointed out fossil localities. The Arthur Shenk family allowed collecting on their property. Gerry Smith, Bruce Wilkinson, Joe McGowan, and Dwight Taylor made helpful suggestions in discussions. The paper was edited by G.R. Smith and Nancy Friedland and prepared for publication by Nancy Friedland.

The Scott Turner Fund, University of Michigan, provided financial assistance.

LITERATURE CITED

Armstrong, R.L., W.P. Leeman, and H.E. Malde. 1975. K-Ar dating, Quaternary and Neogene volcanic rocks of the Snake River Plain, Idaho. Amer. J. Sci., 275:225-251.

Bailey, R.M., and C.E. Bond. 1963. Four new species of freshwater sculpins, genus *Cottus*, from western North America. Occ. Pap., Mus. Zool. Univ. Michigan, 634:1-27.

Beaulieu, J.D. 1972. Geologic formations of eastern Oregon (east of longitude 121 degrees 30 minutes). Oregon Dept. Geol. Min. Indus. Bull., 73:1-80.

Bowen, R.G., W.L. Gray, and D.G. Gregory. 1963. General geology of the northern Juntura Basin. *In* J.A. Shotwell (ed.), The Juntura Basin. Trans. Amer. Philos. Soc., 53(1):22-34.

Bryan, K. 1929. Geology of reservoir and dam sites with a report on the Owyhee irrigation project, Oregon. U.S. Geol. Surv. Water Sup. Pap. 597A:1-89.

Cope, E.D. 1870. On the fishes of a fresh water Tertiary in Idaho, discovered by Capt. Clarence King. Proc. Amer. Phil. Soc., 11:538-547.

Corcoran, R.E., et al. 1962. Geology of the Mitchell Butte quadrangle, Oregon. Oregon Dept. Geol. & Min. Indus., Map GMS2.

Kittleman, L.R., Jr., et al. 1965. Cenozoic stratigraphy of the Owyhee region, southeastern Oregon. Univ. Oregon Mus. Nat. Hist. Bull., 1:45 pp.

Kittleman, L.R., Jr., et al. 1967. Geologic map of the Owyhee region, Malheur County, Oregon. Univ. Oregon Mus. Nat. Hist. Bull., 8.

Lundberg, J.G. 1975. The fossil catfishes of North America. Univ. Michigan Mus. Paleont. Pap. Paleont., 11:1-51.

Miller, R.R., and G.R. Smith. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occ. Pap. Mus. Zool. Univ. Michigan, 654:1-24.

Robbins, C.R., and R.R. Miller. 1957. Classification, variation, and distribution of the sculpins, genus *Cottus*, inhabiting Pacific slope waters in California and southern Oregon, with a key to the species. California Fish & Game, 43(3):213-233.

Smith, G.R. 1975. Fishes of the Pliocene Glenns Ferry Formation, southwest Idaho. Univ. Michigan Mus. Paleont. Pap. Paleont., 14:1-68.

Wheeler, H.E., and E.F. Cook. 1954. Structural and stratigraphic significance of the Snake River capture, Idaho-Oregon. J. Geol., 62:525-536.

PAPERS ON PALEONTOLOGY: NO. 14

G.R. SMITH: GLENNS FERRY FISHES
P.G. KIMMEL: DEER BUTTE FISHES