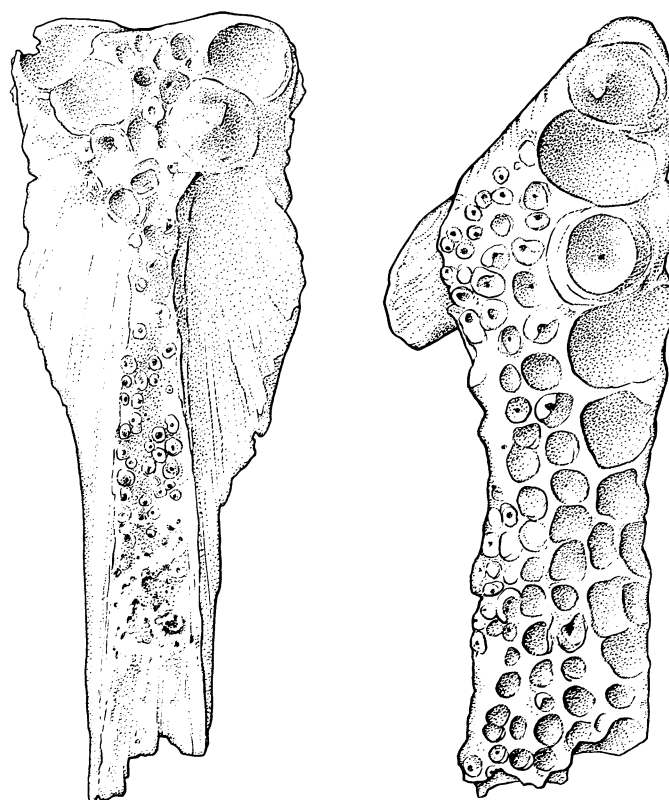


FISHES OF THE MIO-PLIOCENE RINGOLD FORMATION,
WASHINGTON: PLIOCENE CAPTURE OF THE
SNAKE RIVER BY THE COLUMBIA RIVER

GERALD R. SMITH, NEIL MORGAN, and ERIC GUSTAFSON



Esox columbianus

PAPERS ON PALEONTOLOGY — RECENT NUMBERS

22. Systematics of the Fissiculate Blastoidea by *D. Bradford Macurda* (1983)
23. Epizoans on the Brachiopod *Paraspirifer bownockeri* (Stewart) from the Middle Devonian of Ohio by *Diana K. Sparks, Richard D Hoare, and Robert V. Kesling* (1980)
24. Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming by *Philip D. Gingerich (ed.) and others* (1980)
25. Dimorphic Middle Devonian Paleocopan Ostracoda of the Great Lakes Region by *Robert V. Kesling and Ruth B. Chilman* (1987)
26. The Clarkforkian Land-Mammal Age and Mammalian Faunal Composition across the Paleocene-Eocene Boundary by *Kenneth D. Rose* (1981)
27. The Evolutionary History of Microsypoidea (Mammalia, ?Primates) and the Relationship between Plesiadapiformes and Primates by *Gregg F. Gunnell* (1989)
28. New Earliest Wasatchian Mammalian Fauna from the Eocene of Northwestern Wyoming: Composition and Diversity in a Rarely Sampled High-Floodplain Assemblage by *Philip D. Gingerich* (1989)
29. Evolution of Paleocene and Eocene Phenacodontidae (Mammalia, Condylarthra) by *J. G. M. Thewissen* (1990)
30. Marine Mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: Stratigraphy, Age, and Paleoenvironments by *Philip D. Gingerich* (1992)
31. Terrestrial Mesonychia to Aquatic Cetacea: Transformation of the Basicranium and Evolution of Hearing in Whales by *Zhexi Lou and Philip D. Gingerich* (1999)
32. Fishes of the Mio-Pliocene Ringold Formation, Washington: Pliocene Capture of the Snake River by the Columbia River by *Gerald R. Smith, Neil Morgan, and Eric Gustafson* (2000)

FISHES OF THE MIO-PLIOCENE RINGOLD FORMATION, WASHINGTON:
PLIOCENE CAPTURE OF THE SNAKE RIVER BY THE COLUMBIA RIVER



Frontispiece (top): White Bluffs, east of the Columbia River, Franklin County, Washington.

Frontispiece (bottom): Snake River, looking downstream toward the Oxbow and Hells Canyon, Adams County, Idaho, and Baker County, Oregon.

**FISHES OF THE MIO-PLIOCENE RINGOLD FORMATION,
WASHINGTON: PLIOCENE CAPTURE OF THE
SNAKE RIVER BY THE COLUMBIA RIVER**

GERALD R. SMITH

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48109-1079

NEIL MORGAN

Taunton Bench Project, 300 E. Fir
Othello, Washington 99344

and

ERIC GUSTAFSON

1795 West 17th
Eugene, Oregon 97402

UNIVERSITY OF MICHIGAN
PAPERS ON PALEONTOLOGY NO. 32

2000

Papers on Paleontology No. 32

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48109-1079

Philip D. Gingerich, Director

Published December 22, 2000



TABLE OF CONTENTS

<p>Frontispiece ii</p> <p>Title page iii</p> <p>Table of Contents v</p> <p>List of Figures vi</p> <p>List of Tables vi</p> <p>Abstract vii</p> <p>I. Introduction 1</p> <p style="padding-left: 20px;">Institutional Abbreviations 2</p> <p style="padding-left: 20px;">Acknowledgments 2</p> <p>II. Ringold Paleontology in the Pasco and Quincy Basins 5</p> <p>III. Description of Localities and Collections 7</p> <p style="padding-left: 20px;">Priest Rapids Dam 7</p> <p style="padding-left: 20px;">River Road Local Fauna 7</p> <p style="padding-left: 20px;">White Bluffs Local Fauna 7</p> <p style="padding-left: 20px;">Blufftop Local Fauna 7</p> <p style="padding-left: 20px;">Taunton Local Fauna 8</p> <p style="padding-left: 20px;">Moses Lake 8</p> <p style="padding-left: 20px;">Lind Coulee 9</p>	<p>IV. Fish Species Accounts 11</p> <p style="padding-left: 20px;">Family Acipenseridae 11</p> <p style="padding-left: 20px;">Family Cyprinidae 11</p> <p style="padding-left: 20px;">Family Catostomidae 15</p> <p style="padding-left: 20px;">Family Ictaluridae 16</p> <p style="padding-left: 20px;">Family Salmonidae 20</p> <p style="padding-left: 20px;">Family Esocidae 20</p> <p style="padding-left: 20px;">Family Centrarchidae 24</p> <p>V. Biogeography 29</p> <p style="padding-left: 20px;">Biogeographic Background on Ringold Fishes ... 29</p> <p style="padding-left: 20px;">Ringold and Snake River Faunas 31</p> <p style="padding-left: 20px;">Estimation of Hydrographic Connections 31</p> <p>VI. Ringold History and Pliocene Drainage 35</p> <p style="padding-left: 20px;">Columbia River and Pasco Basin 35</p> <p style="padding-left: 20px;">Timing of the Snake River Capture 36</p> <p style="padding-left: 20px;">Connections to the Hudson Bay Drainage 37</p> <p style="padding-left: 20px;">Pliocene Climate of the Pasco Basin 37</p> <p>VII. Significance for Models of Geographic Differentiation 39</p> <p>VIII. Summary and Conclusions 41</p> <p>IX. Literature Cited 43</p>
--	---

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>	<u>Figure</u>	<u>Page</u>
1. Map of Columbia Basin with Ringold Formation	3	8. <i>Catostomus macrocheilus</i>	17
2. Topographic and stratigraphic relationships of Ringold faunas.	6	9. <i>Ameiurus reticulatus</i> n. sp.	18
3. <i>Acipenser transmontanus</i>	12	10. <i>Oncorhynchus rastrosus</i>	20
4. <i>Mylocheilus heterodon</i> n. sp.	13	11. <i>Esox columbianus</i> , n. sp.	21
5. <i>Ptychocheilus arciferus</i>	14	12. <i>Esox columbianus</i> , n. sp.	22
6. <i>Klamathella milleri</i> , <i>Acrocheilus latus</i> , <i>Lavinia</i> <i>hibbardi</i>	15	13. <i>Archoplites molarus</i> n. sp.	25
7. <i>Chastmistes</i> cf. <i>batrachops</i>	16	14. <i>Archoplites molarus</i> n. sp.	26
		15. <i>Archoplites molarus</i> n. sp.	27

LIST OF TABLES

1. Pliocene fishes of the Glenns Ferry and Ringold Formations	32
---	----

ABSTRACT

Three rich, warm-water fish faunas occur in the Pliocene section of the Ringold Formation, near the Columbia River-Snake River confluence in south-central Washington. The fish fossils are in or near the Pasco Basin, where they accompany three mammalian local faunas of Blancan land mammal age. The White Bluffs local fauna is the earliest of the three Pliocene faunas. It is known from many localities at about 182 m (600 ft) elevation in fluvial sediments in the bluffs east of the Columbia River from 9 to 29 km north of Richland, in Franklin County, Washington. The age of the White Bluffs fauna is estimated to be 4.5 Ma. The White Bluffs fishes include *Acipenser transmontanus* (sturgeon), *Esox columbianus* n. sp. (muskellunge), *Chasmistes* cf. *batrachops* (lake sucker), *Ameiurus reticulatus* n. sp. (bullhead catfish), and *Archoplites molarus* n. sp. (sunfish). The Blufftop Locality and local fauna occurs near the northern localities of the White Bluffs local fauna in the Pasco Basin, stratigraphically higher in the Ringold Formation, at 242 m (800 ft) in elevation. Its age is middle Pliocene, about 3.7 Ma. The Blufftop fish fauna is lacustrine, and includes *Acipenser transmontanus*, *Esox columbianus*, *Catostomus macrocheilus* (largescale sucker), *Chasmistes* cf. *batrachops*, *Ptychocheilus arciferus* (northern pikeminnow), *Mylocheilus heterodon* n. sp. (Ringold peamouth chub), *Ameiurus reticulatus*, and *Archoplites molarus*. The Taunton Locality is between the Pasco and the Quincy Basins, in Adams County, Washington, 27 km north of the Blufftop locality. It is stratigraphically the highest of the three faunas, at 285 m (933 ft) in elevation. Its age is late Pliocene, 2.8-3.0 Ma. Fishes of the Taunton local fauna inhabited rivers and floodplains. The Taunton fish fauna includes all of the White Bluffs and Blufftop fish species, with the added presence of *Klamathella milleri* (Snake River chub), *Acrocheilus latus* (Snake River chiselmouth chub), and *Lavinia (Idadon) hibbardi* (Snake River hitch).

The Pliocene White Bluffs section of the Ringold Formation contains no salmonid fishes, indicating its separation from the lower Columbia River and the Pacific Ocean by temperature and hydrographic barriers. In the Miocene, the large salmon *Oncorhynchus (Smilodonichthys) rastrosus* occurred in the River Road local fauna near the base of the White Bluffs. *Oncorhynchus rastrosus* is known otherwise from marine and freshwater deposits along the Pacific coast; its presence suggests a connection between the eastern Pasco Basin and the Pacific in the late Miocene.

The White Bluffs and Blufftop faunas share only six of their eight genera and two of their eight species with contemporaneous faunas of the Snake River Plain, indicating a lack of hydrographic connection between the Clearwater-Salmon drainage and the Snake River Plain during the early and middle Pliocene. The Taunton fauna includes rare bones of three species from the Pliocene fauna of Lake Idaho, suggesting initiation of a connection between the Pasco Basin and Snake River Plain before 2.8 Ma. After the latest Pliocene, *Esox*, *Ameiurus*, *Idadon*, *Klamathella milleri*, *Mylocheilus heterodon*, and *Archoplites* became extinct in the Pasco Basin and Columbia drainage. *Acipenser*, *Catostomus*, *Chasmistes*, *Acrocheilus*, *Mylocheilus caurinus*, and *Ptychocheilus* survived in the Recent Columbia-Snake River drainage. Two of five measurable lineages changed morphologically during the Pliocene period represented in the Pasco Basin. Differentiation of the Columbia and Snake River forms was initiated by isolation in the late Miocene or before.

I

INTRODUCTION

Late Cenozoic volcanic, tectonic, and hydrologic events in the Columbia Basin created a sequence of interbedded volcanic and sedimentary units providing evidence for shifting channels, dissociation of drainages, and stream captures (Fecht et al., 1985; Waitt and Swanson, 1987). This hydrographic history is important to understanding the time scale for evolution of fish faunas in the region (Smith et al., 1984) because origin of new species depends, in part, on the duration of isolation of populations in different drainages. In this study, we describe late Miocene and Pliocene fish fossils from the eastern Ringold Formation in the Pasco and Quincy basins, near the center of the Columbia Basalt Basin. We discuss fish biogeography in relation to climatic and hydrographic history of the lower Columbia River, the upper Columbia River, the Clearwater-Salmon River, and the Snake River after deposition of the Columbia River Basalt Group.

The Columbia River history interested early geomorphologists because of the circuitous routes of the Spokane and Columbia rivers around the northern margin of the Columbia basalts and incision of the Columbia and Yakima rivers through folds on the Columbia Basalt Plain (Fig. 1; Flint, 1938; Waters, 1955; Mackin, 1961). Subsequent mapping of dated basalts and identification of sources of many intercalated sedimentary units provided a detailed 15 million year history of migrating channels of the Columbia, Yakima, Palouse, and Clearwater-Salmon rivers across the Columbia Basin (Schmincke, 1967; Swanson et al., 1980; Fecht et al., 1985; Waitt and Swanson, 1987). Fossil fishes are linked to sedimentary responses to constructional topography created by Columbia Group basalt flows, Cascade siliciclastic volcanics and uplift of east-west anticlines in the western basin (Reidel, 1984). But the fish faunas reported here raise questions about how the eastern Pasco Basin was connected to the Snake River, the Columbia River, and the sea in the Pliocene.

One of the largest drainage changes in the Columbia drainage history involves capture of the Snake River. The Plio-Pleistocene history of the Snake River in relation to the Columbia became a focus of biogeographic research after Wheeler and Cook (1954) demonstrated that incision of Hells Canyon is a

young feature that changed the west-flowing Snake River to a north-flowing Columbia River tributary (Malde, 1991). Fossil and recent aquatic organisms from Idaho, Oregon, California, and Nevada were studied to test the Pleistocene capture hypothesis of Wheeler and Cook (Taylor 1960, 1985; Miller, 1965; Miller and Smith, 1967; Smith, 1981a,b; Taylor, 1985; Taylor and Bright, 1987; Wagner et al., 1997) with qualified support. But Repenning et al. (1995) argued that the Hells Canyon connection was as old as Pliocene or late Miocene and that previous drainage from the western Snake River Plain was directly south through Nevada or Utah, then west to California.

New concepts of stratigraphy and evolution emerged from these studies. It was demonstrated that organic evolutionary change is slow relative to frequent tectonic and drainage changes (Taylor, 1960, 1985), providing a new framework for analysis of relative chronology of evolutionary and geological change. Detailed correlations of mammalian stratigraphy and magnetic reversal (Repenning et al., 1995) enabled refinement of hypotheses about chronology.

The Ringold faunas reported here bear on drainage history because the fishes lived in the Pasco and Quincy basins, less than 80 km north of the present confluence of the Columbia River with the Clearwater-Salmon-Snake River (Fig. 1) in sediments with good stratigraphic control (Gustafson, 1978; Tallman et al., 1979; Myers/Price et al., 1979; Morgan and Morgan, 1995). Although the faunas are limited to the east side of the basin, their lengthy Pliocene persistence in the White Bluffs and eastern Saddle Mountains areas contribute to the history of the Columbia, Clearwater, Salmon, and Snake drainages (Fig. 1) during the period of interest here. The sediments containing the fish reported here were apparently independent of the Columbia, which flowed southwest through the lower Yakima basin to the Columbia River Gorge area near Goldendale, during early Ringold history (Fecht et al., 1985: 34, fig. 12) and possibly later (Reidel, 1984, pers. comm.).

The eastern Ringold sediments are associated with the Clearwater drainage (Fecht et al., 1985; Waitt and Swanson, 1987). The Clearwater-Salmon River flowed westward through various channels across the Palouse slope to the eastern Pasco

Basin through much of the late Miocene (Fecht et al., Waitt and Swanson, 1987), then southward through Wallula Gap (Fig. 1), but its Late Miocene and early Pliocene locations are not entirely clear. "The composition of gravel clasts indicative of the ancestral Clearwater-Salmon River are rarely found in the Snipes Mountain conglomerate" near the lower Columbia west of the Pasco basin and south of Yakima.

The pattern of presence and absence of fishes in the Pasco Basin may help evaluate hypotheses about the Clearwater-Salmon River sedimentation in the Pasco Basin. We investigate hydrologic barriers by examining the relationships of the Ringold fishes to surrounding faunas. Evolved differences between sister species in adjacent drainages indicate lack of gene flow and therefore lack of aquatic connections. Absence of species and genera known to be in surrounding drainages indicates ecological or hydrographic barriers. Absence of migratory salmon known to be in the eastern Pacific indicates barriers. Temperature requirements of the Ringold fishes, inferred from the temperature requirements of their modern relatives and oxygen isotopes in fossil bone, constrain hypotheses about the kinds of habitats, habitat barriers, and sources of waters in the basin.

INSTITUTIONAL ABBREVIATIONS

Fossils and comparative specimens are deposited in:
UM — University of Michigan Museum of Paleontology
UMMZ — University of Michigan Museum of Zoology
UWBM — University of Washington Burke Museum

ACKNOWLEDGMENTS

Illustrations of fish bones and the map were prepared by Bonnie Miljour. Rosario Cervantes assisted with the collection of fossils. James K. Morgan assisted with extensive field work, stratigraphic information, useful discussions, and helped with the manuscript. William Sanders of the University of Michigan Museum of Paleontology assisted in fossil preparation, Jonathon Bloch and Ross Secord sorted, counted, and catalogued many Taunton and Blufftop specimens. Karl Fecht, Steve Reidel, and Kevin Lindsey were tremendously helpful in reviewing the manuscript and the hypotheses presented here, but they are not responsible for errors that still remain. Catherine Badgley read the manuscript and made helpful suggestions. Cheryl Zello organized the Literature Cited.

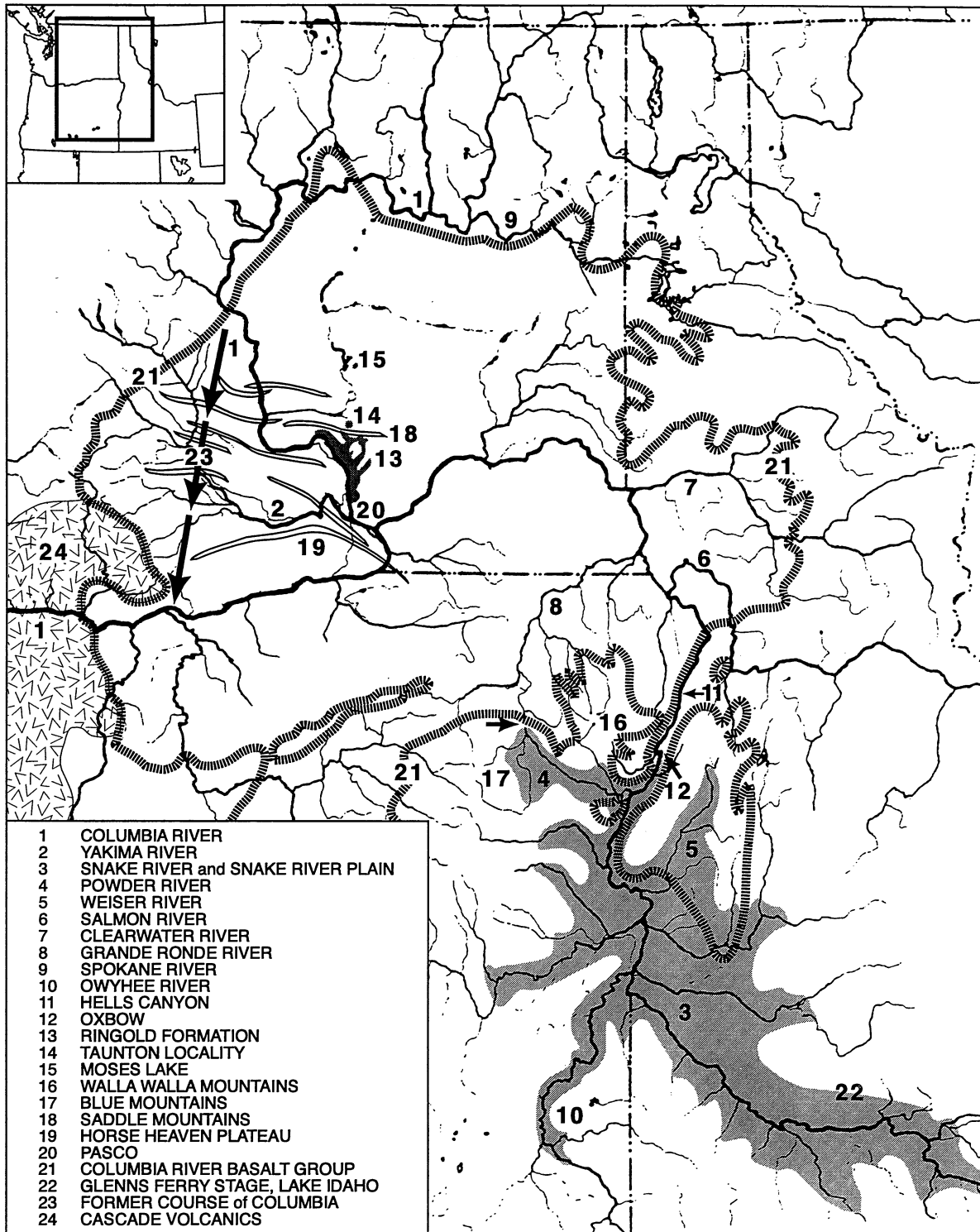


FIGURE 1 — Map of Columbia Basin with Ringold Formation and related drainages.

II

RINGOLD PALEONTOLOGY IN THE PASCO AND QUINCY BASINS

The Pasco Basin became the center of subsidence in the Columbia Basin in the late stages of deposition of the Columbia River Basalt Group in the late Miocene, at 8.5 Ma (McKee et al., 1977). It then became the site of deposition of the Ringold Formation, 300 m of fluvial and lacustrine silts, sandstone, and conglomerates (Newcomb et al., 1972) with some interbedded paleosols (Lindsey, 1991). Ringold sediments are widespread and not thoroughly explored for fossils, but in Franklin, Benton, and Adams counties, Washington, three rich, Pliocene fish horizons (Fig. 2a), several less productive localities, and one Miocene fish locality have been collected. These Ringold sediments were deposited in Hemphillian through Blancan time, as the gradient of the Columbia and Salmon-Clearwater River systems was reduced (Gustafson, 1978; Fecht et al., 1985; Waitt and Swanson, 1987). Sedimentation has been attributed to Late Miocene and Pliocene subsidence of the Pasco basin and uplift and folding of the Horse Heaven anticline (Flint, 1938; Warren, 1941; Waitt and Swanson, 1987) in response to NNW-SSE compression (Camp, 1981; Camp and Hooper, 1981).

Gustafson (1978) studied the Late Miocene River Road local fauna, including bones of fossil rhinoceros and migratory Pacific salmon from the base of the White Bluffs section. Ringold/Pasco drainage was tributary to the lower Columbia River at this time according to Fecht et al. (1986, fig. 13). The upper Columbia did not enter the White Bluffs area until 5 Ma (Waitt and Swanson, 1987, fig. 8) or later (Reidel, 1984) so was probably not a source of White Bluffs or Taunton sediments. The middle of the White Bluffs section includes a gravel unit with clasts suggesting sources in the Clearwater-Salmon system (Gustafson, 1978; Waitt and Swanson, 1987).

The stratigraphically lowest Pliocene localities in the bluffs on the east side of the modern Columbia River (Fig. 2a, 2b), are referred to as the White Bluffs local fauna (Gustafson, 1978). The middle Pliocene localities are included in the Blufftop local fauna, the name of which reflects the modern topographic position of these localities. The stratigraphically and topographically highest is the Taunton Local Fauna at Taunton Bench on the north side of the Saddle Mountains anticline, 27 km north of Blufftop. The White Bluffs and Blufftop sediments were described as the Ringold Formation by Merriam and Buwalda (1917) and studied by Newcomb (1958), Brown and McConiga (1960), Newcomb et al. (1972), Fry and Gustafson (1974), Tedford and Gustafson (1977), and Gustafson (1978, 1985). The Taunton sediments, between the Pasco and Quincy Basins, were referred to as the Ringold Formation by Culver (1937) and Morgan and Morgan (1995).

The Ringold Formation extends north and west of Taunton (Grolier and Bingham, 1971). Collections of fossil fish bones from northern Ringold sediments at Lind Coulee and Moses Lake are deposited in the Burke Museum. Three species of fishes similar to those reported here were identified from Moses Lake by R. R. Miller (Gustafson, 1978). Fish data presented below suggest no significant isolation between the Pasco and Quincy basins by the Saddle Mountains anticline.

Prior paleontological interest in the Ringold faunas has focused on the diverse Blancan mammal remains, listed below (Fry and Gustafson, 1974; Tedford and Gustafson, 1977; Gustafson, 1978, 1985; Morgan and Morgan, 1995).

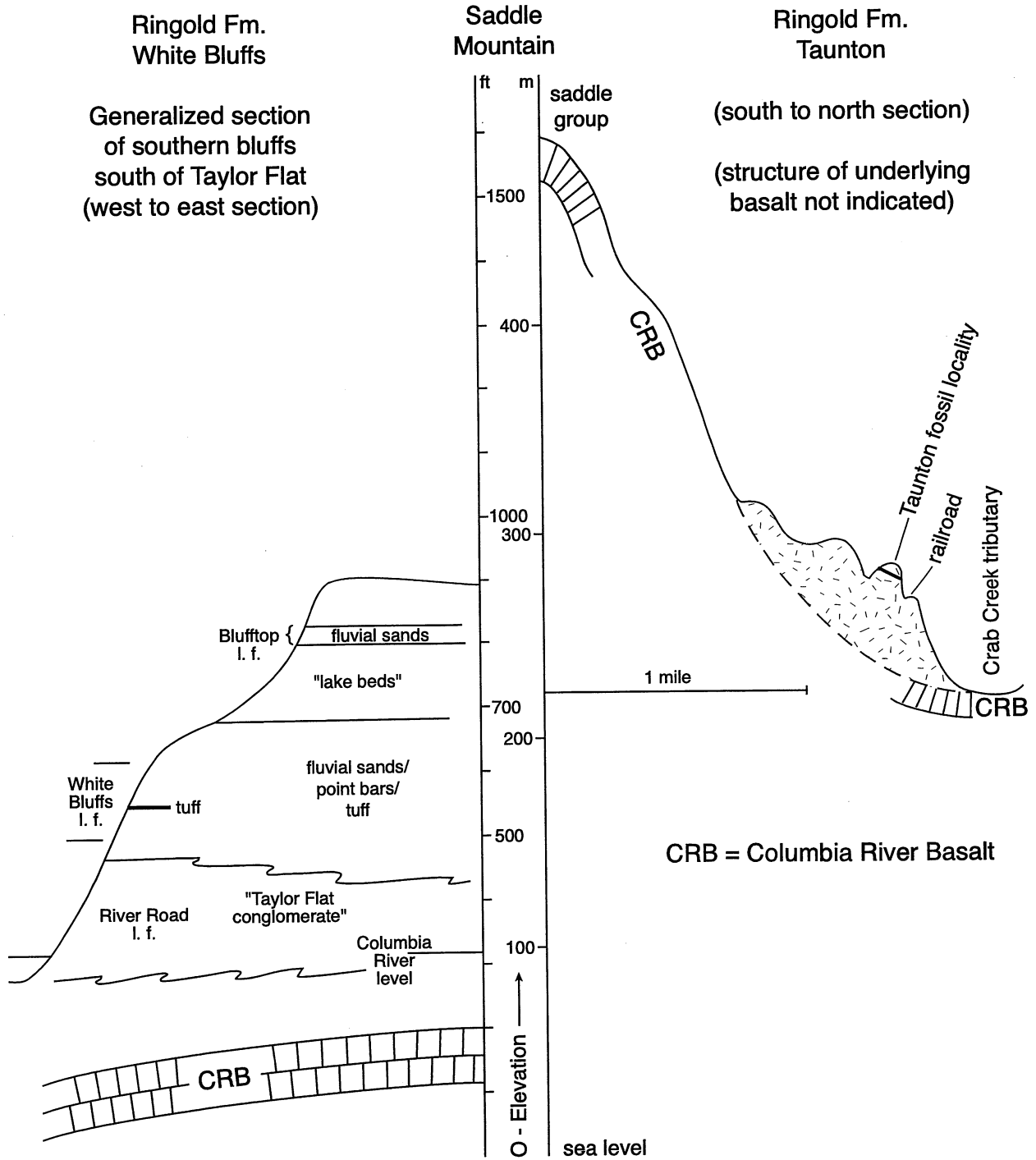


FIGURE 2 — Topographic and stratigraphic relationships of Ringold faunas. Vertical scale exaggerated.

III

DESCRIPTION OF LOCALITIES AND COLLECTIONS

Priest Rapids Dam.— The earliest known fish specimen from the vicinity is a pharyngeal arch collected by Steve Reidel from a thin, fluvial sedimentary unit within the basalts dated at about 15 Ma near Priest Rapids Dam, Yakima County, Washington (Karl R. Fecht, Hanford AEC Reservation, personal communication, with photographs). The pharyngeal arch is complete, and readily recognizable as belonging to a 40 cm long specimen of the pikeminnow, *Ptychocheilus*.

River Road Local Fauna.— Gustafson named the Late Miocene River Road Local Fauna from basal sediments under the Taylor Flat Conglomerate at White Bluffs (UWBM CO479). The Miocene rhinoceros, *Teleoceras*, is the basis for the age determination. Also present were two right dentaries, 136 mm and 124 mm long, and a vertebra 40 mm in diameter of *Oncorhynchus* (*Smilodonichthys*) *rastrosus*. This giant Pacific salmon is known otherwise from the Miocene of coastal California and inland southern Oregon (Cavender and Miller, 1972; Starley and Smith, 1993). It was an anadromous fish more than 1 m long (Cavender and Miller, 1972).

White Bluffs Local Fauna.— Numerous White Bluffs localities occur from about 9 km to 28 km north of Richland in Franklin County, Washington, at 150-194 m (500-640 ft) (Gustafson, 1978). The localities are all in the bluffs east of the Columbia River. They are documented as University of Washington Burke Museum (UWBM) localities A3030, A5132, A5135, A6503, A6520, A8811, A8819, A9328, and A9851, many of which were mapped by Gustafson (1978, fig. 2). All of Gustafson's localities and presumably those of the other collectors as well are from channel, floodplain, and lake sediments within 50 ft of the White Bluffs tuff layer (Gustafson, 1978), above the Taylor Flats Conglomerate (fig. 2, Gustafson, 1978). There are two primary collecting levels. The Ringold Formation has experienced deformation sufficient to alter relative elevations by only a few tens of feet (Brown and McConiga, 1960). Isolated White Bluffs fish fossils were collected by V. S. Mallory in 1963, B. Witte in 1967, E. Gustafson in 1969-72, S. W. Robinson in 1971, and W. E. Fry in 1972, and deposited in the University of Washington Burke Museum. R. R. Miller previously identified a sample of White Bluffs fishes as *Ictalurus*

(=*Ameiurus*), *Archoplites*, and a "large unidentified salmonid" (here identified as *Esox*) (Gustafson, 1978:13-14).

Twenty-seven species of mammals, including *Scapanus* (mole), *Hypolagus ringoldensis* and *Nekrolagus* cf. *progressus* (rabbits), *Paenemarmota* or *Marmota* (woodchuck), *Spermophilus? russelli* and *Amnospermophilus hanfordi* (squirrels), *Thomomys* cf. *gidleyi* (pocket gopher), *Castor californicus* and *Dipoides rexroadensis* (beavers), *Peromyscus nosher* (deer mouse), *Neotoma* cf. *quadriplicatus* (woodrat), *Ophiomys mcknighti* (vole), *Borophagus* and *Canis davisi* (canids), *Ursus* cf. *abstrusus* (bear), *Felis* sp. and a machairodontine (cats), *Trigonichthys cooki* (mustellid), *Megalonyx rohrmanni* (sloth), *Mammut americanum* (mastodon), *Equus* (*Dolichohippus*) cf. *simplicidens* (zebra), *Platygonus pearcei* (peccary), *Megatylopus* cf. *cochrani* (camel), and *Bretzia pseudalces* (deer), were recorded from the White Bluffs by Gustafson (1978).

Gustafson showed that the White Bluffs mammals are more primitive than those from the Hagerman local fauna, Idaho. Morgan and Morgan (1995) compiled additional evidence for an age of 4.0-4.5 ma for the White Bluffs localities, based especially on the mammalian stratigraphy of Repenning (1987). The White Bluffs local fauna also includes fossil turtles, lizards, and frogs. Fossil fish, like other fossils, occur as sparse, disarticulated elements in the White Bluffs sediments, unlike at Blufftop and Taunton, where fishes are represented by concentrations of thousands of disarticulated bones.

Blufftop Local Fauna.— The Blufftop local fauna occurs in the SE 1/4 NE 1/4 Section 3, T. 12 N, R. 28 E, in Franklin Co., Washington, at 242 m (800 ft) elevation, Savage Island 72 minute Quadrangle (Fig. 2b; Gustafson, 1985). Additional localities include the Orchard or Haymaker's Orchard, about 1 mile north of the south end of the Bluffs, and the Ellner locality, UWBM CO149, (Fig. 2b; Gustafson, 1985). Most of the fish have been recovered from the two main sites, at two adjacent excavations in Pliocene lacustrine sediments — University of Washington Burke Museum localities CO150 and CO155, discovered by John Rensberger and Rick Forester. Gustafson (1985) reported other vertebrates from these sites

including *Paracryptotis rex* and *Sorex powersi* (shrews), *Ophiomys* cf. *mcknighti* (vole), as well as rabbit and deer. Gustafson recognized that this fauna was younger than the White Bluffs fauna and older than the Taunton fauna. He correlated these fossil localities to the Gilbert Reversed Epoch below the Cochiti event, based on correlations with a marker bed of Brown and McConiga (1960) and their paleomagnetic studies. Morgan and Morgan (1995) and Repenning (1995) also estimated the age of the Blufftop beds to be about 3.9 Ma based on mammalian remains and paleomagnetic stratigraphy. Blufftop fish fossils were recovered in great abundance in 1988 and 1997 by Neil H. Morgan, James K. Morgan, and Rosario Cervantes. Fossils are deposited in the University of Washington Burke Museum (UWBM) and the University of Michigan Museum of Paleontology (UM). Gustafson (1985) reported catfish, sunfish, and an unidentified salmonid from the Blufftop fauna. The unidentified salmonid fossils are muskellunge, *Esox*, described below. There are no salmonid fossils among the many thousands of Pliocene fish bones in the White Bluffs, Blufftop, and Taunton faunas.

Taunton Local Fauna.— The Taunton local fauna (UWBM locality A9236) is found between the Pasco and Quincy Basins, on the north slope of the Saddle Mountains anticline, 27 km north of Blufftop, 0.8 km E of Taunton, 13 km WSW of Othello, in southwestern Adams County, Washington. Culver (1937) extended the concept of the Ringold Formation widely, to include the Quincy Basin. Tedford and Gustafson (1977) described the Taunton sediments SW of Othello as “flat-lying fluvial deposits resembling those of the stratotype Ringold Formation at White Bluffs on the Columbia River.” Morgan and Morgan (1995) assigned the Taunton sediments near Othello to the Ringold Formation on the basis of symmetry across the Saddle Mountains anticline and similarity of context, lithology, paleomagnetism, age, and fauna. The Taunton excavation occurs in a 1 m layer of fluvial sediments on the north-facing crest of Taunton Bench, T. 15 N, R. 28 E, ctr. Sec. 8, at an elevation of 283–285 m (931–935 ft). The site is 9 km south of the southern outlet of the Drumheller Channels of the scablands eroded by Pleistocene catastrophic floods (Bretz 1923–1969). The sediments of Taunton bench were exposed in part by the floods.

During 1988–1992, the Taunton Bench project (N. H. Morgan, J. K. Morgan, R. Cervantes) recovered approximately 500,000 fish fragments from over 400 cubic yards of sediments excavated by layer and dry screened through 2", 1/4", 1/8", and standard window screen meshes. Most of the fossils were recovered from an allochthonous clay and fine clay-ball layer with little sand and rare basalt clasts, eroded into a basal clay layer. The fossiliferous layer was overlaid by a lighter clay with more sand, which was overlaid by a dark, coarse layer of clay, basalt sand, pebbles, and larger, dispersed fossils. The section was capped by a poorly-sorted coarse layer with limonite stain, then about 2 feet of disturbed overburden. The up-

per lenses were gently cross-bedded; flow direction was to the west. Personnel of the Taunton Bench Project sorted and catalogued fossils according to sedimentary unit and grid-map location of origin and deposited them in the University of Washington Burke Museum and the University of Michigan Museum of Paleontology.

Tedford and Gustafson (1977) and Gustafson (1985) reported 12 species of mammals from near the top of the 50 m thick Ringold beds at the Taunton site. Gustafson (1978) correlated the fauna with either the Hagerman l.f. of Idaho (below the Gilbert/Gauss boundary) or the Sand Point l.f. of Idaho (in a reversed interval above the Gilbert/Gauss boundary), 3.0–3.4 Ma, referring to a nearby paleomagnetic section of Packer and Johnston (1979). The microtine rodents, *Mimomys* (*Ophiomys*) *taylori*, from Taunton are identical to specimens from the Sand Point local fauna on the Snake River Plain. Examples from the Hagerman local fauna are slightly more primitive in some aspects of the teeth. White (1987, 1991) and White and Morgan (1995) suggested age correlation with the Hagerman local fauna on the basis of rabbit evolution. Repenning et al. (1995) suggested an age of the Taunton fauna of about 2.8 Ma. Morgan and Morgan (1994) assigned the Taunton l.f. to the Kaena subchron of the Gauss chron, biostratigraphically between the Hagerman l.f. and Grand View l.f. of the Snake River Plain. They estimate the age to be between 2.8 and 3.0 Ma, similar to the Sand Point l.f., based on mammalian evidence (Repenning, 1987) and lateral correlation with Packer and Johnson's (1979) paleomagnetic section 0.75 km west of the Taunton fossil beds (Packer, 1979).

The Taunton mammalian fauna is now known to include 45 species (Morgan and Morgan, 1995) — two shrews, five rabbits, sloth, three squirrels, two gophers, kangaroo rat, pocket mouse, two beavers, woodrat, vole, muskrat, six mustelids, four canids, bearded dog, bear, raccoon, ringtail, extinct panda (*Parailurus*), three cats, zebra, peccary, two camels, deer, and pronghorn (Tedford and Gustafson, 1977; Gustafson, 1985; White, 1987, 1991; Morgan and Morgan, 1995). These mammals, plus associated turtles, snakes, and birds, indicate lowland, moist, equable mixed forest and grassland depositional environment, perhaps in a semi-arid region. The fish fauna indicates permanent fluvial, floodplain, and oxbow lake habitats with an abundant source of water, warmer winters than today, and long, moderate summers. Morgan and Morgan (1995) list a total of 60 species of vertebrates from the site. Several Taunton fish species, including a catfish and a sunfish, were correctly identified by Paul Principe in a Master's thesis at the University of Massachusetts (1977). Additional Taunton specimens are deposited at the University of Oregon Museum, Eugene, and the Los Angeles County Museum.

Moses Lake.— The Ringold Formation extends considerably north, west, and east of Taunton in the Quincy Basin. A small sample of three species of fishes, at least two of which are probably the same as species of Ringold fishes described

here, were collected at Moses Lake, 36, km north of Othello at an elevation of 364 m (1190 ft) by M. J. Grolier, who tentatively assigned them to the Ringold Formation (letter to R. R. Miller, March 29, 1964). Miller identified them as *Ictalurus* (= *Ameiurus*), *Archoplites*, and unidentified minnow teeth (Miller, unpublished; Gustafson, 1978).

Lind Coulee.— Sediments from the Quincy Basin at Lind Coulee have also been referred to the Ringold Formation

(Grolier and Bingham, 1971). Paleontologists collected fishes for the Burke Museum (UWBM loc. A9325) from Lind Coulee, 20 km north of Othello in the Quincy Basin, Grant/Adams counties, Washington, at about 400 m (1300 ft) elevation. The fossils are catalogued as UWBM 42449, 72080, and 72081. The fish species, *Catostomus* (suckers), *Mylocheilus* (minnows), *Ameiurus* (catfish), and *Archoplites* (sunfish) are similar to those at Taunton.

IV

FISH SPECIES ACCOUNTS

Final identifications of the fish fossils are based on comparisons with fossils and recent osteological specimens in the Museum of Paleontology and Museum of Zoology at the University of Michigan.

FAMILY ACIPENSERIDAE

Acipenser Linnaeus

Acipenser transmontanus Richardson 1836, white sturgeon
(Fig. 3a, b)

The white sturgeon is represented by bony skull plates and scutes from three Pliocene Ringold localities. External texture of the plates consists of rounded tubercles on radiating ridges, typical of *Acipenser transmontanus*. Plates of American species are similar to each other; the identification is based on geography as well as morphology. Only *Acipenser transmontanus* occurs in the upper Columbia and Snake Rivers today. The fossil specimens have the same texture as head plates and body scutes of Recent *Acipenser transmontanus*, UMMZ 185163 (ca 160 cm long), from the Snake River near Hagerman, Idaho.

This species is often anadromous, migrating into rivers in the spring and out to the sea in the fall, but migration to the sea is not obligatory (Carl et al., 1967; Brown, 1971). Suitable spawning habitats range from 10-18°C, with water depth of 5-25 m, mean velocity of 0.8-2.8 m/sec, and preferred substrate of gravel, cobbles, or boulders (Parsley and Beckman, 1994). Adults tolerate temperatures ranging from 0° to 23.3°C (Scott and Crossman, 1973). Growth is slow, e.g., 65 cm body length and 8.5 kg weight by the 8th year (approximate age of the fossil specimens). The maximum known size is an anadromous specimen, 670 kg, from the Fraser river (Scott and Crossman, 1973).

Referred Material.— **White Bluffs l.f.:** UWBM 79561 (CO 623), scute, 19 x 10 mm. **Blufftop l.f.:** UWBM 56098, scute, 20 x 10 mm; UWBM 56099, scute, 19 x 18 mm; UWBM 81829, scute, 18 x 22 mm; UWBM 81853, scute, 15 x 24 mm; UWBM 84081, 1 dorsal head plate, 15 mm x 38 mm (UWBM loc. CO155, Fig. 3a); UM 103932, dorsal head plate, 7 mm x 24 mm, (UWBM loc. CO150, Fig. 3b); UM 103934, 1 scute, 16

mm long; UM 105015, 7 scutes; UWBM 84082-88, 7 scutes. **Taunton l.f.:** UWBM 84089, plate, 25 mm x 22 mm.

FAMILY CYPRINIDAE

Mylocheilus Agassiz 1855

Mylocheilus heterodon new species, Ringold peamouth chub
(Fig. 4a-4g)

Mylocheilus is represented in the Blufftop and Taunton assemblages by small pharyngeal arches bearing extraordinarily modified molariform pharyngeal teeth. The teeth are the most specialized teeth known in fossil or Recent *Mylocheilus*, and along with *Stypodon*, the stump-tooth minnow of Coahuila, Mexico, the most specialized pharyngeal teeth known in North American cyprinids. *Mylocheilus* is currently known from several Miocene and Pliocene species from the Lahontan and Bonneville basins, Snake River Plain, and Klamath region, as well as the Recent *Mylocheilus caurinus* of the Columbia drainage. The fossil forms each possess apomorphies making it unlikely that any is directly ancestral to the modern form.

Mylocheilus bones and teeth are abundantly represented at Blufftop and Taunton, but no specimens have been collected from the White Bluffs local fauna. This implies that the lineage appeared in the drainage about four million years ago, fully specialized and remarkably different from the Miocene and Pliocene relatives to the south, in the Snake, Lahontan, Bonneville, and Klamath drainages. We infer derivation from the north. *Mylocheilus* has long been regarded as part of the western clade of North American minnows (Coburn and Cavender, 1993), but mtDNA sequences indicate that it is an ancient relative of the shiner clade centered in eastern North America (T. Dowling, unpublished data; Smith et al., in press).

Diagnosis.— Recognized as *Mylocheilus* by the short anterior limb and the short dorsal limb of the pharyngeal arch, the enlarged molariform second and third teeth, which are round or elliptical in cross-section, with smooth, flat crushing surfaces (unique among North American Cyprinidae). *Mylocheilus heterodon* differs from all other *Mylocheilus* and *Mylopharodon*, and all other known fishes, in the unique enlargement of the second pharyngeal tooth, its length approximately equal to the

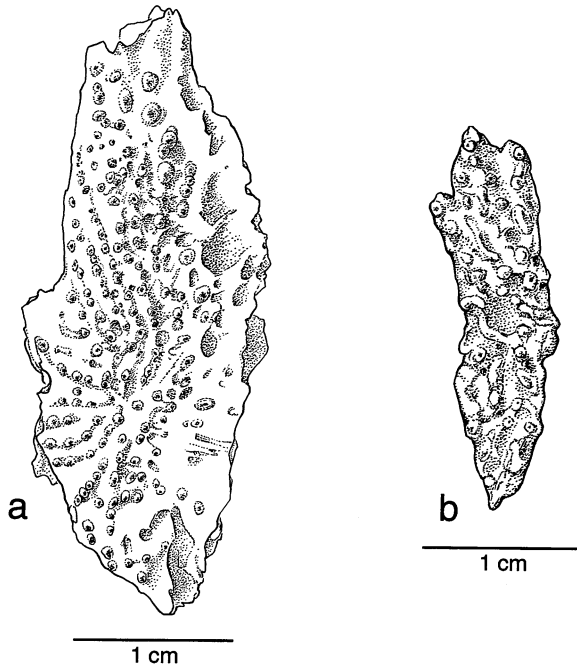


FIGURE 3 — *Acipenser transmontanus* from Blufftop, dermal plates: a, UWBM 84081; b, UM 103932.

length of the anterior limb of the arch, extending along the arch to occupy up to 50% of the length of the tooth row, spanning the space normally occupied by the first two teeth (Fig. 4a-c). The following (more posterior) tooth is flattened in all but juvenile specimens; the last two teeth are pointed and slightly hooked — the plesiomorphic form in American minnows. Molar teeth underlain by massive, striated bone with reduced nutrient spaces as in mollusk-crushing minnows. Tooth formula: 4 teeth in major row; 0 or 1 tooth in minor row.

Holotype and Type Locality. — UM 103970 (Fig. 4a), from the Blufftop local fauna, UWBM loc. CO150, Section 3, T. 12 N, R. 28 W, Franklin Co., Washington, 242 m elevation, collected by N. Morgan, J. Morgan, and R. Cervantes. A nearly complete left pharyngeal arch, 11 mm, missing part of the dorsal limb. Anterior limb, 3 mm long and not offset at an angle, its articular surface 2 mm long and slightly offset; anterior tooth flat and beveled slightly dorsally at its terminus, 2.3 mm long (from its attachment to top of cap), and 3 mm wide in its widest dimension, parallel to the main axis of the arch; second tooth flat at its terminus, 2.3 mm long, and 1 mm wide; third tooth 2.9 mm long, pointed and slightly hooked at its terminus; fourth tooth missing, its base 0.5 mm wide. No minor teeth or minor tooth scars. Pharyngeal arch evenly curved laterally and mesially; no sharp bends or inflections. Nutrient pores under posterior three teeth; major tooth underlain by massive striated bone. Major tooth oriented to crush in apposition to its complement on the opposing arch, as in other *Mylocheilus*, but unlike other North American minnows; action of other teeth unknown.

Paratypes. — (From Blufftop local fauna, UWBM locality CO155): a 10 mm pharyngeal arch with three teeth (Fig. 4b), the enlarged tooth 2 mm long (UWBM 81835); right pharyngeal arch 9.5 mm long (UWBM 81965); left pharyngeal 8 mm long with one tooth (UWBM 82133); right pharyngeal 6 mm long with three teeth, the largest 1.1 mm in diameter (UWBM 82137).

Description of other elements. — Dentaries, inferred by size, abundance, and similarity to other *Mylocheilus*, to belong to *Mylocheilus heterodon*, have a flared gnathal margin and a bony shelf along the ventral margin, containing the lateralis canal and pores (Fig. 4e, 4f). Numerous basioccipitals are preserved and are assigned to *Mylocheilus heterodon* on the basis of size and abundance. They are similar to basioccipitals of *Mylocheilus caurinus*, but have more massive basioccipital platforms; the process for pharyngeal muscle attachment extends posteriorly as a large, laterally-compressed, spatula, rounded in lateral view, as in *Mylocheilus caurinus*. The basioccipital is not dorso-ventrally compressed like *Ptychocheilus* but is more robust, with harder periosteal bone (for muscle attachment) than in *Gila* or *Lavinia*. The posterior process is slender and asymmetrical (stronger on the left, i.e., notched on the right) at its attachment to the basioccipital centrum. There is an unusually strong vertical ridge for muscle attachment on each side of the basioccipital centrum. Fragments of Weberian ribs are referred questionably to *Mylocheilus*. — they are cyprinids with long slender rib elements and restricted dorsal keels, unlike *Ptychocheilus* or *Lavinia*. A large sample of extremely ossified supra-orbitals is assigned to *Mylocheilus* on the basis of bone texture, half-moon shape, and the presence of a distinct ventral fossa near the mesial edge, as in *Mylocheilus caurinus*.

Change through time. — The Blufftop specimens are as described in the holotype. The arch and teeth are oriented as in *Mylocheilus robustus* and *M. caurinus*. Three Taunton specimens differ in that the portion of the arch under the large tooth is inflected to lie straight back in the plane of the tooth, rather than being flared ventrally as in other minnows (Fig. 4a-c). The arch supporting the large tooth has nutrient foramina closed by massive bone growth. The Taunton specimens show more extreme enlargement of the large tooth, possible loss of the fourth tooth, and possible loss of the minor tooth. The specimens are abraded in a way that makes the tooth count ambiguous, but available evidence suggests a count of 0,3-3,0 rather than 1,4-4,1 as in the Blufftop *Mylocheilus heterodon* (Fig. 4a). The characteristics of the Taunton *Mylocheilus* show no sign of genetic influence from *Mylocheilus robustus* (or *inflexus*) of the Snake River Plain, Klamath area, or Great Basin. The Blufftop and Taunton *Mylocheilus* grew to lengths of about 30 cm. *Mylocheilus robustus* grew to lengths of about 60 cm.

Referred Material. — **White Bluffs l.f.:** UW locality CO150. UM 103970, left pharyngeal arch with three teeth, 11 mm (holotype, described above, Fig. 4a); UM 103972, 1 left and 8 right pharyngeal arches, width of largest tooth 1 mm-2.5 mm. UWBM 86633, 1 right pharyngeal arch, 8 mm (Paratype, Fig. 4b). **Blufftop l.f.:** UW locality CO155. UWBM 81835,

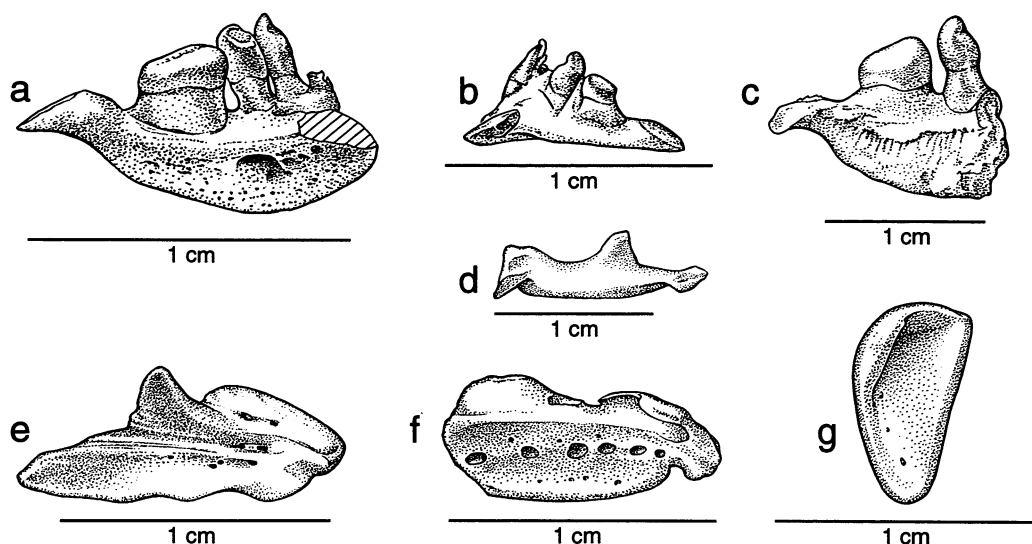


FIGURE 4 — *Mylocheilus heterodon* n. sp.: a, Holotype, UM 103970, left pharyngeal arch with three teeth, White Bluffs; b, UWBM 86633, paratype, right pharyngeal arch, White Bluffs; c, UM 103975, left pharyngeal arch, Taunton; d, UM 103974, right maxilla, mesial view, Taunton; e, UM 103977, left dentary, mesial view, Taunton; f, UM 103977, right dentary, ventrolateral view, Taunton; g, UM 103980, left supraorbital, ventral view, Taunton.

81965, 82133, and 82137, pharyngeal arches described as paratypes, above. UM 103973, 1 left arch with three major teeth and one minor tooth, width of largest tooth 3 mm, and a right arch with 4 major teeth, the largest 1 mm wide. UM 105156, 5 right pharyngeal arches. **Taunton l.f.:** UWBM 84194-84196, 3 maxillae 5-13 mm; UM 103974, 4 maxillae 6-13 mm (13 mm, Fig. 4d); UM 103975, 1 left pharyngeal arch, 15 mm (Fig. 4c); UWBM 84197-84201, 48 pharyngeal arches and teeth; UM 103976, 49 pharyngeal arches and teeth; UWBM 84202-84206, 5 dentaries 10-12 mm; UM 103977, 3 dentaries (Fig. 4e, 4f); UWBM 84207-84220, 127 basioccipitals; UM 103978, 116 basioccipitals; UWBM 86622-86623, 2 Weberian rib fragments, 7 mm, identity uncertain; UM 103979, 3 Weberian rib fragments, 2-12 mm, identity uncertain; UWBM 86624-86626, 44 supra-orbitals; UM 103980, 33 supra-orbitals (Fig. 4g).

Ptychocheilus Agassiz 1855

Ptychocheilus arciferus (Cope) northern pikeminnow
(Fig. 5a-5e)

Ptychocheilus includes North America's largest minnows; it currently lives in many of the larger Pacific Coast drainages, from the Colorado River to the Nass River in British Columbia. Fossil *Ptychocheilus* appear in the Columbia Basin at 15 Ma, documented by a remarkable complete pharyngeal arch collected at Priest Rapids by Steve Reidel. The Priest Rapids specimen is diagnosed as *Ptychocheilus* by the large size, elongate canine teeth slightly hooked, 4,1 tooth formula, long slen-

der anterior limb, and arch enlarged and strengthened under the first two teeth, anterior to the shallow lateral ala (Fig. 5e). This record establishes the modern form of *Ptychocheilus* to be twice as old as previously known.

In the late Miocene and Pliocene, *Ptychocheilus* lived in the Bonneville and Lahontan areas as well as the eastern and western Snake River Plain (Smith et al., in press; Hearst and Smith, in press). *Ptychocheilus arciferus* is known as early as the late Miocene in Idaho and Oregon (Smith, 1975; Kimmel, 1975). The fossils from the Pasco Basin are not different enough to diagnose as a new species. The pharyngeal bones and teeth and dermethmoid are indistinguishable from those of *Ptychocheilus arciferus* of the western Snake River Plain, which has more elongate pharyngeal, facial, and pterygoid bones than *Ptychocheilus oregonensis* of the modern Columbia drainage.

The four living species of *Ptychocheilus* reach the largest sizes of any North American minnows. *Ptychocheilus lucius* of the Colorado River and *P. arciferus* of the Snake River Plain reached lengths of 1.8 m and 1.2 m, respectively (Sigler and Miller, 1963; Smith 1975). A dentary and pharyngeals of the Ringold *Ptychocheilus* indicate lengths of about 50 cm in length; modern *Ptychocheilus oregonensis* of the Columbia River drainage reach up to 40 cm in standard length (UMMZ 179588). This species was present in the basin at 15 Ma; it is not yet known from the White Bluffs local fauna; it is rare at Blufftop and uncommon at Taunton.

Referred Material.— **Blufftop l.f.:** UM 103981, pharyngeal arch with 4 teeth in the major row and 2 teeth in the minor row (Fig. 5a). **Taunton l.f.:** UM 103982, pharyngeal arch, 13 mm (Fig. 5c); UM 107755, right pharyngeal arch, 19 mm (Fig.

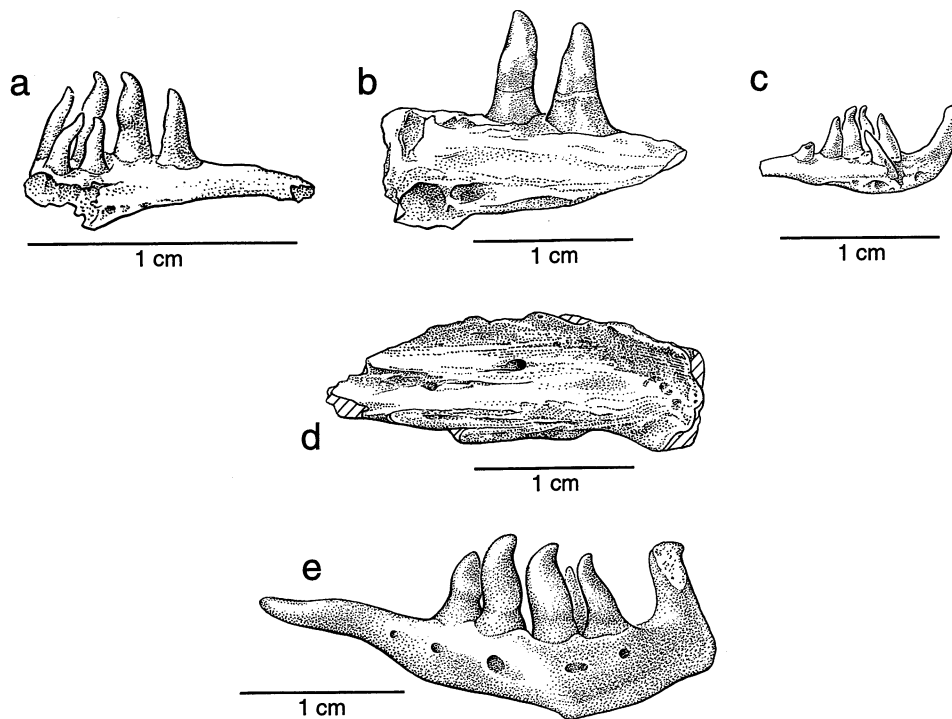


FIGURE 5 — *Ptychocheilus arciferus*: a, UM 103981, right pharyngeal, Blufftop; b, UM 107755, right pharyngeal arch, Taunton; c, UM 103982, left pharyngeal, Taunton; d, UM 103983, left dentary, White Bluffs; uncatalogued Hanford specimen of left pharyngeal arch, Priest Rapids.

5b); UM 103983, left dentary, 24 mm (Fig. 5d); UWBM 84221, left dentary, 13 mm; UM 103984, 25 pharyngeal fragments and teeth, 3-19 mm; UWBM 84222-84227, 30 pharyngeal fragments and teeth, 4-25 mm; UWBM 84228, 1 dermethmoid, 5 mm; UM 103985, 1 opercular fragment, 11 mm, identity uncertain.

Klamathella Miller 1945

Klamathella milleri (Smith) 1975, Snake River chub
(Fig. 6a)

The Taunton fauna includes a small chub with closely spaced, hooked teeth, apparently with a tooth formula of 2,5-5,2. The arch is less elongate and the teeth are closer together than in *Ptychocheilus*. The pharyngeal bones and teeth cannot be distinguished from those of *Klamathella milleri* of the Glenns Ferry Formation. The Ringold *Klamathella* grew to a length of about 30 cm. *Klamathella milleri* is most similar to *Klamathella coerulea* of the Klamath Basin, with which it shares the inner row of pharyngeal teeth (formula 2,5-5,2); they are not closely related to *Siphateles bicolor* of the Lahontan and (modern) Columbia basins. *Siphateles bicolor* lacks the inner row of pharyngeal teeth (formula 0,5-5,0 or 0,5-4,0). According to molecular data obtained by T. Dowling, *Klamathella* is the sis-

ter group to *Acrocheilus*. The shape of the pharyngeal arches and shape of the bones of the skull roof and lateral ethmoids support this sister-group relationship.

Referred Material. — **Taunton l.f.:** UM 103986, 1 pharyngeal fragment, 10 mm (Fig. 6a); UWBM 84229-84230, 2 pharyngeal fragments with one tooth, 7-12 mm; UWBM 84231, 1 arch with 1 tooth and two detached teeth (identification uncertain).

Acrocheilus Agassiz 1855

Acrocheilus latus (Cope), Snake River chiselmouth chub
(Fig. 6b, c)

The Taunton sample includes two fragments of pharyngeal arches with one tooth each and four detached teeth that are not differentiable from arches and teeth of *Acrocheilus alutaceus* of the Columbia River basin or *Acrocheilus latus* of the Pliocene, western Snake River Plain. The teeth are more compressed than those of *Lavinia*, with smooth, narrow grinding surfaces, and a small terminal hook directed posteriorly. The terminal hook is less developed than in *Lavinia*. The teeth are not as elongated as *Orthodon* and the arch is slenderer and more robust than *Orthodon*. One of the arches has a pit mesial to the second tooth, but with no sign that it was a base for an inner

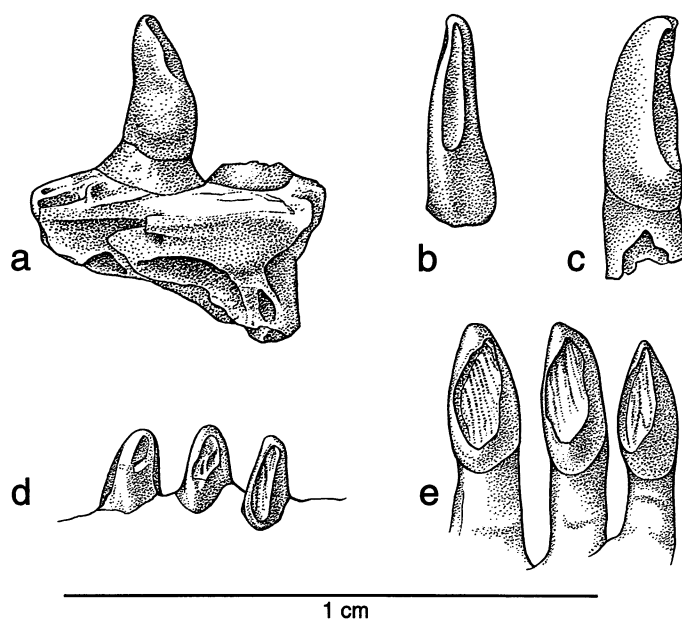


FIGURE 6 — *Klamathella milleri*: a, UM 103986, Left pharyngeal, Taunton; *Acrocheilus latus*., b, c, UM 103987, Taunton; *Lavinia hibbardii*, d, UM 103988, Taunton; *Lavinia hibbardii*, e, UM 62063, Glens Ferry Formation, Idaho.

tooth. No other western minnows have teeth of this shape. Additional material (dentaries) will be necessary to assign the Pasco Basin fossils to either *A. latus* or *A. alutaceus*. The fossil and recent forms are assumed to represent the same lineage for the analysis in Table 1. The modern form reaches a standard length of 272 mm (UMMZ 177110). The Taunton fossils represent fishes about 120 mm in standard length.

Referred Material.— **Taunton l.f.:** UM 103987, two detached teeth (Figs. 6b, c); 1 arch with 1 tooth.

Lavinia Girard 1854

Lavinia (Idadon) hibbardii (Smith) 1975, Snake River hitch (Fig. 6d)

The Taunton fauna includes a small pharyngeal arch with strongly striated teeth as in *Lavinia hibbardii* of the Glens Ferry Formation of the Snake River Plain, Idaho. The teeth are more rounded in cross-section and less hooked terminally than *Lavinia* of California. The striations on the grinding surfaces are better developed than those in California *Lavinia*, being indistinguishable from specimens of *Idadon hibbardii* (Fig. 6e) of the Snake River Plain. *Idadon hibbardii* was described by Smith (1975) and was diagnosed by striated grinding surfaces on the pharyngeal teeth. *Lavinia exilicauda* of the Sacramento drainage and specimens from the Salt Lake Formation have apparently homologous, though weakly expressed, striations. Other osteological similarities suggest that *Idadon* should be synonymized with *Lavinia*.

Referred Material.— **Taunton l.f.:** UM 103988, 1 pharyngeal arch with 3 teeth (Fig. 6d).

FAMILY CATOSTOMIDAE

Chasmistes Jordan 1878

Chasmistes cf. *batrachops* Cope, Fossil Lake Sucker (Fig. 7a-b)

Lake suckers, *Chasmistes*, are represented by uncommon material in all three local faunas. The genus is known from many Great Basin and Columbia Basin localities from Pliocene to Recent (Miller and Smith 1981). *Chasmistes batrachops* is a morphologically primitive form that seems to be represented in the Pliocene to Pleistocene Great Basin of California, Nevada, and Oregon. *Chasmistes* species are large suckers with terminal mouths and gill rakers adapted to feeding on plankton. The diagnostic bone shapes reflect morphological modifications for nektonic rather than benthic feeding. The fossils from White Bluffs, Blufftop, and Taunton are similar to the morphologically generalized *Chasmistes* cf. *batrachops* of the Snake River Plain and elsewhere in the west, and are treated as the same in the analysis in Table 1. The Pasco Basin dentaries are shorter and the maxillae are shorter with a less anteriorly oriented premaxillary process than in *Chasmistes spatulifer* of the Snake River Plain. The Ringold lake sucker grew to a length of about 40 cm.

Referred Material.— **White Bluffs l.f.:** UWBM 40374 (pt.), anterior part of a right maxilla, 8 mm, with obtuse angled anterodorsal process and anteriorly angled premaxilla process,

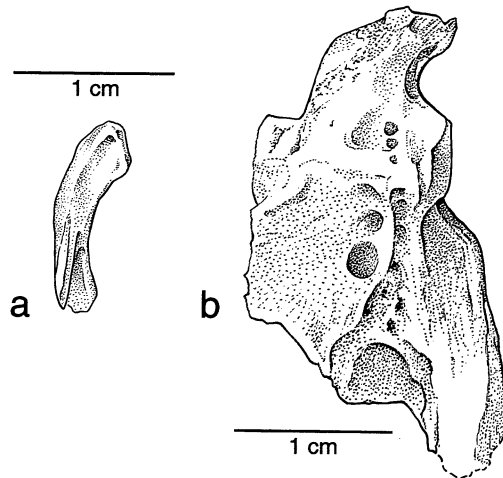


FIGURE 7 — *Chasmistes* cf. *batrachops*. Blufftop.: **a**, UM 103991, left dentary; **b** UM 109684, right hyomandibular.

diagnostic of the genus. UWBM 40374, basioccipital with *Chasmistes* or *Deltistes* ventral keel; UWBM 40384 (pt.), unallocated catostomid partial opercle, 5 mm. **Blufftop l.f.:** UM 103989, 2 fragments of right second ribs of the Weberian apparatus; UM 103990, 1 right dentary; UM 103991, 1 left dentary, 18 mm (Fig. 7a); UM 149682, anterior fragment left maxilla; UM 149684, 1 partial right hyomandibula (Fig. 7b); UM 149683, 1 right articular-angular; UWBM 84240, 1 partial left pharyngeal arch, 28 mm; UM 105155, left maxillary fragment; UM 149685, 4 Weberian rib fragments; UWBM 84232-84237, 6 Weberian rib fragments; UWBM 84239, left hyomandibular fragment; UM 105168, 1 urohyal; UWBM 84238, urohyal; UM 105169, 1 palatine. **Taunton l.f.:** UM 103992, 1 left maxilla, 11 mm.

Catostomus LeSueur 1817

Catostomus macrocheilus Girard, largescale sucker
(Fig. 8a-f)

Catostomus macrocheilus was described from Recent specimens collected in the Columbia River drainage at Astoria, Oregon. The species is diagnosed by the lack of anterior expansion of the dentary, the postero-mesial orientation of the premaxillary process of the maxilla, and the lack of development of the ventral keel of the maxilla. A diversity of Blufftop and Taunton specimens record its presence in the Columbia River drainage 3.9 ma and 2.9 ma, respectively. It first appears on the Snake River Plain in the late Pliocene Bennett Creek and Sand Point local faunas, then later from the latest Pliocene Grand View local fauna at Jackass Butte (Smith, 1975) and the early Pleistocene Froman Ferry local fauna (Repenning et al., 1995). The Ringold specimens grew to a length of about 35 cm, slightly smaller than modern relatives.

Referred Material.— **Blufftop l.f.:** UWBM 84241-84242, 2 right partial dentaries; UWBM 84243, left dentary (Fig. 8a); UWBM 84244, left dentary; UM 103993, 1 right partial dentary 24 mm (Fig. 8b); UM 105154, 2 right dentary fragments; UM 103994, 1 left preopercle, 30 mm; UM 103995, 1 right pterotic, 25 mm; UWBM 84245, 1 right hyomandibula, 43 mm; UWBM 86621, 1 left prootic, 23 mm; UWBM 84246-84248, 3 partial parasphenoids, 24-47 mm; UM 103996, 2 anterior fragments right maxillae, 13-15 mm; UM 103997, left maxilla, 23 mm, (Fig. 8d); UM 103998, left hyomandibular, 45 mm (Fig. 8c); UWBM 84249, right maxilla, Fig. 8e; UWBM 84250, right supratemporal, 22 mm; UM 105166, 2 partial Weberian ribs; UM 105167, pharyngeal arch fragment; UWBM 86639, pharyngeal arch fragment; UM 105170, 2 left maxillae, 13, 15 mm; UWBM 84251-84253, 3 maxillae, 15-22 mm; UM 105171, premaxilla, 16 mm. **Taunton l.f.:** UWBM 84254-84265, 12 maxillae; UM 103999, 12 maxillae; UM 149687, left maxilla, Fig. 8f; UWBM 84266-84274, 9 dentaries; UM 104000, 10 dentaries.

Catastmidae indet.

The following catostomid bones are not differentiable between *Catostomus* and *Chasmistes*: **Blufftop l.f.:** UM 104001, 2 metapterygoids 28 mm, 31 mm; UWBM 84275-84276, 4 basioccipitals 21-27 mm; UWBM 84279-84281, 3 partial cleithra, 22-28 mm; UWBM 84282, 1 prevomer 21 mm; UM 104002, 4 palatines, 12-17 mm; UWBM 86635-86638, 4 palatines; UWBM 84283, 1 epibranchial 11 mm; UM 105172, 1 pro-otic; UWBM 84284, 1 pro-otic; UM 105173, 1 tripus; UM 105174, 1 supra-occipital; UWBM 84285, 1 supra-occipital; UWBM 84286, 1 preopercle; UM 105175, 1 postcleithrum; UWBM 86627, 1 epiotic. **Taunton l.f.:** UWBM 84287-84288, 86618-86620, 10 palatines; UM 104003, 11 palatines; UWBM 84289, 1 parasphenoid, 18 mm; UWBM 84290-84291, 2 basioccipitals; UM 104004, 3 basioccipitals; UWBM 84292-84298, 7 ceratohyals; UM 104005, 8 ceratohyals; UWBM 84299-84305, 7 opercles; UM 104006, 8 opercles; UWBM 84306-84307, 2 hyomandibulae; UM 104007, 2 hyomandibulae; UWBM 84308-84309, 2 retroarticulars; UM 104008, 2 retroarticulars; UWBM 84310-84311, 2 partial second Weberian vertebrae; UWBM 84312, 1 partial cleithrum.

FAMILY ICTALURIDAE

Ameiurus Rafinesque 1820

Ameiurus reticulatus new species, Ringold bullhead
(Fig. 9)

The bullheads, *Ameiurus* (referred to as *Ictalurus* in previous literature, Lundberg, 1992) are rather widely distributed in western North America in the Miocene and Pliocene (Lundberg, 1975, 1992; Baumgartner, 1982). Bullheads are warm-water fishes that became extinct in western U.S. with Pleistocene

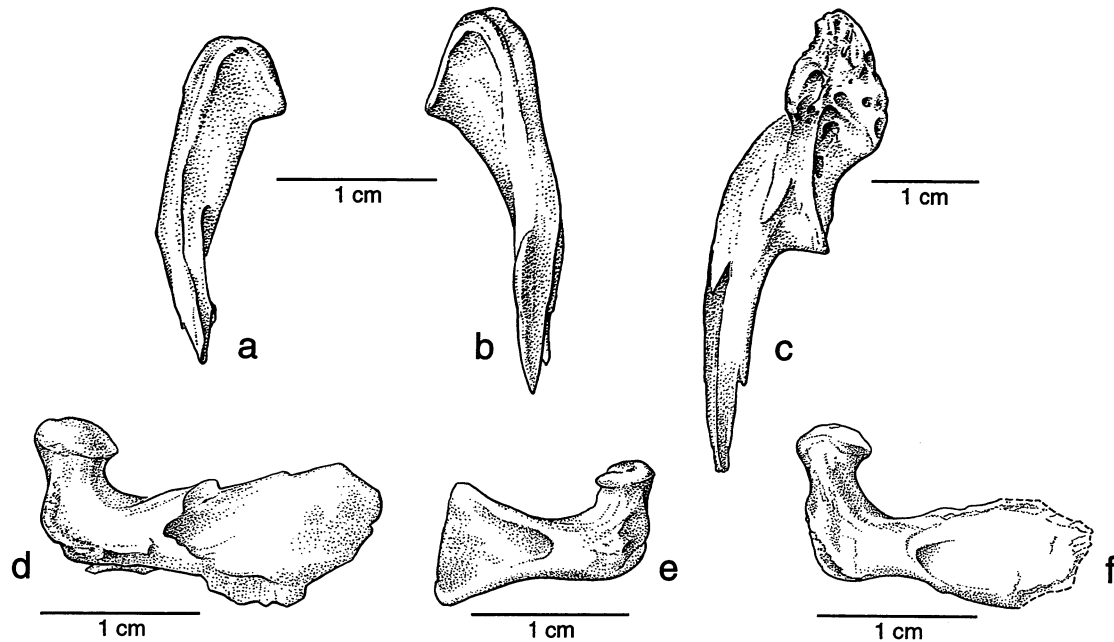


FIGURE 8 — *Catostomus macrocheilus*: a, UWBM 84243, left dentary, Blufftop; b, UM 103993, right dentary, Blufftop; c, UM 103998, left hyomandibular, Blufftop; d, UM 103997, left maxilla, Blufftop; e, UWBM 84249, right maxilla, Blufftop; f, UM 149687, left maxilla, Taunton.

cooling. The lineage on the Snake River Plain is represented by many Miocene and Pliocene fossils (Smith 1975, Kimmel 1975, Smith et al. 1982). Numerous fossils from the three levels in the Ringold Formation represent a related but different lineage.

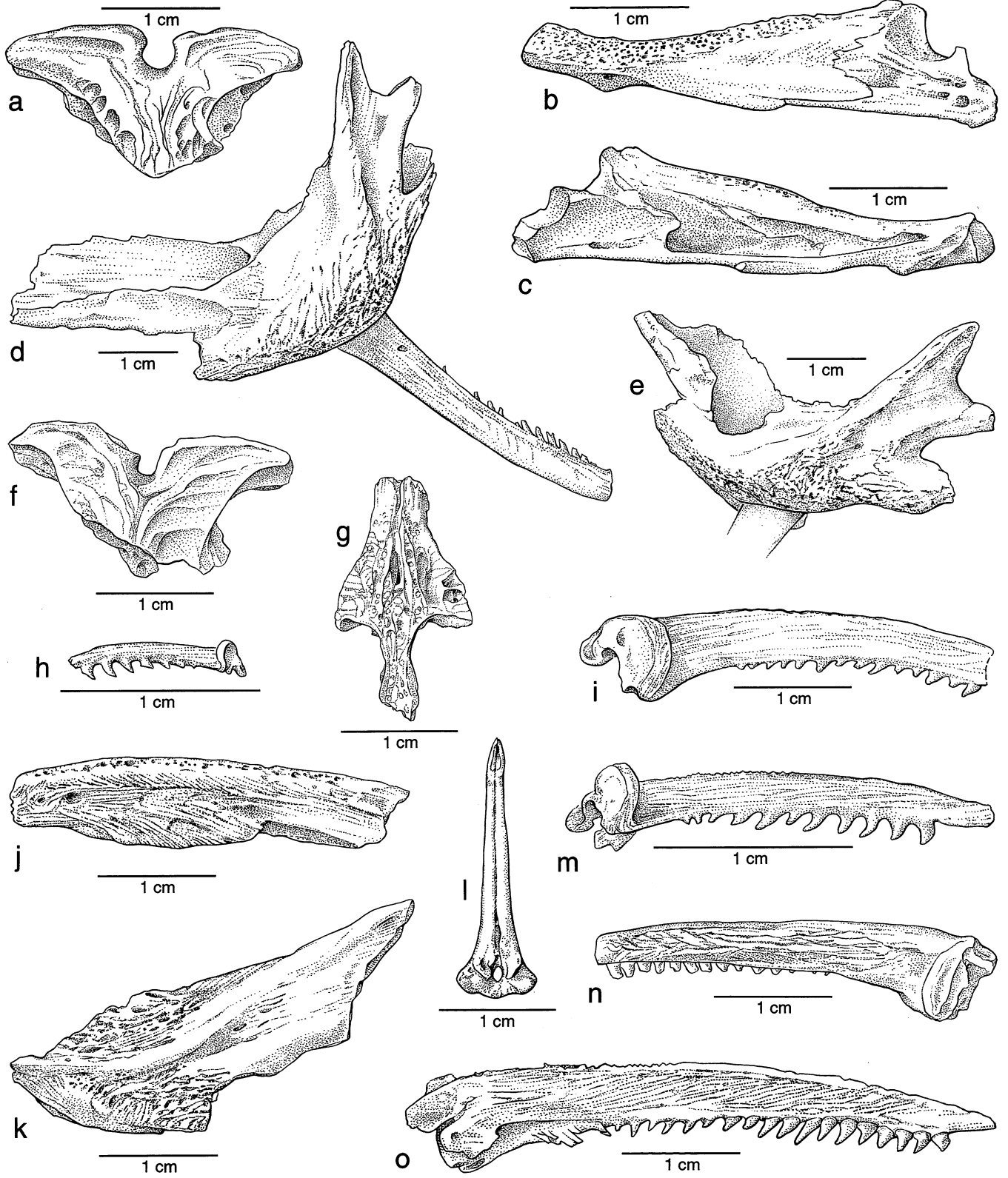
Diagnosis.— A bullhead catfish of the *Ameiurus natalis* group (Lundberg, 1970, 1975, 1992). *Ameiurus reticulatus* differs from all other bullheads in the dense and reticulate sculpturing on the dentary, articular, supraethmoid, cleithrum, pectoral spine base, Weberian vertebrae, and posttemporal (less striate than in other bullheads) and the reduced anterior denticulations on the pectoral spines. Other members of the *natalis* group possess anterior denticulations and sometimes serrae on the pectoral spine. Supraoccipital fontanelle partially open (closed in *vespertinus* and *hazenensis*). Supraoccipital process narrow and more pitted than other bullheads. Dentary with labial edge more rounded than in *vespertinus*. Cleithrum with ornamentation on the lower process of the ascending limb, as on the postventral process (this “middle” process is smooth in other bullheads). Pectoral pocket of cleithrum without raised platform seen in *vespertinus*.

Holotype and Type Locality.— A complete right mandible (UM 104009, Fig. 9b, c), 41 mm long, from the Blufftop local fauna, Franklin Co., Washington, UWBM locality CO150. The dentary is 33 mm long, with a tooth row 22 mm long. The articular-angular is 26 mm long, and 9 mm high at the coronoid process. The dentary is slenderer, with a longer anteroventral crest than in *Ameiurus vespertinus* Miller and Smith

(1967, fig. 6). The toothed surface is flexed anteriorly, the coronoid process rises abruptly ahead of the articulation, and the bone surfaces bear the dense reticulations characteristic of the species.

Paratype.— A nearly complete left cleithrum and attached pectoral spine (UM 104010, Fig. 9d, e) from Washington, Franklin Co., Blufftop local fauna, E. Center Sec. 3, T. 12 N., R. 28 W., 242 m (800 ft) elevation, collected by Neil and James Morgan and R. Cervantes, 1992. The cleithrum is 59 mm long from its anterior border to the broken end of the post-ventral spine, 59 mm to the end of the middle spine, and 54 mm to the end of the upper spine; the pectoral spine is 47 mm long, with strong, evenly spaced, and sometimes bifid posterior denticulations, weak anterior dentations, and dorsal as well as ventral longitudinal striations. The prominence over the pectoral spine flange and the ventral part of the post ventral and middle spines is covered with closely-spaced reticulations.

Description of other elements.— Similar in mature size to *Ameiurus nebulosus* and larger; adults ranging from 250 mm to 400 mm in standard length. The supraethmoid broad, internasally, with a semi-closed anterior notch. Premaxilla not broad, its length about 1/3 its breadth. Palatine short, its length about 3 times its width at the condyle. Supraoccipital process narrow and weakly striate, with many pits. Supraoccipital fontanel partially open, with a narrow groove between its longitudinal ridges. Dense and reticulate sculpturing on the dentary, articular, supraethmoid, cleithrum, pectoral spine base, Weberian vertebrae, and posttemporal. Dentary with labial edge



rounded, the toothed surface not extending out to a sharp labial edge. Articular-angular massive, short, and with an abrupt coronoid process. Cleithrum with post-ventral spine and the lower process of the ascending processes reticulate; post-ventral spine rugose only along the ventral edge and moderately long. Dorsal stridulatory surface of cleithral pocket without raised platform. Pectoral spines with strong, recurved posterior dentations arising from the dorsal half of the mesial groove of the spine. Pectoral spines lacking anterior denticulations and serrae (except in a few small individuals from White Bluffs) and with mesial stridulatory surface nearly flat, not concave. Dorsal pterygiophore and spine, urohyal, and Weberian vertebrae as in other members of the *A. natalis* group (Lundberg 1975).

Discussion.—Lundberg (1992) assigned *Ameiurus vespertinus*, of the Pliocene Snake River Plain, to the *Ameiurus natalis* species group because they share a premaxillary width to length ratio of about 3, posterior cleithral process irregularly and coarsely tuberculate, palatine short, surfaces of supraoccipital process and exoccipital pitted. Baumgartner (1982) added *Ameiurus hazenensis*, from the Miocene Truckee Formation of Nevada to this group. *Ameiurus reticulatus* shares the short palatine and tubercles on the cleithral spine, although these are reduced to the ventral margin of the cleithral spine in the Taunton catfish. *Ameiurus peregrinus* (Lundberg, 1970, 1975) from the Pliocene Juntura basin of Oregon, has strongly developed anterior denticulations on the pectoral spines as in *A. vespertinus*. *Ameiurus reticulatus* from the White Bluffs, Blufftop, and Taunton local faunas show a transition in ornamentation from lowest to highest in the section, yet resemble each other more than any resembles the sequence of *A. vespertinus* from the Chalk Hills and Glens Ferry Formations on the Snake River Plain. In the White Bluffs sample, one of five juveniles in UWBM 34993 and one of five juveniles in UWBM 35196 has anterior denticulations on the pectoral spines. The latest forms in the two areas diverge in cleithral characters but converge in ornamentation of the supraethmoid. None of the forms differ from each other in trophically important characters except for the shape of the dentary. The stridulatory surfaces of the cleithra and pectoral spines differ, implying different sound production.

Referred Material.—**White Bluffs l.f.:** UWBM 35129 (part) 4 spines 6-10 mm; UWBM 35153 spines 7, 9 mm; UWBM 34993, 3 right and 2 left fragmentary pectoral spines, 10-14 mm; UWBM 35135 pectoral spine 12 mm; UWBM 35196 5 spines 6-11 mm; UWBM 35253 dorsal spine 7 mm; UWBM 40305 3 pectoral spines 9, 10 mm; UWBM 40325 spine 6 mm; UWBM 40329 3 pectoral spines, 9, 10 mm; UWBM

40334 3 dorsal spines 3-7 mm; UWBM 84178, dorsal pterygiophore, 20 mm; UM 103967, dorsal pterygiophore, 18 mm; UWBM 40335 fragment left cleithrum (10 mm) and right cleithrum (10 mm); UWBM 40383 cleithrum 7 mm; UWBM 40423 pectoral spine 15 mm; UWBM 42154 2 pectoral spines, 12, 14 mm; UWBM 42156 part, cleithrum 11 mm; UWBM 42258, 4 left and 6 right fragment pectoral spines, 3-14 mm; UWBM 46156 pelvic pterygiophore 9 mm; UWBM 46159 pterygiophore 3 mm, cleithrum 8 mm, unident. bones; UWBM 46163 fragment of left cleithrum, 9 mm; UWBM 46164 dorsal pterygiophore, 6 mm wide, pectoral spine 10 mm; UWBM 46182 left articular/angular, 13.5 mm; UWBM 46193 opercle fragment, 15 mm. **Blufftop l.f.:** UM 104009, right mandible, holotype; UM 104010, left cleithrum and attached pectoral spine, paratype; UWBM 84313, 38 pectoral spines, 8-35 mm; UM 104011, 16 pectoral spines, 7-33 mm; UM 105101, 6 pectoral spines; UWBM 84325, 7 pectoral spines; UM 105058, left pectoral spine, 51 mm (Fig. 9o); UM 105059, right pectoral spine, 39 mm (Fig. 9i); UM 105060, right pectoral spine, 22 mm (Fig. 9m); UM 105061, left pectoral spine, 10 mm (Fig. 9h); UWBM 84314, 21 dorsal spines, 12-29 mm; UM 104012, 6 dorsal spines, 30-46 mm; UWBM 84315, 6 dorsal spine pterygiophores, 11-26 mm; UM 104013, 4 dorsal spine pterygiophores, 20-23 mm; UWBM 84316-84319, 4 cleithra 20-34 mm; UM 104014, 2 cleithra, 25, 29 mm; UWBM 84320-84321, 2 dentaries, 18-29 mm; UWBM 86640, 2 articulares, 17-18 mm; UM 104015, 1 premaxilla, 15 mm; UM 104016, 2 dentaries, 23 mm; 3 articulares, 18-22 mm; UM 104017, 1 urohyal, 15 mm; UM 104018, 1 posttemporal, 19 mm; UM 104019, 1 supraoccipital, 22 mm; UWBM 84327, 1 supraoccipital; UWBM 84323, 1 hyomandibula, 27 mm; UM 105100, 1 Weberian centrum; UWBM 84324, 1 Weberian centrum; UWBM 84326, 1 dentary; UM 105101, Weberian apparatus, 13 mm; UM 105153, articular, 15 mm; UM 105176, frontal fragment, 31 mm; UWBM 84322, 1 Weberian apparatus, 13 mm. **Taunton l.f.:** UWBM 84328-84334, 7 premaxillae, 9-20 mm; UM 104020, 7 premaxillae 7-18 mm; UM 104021, 1 maxilla, 13 mm; UWBM 84335, 37 dorsal spines, 10-24 mm; UM 104022, 15 dorsal spines, 11-20 mm; UM 105056, 1 dorsal spine (Fig. 9l); UWBM 84336, 20 dorsal pterygiophores, 6-21 mm; UM 104023, 15 dorsal pterygiophores, 7-20 mm; UWBM 84337-84376, 50 dentaries, 11-27 mm; UM 104024, 53 dentaries, 11-26 mm; UM 105051, left dentary (Fig. 9j); UWBM 84377-84423, 47 articular-angulars, 7-25 mm; UM 104025, 42 articular-angulars, 11-24 mm; UWBM 84424-84430, 7 Weberian centra, 9-20 mm; UM 104026, 8 Weberian centra, 8-18 mm; UWBM 84431-84455, 25 cleithra, 7-25 mm;

FIGURE 9 — *Ameiurus reticulatus* n. sp.: **a**, UM 105053, dermethmoid, Taunton, dorsal view; **b**, UM 104009, left dentary, Blufftop, holotype, lateral view; **c**, UM 104009, left dentary, Blufftop, holotype, mesial view; **d**, UM 104010, left cleithrum and pectoral spine, Blufftop, anterolateral view; **e**, UM 104010, left cleithrum, Blufftop, posterolateral view; **f**, UM 105054, dermethmoid, Taunton, ventral view; **g**, UM 105052, supraoccipital, Taunton; **h**, UM 105061, left pectoral spine, Blufftop; **i**, UM 105059, right pectoral spine, Blufftop; **j**, UM 105051, left dentary Taunton; **k**, UM 105057 left cleithrum, Taunton; **l**, UWBM 105056, dorsal spine, Taunton, dorsal view; **m**, UWBM 105060, right pectoral spine, Blufftop; **n**, UM 105055, left pectoral spine, Taunton; **o**, UM 105058, left pectoral spine, Blufftop, ventral view.

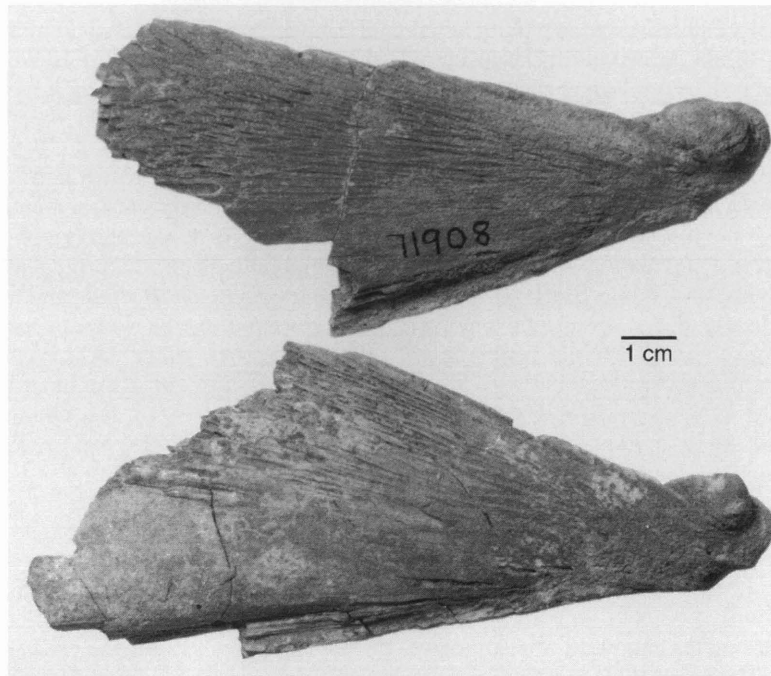


FIGURE 10 — *Oncorhynchus rastrosus*, UWBM 71908, two right dentaries from River Road local fauna.

UM 104027, 13 cleithra, 14-31 mm; UM 105057, left cleithrum (Fig. 9k); UWBM 84456-84466, 243 pectoral spines, 6-25 mm; UM 104028, 191 pectoral spines, 10-28 mm; UM 105055, left pectoral spine (Fig. 9n); UWBM 84467-84472, 24 basioccipitals; UM 104029, 24 basioccipitals; UWBM 84473, 22 supraethmoids, 15-26 mm; UM 104030, 19 supraethmoids, 15-24 mm; UM 105053, 1 supraethmoid (Fig. 9a); UM 105054, 1 supraethmoid (Fig. 9f); UWBM 84474, 6 supraoccipitals; UM 104031, 7 supraoccipitals; UM 105052, 1 supraoccipital (Fig. 9g); UM 105003, 1 urohyal; UM 104004, 3 post-temporals.

FAMILY SALMONIDAE

Oncorhynchus (Suckley)

Oncorhynchus rastrosus (Cavender and Miller)
(Fig. 10)

Two large right dentaries and associated fragments of *Oncorhynchus* (*Smilodonichthys*) *rastrosus* were collected from the River Road Local Fauna by A. Paglieri. This giant salmon is known from the Miocene of California and southern Oregon (Cavender and Miller, 1972; Stearley and Smith, 1993). It was an anadromous planktivore, characterized by deep, triangular dentaries, with teeth reduced to four large tusks in breeding adults (Cavender and Miller, 1972). A landlocked relative lived in the late Miocene Lake Idaho (Smith et al., 1984).

Referred Material.— **River Road l.f.:** UWBM 71908, two right dentaries, 136 mm and 124 mm long, and associated fragments; UWBM 71909, vertebra, 40 mm in diameter.

FAMILY ESOCIDAE

Esox Linnaeus

Esox columbianus new species, Columbia muskellunge
(Figs. 11a-e; 12a-f)

The presence of a large muskellunge in the Miocene of western North America has been known since Cavender, Lundberg, and Wilson (1970) described specimens from the Deer Butte Formation (10 Ma) in southeastern Oregon. The abundance of material in the White Bluffs and the unique apomorphies of this lineage leave no doubt about its presence in the Pliocene Columbia River drainage, after which it became extinct there. The genus *Esox* is known from eastern North America, Europe, and Asia. The Ringold fossils are similar to 100-135 cm specimens of *Esox masquinongy* from the Great Lakes area, but with numerous morphological distinctions. There are two forms of muskellunge in the Laurentian Great Lakes area today, the nominal form, which reaches adult lengths of 75-145 cm and a smaller, ecologically and embryologically distinct form that reaches adult lengths of 57-110 cm in scattered lakes west to Wisconsin (Lebeau, 1992). Examples of 25 different bony elements and numerous teeth have been identified from the Ringold faunas.

Diagnosis.— A large muskellunge with enlarged, fixed (non-hinged) teeth on the anterior part of the vomer and palatine; vomerine teeth small in the narrow band behind the transverse cluster; posttemporal with a nearly straight dorso-lateral margin; pterotic with a short, robust postero-dorsal process, and a weak ventral ridge; hyomandibula with no bony mesial flange at the angle of the opercular and ventral processes and an ob-

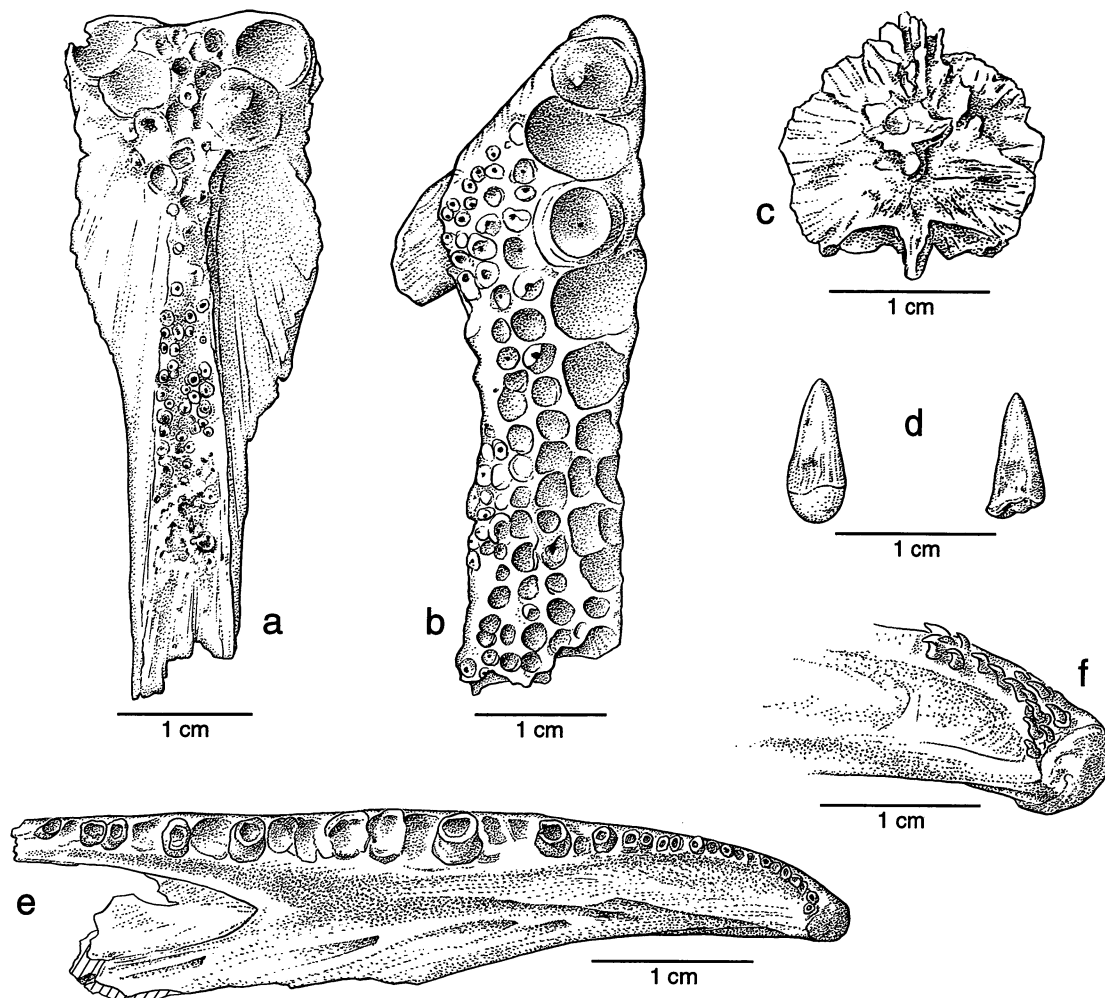


FIGURE 11 — *Esox columbianus*, n. sp.: **a**, UWBM 46178, holotype, prevomer, Ringold Fm., White Bluffs; **b**, UWBM 46179, paratype, right palatine, Ringold Fm., White Bluffs; **c**, UM 103962, supraoccipital; **d**, UWBM 86629, 86630, 2 teeth, Taunton; **e**, UM 103950, left dentary, White Bluffs; **f**, *Esox lucius*, UMMZ 182048, left dentary.

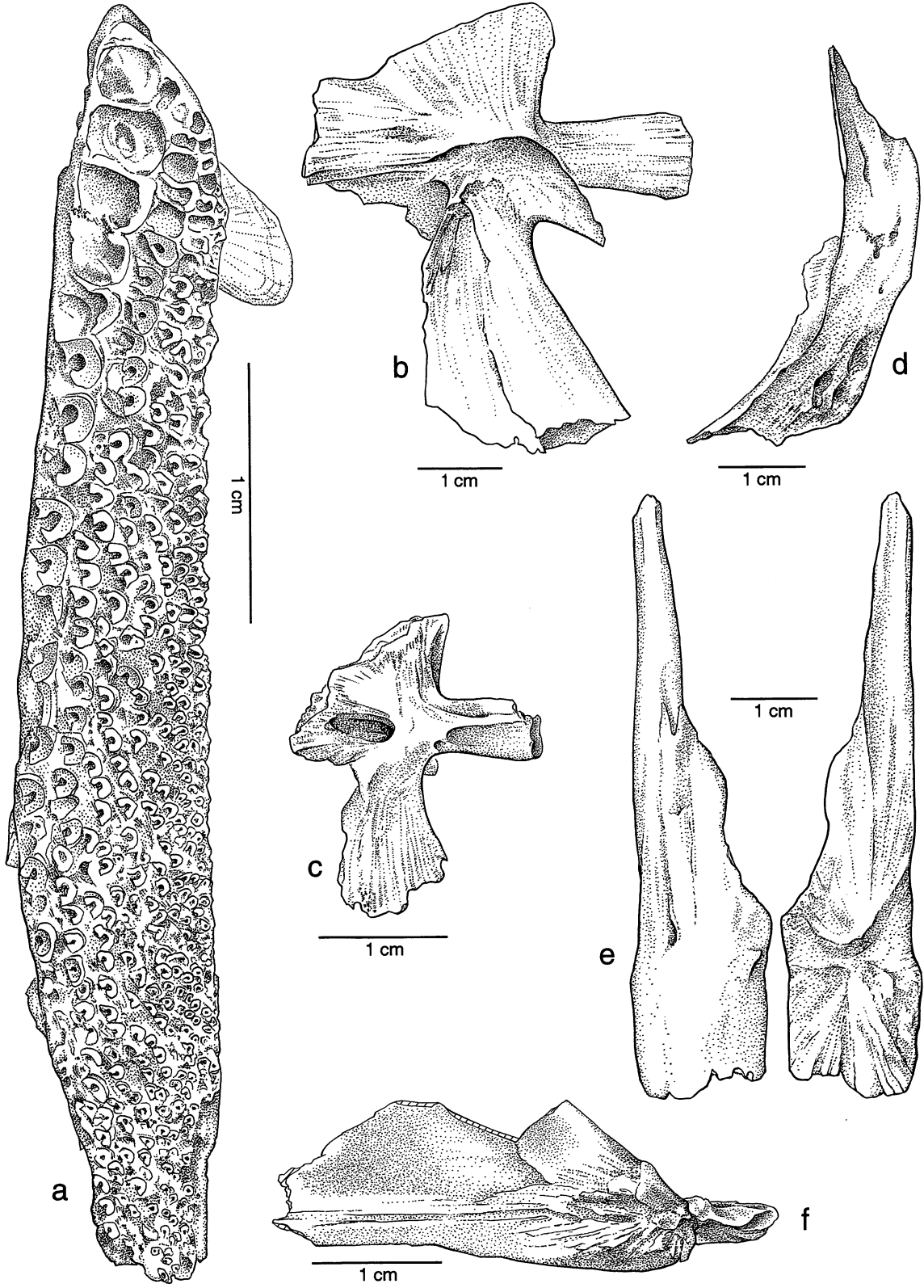
tuse angle between the preopercular and ventral processes; maxilla curved; and no thin mesial flange under the articular condyle.

Type locality.— White Bluffs, Washington, Franklin County, in bluffs on the east side of the Columbia River, in the north side of Baxter Canyon near SE corner, NE 1/4, NW 1/4, Sec. 13, T. 11 N, R. 28 E; Pliocene Ringold Formation, collected by Willis E. Fry, April 17, 1972; UWBM locality A9851. Specimens weathered out at a thick section of cross-bedded sands and some gravel.

Holotype.— UWBM 46178 (Fig. 11a), a nearly complete prevomer with one fixed tooth present, four large empty sockets for fixed teeth, and numerous sockets for small, hinged teeth. The bone is 51 mm long (posterior end missing), 18 mm wide at the toothed head, 18 mm wide at the mid-vomerine flanges. Five large fixed teeth are 5 mm in diameter at their bases; nu-

merous small, hinged teeth are 0.3-2.0 mm in diameter at their bases. The median longitudinal band of hinged teeth is 6 mm wide at its widest point posteriorly and 2 mm wide at the anterior constriction. The remaining fixed tooth is over 9 mm long (tip broken), and round in basal cross-section. The median tooth band is 2-5 tooth rows wide; sockets for 2 mm hinged teeth are located at the anterior edge as well as posteriorly among the larger teeth.

Paratype.— UWBM 46179 (Fig. 11b), anterior portion of a right palatine with two incomplete large, fixed teeth, three replacement sockets for large fixed teeth, and numerous small empty bases for hinged teeth. The bone is 51 mm long, 19 mm maximum width, including the maxillary process, and 14 mm wide at the widest part of the tooth row. The large teeth are 6 mm in diameter at their bases, the most complete one is 10 mm long (tip broken) and round in cross section, but with weak



anterior and posterior keels. The bases of the hinged teeth are 1-3 mm in diameter. *Esox columbianus* has a shorter palatine, with fewer tooth rows than the forms of *Esox masquinongy*.

Description.— The large palatine and prevomer (types) are similar to recent *Esox masquinongy* of similar size (135 cm total length) from Lake of the Woods, Minnesota, in the number, position, and size of teeth, especially the large fixed (non-hinged) teeth on the palatine and vomer (Cavender et al., 1970). The Columbia fossils differ from the small, lacustrine form of unnamed *Esox* (Lebeau, 1992) in that the fixed teeth appear more rounded and the vomerine teeth are smaller at the narrow, anterior part of the median band (behind the transverse anterior cluster of vomerine teeth), resembling the large fluvial form of *masquinongy*. The bones are not similar to *Esox lucius* (Fig. 11f), *niger*, or *americanus*, which have no enlarged, fixed teeth on the palatine (Cavender et al., 1970, fig. 2) and vomer, and which have a broad median band of small teeth behind the head of the vomer. The posttemporal has a nearly straight dorso-lateral margin like the large fluvial *masquinongy*, and unlike the concave margin of the lacustrine *masquinongy*. The fossil pterotic has a shorter and more robust postero-dorsal process than the lacustrine *masquinongy*, and a weaker ventral ridge, like the fluvial *masquinongy*, compared to the lacustrine *masquinongy* and *lucius*. *Esox columbianus* has a broad dorso-mesial surface under the parietal and frontal, compared to other forms. The posterior (pterotic) condyle of the hyomandibula forms an acute angle with the opercular arm, as in both forms of *masquinongy*, and unlike the 90° angle in *lucius*. The Ringold hyomandibulae are unique in having a more obtuse angle between the preopercular and ventral processes (acute in both forms of *masquinongy*) and absence of a bony mesial flange at the angle of the opercular and ventral processes (present in both forms of *masquinongy*). The ventral limb of the hyomandibula is truncate in the large *masquinongy* and Columbia fossils, but oblique in the lacustrine *masquinongy*. Preopercular pores are more variable than in *lucius* or *masquinongy* and number six or seven; the lower limb of the preopercle is not as sculptured as in the lacustrine *masquinongy*. *Esox columbianus* has a curved maxilla like *Esox lucius* and unlike the forms of *E. masquinongy*. The dentaries and quadrates of *E. columbianus* are like those in *E. masquinongy*. The articular-angular of the fossil resembles the large, fluvial form of *E. masquinongy* in the absence of the thin bony mesial flange under the articular condyle, as in the lacustrine form of *masquinongy*. Frontals of *E. columbianus* have a longer supraorbital edge than other muskellunge. The fossil ceratohyals are shorter, deeper posteriorly, but narrower at the constriction than in other muskellunge. The cleithra of *E. columbianus* are slender as in muskellunge (not *lucius*), but more curved.

Discussion.— *Esox masquinongy* lives in the Laurentian and Ohio River drainages west to the upper Mississippi and Red

River of the North to Lake of the Woods, thence eastward across southern Ontario and Quebec. There are several Pliocene and Pleistocene specimens from the Great Plains. Its relatives, the pikes and pickerels, live in eastern and northern North America to eastern and northern Asia. The presence of this lineage in the Pliocene of south-central Washington near the axis of the lower Columbia River is a new aspect to the puzzle of past hydrology of the Snake and Columbia rivers. *Esox* was absent from the Snake River drainage in the Pliocene (Smith 1975, 1982). The Ringold record is associated with the Columbia drainage. The muskellunge from the Deer Butte Formation of Barstovian age in the Owyhee Reservoir district of Oregon (Cavender et al., 1970), was in a north-trending Basin (Kittleman et al. 1965) apparently in the Columbia drainage, possibly separated from the Snake River Plain by the Owyhee Ridge.

The Columbia muskellunge osteology is similar to the large, eastern, fluvial form of *Esox masquinongy*, not the smaller, lake form of Lebeau, 1992. The Columbia muskellunge reached lengths over 110 cm throughout the time it was represented by deposits at the three Ringold localities. The size and body form indicate low-gradient habitat in elevations lower than 300 m.

Referred Material.— **White Bluffs l.f.:** UWBM 40309, prevomer, 13 mm long; UWBM 40333, partial right palatine, 20 mm; UWBM 46183, fragment left maxilla, 23 mm; UWBM 46173, left quadrate, 16.5 mm wide at the condyle; UWBM 46174, right quadrate, 8 mm wide at the condyle; UWBM 42454, partial left articular/angular, 31 mm long; UWBM 41928, partial right dentary, 33.5 mm long; UWBM 41525, fragment of right premaxilla, 15 mm; UWBM 46171, partial right dentary, 41 mm; UWBM 46165, partial right cleithrum 15 mm; UWBM 40466, lower fragment right posttemporal, 35 mm; UWBM 46180, fragment of left dentary, 34 mm; UWBM 42259, partial vertebra, 15 mm diameter; UWBM 46177, prevomer, 17 mm long; UWBM 46184, partial left epiphyal, 21 mm; UWBM 46185, fragment of right dentary, 13 mm; UWBM 46187, 2 vertebrae, 7.4, 17 mm diameter; **Blufftop l.f. (Locality UWBM CO150):** UM 103968 right exoccipital, 22 mm, and associated right prootic and part of pterotic, 27 mm, post-temporal 35 mm, basioccipital, 14 mm diameter; UWBM 84090, premaxilla, 18 mm; UM 103935, 2 premaxillae, 19-29 mm; UWBM 84091-2, left and right maxillae, 47, 49 mm; UM 103936, right maxilla, 90 mm; UM 103937, left palatine, 49 mm (Fig. 12a); UM 103938, 16 palatines, 14-57 mm; UWBM 84093-84112, 20 palatines, 13-45 mm; UM 103939, left dentary 53 mm (Fig. 11e); UM 103940, 24 dentaries 21-105 mm; UM 103941, prevomer 29 mm; UWBM 84113-84141, 29 dentaries, 16-128 mm; UM 103950, right frontal 70 mm (Fig. 12e); UM 103951, right frontal 26 x 69 mm; UWBM 84142-84145, 4 frontals, 27-50 mm; UWBM 84146-84147, 70 teeth, 5-22; UM 103952, 70 teeth, 5-16; UM 103953, right articular-angular 40

FIGURE 12 — *Esox columbianus* n. sp. White Bluffs: **a**, UM 103937, ventral view of right palatine; **b**, UM 103954, lateral view of left hyomandibular; **c**, UM 103955, mesial view of right hyomandibular; **d**, UM 103956, lateral view of left preopercle; **e**, UM 103950, dorsal (l) and ventral (r) views of right frontal; **f**, UM 103953, right articular-angular.

mm (Fig. 12f); UWBM 84148-84150, 3 articular-angulars 25-33 mm; UM 103954, left hyomandibular 52 x 46 mm (Fig. 12b); UM 103955, right hyomandibular 24 x 20 mm (Fig. 12c); UWBM 84151, 1 hyomandibular, 24 x 35 mm + 3 fragments; UM 103956, left preopercle, 50 mm (Fig. 12d); UM 103957, 5 preopercles, 26-37 mm; UWBM 84152-84157, 6 preopercles, 19-35 mm; UWBM 84158-84161, 4 parasphenoids, 53-35 mm; UM 103958, 3 parasphenoids, 36-72 mm; UWBM 84162-84163, 2 ectopterygoids, 37-42 mm; UM 103959, 2 ectopterygoids, 43-59 mm; UM 103960, 3 cleithra, 49-85 mm; UWBM 84164-67, 4 cleithra, 28-44 mm; UWBM 84168, basioccipital, 19 mm diameter; UM 103961, 2 supracleithra, 27, 52 mm; UWBM 84169-70, 2 supracleithra, 25, 35 mm; UM 103962, supraoccipital, 16 x 16 mm (Fig. 11c); UM 103963, epibranchial, 37 mm; UM 103964, ceratobranchial, 58 mm; UWBM 84171-84176, 6 ceratohyals, 25-47 mm; UM 103965, 7 ceratohyals, 19-42 mm; UWBM 84177, epihyal, 29 mm; UM 103966, epihyal, 29 mm; UM 103971, 1 right prototic; UWBM 84180, post-temporal; UM 105006, supra-occipital 11 x 9 mm; UWBM 84179, supra-occipital; UM 105157, 3 basi-occipitals, 12-14 mm; UWBM 84181-84184, 4 basi-occipitals; UM 105158, right articular-angular, 89 mm; UWBM 84185, right articular-angular, 31 mm; UM 105153, 18 vertebrae; UWBM 84186, 18 vertebrae; UWBM 84187-84188, 2 prevomers, 23, 26 mm; UM 105160, 4 quadrates; UWBM 84189-84193, 5 quadrates; UM 107756, pterotic; UM 105161, caudal fin ray 133 mm long. **Blufftop l.f. (Locality UWBM CO155):** UM 103969, 4 fragments of dentaries, 16-31 mm; UWBM 82118, anterior fragment of right dentary 67 mm long; UWBM 71795, right articular angular 41 mm long; UWBM 81704, supraoccipital, 8 x 8 mm; UWBM 81740, vomer 25 mm long; UWBM 70706, vomer 45 mm long; UWBM 81944, vertebra; UWBM 81885, vertebra **Taunton l.f.:** UWBM 86634, left quadrate fragment, 41 mm; UWBM 86628, left dentary fragment, 37 mm (original length 130 mm); UWBM 86629-86630, 2 teeth (Fig. 11d); UWBM 86631-86632, 2 teeth.

FAMILY CENTRARCHIDAE

Archoplites Gill 1862

Archoplites molarus new species, Ringold sunfish
(Figs. 13-15)

Archoplites is the most common of the western North American sunfishes. It is found from Miocene and Pliocene localities in Washington, Oregon, and Idaho and from the Central Valley and some adjacent streams of California. *Archoplites* is characterized by 5-8 anal spines, a long pelvic spine, small teeth on the vomer, endopterygoid, ectopterygoid, and basibranchial; dentary truncate with small teeth on an anteriorly expanded tooth patch and one small anterior, plus four large ventral lateralis pores; preopercular with a long dorsal limb, 90° angle between the limbs, a strong adductor fossa, normally 6 pores, and small serrations; 3 or 4 predorsal bones; and lacrimal serrate and rounded posteriorly. The genus is morphologically primitive among centrarchids, being a sister group to

Centrarchus (Mabee, 1995) and also similar to *Ambloplites*. The Ringold sunfish have massive pharyngeals and small, molariform teeth, at least in the Blufftop sample; pharyngeal teeth are not known from the other samples. The name *molarus* is from a Latin noun for millstone, referring to the molariform pharyngeal teeth.

Diagnosis.— A large species of *Archoplites*, adults 200-400 mm in standard length, similar to *A. interruptus* and *taylori*. *Archoplites molarus* has a deep mandibular shelf on the preopercle and more divided, slit like postero-median pore of the frontal, and more serrated opercle and supracleithrum (unlike *Centrarchus* and *Ambloplites*). *Archoplites molarus* has serrated posterior edges of the posttemporal and preopercle and smaller teeth (unlike *Ambloplites* but like *Centrarchus*). *Archoplites molarus* has long frontals, opercles, parasphenoid, and jaw bones; a lower supraoccipital; shorter and more robust anterior gill rakers on the first arch; the lower median ridge of the second pharyngeobranchial; and the flattened pharyngeal surface of the posterior parasphenoid and basioccipital (unlike *Centrarchus*). *Archoplites molarus* differs from *Archoplites interruptus* and *taylori* in its reduced and (or) somewhat slit-like lateralis pores on the dentary, articular, posttemporal, preopercle, postero-mesial and posterolateral frontal; and the absence of the postero-mesial lateralis pore on the frontal. The Blufftop population has enlarged pharyngeal bones with small, molariform teeth, similar to *Ambloplites rupestris*.

Holotype.— UM 105007, a right frontal, 17 mm long at the midline, 17 mm long at the orbital rim, and 17 mm wide (Fig. 13a). From the Blufftop local fauna, SE 1/4 NE 1/4 Sec. 3, T. 12 N, R. 28 E, in Franklin Co., Washington; 242 m (800 ft) elevation.

Description of Frontal.— The usual arrangement of pores among centrarchids in this group, from anterior to posterior, includes five: first, at the anterior border; second, a few mm behind the first in the center of the frontal; third, posterior to the second at the median border; fourth, posterolateral to the second near the anterior end of the postero-median longitudinal (epiotic) ridge; and fifth, at the posterolateral corner of the bone. The anterior pore in the holotype of *Archoplites molarus* is large, 3.3 mm wide and 1.4 mm deep; the second (mid-dorsal) pore is 4 mm posterior to the anterior pore and also large, 1.8 mm wide, and 3 mm long; the rim of the third, postero-mesial, pore is thick and long and the pore is slit-like and nearly closed, 2 mm long and 0.5 mm wide; the fifth, posterolateral, pore is 11 mm posterior to the second (mid-dorsal) pore and nearly obsolete. The fourth pore, at the head of the postero-mesial ridge of *Archoplites interruptus* and *taylori*, anterior to the postero-median ridge, is absent, as in *Ambloplites*, *Centrarchus* and *Chaenobryttus*. The orbital rim and the arc at the anterior edge of muscle attachment behind the second pore are thick and marked by sinuous strengthening ridges, unlike other centrarchids except *Archoplites interruptus* and (weakly) *Centrarchus*. The postero-mesial longitudinal ridge is more vertical than in *Ambloplites* or *Archoplites interruptus*. The frontal is dorso-ventrally thickened compared to other centrarchids. The ventral keel is massively thickened, not blade-

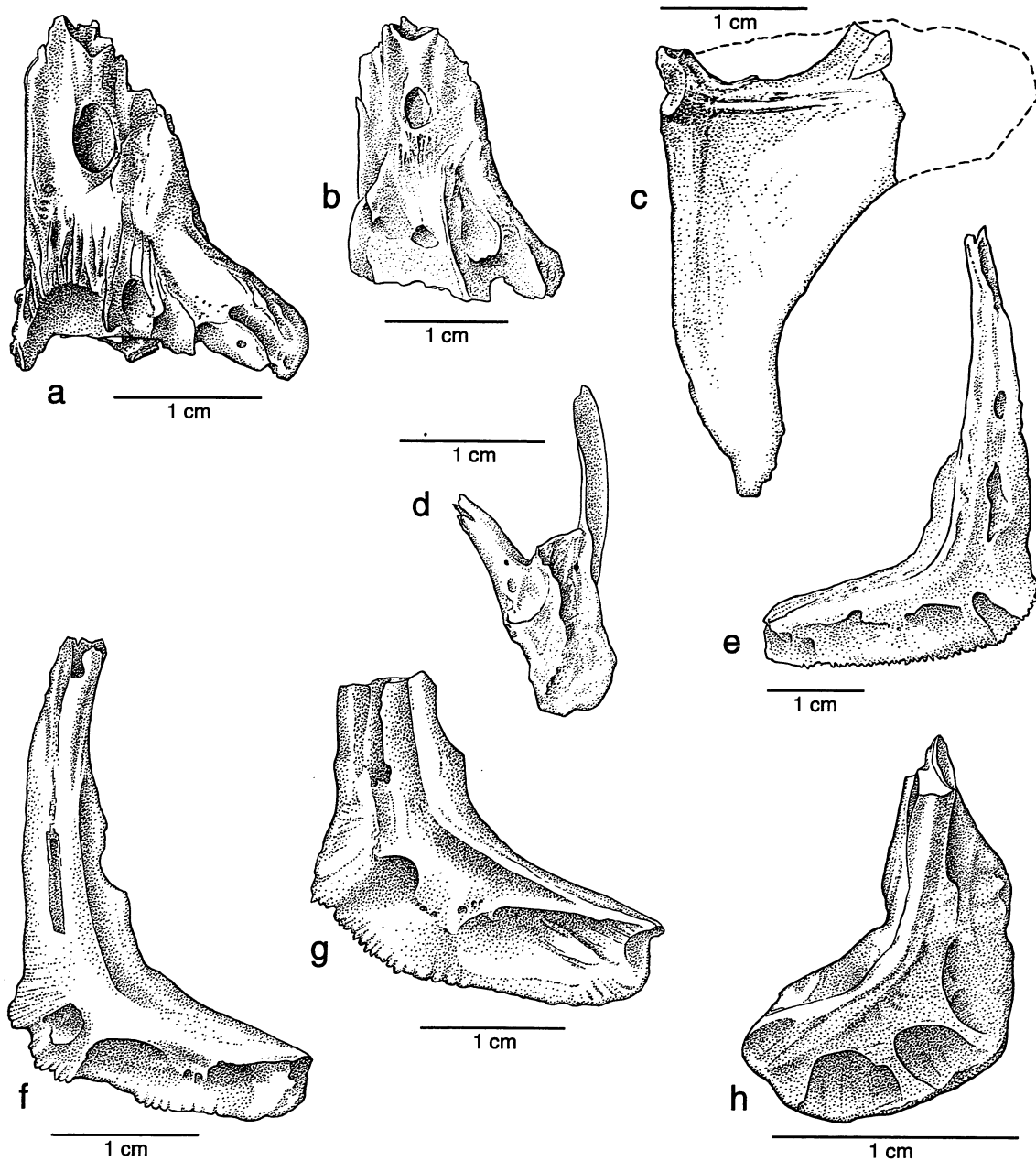


FIGURE 13 — *Archoplites molarus* n. sp.: a, UM 105007, right frontal, Blufftop, holotype; b, UWBM 84494, right frontal, Blufftop; c, UM 105075, right opercle, Blufftop (composite — dashed line represents second specimen); d, UM 105074, right posttemporal, Blufftop; e, UM 105065, left preopercle, Glenns Ferry Formation; f, UM 105094, right preopercle, Blufftop; g, UM 105094, right preopercle, Blufftop; h, UM 105095 left preopercle, Taunton.

like as in *Ambloplites* or *Archoplites interruptus*. The paratypes, UM 105008, a right frontal 20 mm long, and UWBM, a right frontal 26 mm long, match the holotype in all particulars.

Description of other elements. — The premaxillae are similar in shape to *Centrarchus* and other *Archoplites* except that the mesial edge of the ascending process is inflected mesially

at its base. Maxillae are as in *A. interruptus* and *taylori*, but lacking the ridge and notch on the mesial surface posterior to the neck of the bone, and with less extended and pointed mesial ventral processes, especially the anterior. The prevomer has a semilunar tooth patch, laterally extended as seen dorsally or ventrally, its posterior edge is concave and usually smoothly

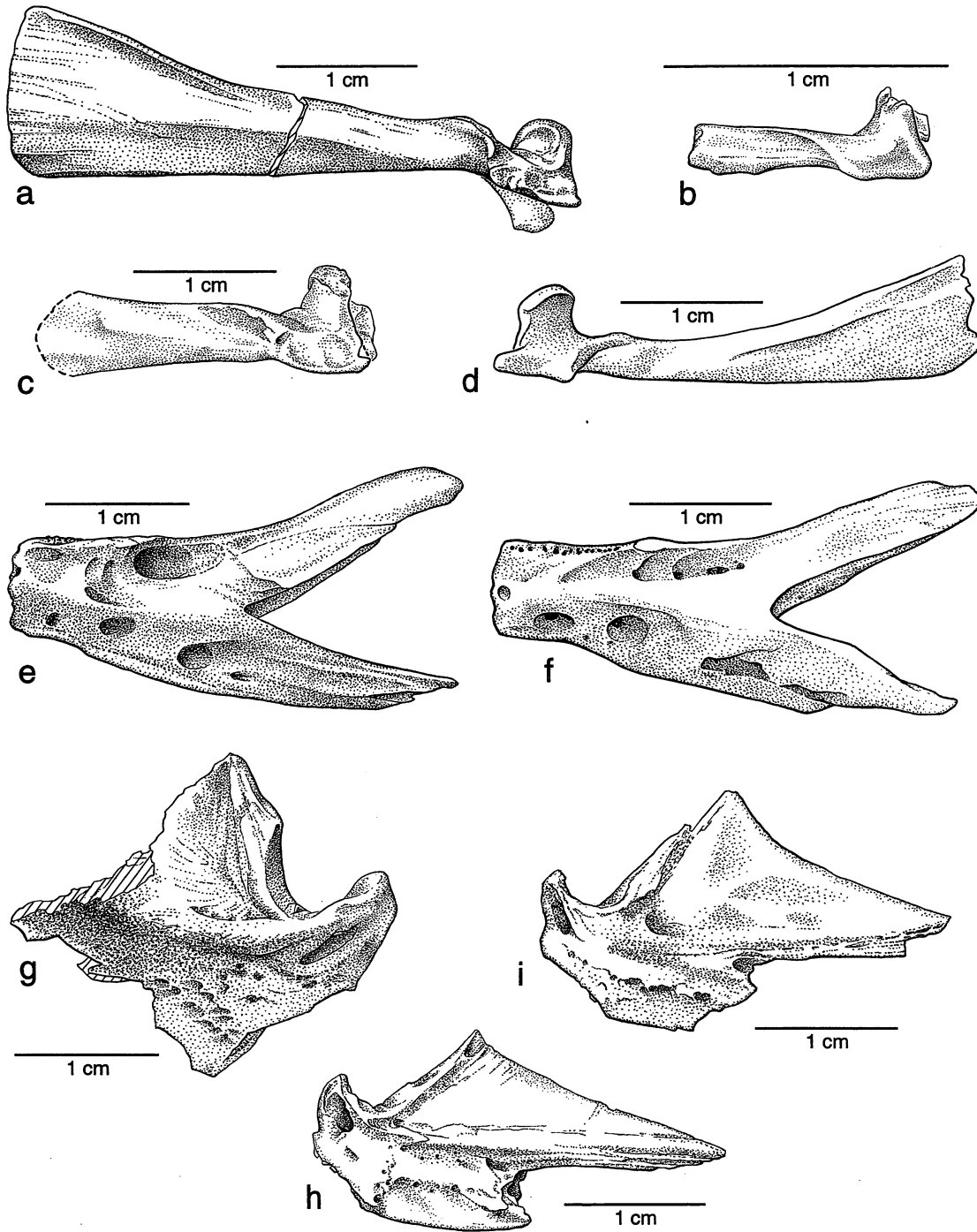


FIGURE 14 — *Archoplites molarus* n. sp.: **a**, UM 105090, right maxilla, Blufftop; **b**, UM 105078, right maxilla, Taunton; **c**, UWBM 105077, right maxilla, Taunton; **d**, UM 105072, left maxilla, Glenns Ferry Formation; **e**, UM 105085, left dentary, Blufftop; **f**, UM 105066, left dentary, Glenns Ferry Formation; **g**, UM 105080, left articular-angular, Taunton; **h**, UM 105084, *Archoplites taylori*, right articular-angular, Glenns Ferry Formation; **i**, UM 105070, *Archoplites molarus*, right articular-angular, Blufftop.

confluent with the vomerine shaft post-ventrally, as in *Centrarchus*, but unlike *Archoplites interruptus* or *taylori*.

Dentaries are elongated and deep anterior to the third pore, compared to *Centrarchus*, with a keeled ventral margin; the

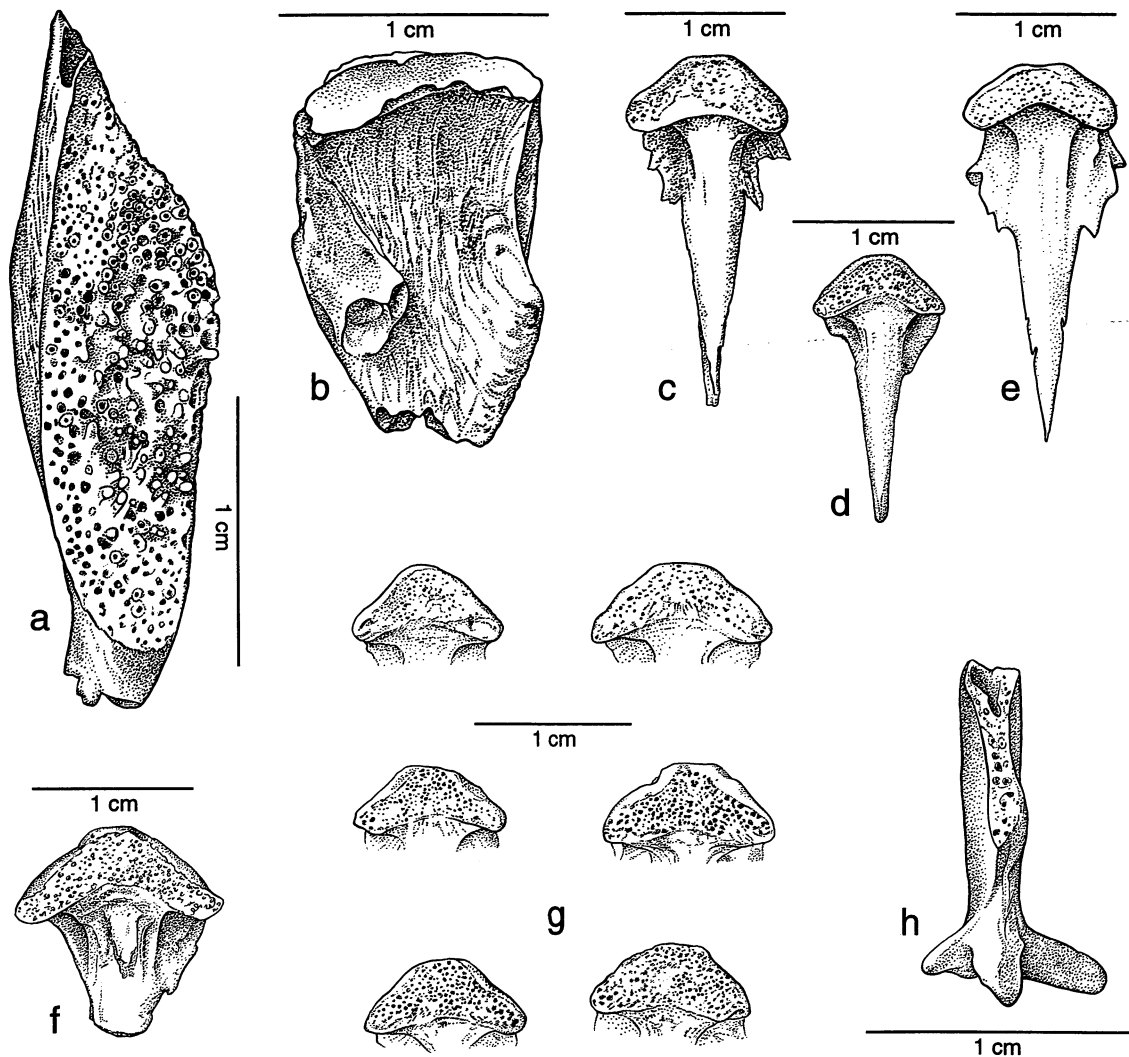


FIGURE 15 — *Archoplites molarus* n. sp.: **a**, UM 105088, lower pharyngeal with molar teeth, Blufftop, posterior up; **b**, UM 105022, upper third pharyngeobranchial, Blufftop, posterior up; **c**, UM 105069, prevomer, Blufftop; **d**, UWBM 105081, prevomer, Taunton; **e**, UM 105067, prevomer, *Archoplites taylori*, Glens Ferry Formation; **f**, UM 105083, *Archoplites molarus*, prevomer, Taunton; **g**, UM 105064, six prevomers, Taunton; **h**, UM 105049, gill raker, Taunton.

posterior part of the tooth patch is abruptly narrow and inflected dorsally as in *interruptus*, but with small pores like *taylori* and *Centrarchus*. Articular-angulars are deeper and shorter, with a larger retroarticular than other *Archoplites*, more like *Centrarchus*; the posterior mandibular lateralis pore is more slit-like and oblique, as in *Centrarchus* and *Archoplites taylori*, rather than round and vertical as in *A. interruptus* or *Ambloplites*. Basioccipital and exoccipital gently striated, without any of the numerous deep pits characteristic of *Centrarchus*, *A. interruptus*, or *A. taylori* or the swollen bullae of *Centrarchus*. Lateralis plate of the posttemporal with weak serrations and shallow canals, but similar to *Centrarchus* in lacking the separate posterior pore from the supracleithral commissure and ventral process to the supracleithrum seen in *A. interruptus* and

taylori. Preopercle flattened, its lateralis pores opening posteriorly and ventrally, more slit-like than *A. interruptus*; *A. taylori* is intermediate. Urohyal with longer antero-dorsal process than *A. interruptus* or *taylori*. Supracleithrum as in *A. interruptus* but posterior serrae weak or absent. Upper and lower toothed pharyngobranchials more massive and with larger, molariform teeth (seen only in Blufftop specimens), unlike the fragile bones and cardiform teeth of *A. interruptus* and *taylori*. Anal pterygiophores and spines more massive than in *A. interruptus*. Supraoccipital, parasphenoid, hyomandibular, quadrate, ceratohyals, and cleithra as in *A. interruptus* and *taylori*.

Referred Material.— **White Bluffs l.f.:** UWBM 28746, spine fragment, 20 mm; UWBM 35106, 3 spines, 6-18 mm; UWBM 35148, right dentary, 20 mm; UWBM 35129 part, 3

spines, 5-13 mm; UWBM 35185, spine, 21 mm; UWBM 40307, 2 ceratohyals, 23, 24 mm; UWBM 40323, 2 cleithra, 11, 13 mm; UWBM 40332, 4 spines, 5-11 mm; UWBM 40334, right dentary, 11 mm; UWBM 40308, 3 dentaries, 9-12 mm; UWBM 40321, dentary, 8 mm; UWBM 40331, left dentary, 7 mm; UWBM 40382, right dentary, 8 mm; UWBM 42156 pt., left cleithrum, 18 mm; UWBM 42262, 3 right dentaries, 7-10 mm; UWBM 46149, right dentary, 1 mm; UWBM 46154, pterygiophore fragment, 4 mm; UWBM 46160, cleithrum, 10 mm; UWBM 46166, pterygiophore fragment, 5 mm; UWBM 46175, spine, 17 mm; UWBM 46176, spine, 33 mm; UWBM 46152, 10 spines, 5-21 mm; UWBM 46153, left premaxilla, 5 mm; UWBM 46155, supracleithrum, 7 mm; UWBM 46157 pt, left cleithrum, 15 mm, urohyal, 8 mm; UWBM 46181, left dentary, 31 mm; UWBM 46189, spine, 13 mm; UWBM 46192, right maxilla, 12 mm; UWBM 46195, pterygiophore, 12 mm.

Blufftop l.f.: UM 105009, 1 basioccipital and 2 exoccipitals; UWBM 84475, 1 basioccipital; UWBM 84476, 7 urohyals; UM 105010, 7 urohyals; UM 105011, 2 supraoccipitals; UWBM 84590, 1 supraoccipital; UWBM 84477, 20 cleithra; UM 105012, 20 cleithra; UM 105074, 1 posttemporal (Fig. 13d); UWBM 84478, 19 posttemporals; UM 105013, 18 posttemporals; UWBM 84479-84492, 14 preopercles; UM 105014, 14 preopercles; UM 105094, 2 preopercles (Figs. 13f, 12g); UM 105075, 1 opercle (Fig. 13c); UM 105076, 1 opercle; UM 105007, 1 frontal (holotype, Fig. 13a); UM 105008, 1 frontal (paratype); UWBM 84493, 1 frontal; UWBM 84494, 1 frontal (paratype; Fig. 13b); UM 105162, 2 frontals; UWBM 84582-84585, 4 frontals; UWBM 84495-94498, 4 epihyals (posterior ceratohyals); UM 105017, 3 epihyals (posterior ceratohyals); UWBM 84499-84500, 2 ceratohyals; UWBM 84578, 1 ceratohyal; UM 105018, 1 ceratohyal; UM 105069, 1 prevomer (Fig. 15c); UWBM 84501, 18 prevomers; UM 105019, 17 prevomers; UM 105099, 2 palatines; UWBM 84577, 1 palatine; UWBM 84502-85513, 12 supracleithra; UM 105020, 12 supracleithra; UWBM 84514-84517, 31 quadrates; UM 105021, 30 quadrates; UWBM 84518-84522, 5 upper pharyngeals; UM 105022, 4 upper pharyngeals (Fig. 15b); UWBM 84523-84552, 30 lower pharyngeals; UM 105023, 31 lower pharyngeals; UM 105088, lower pharyngeal (Fig. 15a); UM 105089, lower pharyngeal; UWBM 84553-84560, 8 anal pterygiophores; UWBM 84579, 1 pterygiophore; UM 105024, 6 anal pterygiophores; UM 105071, anal pterygiophore and spine; UM 105093, 2 pterygiophores; UM 105165, 1 pterygiophore; UWBM 84561-

84567, 7 hyomandibulae; UM 105025, 7 hyomandibulae; UWBM 84568-84572, 5 parasphenoids; UM 105026, 5 parasphenoids; UWBM 84573-84576, 37 premaxillae; UM 105027, 36 premaxillae; UWBM 84591, 8 dorsal spines; UM 105028, 8 dorsal spines; UWBM 84592-84621, 30 articulars; UM 105029, 30 articulars; UM 105070, 1 articular (Fig. 14i); UM 105062, 1 articular; UWBM 84622-84687, 66 dentaries; UM 105030, 58 dentaries; UWBM 84688-84725, 38 maxillae; UM 105031, 38 maxillae; UM 105090, 1 right maxilla (Fig. 14a); UWBM 847726-84735, 250 scales; UM 105032, 250 scales; UM 105033, 1 gill raker; UM 105164, 2 pterotics; UWBM 84580-84581, 2 pterotics; UM 105163, 1 interopercle; UWBM 84587-84589, 3 vertebrae; UM 105100, 4 vertebrae.

Taunton l.f.: UWBM 84736-84739, 33 basioccipitals; UM 105034, 34 basioccipitals; UWBM 84740-84750, 11 urohyals; UM 105035, 14 urohyals; UWBM 84751-84755, 5 cleithra; UM 105036, 4 cleithra; UWBM 84756-84768, 13 posttemporals; UM 105037, 13 posttemporals; UWBM 84769-84844, 76 preopercles; UM 105038, 73 preopercles; UM 105095, 1 preopercle (Fig. 13h); UWBM 84848-85031, 187 ceratohyals; UM 105039, 177 ceratohyals; UM 105064, 6 prevomers (Fig. 15g); UWBM 85032-85039, 82 prevomers; UM 105040, 97 prevomers; UM 105064, 6 prevomers; UM 105079, 12 prevomers; UM 105081, 1 prevomer (Fig. 15d); UM 105082, 1 prevomer; UM 105083, 1 prevomer (Fig. 15f); UM 105096, right palatine; UWBM 85040-85042, 3 supracleithra; UM 105041, 3 supracleithra; UWBM 85043-85317, 275 quadrates; UM 105042, 271 quadrates; UWBM 85318-85324, 77 dorsal and anal pterygiophores; UM 105043, 78 dorsal and anal pterygiophores; UM 105086, 1 anal pterygiophore; UM 105097, 6 pterygiophores; UWBM 86612-86617, 6 pterygiophores; UWBM 85325-85702, 378 premaxillae; UM 105044, 415 premaxillae; UWBM 85703-85717, 154 spines; UM 105045, 150 spines; UM 105080, 1 articular-angular (Fig. 14g); UWBM 85718-85961, 244 articular-angulars; UM 105046, 250 articular-angulars; UWBM 85962-86312, 351 dentaries; UM 105047, 332 dentaries; UM 105085, 2 left dentaries (Fig. 14e); UWBM 86313-86607, 295 maxillae; UM 105048, 280 maxillae; UM 105077, 1 right maxilla (Fig. 14c); UM 105078, 1 right maxilla (Fig. 14b); UM 105087, 1 left maxilla; UM 105091, 20 maxillae; UM 105092, 1 maxilla; UWBM 86608-86611, 4 gill rakers; UM 105049, 5 gill rakers (Fig. 15h); UM 105063, 2 palatines; UM 105050, 6 pelvic pterygiophores.

BIOGEOGRAPHY

Freshwater fish distributions are restricted to lakes, streams, and wetlands. Immigration between drainages occurs through stream captures, shared watersheds and wetlands, marine access, or human transfer (but not on the feet of birds). These colonization modes are often manifest in the resulting patterns of fishes in different habitats, for example, headwater vs. downstream or upland vs. low-elevation patterns. Fishes readily spread through aquatic connections except where blocked by barrier falls or substantial ecological boundaries (e.g., Jordan, 1905; Hubbs and Miller, 1948; Hocutt and Wiley, 1986; Mayden, 1992). Colonization by fishes can proceed on the order of 10^2 to 10^3 km per thousand years, estimating from rates of post-glacial colonization in the Great Lakes (Bailey and Smith, 1981; Smith and Shoshani, 1996; Daniels and Peteet, 1999) and British Columbia (see below).

Biogeographic Background on Ringold Fishes.— Fish fossils in the Pliocene Ringold Formation can contribute to the history of the Columbia River Drainage because we can be confident that fishes rapidly spread where habitat permitted, but did not disperse beyond limits of suitable aquatic connections. Differences between faunas of the Pasco Basin and surrounding drainages required temperature and hydrographic barriers; similarities indicate habitat continuity. The stable continuity of Ringold faunas over 1.7 million years implies relatively thorough sampling of the Ringold depositional system, although the sample localities are geographically limited.

Climate as well as geologic barriers influenced the Ringold fossil fishes. The most significant climatically limiting factors are moisture and temperature. The late Miocene was warm, yet the River Road local fauna contains a salmon, indicating summers free of extreme heat. The Pliocene was a time of decreasing temperatures and increasing seasonality, but the occurrence of large land tortoises in northern Oregon at this time (Orr et al., 1992) indicates frost-free temperatures. Warmwater sunfish and catfish dominated all of the Pliocene Ringold depositional environments sampled; mesothermic minnows, suckers, muskellunge, and sturgeon were present in smaller numbers. All three well-sampled Pliocene Ringold faunas lack coldwater fish such as salmon, trout, whitefish, and sculpins, though we should assume that Pacific salmon migrated to the lower Columbia, and trout, whitefish, and sculpins lived in high-elevation headwaters of the Columbia and Salmon-Clearwater drainages during this period.

The Pliocene faunas represent what are considered two biogeographic groups, in relation to the modern fauna — eastern and western North American fishes. The eastern North American element includes esocids (muskellunge), *Ameiurus* (catfish), and centrarchids (sunfish). The western element includes the white sturgeon, five kinds of western minnows, and two kinds of western suckers. These eastern and western groups reflect post-Pliocene survival, but have no Miocene or Pliocene biogeographic significance.

Five of the Ringold genera, *Ptychocheilus*, *Klamathella*, *Catostomus*, *Chasmistes*, and *Ameiurus* have a long history in the Great Basin and Snake River Plain (Hubbs and Miller, 1948; Smith, 1978; Miller and Smith, 1966; Baumgartner, 1982; Smith et al., 1984; Gobalet and Genenga, 1993, Smith et al., in press). The Pasco and Quincy species can be subdivided into those Pliocene species that were restricted to the drainage downstream (northwest) of Hells Canyon and those that were also found on the Snake River Plain above Hells Canyon (Fig. 1). The forms restricted to the Columbia drainage during the Pliocene are *Acipenser*, *Esox*, *Mylocheilus heterodon*, *Ameiurus reticulatus*, and *Archoplites molarus*. Many forms were found in the Snake but not the Columbia at this time (see below). We must hypothesize tectonic drainage divides, volcanic divides or barrier falls, or extreme habitat differences to explain the unique aspects of the Ringold fauna relative to its neighbors.

The white sturgeon (*Acipenser transmontanus*) is found from Cook Inlet and Anchorage, Alaska, to Monterey, California (Lee et al., 1980). It is the only western sturgeon that penetrates significantly inland — now occurring in the Fraser, Columbia, Snake, and Sacramento. It is a large-river fish found in moderate temperatures. It spawns between 10° C and 18° C. White sturgeon populations are usually migratory, but need not migrate to the sea (Carl et al., 1967; Brown, 1971).

The Ringold pikeminnow bones are not distinguishable from the fossil Snake River form (*P. arciferus*), which is found from the Miocene and Pliocene of the Snake River Plain (Smith 1981; Hearst and Smith, in press) and Miocene of the Salt Lake Formation (McClellan and Smith, in prep.). It is similar to *P. oregonensis*, now found in the Columbia drainage and north to the Skeena and Peace rivers of British Columbia (Scott and Crossman, 1973). *Ptychocheilus* lived in the Pasco Basin 15 m.y.a. and were more widespread to the south in the past (Gobalet and Fenenga, 1993). Today, the genus is found in the

Columbia-Snake, Sacramento, Umpqua, and the Colorado, usually in large river habitats, but the Columbia and Snake River forms occupied lakes as well, from Miocene to Recent (Smith et al., 1984).

The Ringold peamouth chub (*Mylocheilus heterodon*) is related to *Mylocheilus caurinus*, which now ranges from the Columbia-Snake rivers north to the Nass and Peace rivers, and *Mylocheilus robustus*, from the Miocene and Pliocene of the Snake River Plain. Other species of *Mylocheilus* are found in the Miocene and Pliocene drainages of the Salt Lake Formation, western Nevada, Klamath, and Juntura basins (T. Lugaski, unpublished data, McClellan and Smith, in prep., Smith, 1975; Smith and D. Adam, unpublished data). The Pliocene *Mylocheilus* from the Pasco and the Snake basins differ from each other in many characters. The genus is associated with large rivers and lakes.

Three species of Cyprinidae were added to the Ringold faunas in Taunton times. These three evidently came from the Snake River drainage, where they were extremely abundant at the time (Smith et al., 1984). They are represented in the Taunton collections by fewer than a dozen bones and teeth. The chub genus *Klamathella* is native to the modern Klamath drainage and the Pliocene Snake River Plain of western North America. The Ringold *Klamathella* is similar to *Klamathella milleri* of the Pliocene Snake River Plain and *Klamathella coerulea* of lakes and streams in the Klamath system. It is not related to *Siphateles bicolor* of the ancient and modern Lahontan and Klamath basins or the Recent Columbia and Harney drainages (Uyeno and Miller, 1963; Bisson and Bond, 1971; Lee et al., 1980). *Acrocheilus alutaceus*, the chiselmouth chub, is now found in the Columbia, Snake, Harney, and Fraser drainages; its lineage goes back to the Mio-Pliocene Snake River Plain and Salt Lake Formation. *Lavinia hibbardi* was a small chub, especially abundant on the Snake River Plain in the Miocene and Pliocene. These three minnow species, represented by rare fossils of young fishes, appear to be late Pliocene immigrants to the Pasco Basin.

Richardsonius balteatus, the redbase shiner, ubiquitous in the Columbia drainage today, was not found in the Ringold Formation, but was in the Pliocene Glens Ferry Formation. *Richardsonius* is biogeographically important because today it includes differentiated Great Basin and Columbia drainage forms that gained access to the Snake River Plain in the Pliocene, possibly from a connection to the Missouri headwaters (Anderson, 1947; Lemke et al., 1965; Smith, 1981; Smith et al., 1999). Redside shiners are warm-tolerant, aggressive colonizers, less than 12 centimeters long, whose apparent absence from the Pasco Basin bears on estimates of their access to the Columbia and their time of immigration from east of the Rocky Mountains to the west through stream captures.

The lake suckers (*Chasmistes*), are known from the Pliocene Great Basin, Snake River, and Ringold Formation, as well as Recent Klamath, Pyramid, Utah and other Great Basin lakes in western U.S. (Miller and Smith, 1981). The Ringold lake sucker is similar to the morphologically primitive Idaho and Great Basin form, *Chasmistes* cf. *batrachops*. *Chasmistes* did not

colonize the Snake River Plain until the Pliocene (Smith et al., 1984). The genus usually occurs in lakes.

The Ringold largescale sucker (*Catostomus macrocheilus*) is now found in the Columbia, Harney, and lower Snake River to Shoshone Falls, and north to the Skeena and Peace Rivers (Scott and Crossman 1973). This species colonized the Snake River Plain in the late Pliocene (Smith et al., 1984) and the Harney Basin in the Pleistocene (Bisson and Bond, 1971). It now exists in the Snake and Columbia.

The Pliocene Ringold faunas are notable for the absence of migratory Pacific salmon, although *Oncorhynchus rastroros* apparently migrated to the Miocene Ringold Formation. Five salmon species and two trout in *Oncorhynchus* dominated the Columbia in modern times and formerly migrated inland along Pacific Coastal streams as far south as Mexico (Cavender and Miller, 1982). Some of these species of salmon penetrated hundreds of miles inland into the Columbia River and Snake River Plain during the late Miocene (Smith, 1992), Pliocene (rarely, Smith et al., 1984) and Pleistocene to Recent.

Muskellunge (*Esox*) had relatives in British Columbia, Wyoming, and Oregon in the Miocene and earlier (Wilson, 1984; Grande, 1999; Cavender et al., 1970); the Paleogene records date from a time when more of western North America was in the Atlantic drainage. *Esox* apparently became extinct in southeast Oregon in the Miocene (after its occurrence in the Deer Butte Fauna 10 million years ago; it is not in the Juntura fauna) and in Washington in the Late Pliocene. Bones of this species are not found in Late Miocene Poison Creek, Chalk Hills, or Glens Ferry sediments of southwest Idaho.

Western bullhead catfishes in the genus *Ameiurus* range from the middle Miocene of Nevada (Truckee Formation, Baumgartner, 1982) and late Miocene of Oregon (Lundberg, 1975) to late Pliocene of southwest Idaho (Repenning et al., 1995). Seven species survive in warm, usually moist habitats in eastern North America (Lundberg, 1992). The Ringold catfish species was morphologically distinct from its contemporaneous and recent relatives. The northern limits of *Ameiurus* are correlated with isotherms representing a growing period that includes more than 100-180 frost-free days. The central Columbia basin falls within this limitation, but *Ameiurus* is established only in warmwater lakes in the area (Wydoski and Whitney, 1979). The Columbia River, despite elevated temperatures caused by impounded slackwater, is apparently too cool too late in the spring (as measured in degree days) to support *Ameiurus*.

Sunfish, *Archoplites*, were widespread in western U.S. in the early to late Miocene and Pliocene (Smith and Miller, 1985), but are absent from late Pliocene Grand View and Cucumber faunas on the Snake River Plain (Repenning et al., 1995; Smith et al., 1984, respectively). *Archoplites* is now native only in the Sacramento-San Joaquin and Salinas drainages of California. In Pyramid Lake, Nevada, introduced *Archoplites interruptus* survives in warmer, inshore waters. The Ringold sunfish species was morphologically distinct from its contemporaneous and recent relatives. Modern *Archoplites* are inactive from November to April, when the temperature drops below

10°C, but they are active during the 6-month growing season, when the temperature ranges from 10–24°C (Galat et al., 1981). In habitat and growth, Ringold *Archoplites* resembled the introduced black crappies and white crappies (Wydoski and Whitney, 1979) in the Columbia drainage today. These fish spawn above 15°C and 20°C, in reservoirs such as Moses Lake and McNary reservoir, respectively.

The fish of the Ringold Formation are among the richest of Pliocene fish faunas known in western North America. The fossil sturgeon, muskellunge, minnows, suckers, catfish, and sunfish apparently represent a good sample of the medium to large fishes that lived in the original fauna, judged from the large sample size. The absence of salmon from the Pliocene is assured, based on sample sizes in the hundreds of samples. Three of four Miocene specimens are salmonids. The Ringold collections are abraded, but extensive, including many thousands of fish bones ranging across more than 2 million years and several different sedimentary regimes, indicating an effective sampling of all species of medium to large size. The apparent absence of smaller fishes expected in the Columbia basin, such as sculpins and redbreasted shiners is also well established by the large samples recorded here. These fishes had strongly ossified elements, and if they lived in the depositional environment they would be represented as fossils, based on the preservation of hundreds of minute distal pterygiophores, isolated gill rakers, prevomers, and jaw bones of small sunfish, for example. (Disarticulated fish assemblages from fluvial and lacustrine shore face deposits are biased against remains of small fishes, in this case, lampreys, small minnows, sticklebacks, mudminnows, and small sculpins. This size bias is more extreme in dry-screened collections.)

Comparison of Ringold and Snake River Faunas.— The Pliocene faunas of the Ringold Formation and the Snake River Plain are different in both ecology and species composition. The Pliocene Ringold faunas were mainly warmwater and mesothermic fishes — catfish, and sunfish, minnows, suckers, sturgeon, and muskellunge. The Miocene sediments of the Ringold Formation include one possible coolwater fish, *Oncorhynchus rastrosus*. The Ringold Pliocene faunas do not include any of the expected, numerous coolwater fishes from the Pacific coastal or Rocky Mountain drainages. The many coldwater salmonids and sculpins known from the Miocene and Pliocene fish faunas of the Snake River drainage, 300–500 km to the southeast, are completely absent from the huge samples from the Ringold. Furthermore, the contemporaneous sediments of the Snake River Plain from Willow Creek, Oregon, to Hagerman, Idaho, contain salmon, trout, and whitefish, three species of large minnows, four species of large suckers, and more than five species of sculpins not present in the Ringold collections. The Ringold fauna contains a large sturgeon and muskellunge as well as species of minnows, catfish, and sunfish not represented in the Snake River faunas.

The absence of coolwater fishes in the Pasco Basin is a striking contrast to the modern Columbia River fishes and the Pliocene Snake River fishes. The Columbia today is a coldwater river (even in its late 20th Century slackwater state, with tem-

peratures elevated several degrees). The porosity of basalt and gravels generally supports substantial subsurface flow at about the mean annual temperature of the drainage basin. If the Pasco Basin had been fed by streams like those of the modern Columbia tributaries and if there had been winters at nearby high elevations in the Pliocene, the fossil record of the Ringold Formation should be rich in coolwater fishes. Salmon, for example, would have migrated through in cool seasons, and some would have perished en route and after spawning and left a fossil record. The absence of coolwater fishes in the White Bluffs faunas of the Ringold Formation, at a time when cooling climates were bringing subarctic fishes south into Idaho, implies that Ringold environments were warmer, lower in elevation, and experienced no winters, compared to the Snake River Plain. Low elevations and absence of freezing temperatures are supported by the land tortoises with 1 m shells from 4 Ma sediments along the Columbia at Arlington, Oregon (Orr et al. 1992). Large land tortoises cannot survive freezing winters. But habitat barriers are not sufficient to explain the absence of Pacific, Cascadian, and Rocky Mountain fishes from the fauna. Separation from the Pacific, the Snake, and from the upper Columbia by hydrographic barriers is implied. To demonstrate the implied barriers, a more quantitative treatment is presented.

Estimation of Hydrographic Connections by Faunal Similarity.— The comparison of the Ringold and Glens Ferry fish faunas provides evidence concerning connections and disconnections in the hydrographic history of the Columbia River. Modern fishes of the Snake River at Boise and the Columbia River at Pasco illustrate the similarity expected of connected waters with roughly similar habitats: Twenty native species are now found in the Snake River, Idaho, above Hells Canyon between 2000–3000 ft elevation; 21 species are found in the Columbia drainage in the Pasco Basin, Washington, at about 500–1000 ft elevation. Seventeen species are shared by the two regions and seven species are unshared, i.e., found in only one or the other of the drainages. The faunal similarity today between the two drainages, S , is 0.71, where

$$S = \frac{(\text{Shared species})}{(\text{Shared} + \text{Unshared species})} = \frac{17}{24} = 0.71$$

This index of similarity scales from a value of 0 if no species are shared to a value of 1 if all the species in two drainages are shared between the two drainages (Sneath and Sokal, 1973). This high similarity, 0.71, exists notwithstanding the barrier rapids of Hells Canyon and the different elevations and climates of the two regions.

The similarity of the Pliocene Ringold and Glens Ferry faunas is extremely low; $S = 2/30 = 0.07$ during the time of the White Bluffs and Blufftop faunas (Table 1). At the time of deposition of the Taunton fauna, the Ringold-Glens Ferry similarity rose to $S = 6/31 = 0.19$. These values are much lower than the present similarity, $S = 0.71$, and argue against a connection like the modern one. The lack of similarity suggests a

TABLE 1 — Pliocene fishes of the Glens Ferry and Ringold Formations, C = coldwater; W = warmwater; F = fluvial as well as lacustrine.

SNAKE RIVER DRAINAGE GLENNS FERRY FORMATION	PASCO BASIN—COLUMBIA RIVER DRAINAGE TAUNTON, RINGOLD FORMATION	WHITE BLUFFS/BLUFFTOP RINGOLD FORMATION
ACIPENSERIDAE		
—	<i>Acipenser transmontanus</i> CF	<i>A. transmontanus</i> CF
ESOCIDAE		
—	<i>Esox columbianus</i> CF	<i>E. columbianus</i> CF
CATOSTOMIDAE (suckers)		
<i>Deltistes owyhee</i> WF	—	—
<i>Chasmistes spatulifer</i> WF	—	—
<i>Ch. cf. batrachops</i> WF	<i>C. batrachops montanus</i> WF	<i>C. batrachops montanus</i> WF
<i>Catostomus cristatus</i> WF	—	—
<i>Ca. shoshonensis</i> WF	—	—
<i>Ca. macrocheilus</i> ¹ WF	<i>C. macrocheilus</i> WF	<i>C. macrocheilus</i> WF
<i>Ca. arenatus</i> WF	—	—
CYPRINIDAE (minnows)		
<i>Ptychocheilus arciferus</i> . WF	<i>P. arciferus</i> WF	<i>P. arciferus</i> WF
<i>Mylopharodon hagerman</i> . WF	—	—
<i>Mylocheilus robustus</i> W	<i>M. heterodon</i> WF	<i>M. heterodon</i> WF
<i>Idadon hibbardi</i> WF	<i>I. hibbardi</i> WF	—
<i>Idadon condonianus</i> W	—	—
<i>Acrocheilus latus</i> WF	<i>A. latus</i> WF	—
<i>Klamathella milleri</i> WF	<i>K. milleri</i> WF	—
<i>Richardsonius durranti</i> WF	—	—
<i>Orthodon hadrognathus</i> WF	—	—
ICTALURIDAE (catfish)		
<i>Ameiurus vespertinus</i> WF	<i>A. reticulatus</i> WF	<i>A. reticulatus</i> WF
SALMONIDAE (whitefish, trout)		
<i>Oncorhynchus</i> sp. CF	—	—
<i>Oncorhynchus lacustris</i> CF	—	—
<i>Prosopium prolixus</i> CF	—	—
CENTRARCHIDAE (sunfish)		
<i>Archoplites taylori</i> WF	<i>A. molarus</i> WF	<i>A. molarus</i> WF
<i>Archoplites</i> sp. W	—	—
COTTIDAE (sculpins)		
<i>Kerocottus divaricatus</i> C	—	—
<i>K. pontifex</i> C	—	—
<i>K. hypoceras</i> C	—	—
<i>Myoxocephalus antiquus</i> C	—	—
<i>Triglopsis idahoensis</i> C	—	—

¹*Catostomus macrocheilus* occurred at Blufftop and at Taunton. It was shared between the Taunton and contemporaneous (Sand Point) Glens Ferry fauna, but appeared in the Glens Ferry Fauna after Blufftop time, so it was not shared with the contemporaneous Blufftop Fauna.

relatively recent pre-Taunton connection, because 10,000 to 100,000 years would be sufficient to equilibrate the faunas to the present level, all other factors being equal. Although access by downstream (Columbia) species to upstream localities (Snake) could have been blocked by barrier falls, most upstream species would have colonized the drainage below the falls, as parts of the Lake Erie fauna have colonized Lake Ontario over Niagara Falls in the last 14,000 years, for example.

The parallels between the size and latitude of Lake Ontario and Lake Idaho and the possibility of barrier falls to explain the differences between Columbia and Snake river faunas, suggest useful comparison of analogous fish faunas in the Laurentian Great Lakes. Lake Erie (91 species) flows over Niagara Falls to Lake Ontario (84 species), which flows into the St. Lawrence River (86 species in the reach 250 km downstream from Lake Ontario). Lakes Erie and Ontario share 66 species (Bailey and Smith, 1981) and their faunal similarity, S , is 0.61, notwithstanding the 48 m falls. Shoshone falls on the upper Snake River separates 18 species found only below the falls from three species found only above the falls. Twelve species are shared above and below the falls; the similarity of the faunas above and below, S , is $12/33 = 0.36$. Shoshone Falls dates from 15,000 years ago, when it was created by the catastrophic Lake Bonneville flood (Malde, 1965, 1968, 1987, 1991; Scott et al., 1982), but the separation of the upper and lower Snake River drainages dates from much earlier (Taylor, 1985).

Lake Ontario's fish fauna is almost nine times more similar to the St. Lawrence fauna 250 km downstream ($S = 0.61$) than the Lake Idaho fauna is to the White Bluffs/Blufftop fauna ($S = 0.07$), but three times more similar than the Taunton fauna is to Lake Idaho ($S = 0.19$; Table 1). Lake Ontario is unconnected to the Hudson River drainage, but their index of faunal similarity is 0.45. This intermediate similarity value is the consequence of mixing two different stream faunas by post glacial stream captures in the last 17,000 years (Bailey and Smith, 1981; C. L. Smith, 1985); it indicates the expected rate of fish immigration into new drainages following stream capture.

How much of the net dissimilarity of Glenns Ferry and Ringold faunas can be explained by dissimilar habitats? The

Pliocene Snake and Columbia systems (Table 1, Fig. 1) differed significantly in their habitats. The Ringold sediments indicate warm, low-elevation, shallow river and lake habitats, like the Sacramento River. The Glenns Ferry sediments indicate a large, deep lake (like Lake Baikal, but shallower and more southerly) in a climate with winters cold enough to mix 4°C to the bottom, as required by sculpins (Smith et al. 1984; Smith, 1987).

To assess comparable ecological assemblages, we subtract lake-endemics and cold-water salmonids and cottids (sculpins) from the Glenns Ferry diversity and repeat the calculations of S . The 10 fluvial, warmwater fishes (data modified from Smith et al., 1984) give a similarity index value of $2/15 = 0.13$ between contemporaneous White Bluffs/Blufftop and Glenns Ferry faunas. The faunal similarity ($S = 6/15 = 0.40$) between the late Glenns Ferry warmwater fishes and the Taunton fauna represents three times the shared diversity of the earlier Pliocene comparison. It is similar to the comparison of faunas above and below Shoshone Falls of the Snake River. This implies that the first connection between the Snake and Columbia drainages was initiated at about 3 Ma, through a turbulent river.

The biogeographic considerations, above, provide a sense of the possible applications and limitations of fish data to paleohydrographic problems. Aquatic connections in the region are provided by stream captures of diverse scales, from catastrophic lake overflows to large river captures to small, shared, headwater marshes. Fish populations are expected to spread rapidly, on the scale of one-half to three-fourths of a fauna immigrating hundreds of miles per thousand years when the aquatic connections provide favorable habitats. The primary limitations to immigration through aquatic habitat are barrier falls and temperature differences. Therefore, fish distribution patterns can provide evidence of one-way vs. two-way connections, largewater connections vs. headwater connections, and thermal barriers. These comparisons support the hypothesis that the Snake River was captured by a tributary of the Imnaha-Grand Ronde-Salmon drainage about 3 million years ago.

VI

RINGOLD HISTORY AND PLIOCENE DRAINAGE

The Columbia River drainage covers 670,000 km² (258,000 mi²), the sixth largest in North America. The river discharges 75,000 m³/s (265,000 ft³/s), ranking third on the continent. The Columbia drainage freshwater fish fauna is the most diverse in western North America, with 60 species. The 11 species of Miocene and Pliocene fishes in the Ringold faunas represent close relatives of only six of the 60 modern forms. In the context of surrounding faunas the Ringold fossil fishes suggest two hypotheses related to drainage history: (1) The eastern Pasco Basin was separated from the Columbia River and the sea from about 4.5 to about 3 Ma by barrier falls and (or) by elevated temperatures. (2) The Pasco basin was hydrologically separated from the Snake River until the late Pliocene. The conclusion that the Ringold was isolated from the sea and from the upper Columbia is suggested by the absence of any salmon (*Oncorhynchus*) and other coldwater fishes in the known Pliocene Ringold faunas. The conclusion that the Ringold was isolated from the Snake River Plain is based on the faunal contrasts outlined above.

Relationship of the Columbia and Clearwater-Salmon rivers to the Pasco Basin.— The Columbia River Basalt Basin contains a 164,000-174,000 km³ lens (Tallman et al., 1989) of Miocene basalts covering an area of 162,000 km² (62,000 mi²) and thickening to a depth of 4 km near the center, in the Yakima-Pasco area (Waitt and Swanson, 1987). Fecht et al. (1985) and Waitt and Swanson (1987) provide detailed histories of drainage patterns on the western Columbia Basalt Plain. They summarize the long history of segments of the Columbia and Clearwater-Salmon drainage based on numerous studies of intracanyon basalts and lithology of stream clasts in paleochannels. Early stream courses, southwest and westward across the basalt plain, were controlled by three major paleoslopes, especially the westward-dipping Palouse slope, as well as constructional topography formed by repeated eruptions of the Columbia River Basalt and deposition of sediments, and locally emerging topography, especially of the Yakima fold belt (Fecht et al., 1985).

Prior to shift of the center of subsidence to the Pasco Basin in the late Miocene the deepest part of the Columbia Basin was north and west of Priest Rapids (Fecht et al., 1985, fig. 3; Waitt and Swanson, 1987, fig. 8). A well-preserved *Ptychocheilus* pharyngeal was collected by Steve Reidel from sediments dated at about 15 Ma at Priest Rapids dam. This late early Miocene

fossil is the earliest known fish record from the Columbia Basalt Plain. This was a time of low elevation and low relief. Low regional elevations and relief are indicated by low gradient on the Columbia River Basalt flows (Waitt and Swanson, 1987) as well as early and middle Miocene centrarchid fishes collected in Salmon River Canyon, Idaho, Trout Creek, Oregon, and Wells, Nevada. Large, deep-bodied centrarchid fishes are restricted to low gradients and low elevations.

In Late Miocene, as subsidence shifted to the Pasco Basin, it became the topographic low that attracted the major drainages from around the perimeter of the basin: the mainstem Columbia, Yakima, the Clearwater-Salmon-Imnaha-Grande Ronde, Walla Walla, and Umatilla rivers. This subsidence contributed to the deposition of Ringold sediments on the 8.5 Ma Ice Harbor member of the Columbia River Basalt Group (Fecht et al., 1985), perhaps aided by uplift of the Rattlesnake Ridge, Yakima Ridge, and Horse-Heaven Hills. The Columbia flowed through Sentinel Gap (Reidel, 1984), then around the east end of the Umtanum ridge, and southwest to the Columbia River near Goldendale at this time (Schmincke, 1967; Warren, 1941; Campbell, 1979; and Rigby et al., 1979). Fecht et al. (1985) reported evidence of the Columbia River in the Pasco Basin in the Late Miocene to Middle Pliocene (Fecht et al., 1985, figs. 11, 12, 13), but this is inconsistent with warmwater fish fauna and depleted oxygen isotopes.

The Clearwater-Salmon River flowed westward across the Palouse slope of the basalt plain through much of the late Miocene (Fecht et al., 1985). Record of the Clearwater-Salmon River in the White Bluffs section of the Pasco Basin is provided by the Taylor Flat conglomerate (Gustafson, 1978; Tallman et al., 1979) in the earliest Pliocene part of the Ringold Formation. Metavolcanic and quartzite clasts from the east, in Idaho, indicate that the Salmon-Clearwater River deposited the conglomerate. Imbrication direction indicates westward paleocurrents.

Our first White Bluffs fish evidence is the migratory salmon from the Late Miocene Ringold Formation, below the Taylor Flat conglomerate. It suggests discharge westward out of the Pasco Basin, to the lower Columbia River through the path marked by the Snipes Mountain Conglomerate, to the Pacific (Fecht et al., 1985, fig. 12). This drainage was prior to emplacement of the Pliocene basalts of the Simcoe Hills east of Mt. Adams (Waters, 1955; Schmincke 1964, 1967; Fecht et al.

1985, fig. 10-12; Waitt and Swanson, 1987, fig. 8) and prior to the upper Columbia's presence in the White Bluffs area. The Clearwater flowed to the eastern Pasco Basin during much of the Miocene. By 4.5 Ma, the drainage ceased to provide habitat or access for migration of Salmon to the White Bluffs section. The absence of salmon indicates that the topography or basalt fills that contributed to Pliocene sediment accumulation in the White Bluffs and Taunton areas also blocked salmon migration from the Pacific. Fecht et al. (1985:35) attributed continued aggradation to a high relative base level that resulted from (1) absence of Columbia River Basalt volcanism except in the area of the Clearwater Embayment (Swanson et al., 1979; Camp, 1981), (2) continued subsidence and folding of the plateau (Caggiano and Duncan, 1983), (3) uplift of the Cascade Range, and possibly (4) volcanism in the Columbia River Gorge area that choked the Columbia River with hyaloclastic debris and lava flows (Tolan and Beeson, 1984). The composition of the fish faunas in White Bluffs and Taunton sediments suggests that the Columbia flowed to the White Bluffs area after the cessation of sedimentation and after the capture of the Snake River by the Clearwater-Salmon.

Timing of the Snake River Capture by the Clearwater-Salmon River.— In the latest Miocene the western Snake River Plain was accumulating lacustrine sediments of the Poison Creek Formation, then the Chalk Hills Formation (Malde and Powers, 1962) south and east of tectonic activity in eastern Oregon and adjacent Idaho (Kirkham 1931a, b; Camp and Hooper, 1981). Fish fossils in Poison Creek and Chalk Hills sediments (Smith and Cossel, 2000) indicate low elevations and equable lacustrine environments with coexistence of diverse salmon, char, trout, suckers, minnows, catfish, sunfish, and one sculpin (Kimmel, 1975, 1982; Smith et al., 1984; Smith and Patterson, 1994). Two or three kinds of Pacific salmon in the Chalk Hills Formation indicate cool summers and an intermittent connection to the Pacific Ocean. These salmonids include a form with coarse gill rakers somewhat like *Oncorhynchus keta*; *Oncorhynchus salax*, with gill rakers like *Oncorhynchus nerka*, but longer and more numerous (Smith, 1976); and a dwarf, tusked form related to *Oncorhynchus rastrosus* (Cavender and Miller, 1972; Smith et al., 1984). The dwarf salmon was probably too small (less than 60 cm in length) to have migrated to and from the Pacific. These three kinds of salmon as well as a trout and a sculpin on the Snake River Plain suggest locally cooler summers, while sympatric large sunfish and catfish suggest warmer winters than any nearby environment in modern North America. The nearest parallel might be coastal Oregon with few days colder than a mean of 4° C or warmer than a mean of 25° C.

The relatively rich late Miocene fish fauna of the Snake River Plain is known to share relatives of *Ptychocheilus* and *Oncorhynchus rastrosus* with the Ringold fauna, but no others. Therefore, this was possibly the time of the Snake River's course through southeast Oregon to Northern California, through northwest Nevada, as proposed by Wheeler and Cook (1954) or, more likely, to the upper Klamath and upper Pit as proposed by Tay-

lor (1960, 1985). Faunal evidence suggests that this was later than the Deer Butte Formation (10 Ma) and possibly contemporaneous with the Juntura Formation (Hemphillian). The hypothesis that Lake Idaho flowed from its inlet south into Nevada, bypassing southeast Oregon (Repenning et al., 1995), is not supported by sedimentology, biogeography, or geomorphology. The late Pliocene (3 Ma) capture of the Snake River drainage to the Columbia drainage marked the end of the high stand of the Glens Ferry Lake and its drainage to California.

Livingston (1928, figs. 1, 2, 3), proposed a pre-Hells Canyon course of the Snake to the Columbia through the Burnt, upper Powder, and Grande Ronde rivers west of the Wallula Mountains and east of the Blue Mountains (Fig. 15). Wheeler and Cook (1954) amplified Livingston's (1928) analysis of barbed tributaries (Pine, Indian, McGraw, Wildhorse creeks) of the Snake River near the Hells Canyon capture site ("the Oxbow" north of Robinette), as well as observations of geomorphology in Hells Canyon, the Snake River Plain, southeast Oregon, and northwest Nevada. Wheeler and Cook (1954) dismissed Livingston's (1928) Grande Ronde hypothesis because of lack of barbed tributaries on the Burnt River. But this lack is not relevant because the Burnt River was submerged by the Powder River embayment of Lake Idaho, which extended northwest to the North Powder River. The upper Powder River is a major barbed tributary, flowing at an acute angle and reversed direction to the trunk stream, indicating reversal of drainage direction, as noted by Livingston.

Therefore, Livingston's (1928) hypothetical connection from the Snake River northwest through the Powder River to the Grande Ronde is a possibility. If it occurred, it was after the Blufftop fauna, which was isolated from the Snake River Plain, and before the Late Pliocene capture of Lake Idaho at the Oxbow, by the Imnaha-Salmon-Clearwater. Livingston's connection from the Snake to the Grande Ronde at Telocaset Pass, now 3500 ft, (1075 m) was rejected by Wheeler and Cook (1954), who argued that if the Telocaset Pass had been breached at 3500 ft or higher and eroded to that level, the capture of the high stand at the oxbow, at 3300 ft would have been unlikely. Newer estimates of the maximum elevation of Pliocene Lake Idaho range from 3500 ft to 3800 ft (1075-1160 m) (Smith et al., 1982; Jenks and Bonnichson; 1989). These elevations make the proposed flow through Telocaset Pass dependent upon estimates of relative uplift of the Blue Mountains-Wallowa-Seven Devils areas. If the Snake flowed to the Pasco Basin through Telocaset Pass as suggested by Livingston, the connection was the basis for appearance of Lake Idaho fishes at Taunton. This route, if it existed, was stable and short lived, because the capture of Lake Idaho through Hells Canyon probably occurred no later than about 2 Ma, according to Malde (1991) and Othberg (1986). Wheeler and Cook's early Pleistocene estimate for the capture through Hells Canyon was based on Lupher and Warren's (1942) interpretation of small, early Pleistocene channels in the Snake River Canyon, earlier than the Snake River Drainage north from Lake Idaho (Wheeler and Cook, 1954:533-534; Malde, 1991).

The Pleistocene estimate was questioned by Repenning et al. (1995), who concluded that Hells Canyon was connected to the Columbia and Snake drainages in the Late Pliocene, based on similarity of fossil muskrat from the Taunton local fauna to contemporaneous teeth from the Glens Ferry formation. The Taunton fishes support the late Pliocene date of Repenning et al. (1995) for the advent of a Lake Idaho-Pasco connection through either the Grande Ronde or Hells Canyon. The appearance of three Glens Ferry minnow species as fossils in the Late Pliocene Taunton fauna suggests a newly acquired connection between the Pasco Basin and the Glens Ferry Fauna prior to Taunton time. Discussions of faunal similarity (above) and the absence of other Glens Ferry fishes in the Taunton fauna indicate that the connection was prior to 3.0 Ma or that a substantial ecological barrier remained. Estimated gradients (ignoring possible isostatic changes, Wood, 1994) are calculated from the site of the capture, the Oxbow at the head of Hells Canyon, to the Pasco basin at the Taunton locality. Maximum elevations of Pliocene Lake Idaho sediments range from 3500 ft (1075 m) on the south shore (Smith et al. 1984) to 3700 (1128) on the north shore (Gallegos et al., 1987; Wood, 1994). Water-lain basalts are recorded at 3800 ft (1160 m) on the south shore by Jenks and Bonnicksen (1989). The elevations of Ringold sediments at Taunton, Moses Lake, and Lind Coulee are 931 ft (283 m), 1190 ft (364 m), and 1300 ft (400 m), respectively. Assuming an intermediate value for lake level and no uplift (but see Camp and Hooper, 1981) the estimated gradient at Taunton time would have been about $825 \text{ m}/370 \text{ km} = 2.2 \text{ m/km}$ ($2669 \text{ ft}/230 \text{ mi} = 11.6 \text{ ft/mi}$). The present gradient from the Oxbow to the Snake-Columbia confluence averages about $435 \text{ m}/370 \text{ km} = 1.2 \text{ m/km}$ (6 ft/mi). The gradient through the main section of Hells Canyon today is about 2.1 m/km (11 ft/mi). The steep-walled canyon and high input of large clasts create frequent torrential rapids in Hells Canyon. These conditions would have been most severe early in the history of the Snake River connection.

Connections to the Hudson Bay drainage.— In the early Pliocene, at least three kinds of arctic lacustrine sculpins (*Myoxocephalus*, *Triglopsis*, and *Kerocottus*) and whitefish (*Prosopium*) immigrated to the Snake River Plain (Smith et al., 1984; Smith, 1987). The fishes of the Ringold Formation bear on whether the Hudson Bay fauna moved south on the east or west side of the Idaho Batholith. The sculpins would not have tolerated temperatures much above 12°C. Their immigration required an early Pliocene connection between the Snake River and the north. The lack of Salmon River gravels in the early Pliocene at Lewiston (Webster et al., 1987) suggests that the arctic connection was not through the Lewiston or Pasco basins, but rather through the Missouri River to Salmon River headwaters and thence to Lake Idaho. The nearest related fish offering biogeographic evidence of this connection is *Triglopsis thompsoni*, which reaches its southwest limit in Waterton Lake, in the Saskatchewan drainage in Waterton Lakes/Glacier National Park. A Salmon River connection to Saskatchewan drainage headwaters (Anderson, 1947), as Pliocene cooling forced

arctic fishes south, is a possibility. Immigration of eastern North American fishes (see *Richardsonius* above) and mollusks to the Salmon, Snake, and Bonneville basins, was possible when western Montana tributaries to the Missouri flowed to the Saskatchewan drainage, prior to the Pleistocene (Lemke et al. 1965; Smith, 1981:177; but see Taylor, 1985 and Taylor and Bright, 1987).

It is also possible that the immigration of northern fishes to the Snake River Plain was through headwater captures from the Missouri to eastern Snake River headwaters, for example, at Henrys Lake. The Bonneville Basin was not the source of coldwater fishes of the Glens Ferry Formation, although the Bonneville Basin eventually gained the eastern species from the upper Snake River. The late Miocene Salt Lake Group in northern Utah (McClellan 1977) has many faunal similarities to the Miocene Chalk Hills fauna of the western Snake River Plain, but the eastern and western Snake River Plains were separated from the East by a barrier in the Late Miocene (Taylor, 1985). Furthermore, the Salt Lake Formation depositional system was low in elevation (based on the presence of catfish and sunfish; McClellan and Smith, in prep.) and lacked the sculpins that occurred in the Chalk Hills and Glens Ferry formations. The floodplain sediments at Hagerman indicate upper Snake River drainage into Lake Idaho in the late Pliocene. The appearance of northern fishes in the Glens Ferry Formation indicates integration of drainage of the Eastern and Western Snake River Plain in the earliest Pliocene.

Pliocene Climate of the Pasco Basin.— The salient climatic indicators of the Ringold fish faunas are the absence of coldwater fishes — salmon, trout, whitefish, and sculpins — and the dominance of warmwater fishes — sunfish and catfish. Salmon, trout, charrs, whitefish, and sculpins are coldwater fishes that are especially diverse and abundant in the Columbia River (and western valleys north of 41°N and mountains north of 37°N) today. Recently (but prior to anthropogenic destruction), salmonids were diverse in most coastal drainages south to Monterey, California (Lee et al., 1982), and in mountain drainages south to Mexico (Cavender and Miller, 1982); American sculpins are currently at their most diverse in Washington and Oregon. Sunfish and catfish are not native to the Columbia Plateau in Pleistocene-Recent times. They are abundant in warm streams lower than 1100 m, especially in southeastern and midwestern U.S., and have been successfully introduced into low-elevation and warm desert localities in western U.S., including the warmer lakes and reservoirs in Washington and Oregon (Wydoski and Whitney, 1979).

Salmonids and sculpins are northern fishes, limited at the southern extent of their ranges by hot summers. Absence of trout, salmon, whitefish, and sculpins in the Ringold faunas indicates normal daily temperatures exceeding 27°C (80F) during the warmest month, with at least 30 days in which air temperatures exceeded 32°C (88F) in the Pasco Basin. These limits are estimated from summer temperature parameters most closely correlated with the southern distributional limits of salmonids in North America today (Smith and Patterson, 1994).

The absence of salmonids and cottids and moderately heavy ^{18}O signatures for water (see below) also suggests that the northern Columbia drainage did not bring coldwater from northern Rocky mountain tributaries into the Pasco Basin as they do today. This conclusion requires more investigation.

Catfish and sunfish are warmwater fishes whose northern limits are determined by the length of the growing season (Smith and Patterson 1994). The success of *Archoplites* in the Ringold Faunas, compared to Pyramid Lake, for example (where they are less successful than salmonids, Galat et al., 1981) indicates that the Ringold environment had warmer summers and winters than modern Pyramid Lake, i.e., a freeze-free period possibly spanning the entire year, at least during the time when large tortoises lived in the White Bluffs and near the lower Columbia (Merriam and Buwalda, 1917; Orr et al., 1992). The dominance of large catfish and sunfish suggests freeze-free growing seasons in excess of 270 days, as estimated from the correlation between growth of modern representatives of these fishes and growing season (climatic data from U.S. Commerce Dept., 1968; Smith and Patterson, 1994). If Pliocene climates were cyclic during the deposition of the Ringold formation, then winter periods were essentially frost-free at least during long, warm periods in the cycle. Known Ringold fish localities represent only these warm habitats over a period of nearly 2 million years.

The presence of muskellunge is correlated with areas that receive at least 5 cm of rainfall each month and 75-100 cm per year. White sturgeons require water temperatures lower than 23.3°C (Scott and Crossman, 1973) and large-river habitat, which in turn requires substantial runoff in the drainage each

month. Sturgeons are found in the Columbia drainage today, in cool waters originating at high elevations and flowing through desert regions. These fishes indicate abundant moisture, substantially more annual precipitation ($>80\text{ cm}$), and lower lake evaporation ($<80\text{ cm}$) than in east-central Washington today (30 cm and 100 cm respectively).

Preliminary oxygen isotope values in fish tooth and bone apatite from Blufftop indicate that the oxygen isotopic composition of the water ranged from about $\delta^{18}\text{O}_{\text{H}_2\text{O}} = -5$ to -8 SMOW ; values from Taunton tooth and bone apatite ranged from about $\delta^{18}\text{O} = -3$ to -5 (W. P. Patterson, unpublished data). Sunfish growth temperatures estimated for one limited time indicate ambient monthly summer temperatures to 25°C and winter temperatures to -8°C on the Snake River Plain, based on $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of -8 to -16 SMOW (Smith and Patterson, 1994). The Blufftop to Taunton values of $\delta^{18}\text{O}$ are more enriched than on the Snake River Plain, with enrichment increasing during the Pliocene, consistent with low surface elevations and warm winters in the Pasco Basin. The most plausible interpretation of faunal and isotopic data is that the Pasco Basin was low in elevation and warm while the Snake River Plain, to the south, was higher in elevation (but lower than today, based on the presence of abundant sunfish and catfish) and cool (based on abundant trout, whitefish, and sculpins). Shells and fish bones from the Pasco Basin might be expected to show negative values for $\delta^{18}\text{O}$ after diversion of the Snake River into the basin, reflecting the influx of isotopically negative waters from the Snake River. This was not obvious at 3.0 Ma, suggesting that Lake Idaho was no longer a large, deep lake.

VII

SIGNIFICANCE FOR MODELS OF GEOGRAPHIC DIFFERENTIATION

One goal of this fossil fish research is to see how the rate of divergence of fluvial fishes depends on the rate of major drainage changes. Several studies have shown that lacustrine differentiation of fishes can proceed rapidly (McCune, 1996; McCune and Lovejoy, 1998). There is also evidence that small populations of stream fishes can evolve rapidly under strong selection. Some studies of fish differentiation in western North America have concluded that evolution was frequently rapid, on the scale of Post-pluvial (post-glacial) isolation of populations in desiccating basins, e.g. the Death Valley pupfishes (Miller, 1948). The vicariance perspective, on the other hand suggests that differentiation is slow, on a scale slower than that of major tectonic revolutions (Minckley et al., 1986).

The Great Basin, with its apparent post-pluvial differentiation (Hubbs and Miller, 1948) and Laurentian Great lakes with apparent post-glacial colonization and differentiation (Smith and Todd, 1982) seemed to be good arenas for demonstration of rates of evolution. But controlled tests of these examples were lacking because in these lakes, the most parsimonious interpretation of the initiation of isolation rarely involved examination of conditions more recent than the most recent observed geographic separation. A strong test requires older data on morphological states of differentiation and older geologic data to distinguish between hypotheses involving several possible times. We need to be able to test the hypothesis that the youngest possible vicariance event is not the actual cause of observed differentiation in recent organisms (Klicka and Zink, 1997). Fossils, in addition to cladistics of recent organisms, are necessary to perform this test, when most-recent vicariance events have same patterns as older ones.

When possible causes of separation differ sufficiently over the appropriate range of geological time, cladistic analysis of Recent organisms has the potential to test older against younger vicariance events, as demonstrated in organisms of the lower Mississippi Valley (Mayden, 1985; 1987; Cross et al. 1986). This method is not adequate in a glacially or pluvially generated vicariance like the Great Basin or Laurentian Great Lakes, because similar isolating events have been repeated many times over the past several million years. It is therefore important that the studies of Mayden and colleagues concluded that the temporal scale for differentiation is generally longer than the

temporal scale proposed by Miller (1948) and Smith and Todd (1982). Minckley et al. (1986) correlated western fish biogeography with events over the past 30 million years of Cenozoic tectonic events.

To investigate the question of evolutionary rates we use fossils with reasonable chronological control in the context of drainage connections and disconnections that imply a variety of times of separation of populations in allopatry. This allows us to observe differentiation patterns and compare possible differentiation times more ancient than the most recent. The study of history of fish differentiation in the Columbia River drainage in the past 5 million years indicates a primary role for geographic isolation. When estimated isolation is shorter than 1 or 2 million years, we can demonstrate little divergence. When isolation persists longer than 3 million years, changes are frequently observed, at levels indicative of possible species level differentiation.

Increases in the number of species in a drainage are associated with drainage changes more than approximately 3 million years old. That is, if sister populations become sympatric too soon — after 1 or 2 million years of isolation, the number of species does not increase. But if sister populations become sympatric after several million years, the number of species in one or both drainages increases. Therefore, the correlation between the average time of isolation and number of species in a region should be positive for isolation durations older than 3 million years old, but for isolation durations younger than 3 million years, the correlation should be negative. When gene flow is strong enough or frequent enough to swamp differentiation, species number does not increase in fluvial systems, except by immigration of unrelated or distantly-related species. Theoretical considerations suggest that under strong selection, gene flow would not exert strong suppression of differentiation, and new species should originate more rapidly. However, in western American temperate regions, the fluctuations over the past 5 million years have not been conducive to strong unidirectional selection (Darwin, 1859). There is some indication that under the influence of many climatic reversals, approximately every 100,000 years, differentiation has been suppressed.

VIII

SUMMARY AND CONCLUSIONS

(1) Presence of *Oncorhynchus rastrosus* in the Late Miocene, but lack of any *Oncorhynchus* in the Pliocene provide evidence that the eastern Pasco Basin was connected with the Pacific in the late Miocene, but isolated from the Pacific in the Pliocene by falls and by temperature. In the late Miocene the upper Columbia flowed southwest toward the mouth of the John Day River, bypassing the White Bluffs area. During the Pliocene depositional episodes, no salmon reached the White Bluffs or Taunton section of the Ringold Formation.

(2) The known Pliocene fish fauna of the Pasco and Quincy Basins area is represented by 11 species, mostly in the White Bluffs, Blufftop, and Taunton local faunas. These include sturgeon, *Acipenser transmontanus*; a new species of muskellunge, *Esox columbianus*; a northern pikeminnow, *Ptychocheilus arciferus*; a hitch, *Idadon hibbardi*; a chiselmouth chub, *Acrocheilus latus*; a chub, *Klamathella milleri*; a new species of peamouth chub, *Mylocheilus heterodon*; a lake sucker, *Chasmistes* cf. *batrachops*; a large-scaled stream sucker, *Catostomus macrocheilus*; a new species of bullhead catfish, *Ameiurus reticulatus*; and a new species of sunfish, *Archoplites molarus*.

(3) The Pliocene White Bluffs and Blufftop local faunas contain eight species, two of which (*Chasmistes* cf. *batrachops* and *Ptychocheilus arciferus*) were shared with the contemporaneous Glens Ferry Fauna of the Snake River Plain, Idaho. Three species are clearly divergent sisters to complementary forms on the Snake River Plain (*Mylocheilus heterodon* vs. *robustus*, *Ameiurus reticulatus* vs. *vespertinus*, and *Archoplites molarus* vs. *taylori*), indicating no immigration between populations in the late Miocene through middle Pliocene. These data suggest that there was no connection between the Snake River and the Pasco Basin during the time of the White Bluffs and Blufftop faunas. Morphological differentiation of Snake and Ringold populations of *Mylocheilus* (mollusk crushing chub), *Archoplites* (sunfish), and *Ameiurus* (bullhead catfish), indicate a substantial period of allopatry (at least 2 million years) prior to times represented by fossil samples. Within the Ringold sequence, *Archoplites* (sunfish) and *Mylocheilus* (peamouth chub) show morphological changes over a 1-1.6 million year time span.

(4) The Taunton local fauna consisted of 11 species, six of which were shared with contemporaneous fauna of the Snake River Plain. *Chasmistes*, *Ptychocheilus*, and *Catostomus*

macrocheilus were holdovers from the Blufftop fauna. The addition of three Glens Ferry minnows, *Acrocheilus*, *Idadon*, and *Klamathella* to the Taunton fauna and the simultaneous addition of *Catostomus macrocheilus* to the Snake River Plain from Taunton, suggest a late Pliocene time (approximately 3 Ma) for the connection of the Pasco Basin to the Snake River Plain and Lake Idaho.

(5) Pliocene Ringold faunas were mostly warmwater sunfish, catfish, muskellunge, suckers, and minnows. The contemporaneous Snake River Plain fauna to the southeast included coldwater salmon, trout, whitefish, and sculpins in addition to warmwater suckers, minnows, catfish, and sunfish. The Ringold faunas inhabited warm lowlands, with 270 to 365 freeze-free days in the growing season, but with too many hot days to be tolerated by salmonids and sculpins, i.e., more than 30 days with average air temperatures exceeding 32° C (90° F); mean air temperature of the warmest month exceeding 27° C (80° F), perhaps like the Sacramento or the Ohio river basins. The presence of muskellunge and sturgeon indicate large, permanent aquatic habitats in the basin, supported by rainfall in excess of 80 cm/yr and evaporation less than 80 cm/yr. These faunal elements and associated isotopic evidence suggest isolation of the White Bluffs and Taunton areas from the Columbia River in the early and middle Pliocene.

(6) In the Pliocene, coldwater sculpins and whitefish immigrated from the Hudson Bay drainage south to the Snake River Plain through a drainage connection or capture of the upper Missouri River headwaters by the Salmon River and ultimately, northern tributaries of the Snake River. This connection did not involve the Columbia drainage.

(7) The modern Columbia River was assembled through incision in the Pasco Basin after the capture of the Snake by the Clearwater-Salmon. The Columbia fauna eventually gained or retained 11 of the species from the ancient Snake River fauna (chum salmon, sockeye salmon, redband trout, whitefish, char, peamouth chub, chiselmouth chub, northern pikeminnow (squawfish), redband shiner, mountain sucker, and lake sucker). The lower Columbia retained representatives of three of the large-species lineages that occurred in the Pasco Basin in the middle Pliocene (sturgeon, pikeminnow, largescale sucker). The *Idadon*, *Klamathella milleri*, *Mylocheilus heterodon*, *Ameiurus*, *Esox*, and *Archoplites*, became extinct in the Columbia Basin, probably during the Pleistocene.

IX

LITERATURE CITED

- AGASSIZ, J. L. R. 1855. Synopsis of the ichthyological fauna of the Pacific slope of North America, chiefly from the collections made by the expedition under the command of Capt. C. Wilkes, with recent additions and comparisons with eastern types. *American Journal of Science*, 1855 (2 ser.) 19: 71-99, 215-231.
- ANDERSON, A. L. 1947. Drainage diversion in the northern Rocky Mountains of east-central Idaho. *Journal of Geology*, 55: 61-75.
- BAILEY, R. M., and G. R. SMITH. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 1539-1561.
- BAUMGARTNER, J. V. 1982. A new fossil ictalurid catfish from the Miocene Middle Member of the Truckee Formation, Nevada. *Copeia*, 1982: 38-45.
- BISSON, P. A., and C. E. BOND. 1971. Origin and distribution of fishes of Harney Basin, Oregon. *Copeia*, 1971 (2): 268-281.
- BRETZ, J. H. 1923. The channeled scabland of the Columbia Plateau. *Journal of Geology*, 31: 617-649.
- BRETZ, J. H. 1969. The Lake Missoula floods and the channeled scabland. *Journal of Geology* 77: 505-543.
- BROWN, C. J. D. 1971. *Fishes of Montana*. Big Sky Books, Montana State University, Bozeman, 207 pp.
- BROWN, R. E., and M. W. McCONIGA. 1960. Some contributions to the stratigraphy and indicated deformation of the Ringold Formation. *Northwest Science*, 34: 43-54.
- CAGGIANO, J. A., and D. W. DUNCAN (eds.). 1983. Preliminary interpretation of the tectonic stability of the reference repository location, Cold Creek syncline, Hanford Site. RHO-BWI-ST-19. Rockwell Hanford Operations, Richland, Washington.
- CAMP, V. E. 1981. Geologic studies of the Columbia Plateau: Part II. Upper Miocene basalts distribution, reflecting source locations, tectonism, and drainage history in the Clearwater embayment, Idaho. *Geological Society of America Bulletin*, 92: 669-678.
- CAMP, V. E., and P. R. HOOPER. 1981. Geologic studies of the Columbia Plateau: Late Cenozoic evolution of the southeast part of the Columbia River basalt province. *Geological Society of America Bulletin*, 92: 659-668.
- CAMPBELL, N. P. 1979. Geologic map of the Toppenish Ridge (Plate 10); Geologic map of the North Flank of Saddle Mountains and Smyrna Bench (Plate 11). *In*: J. G. Rigby, K. L. Othberg, N. P. Campbell, L. Hanson, E. Kiver, D. Stradling, and G. Webster (eds.), *Reconnaissance Surficial Geologic Mapping of the Late Cenozoic Sediments of the Columbia Basin*, Washington. Washington Division of Geology and Earth Resources, Olympia, Open File Report 79-3: 1-94.
- CARL, G. C., W. A. CLEMENS, and C. C. LINDSEY. 1967. Freshwater fishes of British Columbia. *British Columbia Provincial Museum Handbook* 5: 1-192.
- CAVENDER, T. M., J. G. LUNDBERG, and R. L. WILSON. 1970. Twonew fossil records of the genus *Esox* (Teleostei, Salmoniformes) in North America. *Northwest Science*, 44: 176-183.
- CAVENDER, T. M., and R. R. MILLER. 1972. *Smilodonichthys rastrosus* a new Pliocene salmonid fish from western United States. *University of Oregon Museum of Natural History Bulletin*, 18: 1-44.
- CAVENDER, T. M., and R. R. MILLER. 1982. *Salmo australis*, a new species of fossil salmonid from southwestern Mexico. *Contributions from the Museum of Paleontology, University of Michigan*, 26: 1-17.
- COPE, E. D. 1870. On the fishes of the fresh water Tertiary in Idaho, discovered by Capt. Clarence King. *Proceedings of the American Philosophical Society*, 11: 538-547.
- COPE, E. D. 1883. On the fishes of the Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake. *Proceedings of the Academy of Natural Science of Philadelphia*, 35: 134-167.
- CROSS, F. B., R. L. MAYDEN, and J. D. STEWART, 1986. Fishes in the western Mississippi drainage. *In*: C. H. Hocutt and E. C. Wiley (eds.), *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, New York, pp. 363-412.
- CULVER, H. E. 1937. Extensions of the Ringold Formation. *Northwest Science*, 11: 57-60.
- DANIELS, R. A., and D. PETEET. 1998. Fish scale evidence for rapid post-glacial colonization of an Atlantic coastal pond. *Global Ecology and Biogeography Letters*, 7: 467-476.
- FECHT, K. R., S. P. REIDEL, and A. M. TALLMAN. 1985. Paleodrainage of the Columbia River system on the Columbia Plateau of Washington State: A summary. *Rockwell-Hanford Operations, Richland, Washington, Document RHO-BW-SA-318P*: 1-55.
- FLINT, R. F. 1935. Glacial features of the southern Okanogan region. *Geological Society of America Bulletin*, 46: 169-194.
- FLINT, R. F. 1938. Summary of late-Cenozoic geology of southeastern Washington. *American Journal of Science*, 35: 223-230.

- FRY, W. E., and E. P. GUSTAFSON. 1974. Cervids from the Pliocene and Pleistocene of central Washington. *Journal of Paleontology*, 48: 375-386.
- GALAT, D. L., E. L. LIDER, S. VIGG, and S. R. ROBERTSON. 1981. Limnology of a large, deep, North American terminal lake, Pyramid Lake, Nevada, U.S.A. *Hydrobiologia*, 82: 281-317.
- GALLEGOS, D., P. JOHNSON, S. WOOD, and W. S. SNYDER. 1987. Depositional facies patterns along the Boise front. *Northwest Geology*, 16: 47-59.
- GARDNER, J. N., M. G. SNOW, and K. R. FECHT. 1981. Geology of the Wallula Gap area, Washington. *Rockwell Hanford Operations, Richland, Washington, RHO-BWI-LD-9*: 1-67.
- GILL, T. N. 1862. Notes on some genera of fishes of the western coast of North America. *Proceedings of the Academy of Natural Science, Philadelphia*, 8: 161-168.
- GIRARD, C. F. 1854. Descriptions of new fishes collected by A. L. Heermann, naturalist attached to the survey of the Pacific railroad, under Lieut. R. S. Williamson, U.S.A. *Proceedings of the Academy of Natural Science, Philadelphia*, 7 (4): 129-140.
- GOBALET, K., and G. L. FENENGA. 1993. Terminal Pleistocene - early Holocene fishes from Tulare Lake, San Joaquin Valley, California, with comments on the evolution of Sacramento squawfish (*Ptychocheilus grandis*: Cyprinidae). *PaleoBios*, 15: 1-8.
- GRANDE, L. 1999. The first *Esox* (Esocidae: Teleostei) from the Eocene Green River Formation, and a brief review of esocid fishes. *Journal of Vertebrate Paleontology*, 19: 271-292.
- GROLIER, M. J., and J. W. BINGHAM. 1971. Geologic maps and sections of parts of Grant, Adams, and Franklin Counties, Washington. U. S. Geological Survey, *Miscellaneous Geologic Investigations, Map I-589*.
- GUSTAFSON, E. P. 1978. The vertebrate faunas of the Pliocene Ringold Formation, south-central Washington. *University of Oregon Museum of Natural History Bulletin*, 23: 1-62.
- GUSTAFSON, E. P. 1985. Soricids (Mammalia, Insectivora) from the Blufftop local fauna, Blancan Ringold Formation of central Washington, and the correlation of Ringold Formation faunas. *Journal of Vertebrate Paleontology*, 5: 88-92.
- HEARST, J. M. and G. R. SMITH. in press. Fishes of the late Pleistocene Duck Point Local Fauna, Power County, Idaho: Equable climatic indicator or reworked assemblage? *Idaho Museum of Natural History Occasional Papers*.
- HOCUTT, C. H., and E. O. WILEY (eds.). 1986. *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, New York, 866 pp.
- HUBBS, C. L., and R. R. MILLER. 1948. The zoological evidence. *In: The Great Basin, with Emphasis on Glacial and Postglacial Times*. University of Utah, Salt Lake City, pp. 17-166.
- JENKS, M. D., and W. BONNICHSEN. 1989. Subaqueous basalt eruptions into Pliocene Lake Idaho: Snake River plain, Idaho. *In: V. E. Chamberlain, R. M. Breckenridge, and B. Bonnichsen (eds.), Guidebook to the Geology of Northern and Western Idaho and Surrounding Area*. Idaho Geological Survey Bulletin, 28: 17-34.
- JORDAN, D. S. 1905. *A Guide to the Study of Fishes*. Henry Holt and Company, New York, 2 vols, 624 and 599 pp.
- JORDAN, D. S. 1878. Contributions to North American ichthyology, based primarily on the collections of the United States National Museum. III. B. A synopsis of the family Catostomidae. *Bulletin of the U. S. National Museum*, 1878: 97-237.
- KIMMEL, P. G. 1975. *University of Michigan Papers on Paleontology*, 14: 69-87
- KIMMEL, P. G. 1982. Stratigraphy, age, and tectonic setting of the Miocene-Pliocene lacustrine sediments of the western Snake River Plain, Oregon and Idaho. *In: B. Bonnichsen and R. M. Breckenridge (eds.), Cenozoic Geology of Idaho*. Idaho Bureau of Mines and Geology Bulletin, 26: 559-578.
- KIRKHAM, V. R. D. 1931a. Revision of the Payette and Idaho formations. *Journal of Geology*, 39: 193-239.
- KIRKHAM, V. R. D. 1931b. Snake River downwarp. *Journal of Geology*, 39: 456-482.
- KITTLEMAN, L. R., A. R. GREEN, A. R. HAGOOD, A. M. JOHNSON, J. M. McMURRAY, R. G. RUSSELL, and D. A. WEEDEN. Cenozoic Stratigraphy of the Owyhee Region, Southeastern Oregon, *Bulletin 1, Museum of Natural History, University of Oregon, Eugene*.
- KLICKA, J. and R. M. ZINK. The importance of Recent ice ages in speciation: a failed paradigm. *Science* 277: 1666-1669.
- LEBEAU, B. 1992. Historical ecology of Pike *Esox lucius*, muskellunge *Esox masquinongy*, and maskinonge a new species of *Esox* (subgenus *Mascalongus*) from North America. Ph.D. Dissertation, University of Toronto, 246 pp.
- LEE, D. S., C. R. GILBERT, C. H. HOCUTT, R. E. JENKINS, D. E. McALLISTER, and J. R. STAUFFER, JR. 1980. *Atlas of North American Freshwater Fishes*. North Carolina Biological Survey, Raleigh, Publication 1980-12: 867 pp.
- LEMKE, R. W., W. M. LAIRD, M. J. TIPTON, and R. M. LINDVALL. 1965. Quaternary geology of the northern Great Plains. *In: H. E. Wright Jr., and D. G. Frye (eds.), The Quaternary of the United States*. Princeton University Press, Princeton, pp. 15-27.
- LESUEUR, C. A. 1817. A new genus of fishes, of the order Abdominales, proposed under the name of *Catostomus*; and the characters of this genus, with those of its species indicated. *Journal of the Academy of Natural Science of Philadelphia*, 1: 88-96, 102-111.
- LINDGREN, W. 1898. The mining district of the Idaho Basin and the Boise Ridge, Idaho. U. S. Geological Survey, 18th Annual Report, part 3, pp. 617-719.
- LINDSEY, K. A. 1991. Sedimentation and basin evolution of the late Neogene Ringold Formation, central Columbia Plateau, south-central Washington. *Geological Society of America Abstracts with Programs*, 34 (5): A285.
- LIVINGSTON, D. C. 1928. Certain topographic features of north-eastern Oregon and their relation to faulting. *Journal of Geology*, 36: 694-708.
- LUEDKE, R. G., and R. L. SMITH. 1982. Map showing distribution, composition, and age of late Cenozoic volcanic centers

- in Oregon and Washington. U. S. Geological Survey, Miscellaneous Geologic Investigations, Map I-1091-D.
- LUNDBERG, J. G. 1970. The Evolutionary History of North American Catfishes, Family Ictaluridae. Ph.D. Dissertation, University of Michigan, Ann Arbor, 524 pp.
- LUNDBERG, J. G. 1975. The fossil catfishes of North America. University of Michigan Papers on Paleontology, 11: 1-51.
- LUNDBERG, J. G. 1992. The phylogeny of Ictalurid catfishes: A synthesis of recent work. *In*: R. L. Mayden (ed.), Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford University Press, Stanford, pp. 392-420.
- LUPHER, R. L., and W. C. WARREN. 1942. The Asotin stage of the Snake River Canyon near Lewiston, Idaho. *Journal of Geology*, 50: 866-881.
- MABEE, P. M. 1995. Evolution of pigment pattern development in centrarchid fishes. *Copeia*, 1995: 586-607.
- MACKIN, J. H. 1961. A stratigraphic section in the Yakima Basalt and the Ellensburg Formation in south-central Washington. Washington Division of Mines and Geology, Report of Investigations, 19: 1-45.
- MALDE, H. E. 1965. The Snake River Plain. *In*: H. E. Wright and D. G. Frey (eds.), The Quaternary of the United States. Princeton University Press, Princeton, pp. 255-264.
- MALDE, H. E. 1968. The catastrophic Late Pleistocene Bonneville flood on the Snake River Plain, Idaho. U. S. Geological Survey Professional Paper, 596: 1-52.
- MALDE, H. E. 1987. Shoshone Falls, Idaho: A Pleistocene relic of the catastrophic Bonneville Flood. Geological Society of America Centennial Field Guide, Rocky Mountain Section, pp. 135-137.
- MALDE, H. E. 1991. Quaternary geology and structural history of the Snake River plain, Idaho and Oregon, Chapter 9, *in*: R. B. Morrison (ed.), Quaternary Non-glacial Geology, Conterminous United States. Geological Society of America, The Geology of North America, v. K-2, Boulder, pp. 251-281.
- MALDE, H. E., and H. A. POWERS. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. *Bulletin of the Geological Society of America*, 73: 1197-1219.
- MAYDEN, R. L. 1985. Biogeography of Ouachita highland fishes. *Southwestern Naturalist*, 30: 195-211.
- MAYDEN, R. L. 1987. Historical ecology and North American highland fishes: A research program in community ecology. *In*: W. J. Matthews and D. C. Heins (eds.), Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, pp. 210-222.
- MAYDEN, R. L. 1992. An emerging revolution in comparative biology and the evolution of North American freshwater fishes, pp. 864-890 *in*: R. L. Mayden (ed.) Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford University Press, Stanford, 969 pp.
- McCLELLAN, P. H. 1977. Paleontology and Paleoecology of Neogene Freshwater Fishes from the Salt Lake Beds, Northern Utah. Master's Thesis, University of California, Berkeley, 243 pp.
- McCUNE, A. R. 1996. Biogeographic and stratigraphic evidence for rapid speciation in semionotid fishes. *Paleobiology*, 22: 34-48.
- McCUNE, A. R., and N. R. LOVEJOY. 1998. The relative rate of sympatric and allopatric speciation in fishes: Tests using DNA sequence divergence between sister species and among clades. *In*: D. Howard and S. Berlocher (eds.), Endless Forms: Species and Speciation. Oxford University Press, New York, 470 pp.
- McKEE, B. 1972. Cascadia: The Geologic Evolution of the Pacific Northwest. McGraw-Hill, New York, 394 pp.
- McPHAIL, J. D., and C. C. LINDSEY. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Stikine). *In*: C. H. Hocutt and E. O. Wiley (eds.), The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York, pp. 615-638.
- MERRIAM, J. C., and J. P. BUWALDA. 1917. Age of strata referred to the Ellensburg Formation in the White Bluffs of the Columbia River. University of California Publications, Bulletin of the Department of Geological Sciences, 10: 255-266.
- MILLER, R. R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 68: 1-155.
- 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 University Press, Princeton, pp. 569-581.
- MILLER, R. R., and G. R. SMITH. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occasional Papers of the Museum of Zoology, University of Michigan, 654: 1-24.
- MILLER, R. R., and G. R. SMITH. 1981. Distribution and evolution of *Chasmistes* (Pisces: Catostomidae) in western North America. Occasional Papers of the Museum of Zoology, University of Michigan, 696: 1-46.
- MINCKLEY, W. L., D. A. HENDRICKSON, and C. E. BOND. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. *In*: C. H. Hocutt and E. O. Wiley (eds.), The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York, pp. 519-613.
- MORGAN, J. K., and N. H. MORGAN. 1995. A new species of *Capromeryx* (Mammalia: Artiodactyla) from the Taunton local fauna of Washington, and the correlation with other Blancan faunas of Washington and Idaho. *Journal of Vertebrate Paleontology*, 15: 160-170.
- MYERS, C. W., S. M. PRICE, and 17 others. 1979. Geologic studies of the Columbia Plateau, a status report. Rockwell Hanford Operations, Basalt Waste Isolation Study 4. RHO-BWI-ST-4, Rockwell Hanford Operations, Richland, Washington, 541 pp.
- NEWCOMB, R. C. 1958. Ringold Formation of Pleistocene age in type locality, the White Bluffs, Washington. *American Journal of Science*, 256: 328-340.

- NEWCOMB, R. C., J. R. STRAND, and F. J. FRANK. 1972. Geology and groundwater characteristics of the Hanford Reservation of the U. S. Atomic Energy Commission, Washington. U. S. Geological Survey Professional Paper, 717: 1-78.
- ORR, E. L., W. N. ORR, and E. M. BALDWIN. 1992. Geology of Oregon (Fourth Edition). Kendall/Hunt Publishing Co., Dubuque, 254 pp.
- OTHBERG, K. L. 1991. Late Cenozoic geology and the Tenmile Gravel near Lucky Peak Dam, Idaho. Proceedings of the 22nd Symposium on Engineering Geology and Soils Engineering, pp. 533-545.
- PACKER, D. R. 1979. Paleomagnetism and age dating of the Ringold Formation and loess deposits in state of Washington. Oregon Geology, 41 (8): 119-132.
- PACKER, D. R., and J. M. JOHNSTON. 1979. A preliminary investigation of the magnetostratigraphy of the Ringold Formation. Woodward-Clyde Consultants Report, RHO-BWI-C-42, San Francisco.
- PARSLEY M. J., and L. G. BECKMAN. 1994. White sturgeon spawning and rearing habitat in the lower Columbia River. North American Journal of Fisheries Management, 14: 812-827.
- REIDEL, S. P. 1984. The Saddle Mountains: The evolution of an anticline in the Yakima fold belt. American Journal of Science, 284: 972-978.
- REPENNING, C. A. 1987. Biochronology of the microtine rodents of the United States. *In*: M. O. Woodburne (ed.), Cenozoic Mammals of North America: Geochronology and Biostratigraphy. University of California Press, Berkeley, pp. 236-268.
- REPENNING, C. A., T. R. WEASMA, and G. R. SCOTT. 1995. The early Pleistocene (latest Blancan-earliest Irvingtonian) Froman Ferry fauna and history of the Glenns Ferry Formation, southwestern Idaho. U. S. Geological Survey Bulletin, 2105: 1-86.
- RICHARDSON, J. 1836. The Fish, in Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under the command of Sir John Franklin, R. N. Part 3: 1-327.
- RIGBY, J. G., K. L. OTHBERG, N. P. CAMPBELL, L. HANSON, E. KIVER, D. STRADLING, and G. WEBSTER. 1979. Reconnaissance surficial geologic mapping of the late Cenozoic sediments of the Columbia Basin, Washington. Washington Division of Geology and Earth Resources, Olympia, Open File Report 79-3: 1-94.
- RUSSELL, I. C. 1884. A geological reconnaissance in southern Oregon. U. S. Geological Survey 4th Annual Report, pp. 431-464.
- SCHMINCKE, H.-U. 1967. Flow directions in Columbia River basalt flows and paleocurrents of interbedded sedimentary rocks, south-central Washington. Geologische Rundschau, 56: 992-1019.
- SCOTT, W. B., and E. J. CROSSMAN. 1973. Freshwater Fishes of Canada. Bulletin, Fisheries Research Board of Canada, 184: 1-966.
- SCOTT, W. E., W. D. McCOY, R. R. SHROBA, and M. RUBIN. 1983. Reinterpretation of the exposed record of the last two cycles of Lake Bonneville, western United States. Quaternary Research, 20: 261-285.
- SIGLER, W., and R. R. MILLER. 1963. Fishes of Utah. Utah Department of Fish and Game, Salt Lake City, 203 pp.
- SMILEY, C. J. 1963. The Ellensburg flora of Washington. University of California Publications in Geological Sciences, 35: 159-276.
- SMITH, C. L. 1985. The Inland Fishes of New York State. New York State Department of Environmental Conservation, Albany, 522 pp.
- SMITH, G. R. 1975. Fishes of the Pliocene Glenns Ferry Formation, southwest Idaho. University of Michigan Papers on Paleontology, 14: 1-68.
- SMITH, G. R. 1978. Biogeography of intermountain fishes. *In*: K. T. Harper, and J. L. Reveal (eds.), Intermountain Biogeography: A Symposium. Great Basin Naturalist Memoirs, 2: 17-42.
- SMITH, G. R. 1981a. Late Cenozoic freshwater fishes of North America. Annual Review of Ecology and Systematics, 12: 163-193.
- SMITH, G. R. 1981b. Effects of habitat size on species richness and adult body sizes of desert fishes. *In*: R. J. Naiman and D. L. Soltz (eds.), Fishes in North American Deserts, John Wiley & Sons, New York, pp. 125-171.
- SMITH, G. R. 1987. Fish speciation in a western North American Pliocene rift lake. Palaios, 2: 436-445.
- SMITH, G. R. 1992. Introgression in fishes: Significance for paleontology, cladistics, and evolutionary rates. Systematic Biology, 41 (1): 41-57.
- SMITH, G. R., and J. COSSEL, Jr. 2000. Fishes from the Late Miocene Poison Creek and Chalk Hills formations, Owyhee County, Idaho. Idaho Museum of Natural History, Occasional Papers, in press.
- SMITH, G. R., and R. R. MILLER. 1985. Taxonomy of fishes from Miocene Clarkia lake beds, Idaho. *In*: C. J. Smiley (ed.), Late Cenozoic History of the Pacific Northwest. Pacific Division of the American Association for the Advancement of Science, San Francisco, pp. 75-83.
- SMITH, G. R., and W. P. PATTERSON. 1994. Mio-Pliocene seasonality on the Snake River Plain: Comparison of faunal and oxygen isotopic evidence. Palaeogeography, Palaeoclimatology, Palaeoecology, 107: 291-302.
- SMITH, G. R., and H. SHOSHANI. 1996. Late Pleistocene fishes from the Shelton mastodon site (Oakland County, Michigan) and their ecological context. Contributions from the Museum of Paleontology, University of Michigan 29: 419-443.
- SMITH, G. R., K. SWIRYDCZUK, P. G. KIMMEL, and B. H. WILKINSON. 1984. Fish biostratigraphy of late Miocene to

- Pleistocene sediments of the western Snake River Plain, Idaho. *In*: B. Bonnicksen and R. M. Breckenridge (eds.), *Cenozoic Geology of Idaho*. Idaho Bureau of Mines and Geology Bulletin, 26: 519-541. [Publication issued as an I.B.M.G. open file report in 1982, but the descriptions of new species dates from official distribution in 1984.]
- SMITH, G. R., and T. N. TODD. 1984. Evolution of species flocks of fishes in north temperate lakes. *In*: A. Echelle and I. Kornfield (eds.), *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, pp. 45-68.
- SWIRYDCZUK, K., B. H. WILKINSON, and G. R. SMITH. 1979. The Pliocene Shoofly Oolite: Lake-margin carbonate deposition in the southwestern Snake River Plain. *Journal of Sedimentary Petrology*, 49: 994-1004.
- SWIRYDCZUK, K., B. H. WILKINSON, and G. R. SMITH. 1980. The Pliocene Glens Ferry Oolite II: Sedimentology and oolitic lacustrine terrace deposits. *Journal of Sedimentary Petrology*, 50 (4): 1237-1248.
- SWIRYDCZUK, K., B. H. WILKINSON, and G. R. SMITH. 1981. [Reply] The Pliocene Glens Ferry Oolite: Lake-margin carbonate deposition in the southwestern Snake River Plain. *Journal of Sedimentary Petrology*, 51: 999-1002.
- SNEATH, P. H. A., and R. R. SOKAL. 1973. *Numerical Taxonomy: The Principles and Practice of Numerical Classification*. W. H. Freeman and Co., San Francisco, 573 pp.
- STEARLEY, R. F., and G. R. SMITH. 1993. Phylogeny of the Pacific trouts and salmon (*Oncorhynchus*) and genera of the family Salmonidae. *Transactions of the American Fisheries Society*, 122: 1-33.
- SWANSON, D. A., T. L. WRIGHT, P. R. HOOPER, and R. D. BENTLEY. 1979. Revisions in stratigraphic nomenclature of the Columbia River Basalt group. *U. S. Geological Survey Bulletin*, 1457B: 1-59.
- TALLMAN, A. M., K. R. FECHT, M. C. MARRATT, and G. V. LAST. 1979. Geology of the separation areas, Hanford site, south-central Washington. *Rockwell Hanford Operations, RHO-St-23:133*.
- TAYLOR, D. W. 1960. Distribution of the freshwater clam *Pisidium ultramontanum*. *American Journal of Science*, 258A: 325-334.
- TAYLOR, D. W. 1985. Evolution of freshwater drainages and molluscs in western North America. *In*: C. J. Smiley (ed.), *Late Cenozoic History of the Pacific Northwest*. American Association for the Advancement of Science, Pacific Division, San Francisco, pp. 265-321.
- TAYLOR, D. W., and R. C. BRIGHT. 1987. Drainage history of the Bonneville Basin. *Cenozoic geology of western Utah — sites for precious metal and hydrocarbon accumulations*. Utah Geological Association Publication, 16: 239-256.
- TAYLOR, D. W., and G. R. SMITH. 1981. Pliocene molluscs and fishes from northeastern California and northwestern Nevada. *Contributions from the Museum of Paleontology, University of Michigan*, 25: 339-413.
- TOLAN, T. L., and M. H. BEESON. 1984. Intracanyon flows of the Columbia River Basalt group in the lower Columbia River Gorge and their relationship to the Troutdale Formation. *Geological Society of America Bulletin*, 95: 463-477.
- TEDFORD, R. H., and P. E. GUSTAFSON. 1977. First North American record of the extinct panda *Parailurus*. *Nature*, 265: 621-623.
- UYENO, T., and R. R. MILLER. 1963. Summary of late Cenozoic freshwater fish records for North America. *Occasional Papers of the Museum of Zoology, University of Michigan*, 631: 1-34.
- WAGNER, H. M., C. B. HANSON, E. P. GUSTAFSON, K. W. GOBALET, and D. P. WHISTLER. 1997. Biogeography of the Pliocene and Pleistocene vertebrate faunas of northeastern California and their temporal significance to the development of the Modoc Plateau and Klamath Mountain region. *San Bernardino County Museum Association Quarterly*, 44: 13-21.
- WAITT, R. B., Jr., and D. A. SWANSON. 1987. Geomorphic evolution of the Columbia Plain and River. *In*: W. L. Graf (ed.), *Geomorphic systems of North America*. Geological Society of America Centennial Special Volume, 2, Boulder, pp. 403-416 (Chapter 11).
- WARREN, C. R. 1941. Course of the Columbia River in southern central Washington. *American Journal of Science*, 239: 106-127.
- WATERS, A. C. 1955. Geomorphology of south-central Washington, illustrated by the Yakima East quadrangle. *Geological Society of America Bulletin*, 66: 663-684.
- WEBSTER, G. D., M. J. PANKRATZ-KUHNS, and G. L. WAGGONER. 1982. Late Cenozoic gravels in Hells Canyon and the Lewiston Basin, Washington and Idaho. *In*: B. Bonnicksen and R. M. Breckenridge (eds.), *Cenozoic geology of Idaho*. Idaho Bureau of Mines and Geology Bulletin, 26, Moscow, pp. 669-683.
- WHEELER, H. E., and E. F. COOK. 1954. Structural and stratigraphic significance of the Snake River Capture, Idaho-Oregon. *Journal of Geology*, 62: 525-536.
- WHITE, J. A. 1987. The Archaeolaginae (Mammalia: Lagomorpha) of North America, excluding *Archaeolagus* and *Panolax*. *Journal of Vertebrate Paleontology*, 7: 425-450.
- WHITE, J. A. 1991. North American Leporinae (Mammalia: Lagomorpha) from late Miocene (Clarendonian) to latest Pliocene (Blancan). *Journal of Vertebrate Paleontology*, 11: 67-89.
- WHITE, J. A., and N. H. MORGAN. 1995. The Leporidae (Mammalia, Lagomorpha) from the Blancan (Pliocene) Taunton Local Fauna of Washington. *Journal of Vertebrate Paleontology* 15: 366-374.
- WILSON, M. V. H. 1984. Osteology of the Palaeocene teleost *Esox tiemani*. *Palaeontology* 27: 597-608.
- WOOD, S. H. 1994. Seismic expression and geological significance of a lacustrine delta in Neogene deposits of the western Snake River Plain, Idaho. *American Association of Petroleum Geologists Bulletin*, 78: 102-121.
- WYDOWSKI, R. S., and R. R. WHITNEY. 1979. *Inland fishes of Washington*. University of Washington Press, Seattle, 220 pp.

