FISHES OF THE MIO-PLIOCENE WESTERN SNAKE RIVER PLAIN AND VICINITY

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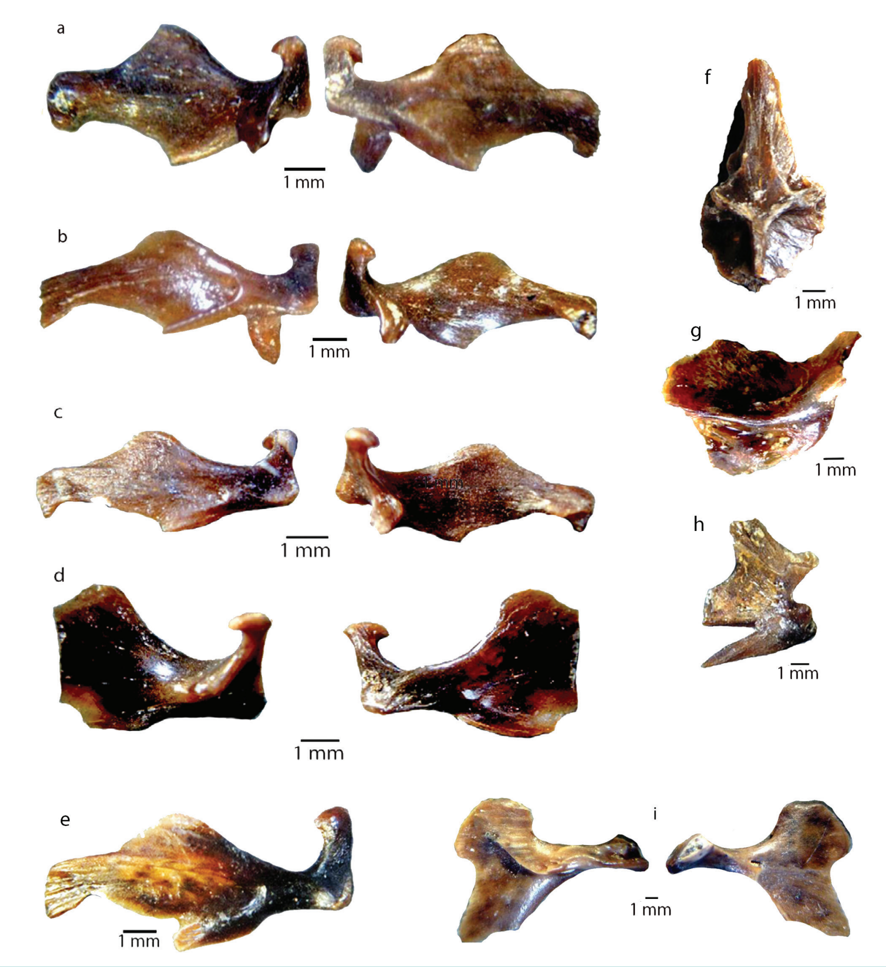

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, 204 no. 5

Ann Arbor, July 26, 2019
ISSN 0076-8405

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KEATING, ALWAYS WELCOME INN, AND IMBLER FISH PALEOFAUNAS, NE OREGON: TESTS OF MIOCENE-PLIOCENE DRAINAGE CONNECTIONS

By

Jay Van Tassell[1] and Gerald R. Smith[2]

ABSTRACT

A persistent puzzle in the study of late Miocene and Pliocene hydrography of the Pacific Northwest United States involves timing and location of connections among the many drainage basins containing sediments and fossils. The Keating, Imbler, and Always Welcome Inn faunas are important datum points that link the Western Snake River Plain to the interior Columbia River Basin. The sites lie in a tectonically active region with punctuated periods of volcanic activity that have periodically disrupted drainage, forcing new connections that allowed faunal interchange between hydrologic basins. Late Miocene to Pliocene fossils from the Keating (Lower Powder), Always Welcome Inn (Baker), and Imbler (Grande Ronde Valley) of northeast Oregon, the Oregon-Idaho Graben and Drewsey-Juntura Graben, Oregon, and lakes of the Western Snake River Plain reveal patterns as well as conflicting evidence. Discovery of distinctive fish groups in the middle Miocene Oregon-Idaho Graben documents the beginning of their appearance in the area following a long period of Oligocene high elevation, cold, and aridity. The pattern of fish dispersal through many regional fossil localities provides baseline evidence of where and when drainage connections might have existed through headwater connections and lake spillovers. Central to this study are 10 species of cool- and warm-water fishes recovered from the Always Welcome Inn site—two species of suckers (Catostomidae), four minnows (Cyprinidae), a char (Salmonidae), a sculpin (Cottidae), and two sunfishes (Centrarchidae). Topographic, geologic, fish, and diatom evidence suggests many possible connections first from the Oregon-Idaho Graben; then the Drewsey-Juntura Graben, Oregon, and Ellensburg Formation, Washington; later from the Western Snake River Plain, Idaho and Oregon; and the Keating, Baker, and Imbler sites, northeast Oregon; and Pasco basin, Washington, prior to the late Pliocene when the Glenns Ferry lake spilled into Hells Canyon. These drainages might have been connected in the Miocene and Pliocene when climates were wet and lake levels were high, and in times of deflation and re-routing after episodes of volcanic activity. The species and characteristics of most of the fishes in the Always Welcome Inn local fauna, 4.5 Ma, near Baker, suggest earlier dispersal along a wide zone of northwest- and north-trending faults and several large, inferred, pull-apart basins between Weiser, Idaho, on the south and Elgin, Oregon, on the north. Topography suggests an additional northward drainage connection at the site of The Summit, the pass between the Keating and Grande Ronde Valleys. The characteristics of the fish fossils in the ~3.8–3.7 Ma Imbler local fauna of the Grande Ronde Valley suggest a connection with the Columbia River drainage in the middle Pliocene or earlier. In Grande Ronde Valley, presence of planktonic diatoms with affinities to Glenns Ferry Lake diatoms just above older sediments containing the Imbler fish fossils indicate a change to deep-water lake environments and suggest possible dispersal between the Powder River arm of the Glenns Ferry Lake and the Grande Ronde Valley via Telocaset Pass (the lowest pass between the Baker and Grande Ronde Valleys). This could have occurred during a wet climate period that peaked at about 3.7 Ma, but after fish dispersal via the Oregon-Idaho and Drewsey-Juntura grabens. There is evidence that prior drainage connections existed between Keating and Baker Valleys and the Columbia River drainage in the late Miocene and Pliocene as a result of stream pathways created by tilting and faulting.

KEY WORDS: *Ptychocheilus, Acrocheilus, Mystocheilus* n. gen., *Catostomus, Pantosteus, Salvelinus, Prosopium, Cottus, Archoplites*, Oregon-Idaho Graben, Drewsey-Juntura Graben, Snake River Plain, Chalk Hills Formation, Glenns Ferry Formation.

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[1] La Grande, OR 97850

[2] University of Michigan, Ann Arbor, MI 48108 (grsmith@umich.edu)

INTRODUCTION

The late Miocene and Pliocene in eastern Oregon was a time of active tectonics, volcanism, block faulting, changing climate, and fluctuating lake levels. These processes resulted in drainage blockages and stream captures that shifted river courses. This paper explores implications of fish and other fossils at three sites in the Lower Powder (Keating), Baker, and Grande Ronde Valleys of northeast Oregon, regarding drainage connections and the dispersal of fish and other organisms between the Oregon-Idaho Graben, Drewsey-Juntura Graben, Western Snake River Plain, and lower Columbia River basins during this critical period in geological history of the Pacific Northwest (Fig. 1a, b, Fig. 2). The sites lie in a tectonically active region with punctuated periods of volcanic activity that have periodically disrupted drainage, forcing new connections between hydrologic basins that allowed faunal interchange. The spillover of the large Glenns Ferry lake from the western Snake River Plain into the Columbia River system (Wheeler and Cook, 1954; Barrash et al., 1983; Wood, 2000; Smith et al., 2000) was a dominant hydrographic event in this history.

Edward D. Cope (1870; 1884a, b), after describing large fish bones collected by the Hayden expedition and the King survey, proposed that a large Tertiary lake, which he named “Lake Idaho,” occupied the Western Snake River Plain. Lindgren and Drake (1904) divided the Lake Idaho sequence into two units, separated by an unconformity. Malde and Powers (1962) named the late Miocene Lake Idaho unit the Chalk Hills Formation and the Pliocene Lake Idaho unit the Glenns Ferry Formation and added several other volcanic and sedimentary marker beds. These large rift lakes dominated fish diversity in the Pacific Northwest; most modern species in the region descended from them, although many of the lake species are now extinct. Because the Chalk Hills and Glenns Ferry lake beds were in different parts of the Western Snake River Plain (WSRP) and are separated in some localities by an unconformity representing an approximately 1.5 m.y. hiatus (Stearley and Smith, 2016), they are considered to represent two separate lakes (Lindgren and Drake, 1904; Malde and Powers, 1962). New evidence suggests that the formations, which extend over more time than the lake beds, may have been separated by only 150–250 ka of known time in some areas (Nate Carpenter, written communication, 2018). The presence of the salmon, *Oncorhynchus salax,* in both lakes implies fluvial continuity between them and at times the Pacific Ocean (Stearley and Smith, 2016). Prior to the Chalk Hills lake, the late Miocene Poison Creek Formation (9.5–8.9 Ma) includes diatomites (Buechler et al., 2007) and fluvial deposits representing an early phase of subsidence, aquatic habitats, and fish life in the Western Snake River Plain (WSRP), (Table 1).

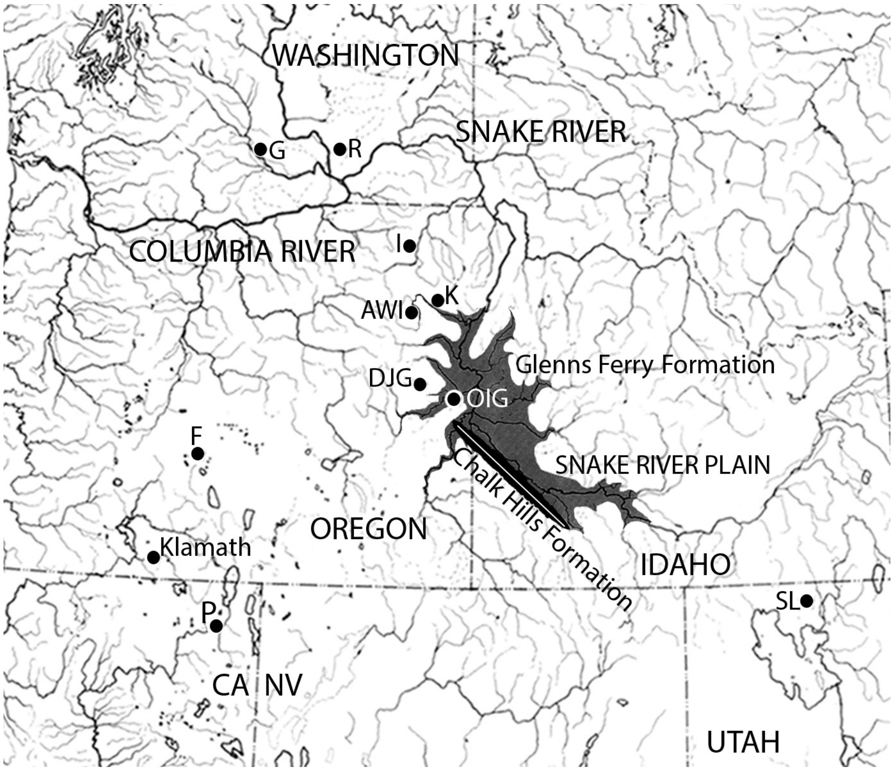

Figure 1a.—Location of Miocene and Pliocene fossil sites in northeast Oregon and vicinity relative to modern river drainages. AWI, Always Welcome Inn; DJG, Drewsey-Juntura Graben; G, Granger Clay Pit, Ellensburg Formation; F, Fossil Lake; I, Imbler; K, Keating; OIG, Oregon-Idaho Graben; P, Pit River, Sacramento drainage; R, Ringold Formation; SL, Salt Lake Formation.

Many of the species of fishes in the Miocene lakes were originally derived from the Sacramento and Klamath river faunas (Wheeler and Cook, 1954; Taylor, 1985; Smith et al., 1982, 2000; Spencer et al., 2008; Stearley and Smith, 2016), mostly through a major structural feature, the Oregon Idaho-Graben (Cummings et al., 2000) and yet to be identified paleo-drainages across southern Oregon. Additional species possibly colonized through the Deschutes and Columbia drainages.

A puzzle in the study of the geologic history of the late Miocene and Pliocene drainages of eastern Oregon and adjacent Idaho involves the timing and location of connections between different phases of the large lakes and the Columbia River drainage basin. Livingston (1928) studied the topography and proposed Pliocene Glenns Ferry Lake drainage through northeast Oregon via the Burnt and Powder Rivers and then through Telocaset Pass, the low point between the Baker and Grande Ronde Valleys, into the Grande Ronde River and the Columbia River system (Figs. 2, 3), the area that is the focus of this paper. He suggested that the lake outlet later switched to Hells Canyon when a tributary of the Clearwater-Salmon River system eroded headward and the Snake drainage spilled from the Glenns Ferry Lake into the Clearwater-Salmon River system at the start of the Quaternary. Wheeler and Cook (1954) argued that Livingston's proposed early drainage course was improbable because there are no barbed tributaries in the Burnt River and because Telocaset Pass is at a higher elevation than the Oxbow in Hells Canyon, which both Livingston (1928) and Wheeler and Cook (1954) proposed as the point of capture at the start of the Quaternary. The maximum elevation of the Glenns Ferry lake deposits during the Pliocene (not adjusted for faults) ranged between 1070 and 1160 m (Smith et al., 1982; Jenks and Bonnichsen, 1989). Post-Glenns Ferry cinder cones and flows on the north margin of the WSRP north of Vale are tilted to the south, implying uplift here. It is possible that the critical area between the John Day and Malheur River has been considerably uplifted since the Pliocene (Mark Ferns, Written Communication, Dec. 31, 2018). The upper Powder River flows at an acute angle in a reversed direction to the trunk stream, which indicates a capture as noted by Livingston (1928). Smith et al. (2000) observed that Livingston's (1928) proposed drainage is not consistent with the paucity of shared fish species, in contrast to the diversity that would be expected as a consequence of a through-flowing river. Wheeler and Cook wrote to Carl L. Hubbs, searching for fish evidence that might bear on this problem (C. L. Hubbs letter, UMMZ) but at that time there was no fossil evidence. Wheeler and Cook (1954) also pointed out that: (1) there are no known lacustrine sediments in the Baker and Keating Valleys that can be related to the Snake River's history and (2) that there is no evidence that a stream as large as the Snake River ever flowed down the

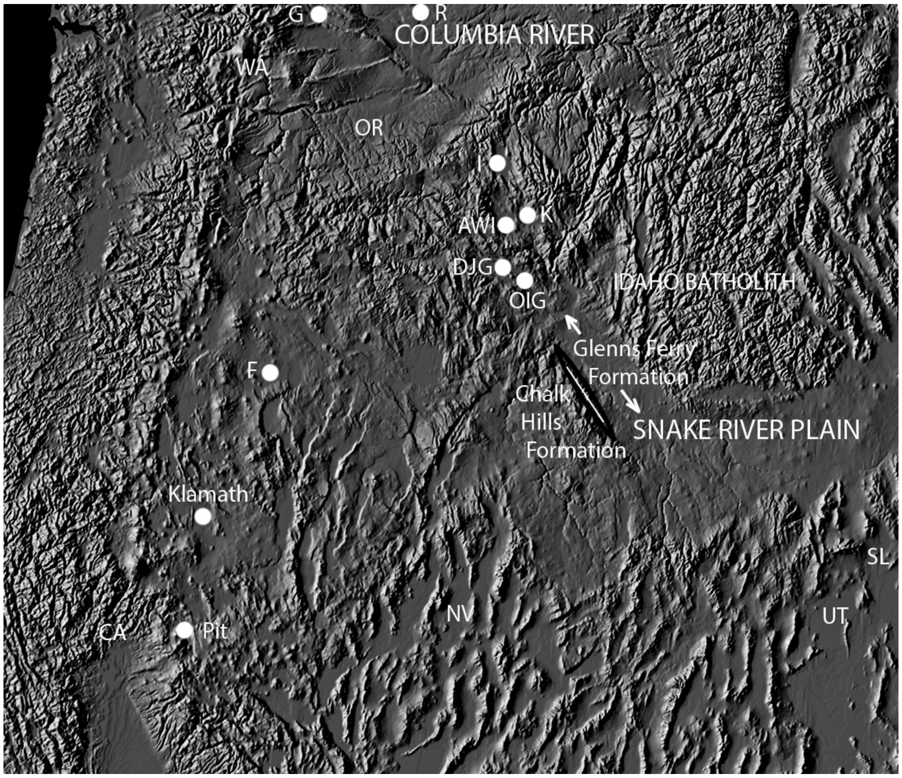

Figure 1b.—Shaded relief map showing sites of Miocene and Pliocene basins and fish paleofaunas in the Northwest. AWI, Always Welcome Inn; DJG, Drewsey-Juntura Graben; G, Granger Clay Pit, Ellensburg Formation; F, Fossil Lake; I, Imbler; K, Keating; OIG, Oregon-Idaho Graben; P, Pit River, Sacramento drainage; R, Ringold Formation; SL, Salt Lake Formation; standard abbreviations for state names.

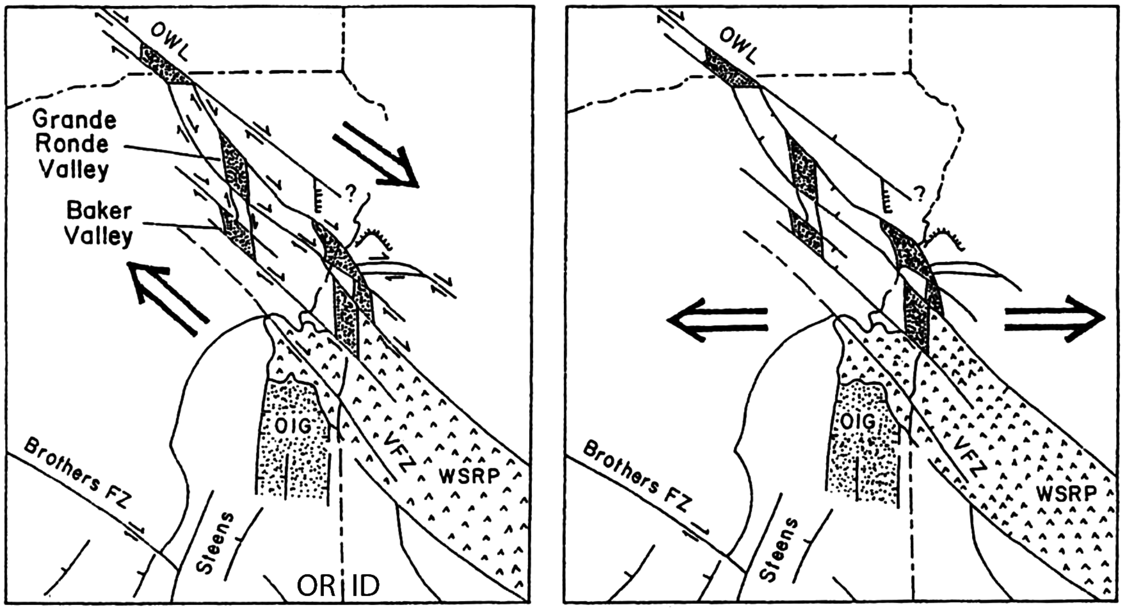

Figure 2.—Tectonic models for northeast Oregon between the Western Snake River Plain (WSRP) and the Snake River. Left, based on the strike-slip basin model of Mann and Meyer (1993), right, and the extension model based on Hooper and Conrey (1989). Both models indicate likely stream courses and fish dispersal pathways in the Late Miocene and Pliocene. OWL: Olympic-Wallowa Lineament; OIG: Oregon-Idaho Graben; VFZ: Vale Fault Zone

Grande Ronde Valley. Late Miocene lake deposits are present in the Baker and Keating Valleys but were thought not to be related to lakes of the WSRP (Lindgren, 1901; Gilluly, 1937).

Reidel et al. (1994) and Reidel and Tolan (2013) suggested a variation of Livingston's ancestral drainage from the Snake River to the Columbia drainage basin. Their proposed drainage route follows the Burnt River to the Baker Valley and then heads west of the Grande Ronde Valley near La Grande, Oregon, down the drainage of the Umatilla River into the Columbia River. They proposed that this was a long-standing connection during the Miocene. They suggested that although the paleochannel was directed back and forth by Columbia River flood basalt lava flows, there was a consistent connection with the lower Columbia west of the Cascade Mountains during the Miocene. This connection would have been active as early as 16 Ma, after deposition of the Grande Ronde Basalts, and continued through the time of the 8.5 Ma Ice Harbor Basalt (Fecht et al., 1987; Reidel and Tolan, 2013) during the time of the Poison Creek fluvial deposits and Chalk Hills Lake. This connection is hypothesized to have lasted until the beginning of the Pliocene (Fecht et al., 1987; Reidel and Tolan, 2013).

The data in Table 1 suggest that the catfish (*Ameiurus*), pikeminnow (*Ptychocheilus*), dace (*Rhinichthys*), mountain sucker (*Pantosteus*), and sunfish (*Archoplites*) may have dispersed between the Drewsey-Juntura Graben in southeast Oregon to the Columbia River drainage basin sometime between 13–10 Ma. The minnow *Klamathella* may have followed the same route between the Columbia River basin to or from the WSRP between 10.5–7.5 Ma. These fish may have followed the route proposed by Reidel et al. (1994) and Reidel and Tolan (2013). The fish may also have dispersed up the Malheur River into the John Day River system and down into the lower Columbia. Fish fossils in 3.8–3.7 Ma sediments from a water well near Imbler, Oregon, provide evidence of a connection between the Grande Ronde Valley and the Columbia River drainage basin during the middle Pliocene (Van Tassell et al., 2001). These pikeminnow, catfish, and sunfish bones are similar taxonomically and ecologically to their counterparts in Pliocene Blufftop (3.6 Ma) and Taunton (3.3 Ma) local faunas of the Ringold Formation of south-central Washington. That evidence suggests a connection between the Grande Ronde Valley and the Columbia River drainage basin during or prior to ~3.6 Ma. This drainage connection may have followed the route of the present-day Grande Ronde River into the tributary of the Salmon River which later became the Hells Canyon segment of the Snake River after the Glenns Ferry lake spilled into the Salmon River system.

The Imbler fish fauna also contains fossils of cool-water whitefish (*Prosopium* sp.). Whitefish are found in Glenns Ferry lake deposits, but not in the contemporaneous Ringold Formation, Washington. They may have lived in the cool headwater reaches of the Grande Ronde and Powder Rivers before the middle Pliocene. Van Tassell et al. (2001) described two Miocene diatoms (*Aulacoseira jouseana* and *Tetracyclus stellare* var. *eximia*) along with Pliocene planktic diatoms (*Stephanodiscus* sp. and *Aulacoseira* sp. aff. *A. solida*) with affinities to those in the Glenns Ferry lake in the layer above the horizon that contains the fish fossils in the Imbler well.

TABLE 1.—Selected Neogene fish present in Pacific Northwest U.S. paleofaunas (from Carpenter and Smith, in preparation, this volume.)

Localities	Modern Drainage	STATE	NALMA	AGE Ma	Acipenser	Ameiurus	Orthodon	Ptychocheilus	Mylopharodon	Siphateles	Lavinia	Gila / Klamathella	Klamathella	Acrocheilus	Mystocheilus	Richardsonius	Mylocheilus	Rhinichthys	Oregonichthys	Deltistes	Chasmistes	Catostomus	Pantosteus	Prosopium	Paleolox/Salvelinus	Oncorhynchus trout	Oncorhynchus salmon	Esox	"PLIOPLARCHUS"	Archoplites	Cottus	Myoxocephalus	Kerocottus	NUMBER OF SPECIES
Ringold Fm.	Columbia River	WA	BL	4.8-3.0	X	X		X			X		X	X			X				X	X					X	X		X				12
Imbler	Grande Ronde River	OR	BL	3.6-3.5		X		X																X						X				4
Glenns Ferry Fm.	Snake River	ID/ OR	BL	4.5-1.8		XX	X	X	X		X		X	X		X	X	X		XX	X	X	XX	XX		X	XX			XX	X	XX	XX XXX	32
Upper Yonna Fm.	Kalamath River	OR	BL	4.5-3.3													X					X				X								3
Always Welcome Inn	Powder River	OR	BL	4.5-4.4				X						X	X			X				X	X		X					XX	X			10
Upper Alturas	Sacramento	CA	BL	4.8-4.5				X		X	X		X								X	X				X					X			8
Christmas Valley	Fort Rock Basin	OR	HH	5.0-4.9						X											X	X				X								4
Krebs Ranch	Columbia River	OR	HH	5.9-5.0		X																X					X	X		X				5
Chalk Hills Fm.	Snake River	ID	HH	8.1-6.0		X	X	X	X		X			X			X			XX	X	X			X	X	XXX			X	X			18
Rome Beds	Owyhee River	OR	HH	8.1-6.5		X		X																					X	X				4
Keating Local Fauna	Grande Ronde	OR	HH	8.6-8.1								?										?									X			3
Ellensburg Fm.	Yakima River	WA	CL	10.5-10		X		X	X		X		X										X							X				7
Poison Creek	Snake River	ID	CLHH	11.5-8.1		XX	X	X	X					X			X					X			X					X				10
Drewsey-Juntura Graben	Malheur River	OR	CLHH	13.6-7.25		XX	X	X	X		X	X		X	X		XX		X	X	X	X	X		X			X		X				19
Oregon-Idaho Graben	Owyhee River	OR	CLHH	15.9-12.8		X		X			X														X			X	X	X				7
		STATE	NALMA	AGE Ma	Sturgeon	Catfish	Blackfish	Pikeminnow	Hardhead	Tui Chub	Hitch	Chub	Chub	Chiselmouth	Chub	Shiner	Peamouth	Dace	Oregon Chub	Lost R Suckers	Lake Suckers	River Suckers	Mtn. Suckers	Whitefish	Char	Trout	Salmon	Muskellunge	Large Sunfish	Small Sunfish	River Sculpin	Sculpins	Lake Sculpins	SPECIES

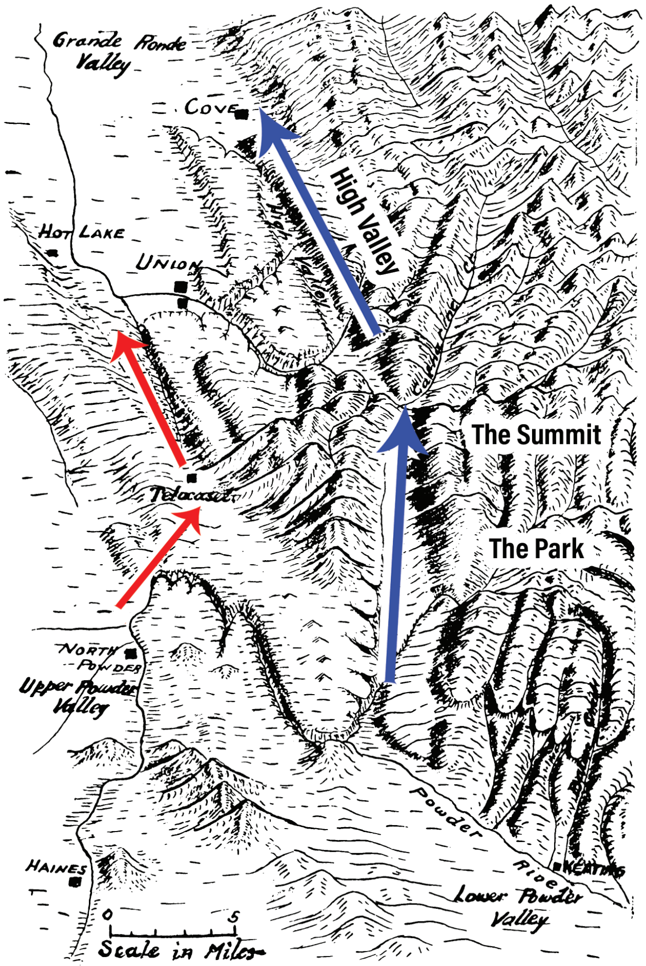

Figure 3.—Livingston's (1928) proposed a former course of Catherine Creek. Telocaset, to the west of Catherine Creek (red arrows), is the low point where Livingston suggested that Lake Idaho drained out of the Powder Valley into the Grande Ronde Valley and the Columbia River system. Blue arrows show the proposed connection between the Keating paleofauna and the Grande Ronde Valley across the Summit (See Fig. 17). The physiographic diagram is from Livingston (1928).

The Miocene diatoms may have been reworked from Miocene outcrops submerged by the Weiser embayment of the Glenns Ferry Lake and washed into the Grande Ronde Valley. The Pliocene planktic diatoms with affinities to those in the Glenns Ferry lake suggest a rapid increase in water depths after the fish bones were deposited. This evidence suggests a possible aquatic connection between the Glenns Ferry Lake and the Grande Ronde Valley at or prior to ~3.6 Ma. It is also possible that the Miocene diatoms were aerially transported (Van Tassell et al., 2001).

Wheeler and Cook (1954) suggested that the timing of the Snake River capture through Hells Canyon took place at the start of the Quaternary. This hypothesis is roughly consistent with: (1) stratigraphic evidence for a drop of ~120m in the level of the Glenns Ferry Lake (Wheeler and Cook, 1954; Malde, 1991; Othberg, 1994) and (2) the dispersal of the snail *Fisherola nuttalli* upstream from the Columbia River drainage to the western Snake River Plain (Taylor, 1985; Othberg, 1988; Malde, 1991). Recent workers (Hearst, 1999; Wood and Clemens, 2002) suggested that drainage of the Glenns Ferry Lake into the Salmon River started at ~2.75–2.5 Ma. Repenning et al. (1995) suggested that spillover happened during the late Pliocene, based on the dispersal pattern of the muskrat *Pliopotamus*, which immigrated up the Sacramento River drainage to the Snake River Plain at Hagerman, Idaho, around 4.2–3.6 Ma and then moved to the Columbia River drainage, where it is found in the 3.3 Ma Taunton local fauna, but muskrats do not require water to disperse. The location of the spillover of the Glenns Ferry Lake into the tributary of the Clearwater-Salmon River system that would become Hells Canyon has also been questioned. Wood (1994) suggested that the outlet was closer to Weiser, Idaho, rather than at The Oxbow.

Smith et al. (2000) studied Pliocene fish fossils in the Pasco Basin of Washington which provided evidence concerning timing of the Glenns Ferry Lake-Snake River-Columbia drainage basin connection. The large salmon, *Oncorhynchus rastrosus*, was in the Late Miocene or early Pliocene Ringold Formation, but lack of salmon or other cool-water fishes in other Ringold sediments, despite samples of thousands of fossil fish bones, indicates that the eastern Pasco Basin was isolated from the Pacific coastal streams in the middle and late Pliocene. It is possible that the cutoff resulted from contemporaneous folding of the Yakima fold belt (Mark Ferns, 2019, written communication). Temperature differences were also a factor. The known Pliocene fish fauna of the Pasco and Quincy Basins is represented by 11 species, mostly in the 4.5–4.3 Ma White Bluffs, ~3.6 Ma Blufftop, and 3.3 Ma Taunton local faunas. Six of the eight widespread White Bluffs and Blufftop fish genera (*Ameiurus, Chasmistes, Catostomus, Mylocheilus, Ptychocheilus,* and *Archoplites*) were also present in the contemporaneous Glenns Ferry Fauna of the WSRP. The Taunton local fauna consisted of 11 genera, nine of which were shared with contemporaneous fauna of the Snake River Plain. *Ameiurus, Chasmistes, Catostomus* cf. *macrocheilus, Ptychocheilus, Mylocheilus*, *Acrocheilus, Lavinia, Klamathella*, and *Archoplites*. The addition of three Glenns Ferry minnows (*Acrocheilus, Lavinia*, and *Klamathella*) to the 3.3 Ma. Taunton fauna and the later reverse dispersal of *Catostomus* cf. *macrocheilus* to the Snake River Plain from the Pasco Basin indicate late Pliocene time for the connection of the Pasco Basin to the Snake River Plain and the Glenns Ferry lake (Table 1).

This extensive overlap of species illustrates three useful points for this investigation: (1) Species occur in common when drainage elevation and size permit aquatic connections that facilitate dispersal, for example, the three largest species in the Ringold environments, the sturgeon, salmon, and

Muskellunge did not colonize the Glenns Ferry lake through Hells Canyon. (2) Temperature differences limit the numbers of species shared. Pliocene Ringold faunas were mostly warm-water sunfish, catfish, Muskellunge, suckers, and minnows (Table 1), but many cold-water species from the WSRP were excluded from the Pasco Basin by its warm temperature, and (3) three species of Ringold fishes, *Mylocheilus heterodon* (chub with molar teeth), *Ameiurus reticulatus* (catfish), and *Archoplites molarus* (sunfish with molar teeth), are divergent relatives of forms on the Snake River Plain, *Mylocheilus robustus*, *Ameiurus vespertinus*, and *Archoplites taylori*. Relatives of these three WSRP species in the late Miocene Ellensburg Formation of Washington (10.2 Ma) emphasize the isolation of the Ringold and Always Welcome Inn paleofaunas. *Archoplites* in the Always Welcome Inn and Ringold faunas are differentiated from each other and widespread sunfishes. Morphological differentiation of Always Welcome Inn sunfish from Snake River Plain and Ellensburg sunfish suggests a period of allopatry of perhaps a million years of evolution prior to the Always Welcome Inn fauna. Within the Ringold sequence, *Archoplites* and *Mylocheilus* show small morphological changes over 1–1.6 million years (Smith et al., 2000), while the WSRP *Mylocheilus* was actively evolving molar teeth in a unique direction at this time (Smith et al., 1982).

The contemporaneous Always Welcome Inn fauna also included cool-water char, mountain suckers, dace, and sculpin in addition to warm-water suckers, minnows, and sunfish. This suggests that dispersal of cool-water species between the Glenns Ferry lake and other regions could have reached the Blue Mountains and Baker Valley, but did not extend into Pasco Basin habitats of the Columbia River drainage (Smith et al., 2000), apparently because of warm temperature there, even when aquatic connections were available.

This paper presents new information about the fossil fishes from the Lower Powder (Keating), Baker (Always Welcome Inn), and Grande Ronde Valley (Imbler) areas of northeast Oregon. The Keating, Imbler, and Always Welcome Inn faunas are important sites that link the WSRP to the interior Columbia River Basin. They lie in a tectonically active region with volcanic activity that periodically disrupted drainage, forcing new connections between hydrologic basins that allowed faunal interchange. The purpose of the paper is to compare this information with what has been proposed previously and explore implications regarding drainage connections among rivers of eastern Oregon, the Western Snake River Plain, and the Columbia drainage during the late Miocene and Pliocene. Although much of the data for this work come from lake deposits, most fish species live primarily in streams. Most of the connections we infer were fluvial, especially occurring as headwater captures, which are hypothesized when evidence indicates that elevation and slope limited the number of species that dispersed, compared to diversity expected to swim through a through-flowing river.

METHODS

Fossils were collected from the vertical exposure behind the Always Welcome Inn by surface picking or dry screening. Field notes recorded the strata and location of recovered fossils. Bones were identified by comparison with collections from surrounding sites, including the Ringold and Ellensburg Formations, Washington; the Drewsey, Juntura, Sucker Creek, Danforth formations, Oregon; and Chalk Hills and Glenns Ferry formations, Idaho and Oregon. Skeletons of modern fishes in the University of Michigan Museum of Zoology were also compared.

Our goal is to use freshwater fish distributions to test geologic hypotheses about time and place of drainage connections between the Oregon-Idaho Graben, Malheur River Basin, Chalk Hills and Glenns Ferry Lakes, and the Columbia River drainage during the late Miocene and Pliocene. This requires having fossil fish faunas, including some that span several million years, in a group of nearby drainages for which connections have been hypothesized. Because we are interested in time and rates of evolution we include radiogenic dates from local volcanic marker beds and biostratigraphic (mammal, diatom) ages.

We assume:

1) Primary freshwater fishes disperse through their habitats, not overland or by sea.
2) Fish are rarely if ever, dispersed as eggs sticking to bird's feet, or by storms.
3) Fish are most commonly transferred to different drainage systems by stream capture or lake spillover.
4) Fish size is correlated with habitat size; small headwater fish are more readily transferred across high elevations, where large fish are blocked by inadequate water volume.
5) Adult fish have small home ranges except when migrating to spawn; young fish disperse away from high density and predation and are more likely to colonize new areas.
6) Fishes disperse upstream or downstream in about equal frequency, depending on fish size, habitat preference, current velocity, or falls. Therefore, the direction of flow is not evidence for the direction of dispersal.
7) Local extirpation and population fluctuations are common; absence from a collection is weak evidence of absence from a fauna, depending on total sample sizes.
8) Age of a fossil cannot pinpoint the time of species arrival in its drainage basin unless there is strong evidence for its absence in older similar sediments.

LATE MIOCENE (8.6 MA) KEATING FISH FOSSILS
Figure 5

A small number of late Miocene fish fossils was found northeast of the town of Keating in the Keating (Lower Powder) Valley of northeast Oregon (Figs. 1a, b). These fossils (Table 2) came from a diatomite in a sequence of fluvial and lacustrine sediments (Fig. 4) that is located on top of olivine basalt flows that form the basal unit of the Powder River Volcanic Group (Bailey, 1990; Ledgerwood and Van Tassell, 2006; Van Tassell and Ledgerwood, 2009; Ferns and McClaughry, 2013). The fluvial and lacustrine sediments are separated from the overlying layer of late Pliocene-Early Pleistocene gravels by a prominent angular unconformity (Gilluly, 1937; Brooks et al., 1976; Dittrick et al., 2012).

Ash immediately below the diatomite was dated at 8.57 ± 0.07 Ma using ^{40}Ar/^{39}Ar step heat analysis (Ledgerwood and Van Tassell, 2006). This is within the range of the Poison Creek Formation and slightly older than the Chalk Hills lake (about 8.1 Ma) in the Western Snake River Plain. This same ash is found in the Teewinot Formation, Wyoming, just above a basaltic tuff dated at 9.5 Ma (Nate Carpenter, written communication, 2018). The chemical composition of the ash suggests that it came from the Twin Falls volcanic center in Idaho (Nash and Perkins, 2012).

The Keating fishes include a minnow, a probable sculpin (*Cottus*), and an unidentified pelvic girdle (Fig. 5). The part and counterpart of the minnow fossil (Figs. 5a, b) are preserved in diatomite. It has a standard length of about 73 mm and a cyprinid-shaped dentary with no sensory pores. There are approximately 32 vertebrae; 8 or 9 dorsal-fin rays; 8 or 9 pelvic-fin rays, and approximately 9 anal-fin rays. The anal fin is forward and the dorsal fin is slightly behind the pelvic fin. The pectoral fin is ventral, in the cyprinid position, and the opercle shape is like that in other cyprinids. There are no visible teeth, but one possible pharyngeal tooth mold is present. Preservation shows no clear Weberian apparatus and no scales. The broken and compressed thoracic region suggests that the carcass floated in warm water before burial. There is no doubt that it is a minnow (Cyprinidae). The clear surface of the dentary, with no sensory pores, fits the genera *Oregonichthys* and *Rhinichthys*, cool creek inhabitants that could have been washed into a warm lake, but the body shape is not like *Rhinichthys* and the body size is larger than modern *Oregonichthys*. The sculpin is diagnosed by its elongate vertebrae, slender body, and caudal peduncle. The unidentified pelvic girdle is similar to pelvic girdles of Catostomidae, but diagnostic processes are not preserved.

The diatomite from which Keating fish fossils were collected also contains leaves, fruits, nuts, and seeds of maple,

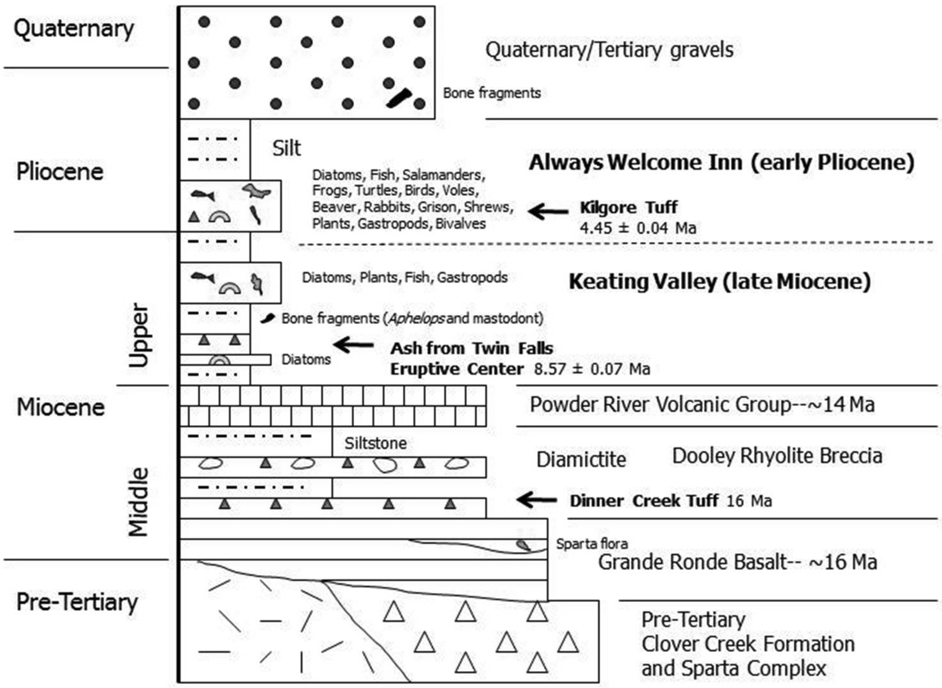

Figure 4.—Geologic units in the Powder Valley area, based on Gilluly (1937); Brooks et al. (1976); Whitson (1988); Bailey (1990); Ledgerwood and Van Tassell (2006); Van Tassell and Ledgerwood (2009); Streck et al. (2011); Nash and Perkins (2012); and Ferns and McClaughry (2013).

Table 2.—Fish fossils from the Keating, Always Welcome, and Imbler paleofaunas.

Family	Scientific Name	Common Name
Keating Local Fauna (Late Miocene, ~8.6 Ma)		
Cyprinidae, minnows	unidentified minnow	—
Catostomidae?, suckers	possible sucker pelvic pterygiophore	—
Cottidae sculpins	*Cottus* sp.	Sculpin
Always Welcome Inn Local Fauna		
Cyprinidae, minnows	*Acrocheilus*	Chiselmouth Chub
	Mystocheilus	Chub
	Ptychocheilus	Pikeminnow
	Rhinichthys	Dace
Catostomidae, Suckers	*Pantosteus*	Mountain Sucker
	Catostomus cf *macrocheilus*	Largescale Sucker
Salmonidae, Salmoninae	*Salvelinus* cf. *confluentus*	Char
Centrarchidae, Sunfish	*Archoplites langrellorum n.* sp.	AWI Sunfish
	Archoplites sp.?	
Cottidae	*Cottus* spp.	Sculpins
Fossil fishes of the Imbler Local Fauna (Middle Pliocene, 3.8-3.7 Ma)		
Ictaluridae	*Ameiurus reticulatus*	Bullhead Catfish
Cyprinidae	*Ptychocheilus* sp.	Pikeminnow
Salmonidae (Coregoninae)	*Prosopium* sp.	Mountain Whitefish

hornbeam, hickory, sweet gum, magnolia, tupelo gum, oak, redwood, swamp cypress, and water chestnut (Gilluly, 1937; Chaney, 1959; Hoxie, 1965).

The Keating diatomite contains three diatoms that were considered potentially diagnostic of the Neogene by Bradbury and Krebs (1982) and/or VanLandingham (1985): *Coscinodiscus miocaenicus, Gomphonema cholnockyites,* and *Opephora glangeaudi*. Other Neogene diagnostic diatoms in the Keating sequence include *Tetracyclus ellipticus* (Moore, 1937) and *Fragillariopsis*, which was listed by D.M. Williams in the Paleobiology Database as present in the Keating Valley diatomite. These diatoms may be the same or very closely related to the diatoms *Tetracyclus ellipticus* var. *latissimus f. minor* and *Fragillariopsis* sp. 1 noted as Neogene diagnostic diatoms by VanLandingham (1985). Four of these diatoms (*G. cholnockyites, O. glangeaudi, T. ellipticus,* and *Fragillariopsis*) are found only in the Miocene.

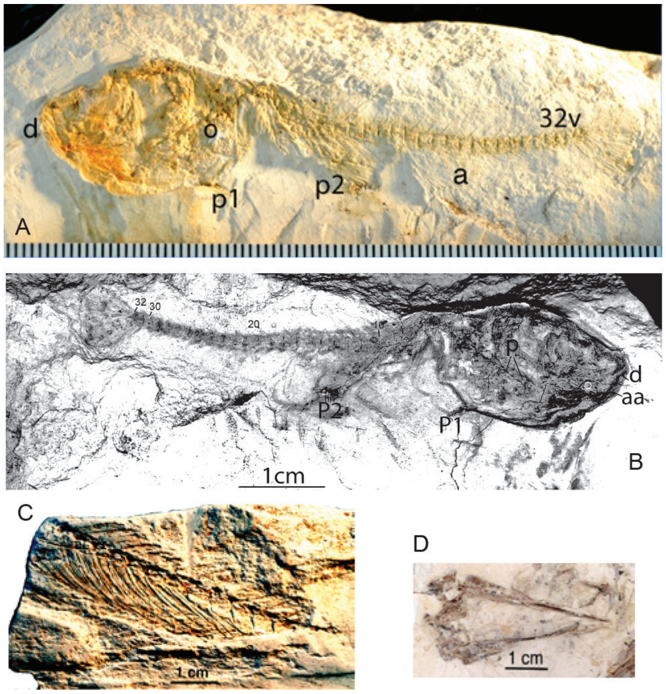

Figure 5.—Late Miocene (~8.6 Ma) Keating fossil fishes. A, B, Keating cyprinid (Hoxie Collection K-4) genus indet., possibly *Oregonichthys*. aa, articular-angular; d, dentary; o, opercle; p, preopercle; p1, pectoral fin; p2, pelvic fin numerals; v, number of post-Weberian vertebrae. C, Keating sculpin mid-body (Hoxie Collection K-71), identified by slender body, elongate vertebrae, short neural and hemal spines. D, Unidentified Keating pelvic girdle (Hoxie Collection K-2); critical processes broken off. (Hoxie Collection K-2).

All five of the Neogene diagnostic diatoms found in the Keating diatomite are present in the 11.5 Ma Truckee Formation diatomite districts located ~75 km east of Reno, Nevada (VanLandingham (1985). Four out of five of these diatoms are present in the 11.3 Ma Mann Creek diatomite, which is ~10 km north-northeast of Weiser, Idaho, and ~50 km southeast of Keating, Oregon. Four out of five of these diatoms occur in the 15.9 Ma Squaw Creek Diatomite member of the Yakima Basalt of Washington (Table 3). In contrast, only two of these Neogene diagnostic diatoms are present in the 11.5 Ma Juntura and Harper diatomites in the Drewsey- Juntura Graben of Oregon. Only one of these diatoms has been found in the 11.5–8.9 Ma Poison Creek Formation and none are present in the 8.2–6.4 Ma Chalk Hills and 4.5–1.7 Ma Glenns Ferry Formations of Idaho. This evidence suggests a relationship between the 8.7–8.6 Ma Keating diatomites and (1) the 11.3 Ma Mann Creek diatomites near Weiser, Idaho, (2) the 11.5 Ma Truckee Formation diatomites, Hazen, Nevada, and (3) the 15.9 Ma Squaw Creek diatomite member of the Yakima Basalt of Washington, but not with the Poison Creek, Chalk Hills, or Glenns Ferry lakes.

Table 3.—Neogene diagnostic Diatoms.

	KEATING					IMBLER	
	Coscinodiscus miocaenicus	*Fragillariopsis*	*Tetracyclus ellipticus*	*Gomphonema cholnockyites*	*Opephora glangeaudi*	*Tetracyclus stellare* v. *eximia*	*Stephanodiscus* sp.
Imbler, OR 3.8–3.7 Ma						X	X
Glenns Ferry, ID. 4.5–1.7							X
Keating, OR 8.7–8.6	X	?	?	X	X		
Manning Cr., Durkee, OR			X				
Brady Hot Springs, NV 9.5	X				X		
Mann Creek, Weiser, ID 11.3	X	X	X		X	X	
"Lower Banbury Basalt", ID				X	X		
Poison Creek, ID 11.5–8.9	X						
Juntura-Harper, OR (DJG) 11.5	X			X			
Truckee, NV 11.5	X	X	X	X	X		
Esmeralda Co., NV 15.1			X				
Sucker Creek, OR 15.9–13.6	X						
Yakima Basalt/ Squaw Cr., WA 15.9	X	X	X	X			

Notes:
1. *Fragillariopsis* sp. 1 marked by "X". *Fragillariopsis* marked by "?".
2. *Tetracyclus ellipticus* var. *latissiumus* f. *minor* indicated by "X". *Tetracyclus ellipticus* indicated by"?".

EARLY PLIOCENE (4.5 MA) ALWAYS WELCOME INN FISH FOSSILS

Discovery and Sampling

Early Pliocene (Blancan) fossil sunfish and minnow bones, charophytes, and ostracodes were discovered in the ~10 m-thick vertical section behind the Always Welcome Inn in Baker City, Oregon (44°47.106'N latitude, 117°48.300'W longitude at ~1050 m [3,440 ft] elevation) in May 2002. A wide diversity of fossils was collected from the Always Welcome Inn site by the faculty and students of Eastern Oregon University, with help from the faculty and students of Pine-Eagle High School in Halfway, Oregon, and other groups between 2002 and 2015 (Table 2). At the beginning of the study, only the fossils exposed on the surface of the outcrop were collected. In 2004, the Always Welcome Inn section was measured with Jacob staff and in 2006 collection of bulk samples began at 0.25 m intervals in the sequence, dry-sieving the sediment at the outcrop through screens with a square mesh measuring 1.5 mm on each side. To obtain a semi-quantitative measure of the number of fossils in each layer, ~0.1-m^3 from each unit was sieved and the fossils in each sample were identified and counted (Van Tassell et al., 2007). In order to assess the lateral variations in fossil content within a single bed, Stubblefield (2012) divided a sunfish fossil-rich unit (2.5–2.75 m) along its length into 1-m-long units, collected samples with a volume of ~0.025-m^3 from each unit, sieved the samples, and identified and counted the fossils in each sample.

Stratigraphy and Age

The stratigraphy at the Always Welcome Inn site was described by Van Tassell et al. (2007). The lower 5 m of the exposure consists of a coarsening-upward sequence of pale yellow, light gray, and light brown diatomites and silts, plus two lignite layers (Fig. 6). The fish bones, diatoms, sponge spicules, ostracodes, gastropods, bivalves, turtle, and beaver (Castor) found in the lower half of the sequence indicate the presence of shallow lake and lake margin environments, with charophytes and other vegetation growing in and around the margins of the water. The upper half of the sequence is characterized by river floodplain and channel sediments that consist of light yellow, light gray, and light brown massive and laminated silts and fining-upward cycles of trough cross-bedded silty fine sand and light yellow, light brown, and light gray massive and laminated silts. These contain fossils of fish, salamanders, turtles, snakes, shorebirds and raptors, and a variety of mammals, including shrews, voles, rabbits, gopher, beaver (*Dipoides*), and a grison. A rib of a mammal about the size of an antelope was found in 2010 in the upper part of the Always Welcome Inn sequence by a high school student from Halfway, Oregon.

Van Tassell et al. (2007) suggested that the age of the Always Welcome Inn sequence was ~4.8–3.7 Ma based on fossils of the microtine (*Ophiomys mcknighti*) in the sequence. Bork et al. (2009) narrowed this age range to ~4.8–4.4 Ma based on further studies of the voles and the beaver (*Dipoides*). The chemical composition of the glass from a pale gray friable ash, 6.6 m above the base of the Always Welcome Inn section, indicates that it is the Kilgore Tuff, which was erupted at 4.45 ± 0.04 Ma from the Heise volcanic center in the eastern Snake River Plain (Nash and Perkins, 2012). This confirms a late Pliocene (Blancan) age for the Always Welcome Inn fossils and places them near the beginning of the Glenns Ferry lake deposition on the central Snake River Plain at about 4.3 Ma.

A new species of sunfish and a new genus and species of minnow were discovered at the site. Van Tassell et al. (2007) added *Acrocheilus* (Cyprinidae), to the list of Always Welcome Inn fish fossils. Since 2007, several new species of fish fossils have been found at the Always Welcome Inn site. These include suckers (*Pantosteus* sp*.*, *Catostomus* cf. *macrocheilus*), a salmonine (*Salvelinus* cf. *confluentus*), a pikeminnow (*Ptychocheilus*), three sculpin preopercles (*Cottus*), and

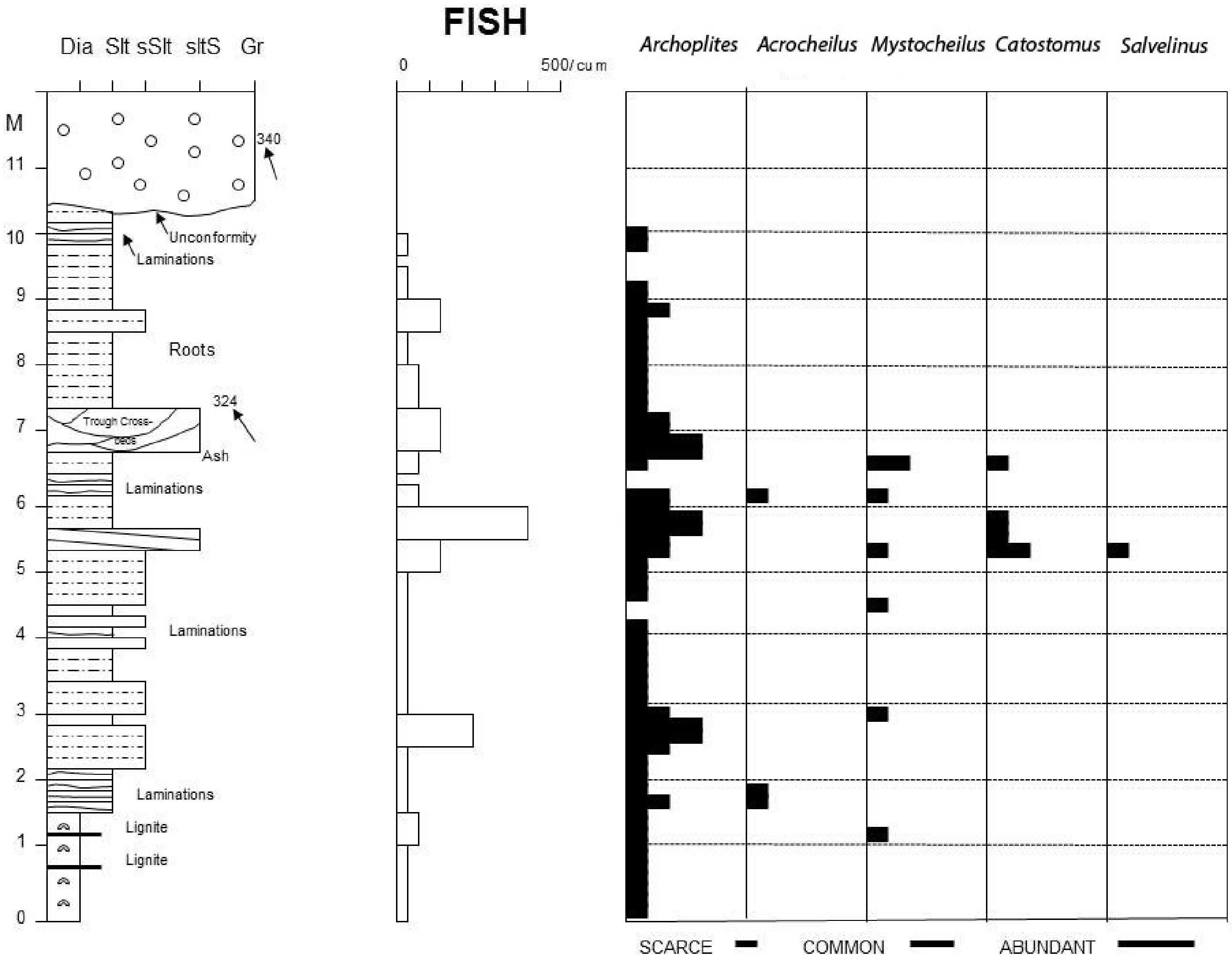

Figure 6.—The Always Welcome Inn sedimentary sequence (modified from Van Tassell et al., 2007), showing the distribution of diatomite (Dia); silt (Slt); sandy silt (sSlt); silty sand (sltS); gravel (Gr); and fish fossils in the sequence. Small numerals 340, 324 are current directions, adjusting for tilting.

a possible second species of sunfish (Centrarchidae). No catfishes (Ictaluridae) have been found (Table 2).

Teleostei
Catostomidae, suckers
Pantosteus sp. Mountain Sucker
Figure 7a

Maxillae of *Pantosteus* (Fig. 7a; UMMP 42395) were among the sucker maxillae collected from the fluvial strata at the Always Welcome Inn site. They are diagnosed by the larger relative depth of the maxilla and size and shape of the anteroventral keel of the bone, compared to slender *Catostomus*. In addition, the external ridge for insertion of the dorsal maxillary muscle on the lateral face of the anteroventral keel is more prominent than in most *Catostomus* (Smith, 1975, fig. 12). The maxilla of *Catostomus* is longer and slenderer (Fig. 7b, UMMP 42394). Fossil *Pantosteus* are known from the Juntura, Ellensburg, and Glenns Ferry formations (Table 1), as well as the Great Basin of Nevada and Pleistocene of southern Colorado and northwest Kansas (Smith et al., 2013). Modern forms live throughout the west from Canada to Mexico and from California to South Dakota. They live in moderate gradient streams over gravel substrate.

Catostomidae
Catostomus cf. *macrocheilus* and *Catostomus* sp., Suckers
Figure 7b-h

Suckers (*Catostomus* cf. *macrocheilus* and *Catostomus* sp.) have been found only in the fluvial portion of the Always Welcome Inn sequence (Fig. 6). The sucker bones include maxillae, Fig. 7a-d, e, Weberian apparatus, quadrates Fig. 7h,

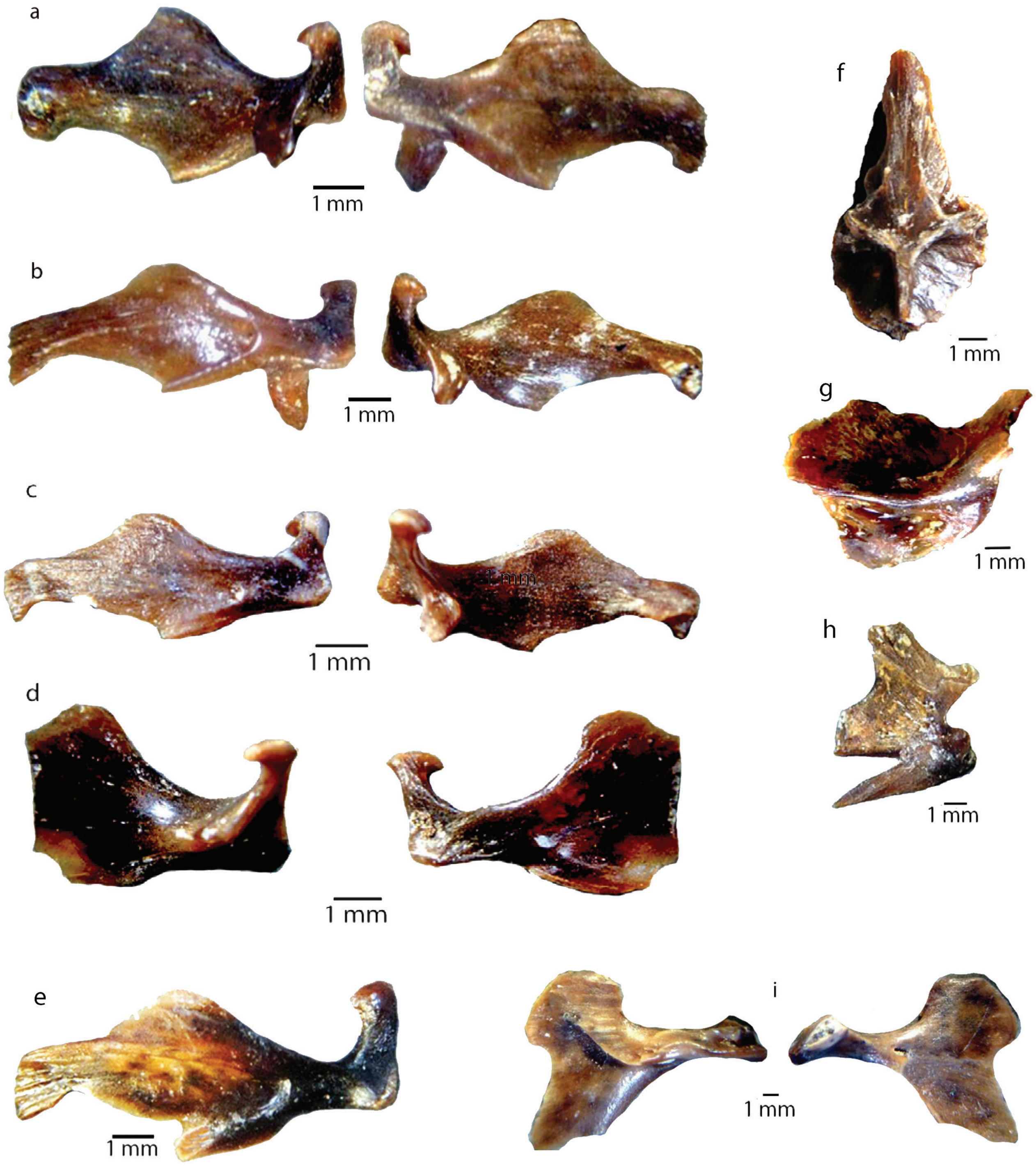

Figure 7.—a, Mountain Sucker (*Pantosteus* sp.) left maxilla (UMMP 42395) from Always Welcome Inn paleofauna. Mesial (on left) and lateral (on right) views of the same bone; b, c, e-i Sucker (*Catostomus* cf. *macrocheilus*) right maxillae from the Always Welcome Inn paleosite (EO-1058; UMMP 42394); b, lateral (L) and mesial (R) views of same maxilla; c, lateral (L) and mesial (R) views of same maxilla; d, mesial (L) and lateral (R) views of *Catostomus* sp., fragment of maxilla; e, lateral view of right maxilla; f, parasphenoid fragment; g, cleithrum fragment; h, nearly complete quadrate (UMMP 42394); i, lateral (L) and mesial (R) view of a right dentary.

pelvic pterygiophores, hyomandibula, and a dentary (Fig. 7i; UMMP 42394). Maxillae of juvenile suckers are also present. Suckers are most common at the base of the fluvial section (5.25–5.5 m) and in the overlying layers (5.5–6 m), but also occur at the base of the overlying channel sequence (6.75–7 m, Fig. 6). Two species might be present; compare Fig. 7e with Fig. 7a-d. Differences might be ontogenetic. Catostomid fragmentary parasphenoid and cleithrum (Fig. 7f, g) are present. Diverse assemblages of *Catostomus* cf. *macrocheilus* are present in the 3.6 Ma Blufftop and 3.3 Ma Taunton local faunas of the Ringold Formation of Washington. *Catostomus* cf. *macrocheilus* first occurs on the WSRP in the late Pliocene after deposition of the Blufftop local fauna of Washington (Smith et al., 2000).

Cyprinidae, minnows
Mystocheilus fresti **Van Tassell and Smith, new genus and species**
Figures 8, 9

Holotype.— A right maxilla (UMMP 42400), approximately 8.6 mm long, in two pieces, broken at the slender neck. The anterodorsal condyle is clearly divided into two distinct condyles (Fig. 8f).

Type locality.— Collected by Terry Frest, Jay Van Tassell, and students from the ~10 m–thick vertical section behind the Always Welcome Inn in Baker City, Oregon (44°47.106’N latitude, 117°48.300’W longitude at ~1050 m [3,440 ft], elevation) in May 2002, and subsequently. found in both the lacustrine and fluvial portions of the Always Welcome Inn sequence in the 1–1.25 m, 2.75–3 m, 4.25–4.75m, 5.25–5.5 m, 6–6.25 m, and 6.5–6.75 m intervals (Fig. 6). It is most abundant in the 6.5–6.75 m layer.

Diagnosis.— The maxilla (Fig. 8f; UMMP 42400) has the antero-dorsal condyle divided into two (Fig. 8f), with the premaxillary arm extending downward and forward below and behind the posterior condyle; the body of the maxilla is slender. The dentaries have an outwardly flared (non-vertical) outer edge of the front and sides of the jaw (Figs. 8a, b, c, e; UMMP 42396), with the mental foramen halfway along its length. The opercles (Fig. 8h; UMMP 42398) and pterotic are more robust than other North American minnows and are highly textured externally with ridges and grooves. The pharyngeal teeth (Figs. 9a, b, g; UMMP 42402) are short, slightly compressed in cross-section, and with robust hooks offset slightly ventrally from the dorsal edge adjacent to the hook. These traits readily separate *Mystocheilus* from all other western North American genera.

Description.— The short, wide-flared dentary traits (Figs. 8a-c, e) are shared by members of the clade containing *Pogonichthys, Mylocheilus,* and *Richardsonius* (Smith et al., 2002). The traits of the maxilla (Fig. 8f) are shared with *Pogonichthys* and *Ptychocheilus*. The hyomandibula has a long concave arch between the opercular condyle and the sphenotic condyle. The palatine (Fig. 8g; UMMP 42397) is elongate and lacks a longitudinal ridge. The angulo-articular has a short concave arch between the articulation and the coronoid; and a straight, posteriorly-directed posterior process. A similar form is found in the Drewsey Formation in the Drewsey-Juntura Graben, Malheur County Oregon. It is not likely that this genus is related to the late Miocene minnow found in the Keating area because of the different opercles and mouth bones.

Paratypes.— Fig. 8e, right dentary; g, palatine; h, left opercle; i, left angulo-articular; j, pterotic; k, partial preopercle (UMMP 42396).

Age.— The locality and specimens at the Always Welcome Inn site are early Pliocene, Blancan (North American Land Mammal Age), dated by tephra and biostratigraphy at 4.5–4.4 Ma.

Etymology.— The genus name, *Mystocheilus* refers to the partially spoon-like (Gr. *Mystos*) dentary of the lower jaw (Gr. *Cheilus*).

The species is named for Dr. Terry Frest (1950–2008), Western American malacologist and paleontologist associated with the Burke Museum of the University of Washington.

Additional material examined.— A hymandibula (Fig. 8d), palatine (Fig. 8g), opercle (Fig. 8h), angulo-articular (Fig. 8 i), pterotic (Fig. 8 j), and a fragment of a preopercle (Fig. 8k) with reduced sensory pores. Numerous provisionally identified isolated teeth (Figs. 9a, b, c?, g, unattached tooth cap, h, unidentified juvenile; UMMP 42402). A small cluster of many associated unidentified fragments were collected together at the time of discovery by Terry Frest.

Cyprinidae, minnows
Ptychocheilus **sp.**
Figure 9e, f

One tooth of a large pikeminnow, *Ptychocheilus*. was found in the 6.5–6.75 m interval and another on the surface at the Always Welcome Inn (Figs. 9e, f; UMMP 42407). *Ptychocheilus* appeared in the Columbia Basin at just after 16 Ma and is known throughout the late Miocene of Washington, Idaho, and Oregon (Smith, 1975; Kimmel, 1975; Smith et al., 2000; Smith et al., 2002). It is diagnosed by the large and elongate canine pharyngeal teeth, round in cross-section and with reduced terminal hooks. In the Ringold Formation of Washington, *Ptychocheilus* fossils are not known from the 4.5–4.3 Ma White Bluffs local fauna, are rare in the 3.6 Ma Blufftop local fauna, and uncommon in the 3.3 Ma Taunton local fauna. *Ptychocheilus* fossils were also in the ~3.8–3.7 Ma Imbler paleofauna of the Grande Ronde Valley of Oregon.

Cyprinidae, minnows
Rhinichthys **sp.**
Figure 10a-f

Rhinichthys (Dace) is a polytypic genus with four modern species in the western United States (Smith et al., 2017).

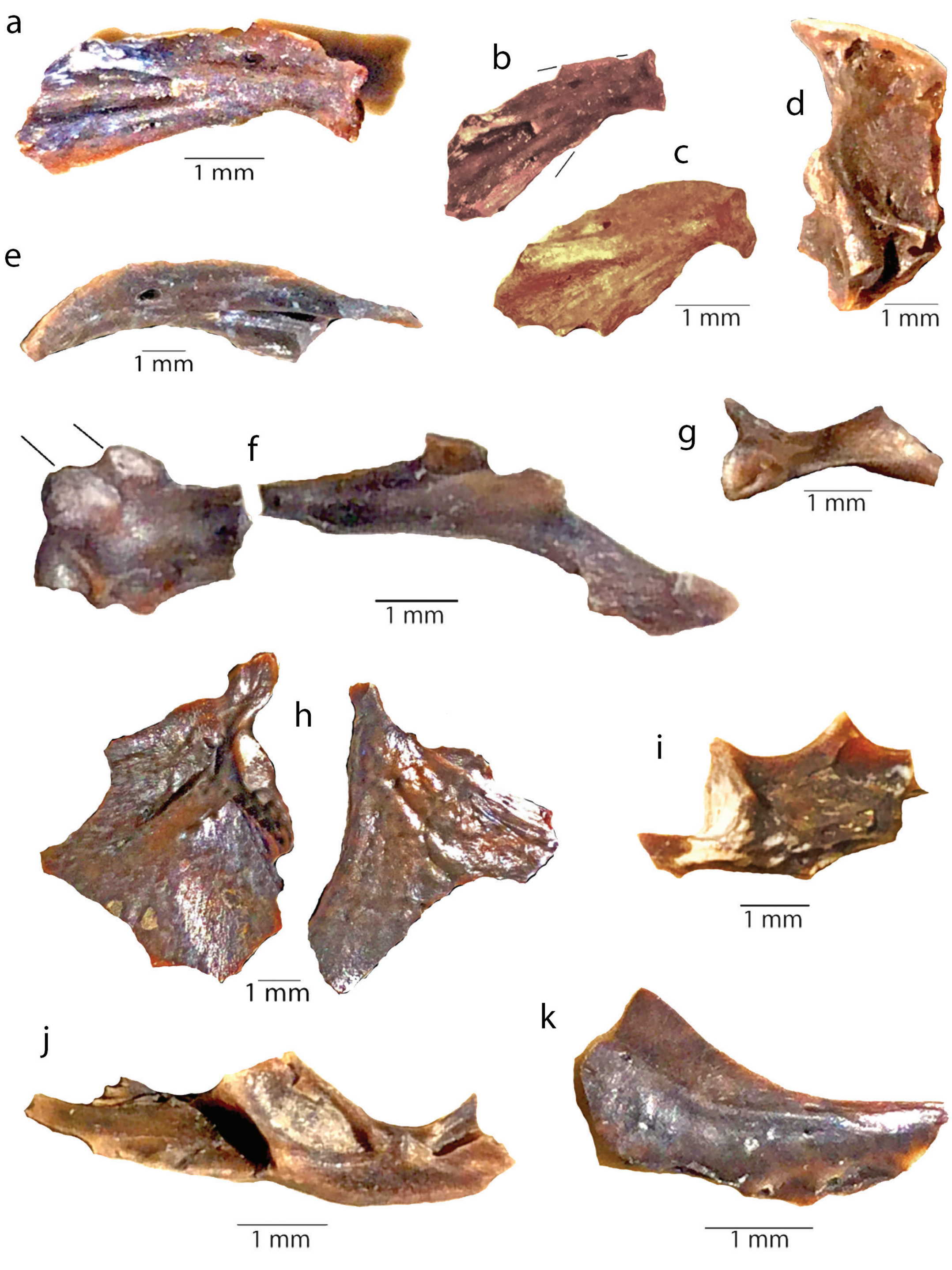

Figure 8.—Head bones of *Mystocheilus* fresti. a, b, c, left dentaries; d, left hyomandibula; e, right dentary; f, right maxilla, (Holotype, UMMP 42400), lines point to double anterodorsal condyles; g, right palatine; h, left opercles (UMMP 42398); i, left articulo-angular; j, left pterotic; k, right preopercle (UMMP 42400).

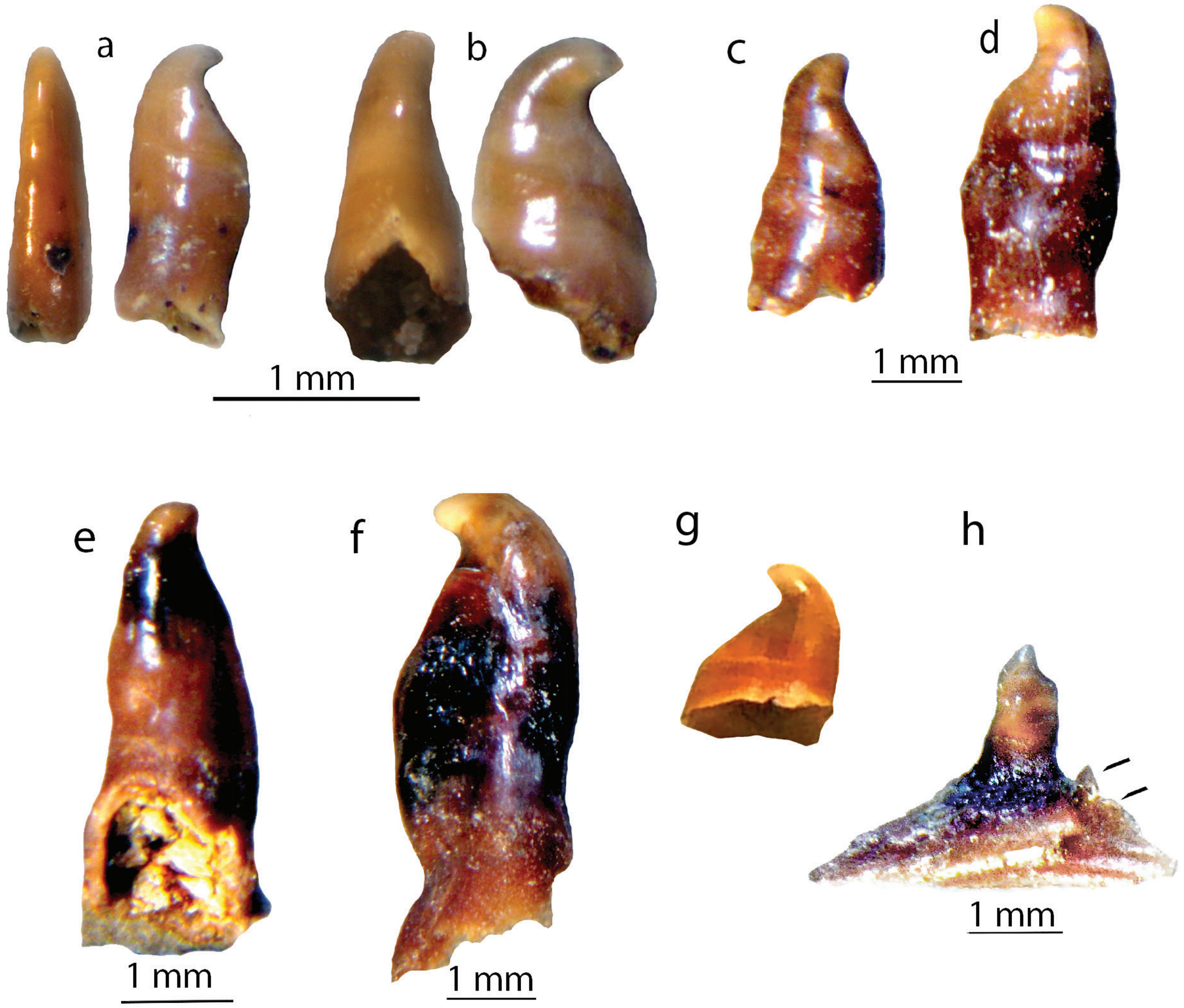

Figure 9.—*Ptychocheilus, Mystocheilus*, and unidentified cyprinid pharyngeal teeth. a, b, g, *Mystocheilus* teeth (UMMP 42402), ventral and lateral profiles of *Mystocheilus* pharyngeal teeth, short, laterally compressed, and with enlarged terminal hooks; c, d, (UMMP 42407); two unidentified teeth *Klamathella?* or *Gila*? elongate, somewhat flattened, with a slight grinding surface, and moderate terminal hook (UMMP 42407, part); e, f, *Ptychocheilus* teeth, elongate, round in cross-section, and with reduced terminal hook; h, unidentified juvenile with two broken teeth in the minor row.

All four species are known from the Columbia-Snake River drainage in northeastern Oregon and southwest Idaho (Smith et al., 2017), two are centered in this region. *Rhinichthys* is represented in the Always Welcome Inn paleofauna by few isolated teeth, which are diagnosed by the presence of a sharp cutting edge on the dorsal side of teeth 2–4, near the reduced terminal hook (UMMP 42406). The pharyngeal tooth formula is usually 4,1–1,4, but no complete arches are known from the Always Welcome Inn paleofauna. *Rhinichthys* sp. fossils are known from the Juntura Formation and the Granger Clay Pit of the Ellensburg Formation, dating back to about 10.2 Ma. in the same system of basins as other members of the Always Welcome Inn paleofauna. They are small, fusiform benthic minnows with small subterminal mouths, preferring moderate current and rubble or gravel bottom. Modern forms of *Rhinichthys osculus* are distributed in all major Western U. S. drainages, from southwestern Canada to southern Arizona and from Colorado to California, and in most individual basins of the Great Basin. Other species of the genus are in Mississippi and Great Lakes drainages and Atlantic coastal streams. Fossils are rare because of their small size and preference for aggradational stream habitats.

Cyprinidae, minnows
Acrocheilus sp.
Figure 10g, h

Teeth of the minnow, *Acrocheilus*, have been found in the 1.75–2 m interval in the lacustrine section and in the 6–6.25 m layer in the fluvial portion of the sequence (UMMP

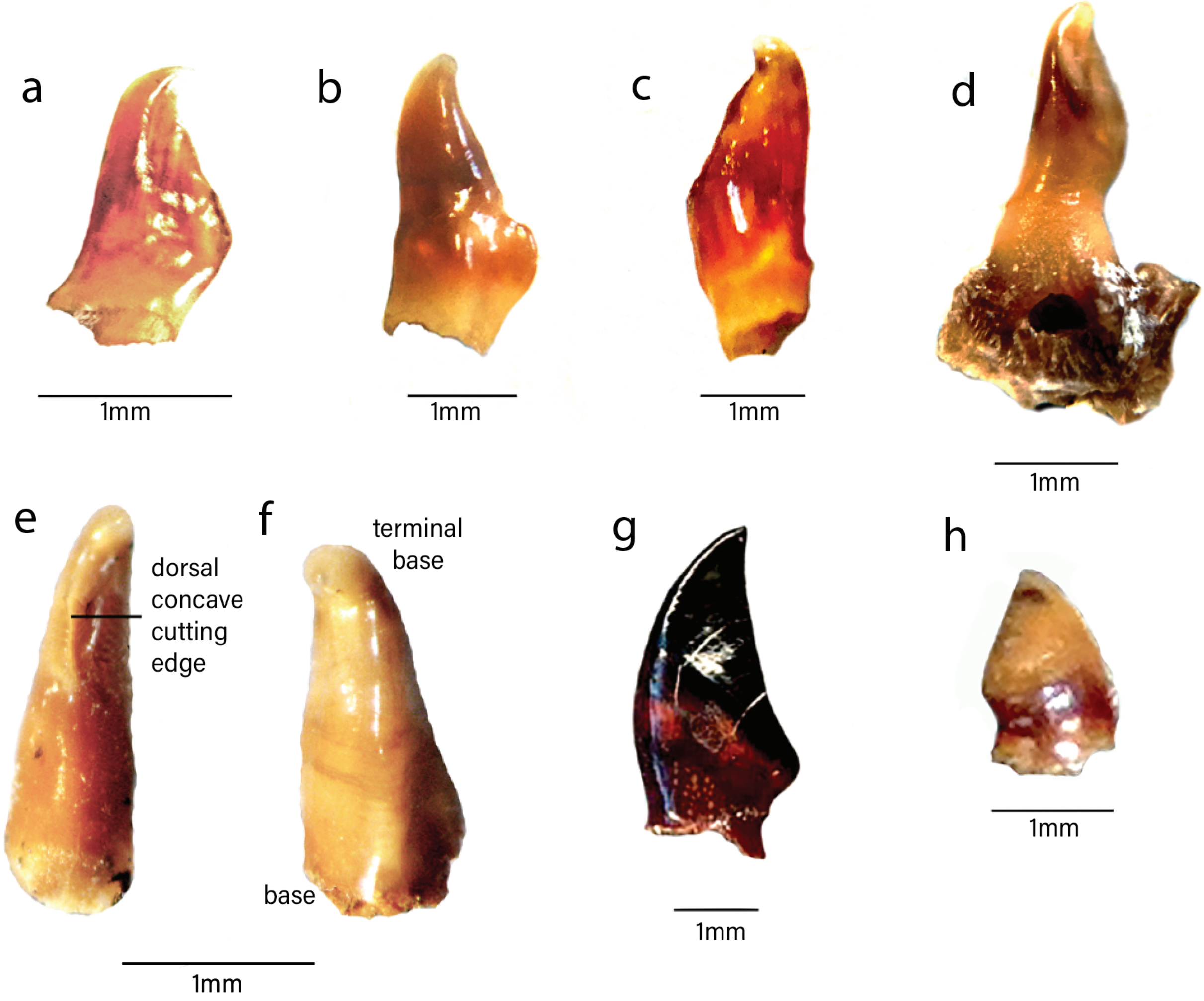

Figure 10.—*Rhinichthys*, *Acrocheilus*, and unidentified teeth. a-f, *Rhinichthys* sp. pharyngeal teeth (UMMP 42406) showing cutting edge adjacent to moderately hooked tip; g, adult *Acrocheilus* sp. tooth (UMMP 42408) showing concave grinding surface and pointed tip; h, juvenile *Acrocheilus* tooth. (UMMP 42408, part).

42408). These teeth resemble those of the Chiselmouth Chub, *Acrocheilus latus* (Cope), of the Miocene and Pliocene, as well as modern *A. alutaceus* of the Snake and Columbia rivers and northward. The teeth are diagnosed by their sharp, concave, dorsal cutting surfaces and the sharp terminal point. *Acrocheilus* was a member of the upper Snake River fauna, Miocene to modern (Smith et al., 1982), but did not appear in the Columbia River drainage until after initiation of erosion of Hells Canyon, marked by its appearance in the 3.3 Ma Taunton local fauna of the Ringold Formation of Washington (Smith et al., 2000).

Salmonidae
Salmoninae: Salmon, Trout, Chars
Salvelinus cf. *confluentus*, Char
Figure 11

Two vertebrae of a salmonid, similar to the Bull Trout *Salvelinus confluentus*, have been found in the 5.25–5.5m interval at the Always Welcome Inn (Fig. 11; UMMP 42409). The growth rings on one of the vertebrae suggest that the fish was about 6 years old. It is identified as a char by the coarse parallel ridges on the vertebrae. They are among the few local genera with recognizable vertebrae. Chars are large, cool-water, predatory, trout-like species distributed widely across northern North America and Eurasia. They are known from Middle Miocene deposits in Nevada, Oregon, and northern Idaho, the Chalk Hills Formation of Idaho and Oregon, and Pleistocene Lake Bonneville, Utah (Stearley and Smith, 2016).

The occurrence of this Northwest predator in the AWI beds and Chalk Hills Formation, but not the Glenns Ferry or Ringold formations, is a significant ecological and biogeographic indicator of isolation by basalt and temperature.

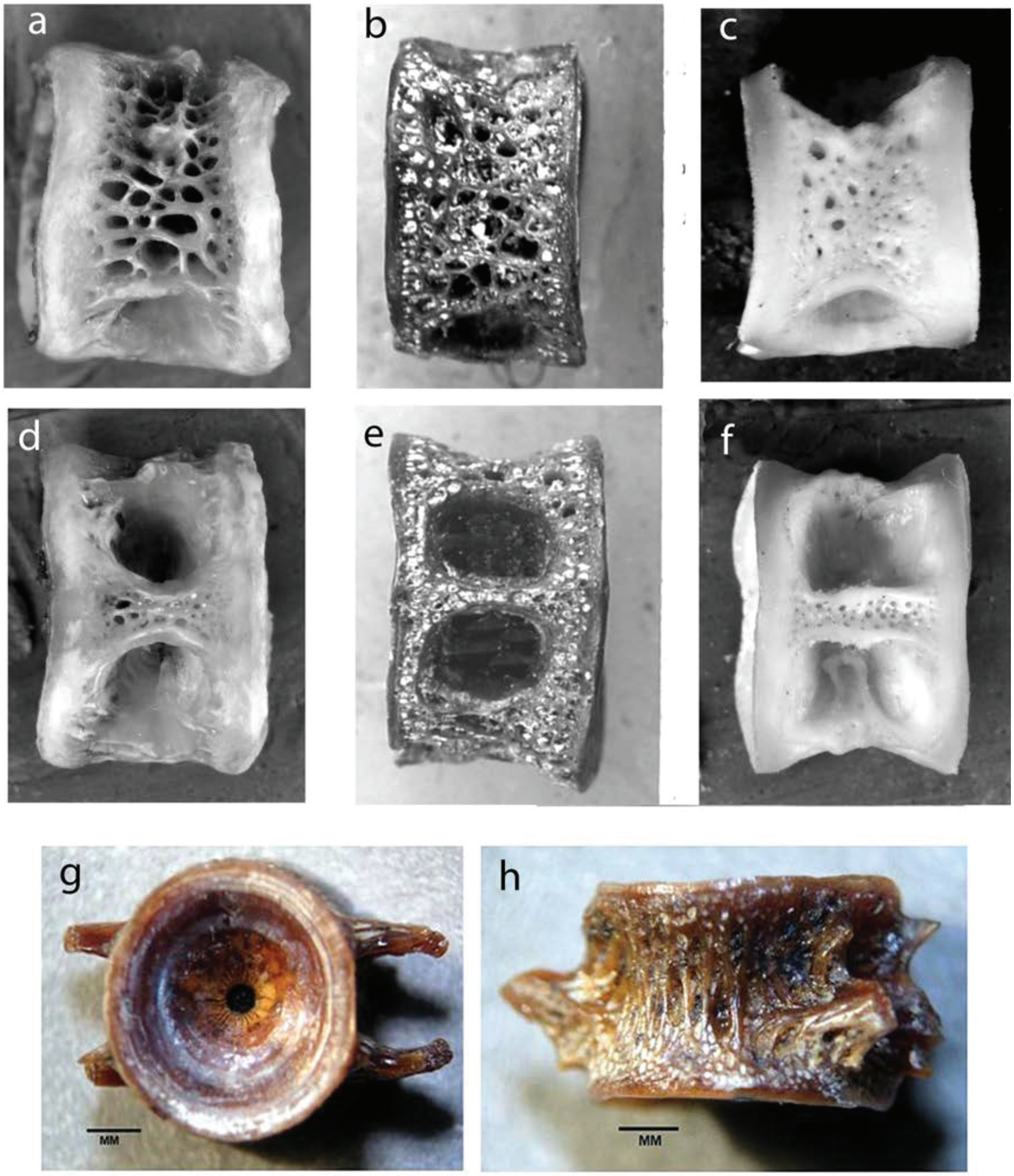

Figure 11.—*Salvelinus* from the Always Welcome Inn paleofauna compared to modern vertebrae; a, modern, b, fossil *Salvelinus* sp., lateral views; c, modern *Oncorhynchus* lateral view; d, e, modern and fossil *Salvelinus* sp., dorsal views; f, modern *Oncorhynchus* dorsal view; g, h, AWI fossil Salvelinus, anterior and lateral views. Anterior view shows about 5 annuli (UMMP 42409).

Centrarchidae, Sunfishes and Bass
Archoplites langrellorum
Van Tassell and Smith, new species
Figures 12, 13

Locality and age.— Oregon, Baker County, Baker City, 44°47.106'N latitude, 117°48.300'W longitude at ~1050 m (3,440 ft) elevation. Blancan North American Land Mammal Age.

Holotype.— A robust left preopercle, Fig. 13b, 8 mm in longest dimension, from the ~10 m-thick sequence at the Always Welcome Inn Local Fauna (Figs. 13b; UMMP 42411).

Diagnosis.— An *Archoplites*, based on the synapomorphic shapes of the dentary, premaxilla, and lacrymal, with serrations

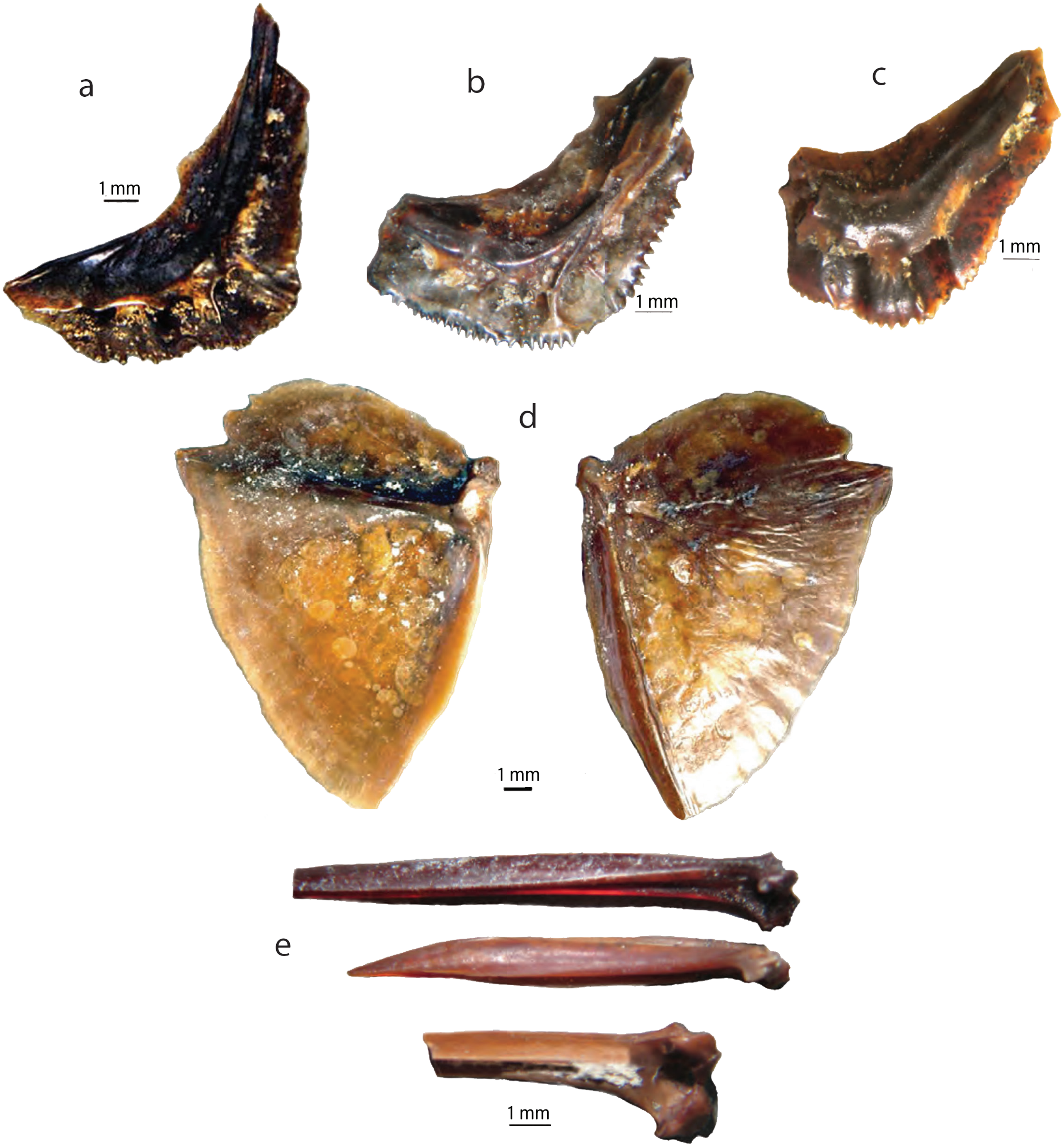

Figure 12.—Fossil bones of sunfish, *Archoplites langrellorum*, from the Always Welcome Inn paleofauna. a, left preopercle (UMMP 42413, part); b, left preopercle, holotype, *Archoplites langrellorum* (UMMP 42411); c, left preopercle (UMMP 42413, part); d, left opercle, mesial (L) and lateral (R) views (UMMP 42413); e, dorsal and anal fin spines.

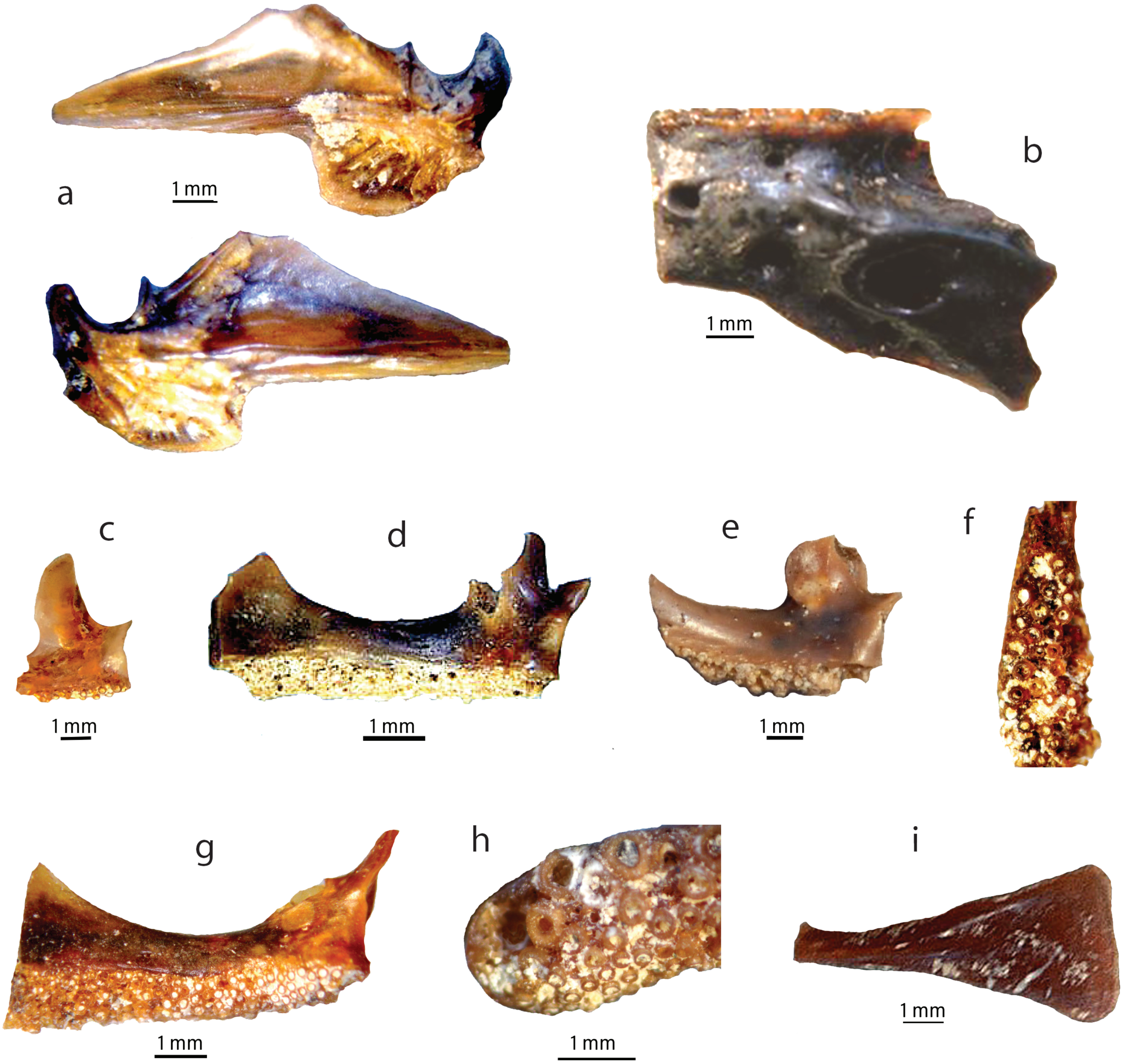

Figure 13.—*Archoplites langrellorum*. a, right Angulo-articular, mesial (top) and lateral (below) views; b, left dentary, lateral view (UMMP 42405); c, d, e, g, left maxillae (UMMP 42412, part); f, partial lower pharyngeal (UMMP 42401); h, partial, anterior part left dentary; i, posterior part of maxilla (UMMP 42412).

on the ventral and posterior edges of the preopercle and lacrymal, *Archoplites langrellorum* differs from *Archoplites taylori, A. molaris,* and *A. interruptus* by the larger, more robust serrations on the preopercle (Smith et al., 2000, fig. 13). There are 24 sharp serrations on the ventral edge, and 15 on the posterior margin of the preopercle (Figs. 12b; UMMP 42411). The sensory pores on the preopercle are smaller (plesiomorphic) than in *A. molaris* or *A. taylori* (Smith et al., 2000, fig. 13). The outer tooth bases of the dentary are approximately twice the diameter of bases of the inner teeth, suggesting enlarged or molariform teeth Figs. 13h; UMMP 42412).

Description.— Van Tassell et al. (2007) suggested that the Always Welcome Inn sunfish, *Archoplites* sp. shared more traits with *A. taylori*, the common Snake River form, than with *A. molarus* of the Ringold formation of the Columbia

River drainage, based on delicate bones, but since then robust sunfish pharyngeal bones have been found that show large tooth bases (Figs. 13f) for possible molar teeth like those of *Archoplites molarus* from the 3.6 Ma Blufftop local fauna of the Ringold Formation of Washington. *Archoplites langrellorum* is a robust sunfish with stout dorsal and anal fin spines (Fig. 12e; UMMP 42414), large serrations on the preopercle (Fig. 12b; UMMP 42411), some molariform pharyngeal teeth (Figs. 13f; UMMP 42401), large teeth on the outer edges of the dentary (Figs. 13h; UMMP 42401) and premaxilla, and a robust horizontal ridge on the mesial side of the opercle (Figs. 12d; UMMP 42413). The teeth on the premaxilla and dentary (Figs. 13d, h; UMMP 42412) are in six or seven rows, with the outer tooth bases approximately twice the diameter of those of the inner teeth. The frontals have a long anterior sensory canal, usually not interrupted in the middle by a pore. The anterior two or three teeth of the premaxilla are much enlarged compared to the rows of small teeth of the premaxilla and dentary. In Fig. 13i, the maxilla is an elongated triangle, but the anterior part of the bone is missing. Bimodal variation (unquantified) in preopercles, lachrymal, dentaries, and premaxillae and robustness of other bones of *Archoplites langrellorum* suggest that two species of sunfishes, a robust channel form and a gracile lake form, may have been present (see below).

Etymology.— Named for Richard and Lynn Langerell, owners of the Always Welcome Inn, who supported Eastern Oregon University field work and made faculty and student paleontologists feel welcome.

Additional material.— Miscellaneous bones, UMMP 42415.

Variation and taphonomy.— Sunfish bones are found in almost every layer at the Always Welcome Inn, with the exception of 4.25–4.5 m, 6.25–6.5 m, and 9.25–9.75 m intervals. They are most abundant in the 2.5–2.75 m layer in the lower lacustrine portion of the sequence and in the 6.75–7 m layer, the base of a channel layer in the upper fluvial portion of the sequence (Fig. 6). The sunfish bones in the lake sediments are delicate and fragile, while a form with robust bones is characteristically found in stream sediments and is common in other layers, especially in the upper fluvial part of the sequence (Van Tassell et al., 2007).

Stubblefield's (2012) data from the 2.5–2.75 m layer (Fig. 14), which is rich in sunfish fossils, shows that scales are the most abundant sunfish fossils (54%) in the 2.5–2.75-m layer, followed by skull bones (26%), spines (14%), and vertebrae (6%). There is considerable variation in the number of sunfish fossils laterally across the layer. These lateral variations may reflect differences in distance from the mouth of the stream that discharged into the area at the time of deposition. High sunfish concentrations may reflect times when nutrients were abundant and water depths were shallow. It is also possible that factors such as different energy levels created by channeling within the stream entering the lake or wave variations along the lakeshore were responsible for the lateral variations in the abundance and types of sunfish fossils found in this layer.

Significance of AWI sunfish pharyngeal teeth.— The Always Welcome Inn robust sunfish has some large tooth-sockets that likely supported molariform teeth on the pharyngeal bones Fig. 13f; UMMP 42401). This trait is shared with *Archoplites molaris* of the Ringold formation in the Columbia River drainage. These differ from *Archoplites* of the Western Snake River Plain and elsewhere. This synapomorphy suggests a sequence of events. First, a drainage connection between the Powder River and Lower Columbia River Basins after the Powder Valley began to form at about 9 Ma and before the deposition of the Always Welcome Inn sequence at about 4.5–4.4 Ma. Next, isolation for a period long enough to account for differentiation from other known A*rchoplites*, which have only small, sharp pharyngeal and other teeth. After an interval of about a million years (Van Tassell et al., 2007) new connections allowed a genetic exchange of the large pharyngeal tooth trait. This constrains the times of secondary contact between the Baker Valley and the Lower Columbia River to about 9–4.5 Ma. One possible time for the first drainage connection is 9–8 Ma when diatomites were deposited during a period of high lake levels in the early Keating Valley. A later contact was possibly when late Miocene stream gravels north of the pass at The Summit were deposited (Fig. 3). Imbrications of the gravel indicate northward stream flow. The Summit gravel sequence grades upward from clasts rich in metachert and other fragments derived from the south to gravels composed of locally derived andesite and basalt fragments. Isaacson (2002) matched this pattern with a similar change in the composition of the sediments deposited in the

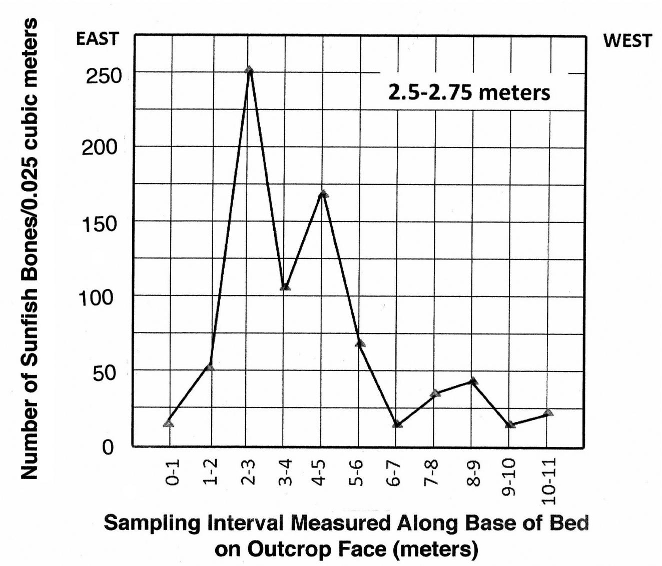

Figure 14.—Lateral variations in the number of sunfish bones within the 2.5–2.75 m layer at the Always Welcome Inn, based on data of Stubblefield (2012).

Grande Ronde Valley between 6.5–6 Ma (Van Tassell et al., 2001) and suggested that the Summit gravels were deposited at about 6 Ma. This evidence supports Livingston's (1928) suggestion that Catherine Creek, which today is a tributary of the Grande Ronde River, once flowed from the Lower Powder (Keating) Valley through the pass and along a course east of the present path of modern-day Catherine Creek into the Grande Ronde Valley. This connection through the Summit between the Powder and Grande Ronde Valleys probably lasted for only a short time before it was blocked by an uplift of a fault block, causing Catherine Creek to divide into the present northwest-flowing Catherine Creek and southeast flowing Big Creek into the Powder River (Fig. 3).

Cottidae, Sculpins
Cottus, sculpins
Figure 15

Sculpins are small, cool-water, northern benthic fishes. They were found in the 6.5–6.75m interval at the Always Welcome Inn (Fig. 15). The AWI sculpin preopercles (UMMP 42410) are unique in possessing a single long posterior spine usually flanked by two short, blunt, closely-spaced spines. Small sensory pores are visible between the long and short spines on one specimen (Fig. 15a). The specimens are variable, one (Fig. 15c) lacks the two short, blunt spines and two (Figs. 15b, c) lack sensory pores. The morphs are distinct from other known sculpins, but as yet undescribed; more examples are necessary to determine their distinctness, variation, number of species, and relationships. Sculpins are small, benthic, cool-water fishes. It is common for them to occur in multi-species assemblages. Their diversity is centered in Oregon in North America, and Lake Baikal in Siberia. Eight species in three genera are found in the Glenns Ferry Formation, one each in the Keating and Chalk Hills faunas, but none in the Ringold Formation of Washington. The AWI *Cottus* is most like *Cottus calcatus* in the Chalk Hills and Glenns Ferry formations and modern *Cottus* of the Columbia drainage, Oregon and Idaho. They show a hint of development of the preopercular armature of the extinct *Kerocottus* of the Glenns Ferry Lake and are most unlike *Myoxocephalus* of the Glenns Ferry lake and the Arctic.

LATE PLIOCENE (3.8–3.7 MA) IMBLER FISH FOSSILS

Fossilized fish bones were found in the Grande Ronde Valley in a water well drilled in 2000 near Imbler, Oregon, at a depth of 138–141 m just above andesitic bedrock (Van Tassell et al., 2001). Most of the fish fossils came from a layer consisting of a mixture of rock fragments, quartz sand, and diatomite. The overlying layer of organic-rich peaty sediments also contains fish fossils, but fewer. Estimates based on the stratigraphic position of the fish fossils relative to ~7.5 Ma and ~3 Ma tephras suggest that the age of the Imbler fish fossils is ~3.8–3.7 Ma.

Four fish species from the Imbler well (Table 2) include a pikeminnow (*Ptychocheilus* sp.), catfish (*Ameiurus* cf. *reticulatus*), a sunfish (*Archoplites* sp.), and a whitefish

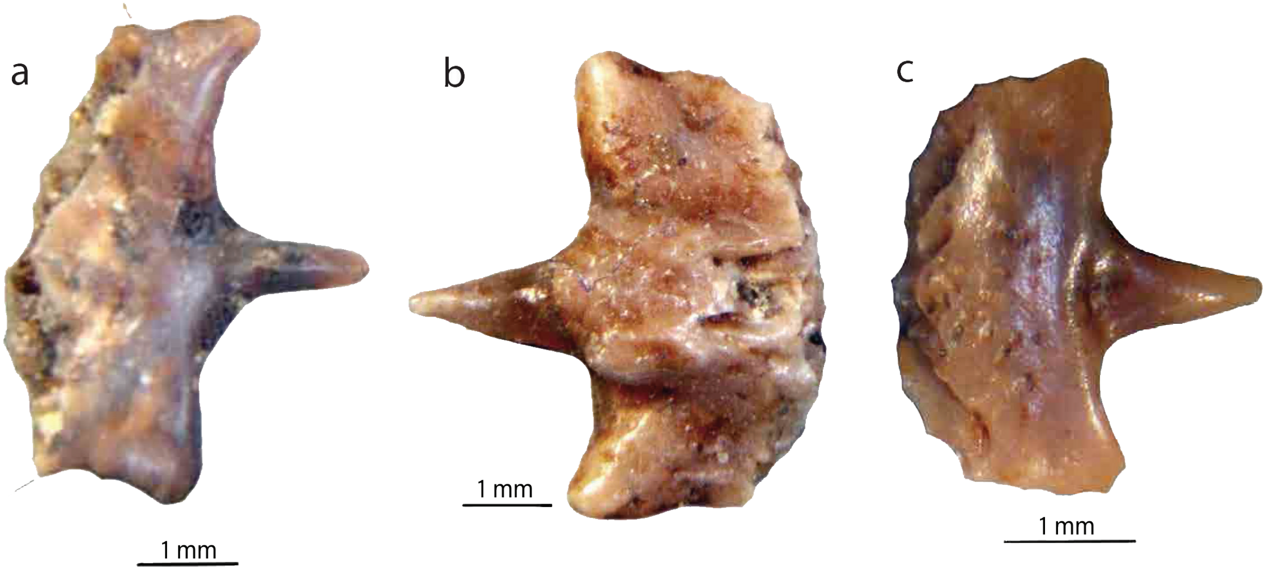

Figure 15.—Sculpin (*Cottus*) bones from the Always Welcome Inn local fauna. a, Fragment of left preopercle showing a central spine flanked by sensory pores and short, blunt spines, missing the dorsal and anterior extensions of the bone, lateral view; b, Fragment of right preopercle with two short, blunt spines and a basal nub, sensory pores not visible, missing the dorsal and anterior extensions of the bone, lateral view; c, fragment of a right preopercle showing a single spine, no short spines, missing the dorsal and anterior extensions of the bone, mesial view (UMMP 42410).

(*Prosopium* sp.). The presence of sunfish and catfish suggests deposition in warm, quiet water; the whitefish required cool, flowing water.

The caniniform pharyngeal tooth of the predaceous *Ptychocheilus* of the Imbler local fauna is not distinguishable from teeth of *P. arciferus* Cope from the Miocene and Pliocene of the Snake River Plain, the AWI paleofauna, and the Ringold Formation in south-central Washington. The supraoccipital bone of the catfish is reticulated on its dorsal surfaces, like those of *Ameiurus reticulatus* of the Ringold Formation; the supraoccipital has a deeper median-dorsal groove or fontanelle, somewhat like *A. vespertinus* from the WSRP. The catfish pectoral spines are striated like *A. reticulatus* and *A. vespertinus*, and the catfish dorsal pterygiophore has characteristics of both species suggesting earlier connections to the Oregon-Idaho Graben and the Ringold Formation. The cleithrum of the sunfish *Archoplites* is similar to other *Archoplites*. The Imbler fauna possibly shared or exchanged species with the modern Columbia River drainage fish fauna along with the contribution from the AWI fauna (Table 1).

The slow growth indicated by the vertebral annual rings of the whitefish *Prosopium* in the Imbler fish fauna is indicative of waters outside its cooler requirements, compared to the other families, perhaps summers were cool enough to allow *Prosopium* to coexist with *Ameiurus* and *Archoplites*, or the whitefish specimens were washed into a warmer ponded lowland environment from a cool, upstream tributary. Two species of whitefish of the genus *Prosopium* were common in Pliocene Glenns Ferry lake but have not been recorded from the warm-water fish faunas of the Ringold Formation, although one is now common in the Columbia River drainage basin and a second species to the north. In general, the presence of the Mountain Whitefish, *Prosopium*, in the ~3.8–3.7 Ma Imbler fauna suggests a possible link to the north. Overall, the other Imbler fishes are somewhat similar to those of the Ringold Formation of Washington. The individual bones of the Imbler pikeminnow, catfish, and possibly sunfish are similar taxonomically and ecologically to their counterparts in the late Pliocene (3.3 Ma) Taunton Local Fauna of the Ringold Formation. On the basis of the proportion of shared species, the Imbler fish fauna is most similar to the ~3.6 Ma Blufftop fauna of the Ringold Formation of Washington. This evidence may indicate a connection between the Grande Ronde Valley and the Columbia River drainage basin during the Pliocene at ~3.8–3.6 Ma.

The diatom-rich layer above the zone with the fish fossils includes abundant benthic and epiphytic diatoms and sponge spicules. The diatoms include *Tetracyclus stellare* var. *eximia, Aulacoseira jouseana,* and rare *Stephanodiscus* sp. None of the diagnostic Miocene diatom genera that occur in the Keating diatomites have been found in this layer (Table 3). *Aulacoseira jousean*a occurs in the 15.9 Ma Squaw Creek diatomite in Washington, the 11.5 Ma Juntura- Harper diatomites of the Drewsey-Juntura Graben, Oregon, the 11.3 Ma diatomites near Weiser, Idaho, the 9.5 Ma Brady Hot Springs diatomite in Nevada, and the 4.7 Ma Yonna Formation and 2.8 Ma Sprague River area of Oregon. *Tetracyclus stellare* v. *eximia* is relatively rare in the Mann Creek diatomite and occurs with other Miocene diatoms that are also found in the Keating diatomites and in the Miocene (11.5 Ma) Truckee Formation of Nevada (VanLandingham, 1985).

The occurrence of the Imbler fish fossils below sediments containing the diatom *Tetracyclus stellare* var. *eximia* suggests the possibility that the fish fossils are similar in age to the Miocene diatomites in the Weiser, Idaho, area. Van Tassell et al. (2001) noted that the diatoms *Stephanodiscus* sp. and *Aulacoseira* sp. aff. *A. solida* in the sediment layer above the fish fossils are possible equivalents of similar (but not necessarily the same) diatoms in the Pliocene Glenns Ferry Formation. This suggests a Pliocene, not Miocene, age. *Stephanodiscus* first appeared at the beginning of the Pliocene, although the genus probably evolved during the latest Miocene (Bradbury and Krebs, 1982; Krebs et al., 1987). Bradbury and Krebs (1982) recognized four possible primitive species of *Stephanodiscus* in the Chalk Hills Formation, but two of these were later assigned to a new fossil genus (*Mesodictyon*) by Theriot and Bradbury (1987).

Van Tassell et al. (2001) answered the question of how Miocene and Pliocene diatoms came to be mixed together in the layer above the Imbler fish fossils by noting that (1) the scarcity of *Aulacoseira jouseana* and *Tetracyclus stellare* var. *eximia* suggests reworking and (2) the presence of *Stephanodiscus* sp. and *Aulacoseira* sp. aff. *A. solida* indicates an abrupt change to deep-water lake environments. This evidence suggests that the Miocene diatoms could have been eroded from the 11.3 Ma Miocene diatomite outcrops near Weiser, Idaho when they were flooded by the Weiser embayment of the Glenns Ferry Lake and were then washed into the Grande Ronde Valley. It is also possible that the diatoms were transported to the Grande Ronde Valley by anticyclonic winds. An aquatic connection, if it occurred, started prior to or at ~3.6 Ma and was short-lived. The route could have been up to the Burnt River arm of the Glenns Ferry Lake, as proposed by Livingston (1928), or up to the Powder River arm of the Glenns Ferry Lake into the Baker Valley, and then over Telocaset Pass into the Grande Ronde Valley and the Columbia River drainage system. The small sample of Imbler fishes is inadequate to test this hypothesis.

SIMILARITY OF FISH PALEOFAUNAS

Table 1 shows the genera identified in selected Late Cenozoic fish faunas in the Pacific Northwest. The Always Welcome Inn paleofauna shares *Mystocheilus* with the Drewsey Formation (Carpenter and Smith, this volume) and an *Archoplites* with molariform pharyngeal teeth in the Ringold Formation. Always Welcome Inn fishes are otherwise part of regional fish fauna, the members of which have varying species diversity depending on the relative sizes of drainages and fossil samples. An axis of dispersal runs north-south from the Oregon-Idaho Graben to the Ellensburg Formation, from prior to 10 Ma to modern times, based on shared fishes. The variable faunal lists reflect possible connections, filtered through elevational barriers and stream captures and separated by ranges that kept the fishes generally isolated. That pattern is common across Basin and Range tectonic regimes (Smith et al., 2002).

LATE MIOCENE AND PLIOCENE DRAINAGE CONNECTIONS AND DISPERSAL OF FISHES AND OTHER ORGANISMS BETWEEN EASTERN OREGON, EASTERN WASHINGTON, AND THE WESTERN SNAKE RIVER PLAIN

Available evidence (Table 1) suggests the possibility of Miocene and Pliocene drainage connections and immigrations of fishes and other animals between southeast and northeast Oregon (Keating, Baker, and Grande Ronde Valleys) during the late Miocene and Pliocene. Some of this evidence is strong, such as the presence of sunfish with molar teeth and *Mystocheilus*. Weaker evidence may be found in the distribution patterns of diatoms and mammals.

Possible Late Miocene (~11.5–8.6? Ma) Drainage Connection.— The presence of *Mystocheilus* only in the 8.5 Ma Trapa Beds of the Drewsey Formation and the 4.5–4.4 Ma Always Welcome Inn local fauna is strong evidence for a direct aquatic connection of some kind between the Drewsey-Juntura Basin and the Baker Valley before 4.5–4.4 Ma. The origin of *Mystocheilus* is not known, so it is not clear exactly when or where this connection began. The presence of *Pantosteus* and *Rhinichthys* in the 11.5 Ma Juntura, 10.3 Ma Ellensburg, and 4.5–4.4 Ma Always Welcome Inn fish faunas support an aquatic connection with the Drewsey-Juntura Basin beginning as early as 11.5 Ma. Drainage changes probably provided sporadic dispersal connections through the changing fault zones in the complex system of faults and extensional basins between Weiser, Idaho, and Elgin, Oregon (Fig. 2). The small number of fish fossils (*Cottus*, an unidentified minnow, and unidentified pelvic bones) found in the ~8.6 Ma Keating Valley fauna to date provide little information about a drainage connection involving Keating.

The occurrence of diagnostic Miocene diatoms in the Keating diatomite, including *Opephora glangeaudi* and, possibly, *Fragillariopsis* sp. 1 and *Tetracyclus ellipticus* var. *latissimus f. minor* (Table 3), provides evidence of a close relationship between the Keating Valley diatomite and the 15.9 Ma Squaw Creek diatomite member of the Yakima Basalt in Washington, the 11.5 Ma Truckee Formation diatomites east of Reno, Nevada, and the 11.3 Ma Mann Creek diatomite near Weiser, Idaho. This may indicate a possible drainage connection between the Weiser area in the Western Snake River Plain and the Keating area sometime between ~11.3 and 8.7–8.6 Ma. The presence of the diagnostic diatoms *Coscinodiscus miocaenicus* and *Gomphonema cholnockites* in the diatomite layer that the Keating fish fossils came from has been suggested as evidence of a possible relationship with the Bully Creek Formation of the Drewsey-Juntura Basin near Harper, Oregon. (VanLandingham, 1985). Nate Carpenter (written communication, 2018) suggested that these diatomites are in the 10–8.1 Ma Upper Bully Creek Formation. This suggests a possible aquatic connection between the Drewsey-Juntura Basin and the Keating Valley between ~10 and 8.7–8.6 Ma. The diatom evidence suggests that possible aquatic connections between the Keating Valley and both the Western Snake River Plain and the Drewsey-Juntura Basin occurred at or before 8.7–8.6 Ma. It is possible, however, that these diatoms were dispersed by wind. There is direct sunfish evidence for early and later connections between the Pasco Basin of Washington and the Always Welcome Inn, based on sunfish pharyngeal teeth (see sunfish species account and Discussion).

Possible Late Miocene (~8.6–4.5 Ma) and Early Pliocene (~4.5–4.3 Ma) Drainage Connections.— A possible late Miocene drainage connection between the 8.1 Ma Chalk Hills lake and Baker Valley may have occurred after the 8.6 Ma Keating Valley local fauna and prior to the 4.5 Ma Always Welcome Inn local fauna. The minnow, *Acrocheilus* sp., sucker (*Catostomus*), and sunfish (*Archoplites langrellorum*) found in the Always Welcome Inn local fauna appear to be relatives of fishes that were connected between to the Ellensburg and Ringold formations, Washington. The unique similarity of the sunfishes in the Ringold and Always Welcome Inn faunas suggest that the Always Welcome Inn fauna was isolated for a considerable time between an early connection between the Western Snake River Plain, the Always Welcome Inn area, and the Pasco Basin at about 10.5–10 Ma and between Always Welcome Inn and Pasco, at ~8.6 Ma. The evidence for a Pliocene drainage connection between the Baker Valley and the Pasco Basin is in the pharyngeal teeth of the sunfish *Archoplites*, which have large tooth sockets for possible molariform teeth in both areas. Since *Archoplites* has been found in the 10.5–10.2 Ma Ellensburg Formation of Washington, the Miocene connection was probably repeated between the Always Welcome Inn and the Columbia River drainage and included drainage connections among the Baker Valley, the Glenns Ferry Formation, and the Pasco Basin in the Pliocene. The presence of the lake sucker *Chasmistes*, which came from Walker Lane, Nevada and California (Smith et al., 2018) and later dispersed to the latest Chalk Hills lake, Glenns Ferry lake, post 7.45 Faust Tuff in the Teewinot Formation, and the 4.5–4.3 Ma White Bluffs local fauna is consistent with this interpretation.

An early Pliocene connection may have been at the same time as the immigration of microtines between the Sacramento River, the WSRP, and the Pasco Basin of Washington at about 4.5–4.3 Ma and has important implications for hypotheses about the immigration of microtines during this period. Microtines dispersed down the Pliocene Pacific coastline as far south as the San Francisco area, where they moved up the Sacramento River to Alturas by 4.5 Ma, reached the Glenns Ferry lake area at Hagerman by 3.7 Ma (Repenning et al., 1995; Repenning, 2003), and then dispersed eastward through Yellowstone Pass during the late Pliocene (Barnosky, 1985; Repenning, 2003). One hypothesis (Repenning, 1987; Repenning et. al., 1995) suggests that microtines also immigrated inland up the Columbia River to the Pasco Basin area by 4.5–4.3 Ma. The microtine species *Ophiomys mcknighti* described by Gustafson (1978) in the White Bluffs fauna of the Ringold Formation, Washington, is similar to the species of *Ophiomys* described in the Always Welcome Inn local fauna by Van Tassell et al. (2007), suggesting that these rodents may have immigrated from the Columbia River system to the Always Welcome Inn area. A second hypothesis, proposed by Bork et al. (2009), is that these microtines bypassed the Columbia River during southward immigration at 4.8 Ma along the Pacific Coast. Perhaps because the ancestral Columbia basin was covered with volcanics derived from the eastern Cascades that flowed into the basin and were redeposited downstream, forming the early Pliocene upper Troutdale Formation (Trimble, 1967; Tolan and Beeson, 1984; Swanson, 1996). According to Bork et al. (2009), the Always Welcome Inn and White Bluffs microtines are members of the group that reached from California to the Snake River Plain, where they dispersed northwestward, entered the Burnt River system, and immigrated northward across the drainage divide into the lower Powder Valley by 4.5 Ma and across the drainage divide and into the Columbia River drainage by 4.3 Ma.

Possible Middle Pliocene Drainage Connection.— Evidence for a connection between the Glenns Ferry lake and the Grande Ronde Valley at ~3.8–3.7 Ma. includes the presence in ~3.8–3.7 Ma Grande Ronde Valley (Imbler) sediments of (1) the Mountain Whitefish (*Prosopium*); (2) the diatoms *Tetracyclus* v. *eximia* and *Aulacoseira jouseana*, which could have come from reworking of middle Miocene outcrops in the vicinity of Weiser, Idaho, that were submerged by the Weiser arm of the Glenns Ferry Lake, and (3) the abundant *Stephanodiscus* sp. and the centric diatom *Aulacoseira* sp. aff. *A. solida*, which have affinities to diatoms in the Glenns Ferry Formation and indicate a rapid rise in water level after the deposition of the Imbler fish fossils. The resemblance of bones of catfish (*Ameiurus* cf. *reticulatus*) and sunfish (*Archoplites langrellorum*) in the ~3.8–3.7 Ma Imbler local fauna to congeners in the 3.3 Ma Taunton paleofauna suggests that a drainage connection occurred between the Pasco Basin and the Grande Ronde Valley (Van Tassell et al., 2001). The appearance of *Catostomus* cf. *macrocheilus* in the Blufftop local fauna of Washington indicates the presence of *Catostomus* in the Pasco Basin (Smith et al., 2000, fig. 8) by 3.6 Ma. *Catostomus* cf. *macrocheilus* in the Blufftop local fauna (Smith et al., 2000, fig. 8) may be the same as *Catostomus* in the 4.5 Ma Always Welcome Inn local fauna (Fig. 8). This evidence links the Grande Ronde and Baker Valley areas. A limited drainage connection possibly occurred in the path proposed by Livingston (1928), between an embayment of the Glenns Ferry lake in the Burnt River drainage near Durkee, Oregon, and the lower Powder Valley, the Always Welcome Inn site, and across Telocaset Pass into the Grande Ronde Valley and the Columbia River drainage (Fig. 3).

The differences between the species of catfish, sucker, and sunfish in the northeast Oregon local faunas from those in the Blufftop and Taunton local faunas of Washington suggests that the drainage links between the Glenns Ferry lake, the Baker and Grande Ronde valleys, and the Columbia River drainage passed through elevational filter barriers. The proportional similarity of the 3.8–3.7 Ma Imbler local fauna of northeast Oregon to those in the 4.5–4.3 Ma White Bluffs and 3.3 Ma Taunton local faunas of Washington (three shared of 12 total taxa) compared to the Imbler fauna and the Glenns Ferry sequence (four shared of 32 total taxa) may indicate that both drainage connections were separated by filter barriers, but the comparisons are hampered by the small Imbler sample size.

Late Pliocene (3.3 Ma) Drainage Connection.— Smith et al. (2000) presented evidence for timing of the drainage connection between the Glenns Ferry lake and the Pasco-Columbia drainage during the deposition of the 3.3 Ma Taunton local fauna based on: (1) the appearance of three Glenns Ferry minnows, the Chiselmouth Chub *Acrocheilus latus*, the hitch *Lavinia hibbardi*, and the chub *Klamathella milleri*, in the Taunton fauna; and (2) the addition to the latest Glenns Ferry Fauna of *Catostomus* cf. *macrocheilus* from the Ringold Formation. Smith et al. (2000) suggested that this evidence indicates that the spillover of the Glenns Ferry lake through Hells Canyon began at about 3.3 Ma, slightly earlier than the early Pleistocene date suggested by previous workers (Wheeler and Cook, 1954; Cook and Larrison, 1954; Othberg, 1988, 1994; Malde, 1991; Othberg et al., 1995; and Taylor, 1985). Additional support for a connection between the two areas at 3.3 Ma is provided by evidence that muskrats immigrated up the Sacramento River Valley at ~4.1 Ma, beginning with *Dolomys*, which is found in the Etchegoin Formation of the Kettleman Hills of California. The small muskrat *Pliopotamys minor* reached the Glenns Ferry Lake at Hagerman, Idaho by 3.7 Ma and immigrated northwestward from there to the Columbia River drainage basin, where it is found in the 3.3 Ma Taunton paleofauna (Gustafson, 1978). Repenning et al. (1995) suggested that the similarity of fossil muskrat teeth from the Taunton paleofauna to contemporaneous muskrat teeth from the Glenns Ferry Formation is evidence that Hells Canyon was connected to the Columbia and lower Snake River drainages in the late Pliocene.

A 3.1 Ma ash in the Grande Ronde Valley sediments is evidence that could support a late Pliocene fluvial connection between the Glenns Ferry lake and the Pasco Basin, following the route proposed by Livingston (1928) through the Burnt River drainage, Baker, and Grande Ronde Valleys of northeast

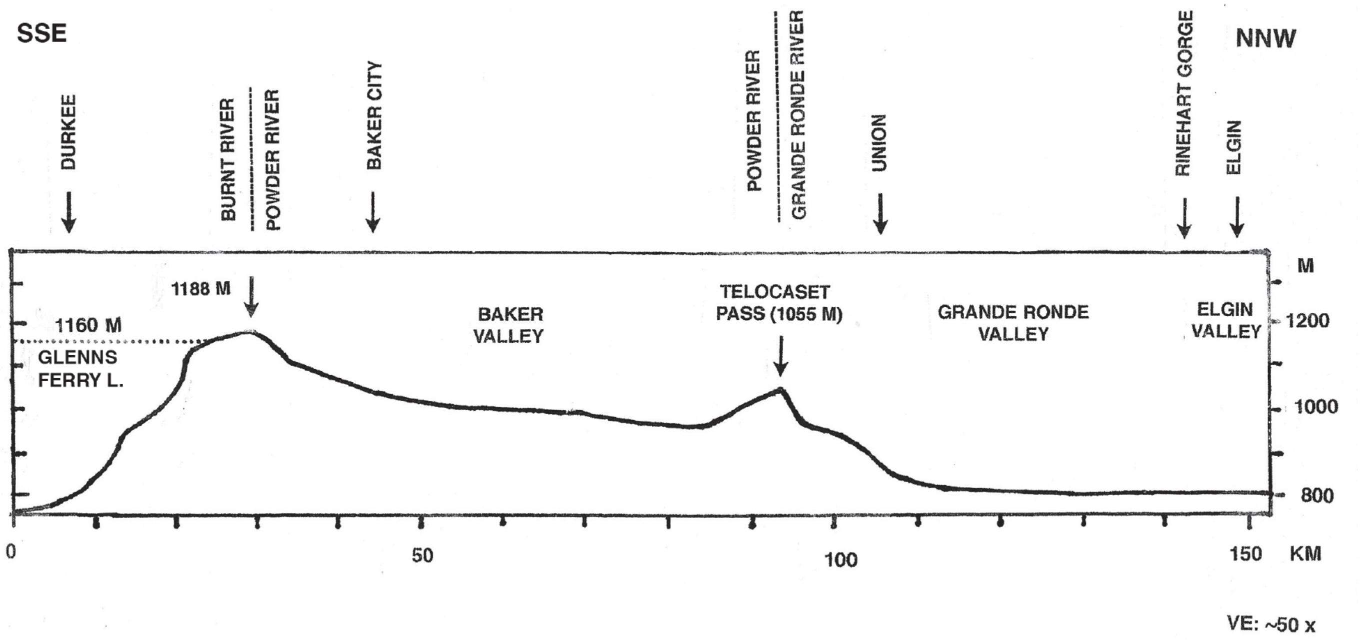

Figure 16.—Short topographic profile along the Burnt, Powder, and Grande Ronde Rivers from Durkee to Elgin, east of the Blue Mountains, Northeast Oregon. Evidence from the Durkee area suggests that the Glenns Ferry lake reached an elevation of 1160 m, ~28 m below the present elevation of the drainage divide between the Burnt and Powder Rivers. See Figs. 3, 16, 17, 18, 19.

Oregon (Fig. 3). Van Tassell et al. (2001) suggested this ash might have been washed in by a river from the Glenns Ferry lake, but it also could be a regional air fall deposit. *Acrocheilus latus* in the Taunton fauna and *Catostomus* cf. *macrocheilus* in the Glenns Ferry Formation is related to the species of *Acrocheilus* and *Catostomus* present in the Always Welcome Inn local fauna. This would support connections (Fig. 2) to explain their dispersal of fish between the Drewsey-Juntura Graben, Western Snake River Plain, and the Always Welcome Inn area. Two or more connections are not mutually exclusive if one was a headwater stream capture.

Early Pleistocene (2.5–2 Ma) Drainage Connection.—The dispersal of the snail *Fisherola nuttalli* upstream from the Columbia River drainage to the Salmon River and into the western Snake River Plain during the early Pleistocene shows that the Snake River was flowing through Hells Canyon between ~2.5–2 Ma (Taylor, 1985; Othberg, 1988; Malde, 1991). This connection may have begun in 2.75 Ma according to Hearst (1999) and Wood and Clemens (2002), and earlier according to Smith et al. (2000). This coincides approximately with the ~120m drop in the level of the Glenns Ferry Lake noted by Wheeler and Cook (1954), Malde (1991), and Othberg (1994).

GEOLOGICAL CONTROL OF LATE MIOCENE TO PLIOCENE DRAINAGE CONNECTIONS FROM THE OREGON-IDAHO GRABEN AND DREWSEY-JUNTURA GRABEN THROUGH NORTHEAST OREGON TO THE COLUMBIA RIVER

Studies of the fossil fishes in the 15.9–13.6 Ma Oregon-Idaho Graben, 13.6–11.3 Ma Drewsey-Juntura Graben, and the 10.5–8.4 Ma Poison Creek Formation of the Western Snake River Plain (Table 1) suggest that these fishes did not live in large or deep lakes. The Sucker Creek Formation in the Oregon-Idaho Graben was deposited starting 15.9 Ma in a swamp that may have covered 2500 square kilometers. Aquatic connections with neighboring regions would have been likely during this period as extension began.

After regional extension began, block faulting played a major role in fish dispersals by regulating the locations and elevations of the passes that drainage connections between the Oregon-Idaho and Drewsey-Juntura grabens, the Keating (Lower Powder) and Baker Valleys, the Grande Ronde Valley, and the Columbia River (Figs. 2, 3, 16). The passes through the drainage divides between the Baker, Keating, and Grande Ronde valleys are complex grabens formed by extension along west-northwest- and east-northeast-trending fault systems. These resulted in the bedrock floor of the Grande Ronde Valley stepping down in a series of fault blocks along the direction of the streams draining into the south end of the basin (Fig. 17). The structures of the east, north, and west sides of the Grande Ronde Valley basin are similar to those of the south side, with additional complexities due to uplifted fault blocks in the bedrock floor near the center of the north end of the basin.

Block faulting along the west-northwest-trending faults in the drainage divide area between the Baker-Keating Valley areas and the Grande Ronde Valley is complex (Fig. 18). The passes at Ladd Canyon and The Summit (Fig. 3) are cut into

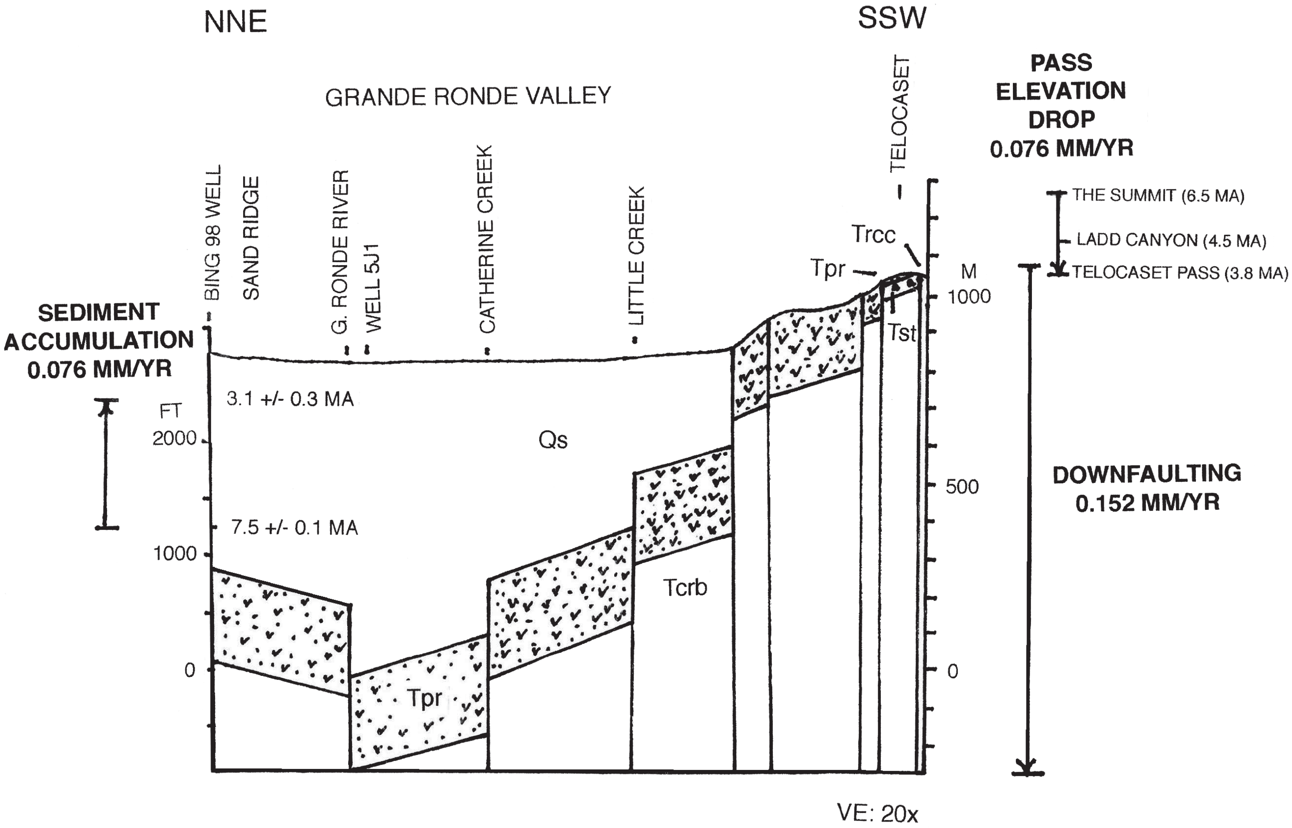

Figure 17.—Generalized geologic cross-section from Telocaset Pass into the Grande Ronde Valley and the rates of down-faulting, sediment accumulation, and pass elevation drop relative to pass at The Summit between the two areas (See Fig. 3).

Tertiary Powder River volcanics. Telocaset Pass is carved into pre-Tertiary metavolcanics (Clover Creek Formation). All of the passes are located on the west sides of fault blocks. Both Ladd Canyon and the pass at The Summit are located adjacent to fault zones. This suggests that the drainage through these areas is not following downthrown fault blocks, but, instead, are following fault zones because it was easier for them to erode through the fractured rocks along the faults. Telocaset Pass is not located close to one of the mapped fault zones in the area. It may be the result of the stream eroding along a fracture zone in the pre-Tertiary bedrock that predates the late Miocene to Recent normal faulting in the area.

Plotting the ~3.8–3.7 Ma date proposed by Van Tassell et al. (2001) for a drainage connection between the Powder and Grande Ronde Rivers through Telocaset Pass at ~3.8–3.7 Ma and Isaacson's (2002) 6.4–5.8 Ma age for time when an aquatic connection between the Powder and the Grande Ronde River drainages was established through the pass at the Summit versus their present elevations provides insights into the formation of these passes. Based on its present elevation, the graph suggests that the pass at Ladd Canyon was formed at ~4.5 Ma (Fig. 19). The data indicate that the elevation of the passes between the Powder and Grande Ronde Valleys dropped relative to the elevation of the pass at The Summit at a rate of ~0.076 mm/yr between ~6.5–3.8 Ma or, alternatively, the elevation of The Summit rose at the same rate relative to Telocaset Pass. This value is roughly half the rate of subsidence between Telocaset Pass and the bedrock floor of the Grande Ronde Valley since about 9 Ma and is similar to the average rate of sediment accumulation in the Grande Ronde Valley near Imbler between 7.5–2.9 Ma (Fig. 18). The observation that the rate of downcutting of the passes is approximately equal to the rate of downfaulting in the basin minus the average rate of sedimentation suggests that the streams in the area may be downcutting in response to changes in equilibrium level (base level) in the adjacent basin.

Periods of wet climate and high lake levels are indicated by deep water diatoms in the Grande Ronde Valley sequence (Fig. 20). For example, the wet period at 4.5 Ma, during the time of the Always Welcome Inn fish fauna, may have raised water levels high enough to provide a path for the immigration of fish and microtines between the Powder and Grande Ronde Valleys. Possible drainage connections between (1) the Oregon-Idaho Graben, Drewsey-Juntura Graben, and Lower Powder (Keating) Valley between 10.3–8.5 Ma, (2) the Lower Powder (Keating) and Baker Valleys with the Columbia River

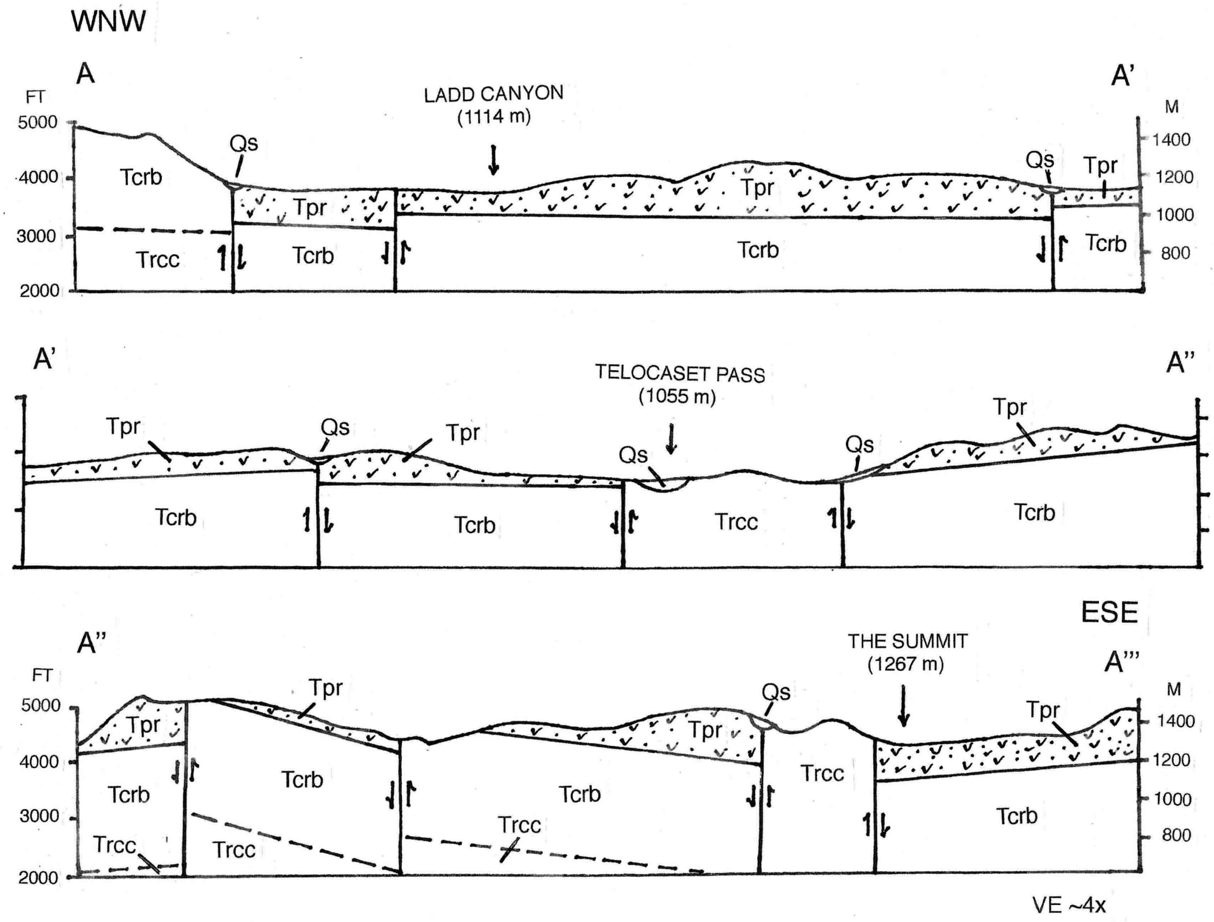

Figure 18.—Generalized geologic cross-section along the drainage divide between the Powder and Grande Ronde Valleys. Qs, Quaternary sediments; Tpr, middle Miocene Powder River Volcanics; Tcrb, Middle Miocene Columbia River Basalt Group; Trcc, pre-Tertiary Clover Creek Formation (See Fig. 3).

drainage via the Grande Ronde Valley at about 9–8.5 and 6.5–6 Ma, (3) the Glenns Ferry Lake (4.3–1.8 Ma), Powder and Grande Ronde Valleys, and the Columbia River at about 3.6 Ma, and (4) the spillover of the Glenns Ferry Lake and drainage through Hells Canyon into the Columbia River starting at 3.3 Ma all match periods of wet climate indicated by diatoms.

The low number of fishes exchanged between the Western Snake River Plain and the Columbia River drainage basin during late Miocene and Pliocene connections through the Lower Powder (Keating), Baker (Always Welcome Inn), and Grande Ronde valleys are not typical of spillovers from one lake to another, which usually result in dispersal of most of the fish species between lakes, unless there is a gradient barrier or falls. A filter connection of the type occurring through the capture of headwaters, rather than spillovers, seems more likely. These headwater connections were probably facilitated by increased streamflow and rapid headward erosion and stream capture during wet climate periods. This hypothesis might explain the prevalence of headwater species (*Cottus, Rhinichthys, Pantosteus, Prosopium*, and *Salvelinus*) that dispersed through the Lower Powder (Keating), Baker (always Welcome Inn), and Grande Ronde valleys in the late Miocene and Pliocene between 9–3.6 Ma.

DISCUSSION

The literature suggests that there may have been multiple drainage connections between the Western Snake River Plain, northeast Oregon, and the Pasco Basin of Washington during the late Miocene to middle Pliocene period, caused by headwater captures. These drainage connections and a later large spillover through Hells Canyon may have occurred as the result of erosion during periods of wet climate and may have been facilitated by regional deflation following volcanic eruptions in the area. The different possibilities are evaluated by considering the habitat requirements of the species of fishes that form the evidence.

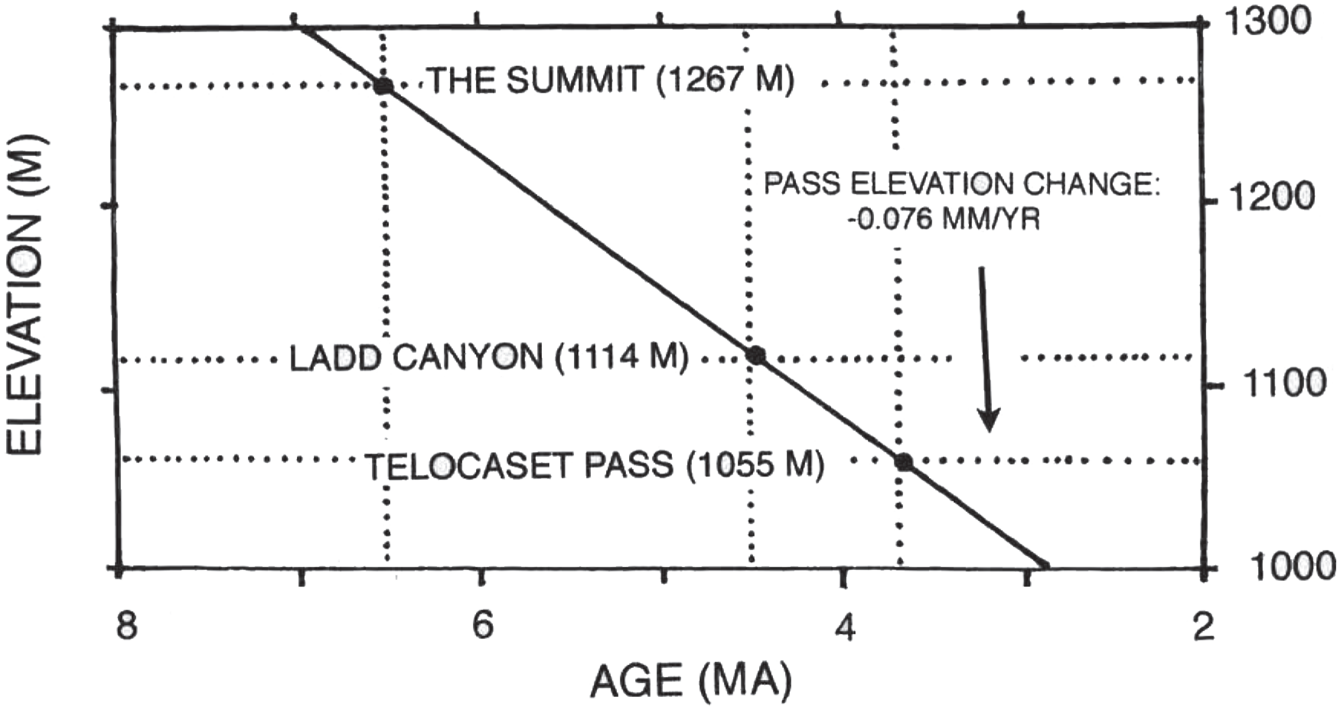

Figure 19. —Graph of pass elevations vs. age (See Figs. 3, 16, 17, 18).

The Keating fish fossils come from a diatomite layer that was deposited during a wet climate period that peaked at ~8.4 Ma based on evidence from the sediments in the Grande Ronde Valley. Additional sampling and study of the late Miocene fish fossils in the Keating Valley and other nearby areas, including the Eagle and Pine Valleys of northeast Oregon, is needed to test the connection of the Drewsey-Juntura Graben and Malheur River Valley areas during this period. The minnows (*Acrocheilus, Ptychocheilus, Rhinichthys*, and *Mystocheilus*), sculpin (*Cottus*), salmonid (*Salvelinus*), and suckers (*Pantosteus, Catostomus*) fossils in the 4.5–4.4 Ma Always Welcome Inn local fauna indicate a past connection with the Drewsey-Juntura Graben, but, as noted by Van Tassell et al. (2007), the overall characteristics of the Always Welcome Inn fish fauna suggest that the fishes were isolated for a long period, perhaps a million years, in the Baker Valley prior to the deposition of the Always Welcome Inn local fauna. The presence of: (1) different but related species of the sunfish *Archoplites* in the Glenns Ferry, Always Welcome Inn, and White Bluff faunas, and (2) different but related species of the catfish *Ameiurus* in the Glenns Ferry fauna and the White Bluffs local fauna indicate the possibility that the connections to the Baker Valley may have extended through the Grande Ronde Valley to the Pasco Basin. When a late Miocene drainage connection could have occurred is not known, but fishes in the 10.2–11.0 Ma Ellensburg Formation indicate that it was prior to 10.2 Ma. Geological evidence suggests that a drainage connection between the Powder and Grande Ronde Valleys may have occurred at The Summit in the headwater area of Catherine Creek, which flowed into the Grande Ronde Valley via a different course than it does today.

Presence in the ~4.5 Ma Always Welcome Inn local fauna of two sunfishes (*Archoplites*), one possibly with unusual molariform teeth similar to those of a sunfish in the 4.5–4.3 Ma White Bluffs, 3.6 Ma Blufftop, and 3.3 Taunton local faunas of the Ringold Formation and one like a Glenns Ferry sunfish, suggests a possible drainage connection between the Baker Valley and a Columbia River during a brief period of wet climate between 4.5–4.3 Ma. The presence of a species of the microtine *Ophiomys* in the early Pliocene Always Welcome Inn local fauna that is similar to *Ophiomys mcknighti* in the White Bluffs local fauna of Washington suggests the possibility that microtines were able to immigrate from the Western Snake River Plain through the Powder (Baker) Valley and across the drainage divide at Ladd Canyon into the Grande Ronde Valley and to the Pasco Basin (or vice versa) at the same time.

The resemblance of the bones of the pikeminnow (*Ptychocheilus*), catfish (*Ameiurus*), and sunfish (*Archoplites*) in the 3.6 Ma Imbler local fauna of the Grande Ronde Valley to those in the 3.6 Ma Blufftop and 3.3 Ma Taunton local faunas suggests drainage from the Grande Ronde Valley into the Pasco Basin area during the late Pliocene. The presence of whitefish (*Prosopium*) in the Imbler fish fauna, the occurrence of reworked late Miocene diatoms from the Drewsey-Juntura Graben along the margins of the Glenns Ferry Lake, and deep-

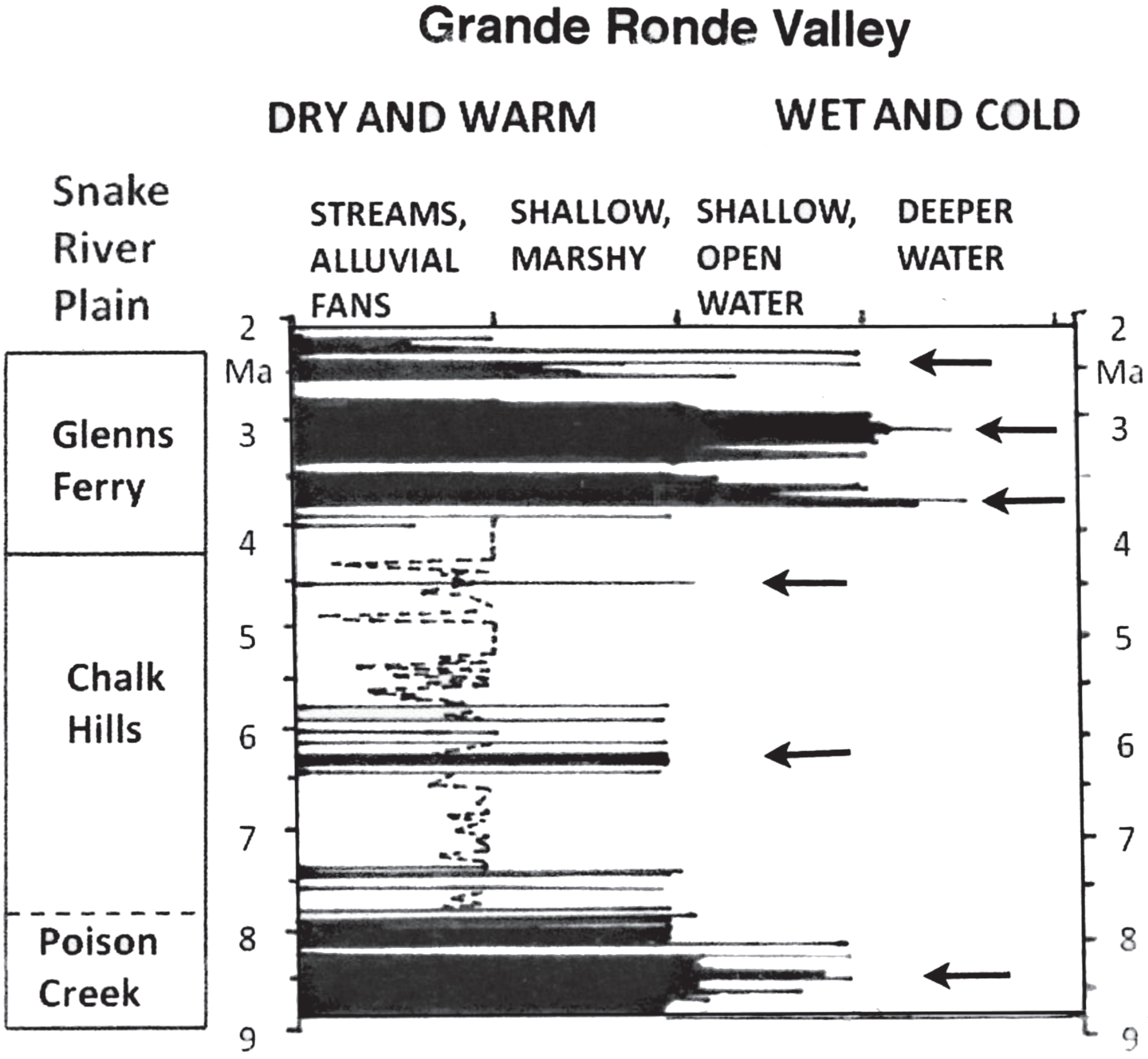

Figure 20.—Lake depths and climate patterns indicated by the types of diatoms in the sediments in the Grande Ronde Valley (from Van Tassell et al., 2001). The Keating, Always Welcome Inn, Imbler, Blufftop, and Taunton fish faunas were all deposited during periods of high lake levels. Six possible dispersal events between lakes on the Western Snake River Plain, northeast Oregon, and the Pasco Basin (arrows) postulated in this paper coincide with periods of high lake levels recorded in the Grande Ronde Valley sedimentary sequence.

water diatoms with affinities to Glenns Ferry Lake diatoms in the sediments just above those containing the Imbler fish fauna indicate an abrupt transition to deep-water lake environments in the Grande Ronde Valley sedimentary sequence. These data suggest a connection at 3.6 Ma between the Glenns Ferry Lake and the Grande Ronde Valley along the route through the Powder River (Baker) Valley and over Telocaset Pass proposed by Livingston (1928). But the use of the connection by only one species of fish from the 32 species in the Glenns Ferry lake requires a stream capture and ecological explanation, not a through-flowing river.

A 2.91 Ma ash present in the Grande Ronde Valley sequence that was washed or blown into the Glenns Ferry Lake provides possible evidence that a drainage connection between the Glenns Ferry Lake and the Grande Ronde Valley occurred at this time. Evidence presented by Smith et al. (2000) suggests that it is more likely that a through-flowing drainage connection from the Glenns Ferry Lake to the Ringold-Columbia paleofaunas was established through spillover into a tributary of the Salmon River that became Hells Canyon, allowing immigration of three minnows (*Klamathella milleri*, *Lavinia hibbardi*, and *Acrocheilus latus*) downstream, and a sucker (*Catostomus* cf. *macrocheilus*) upstream at 3.3 Ma. Muskrats (*Pliopotamus*) moved between the two areas at this time. The drainage connection through Hells Canyon was well-established when the Glenns Ferry Lake flowed into the Salmon and Columbia River drainage during a wet climate period that occurred at about 2.5–2 Ma, permitting the immigration of the snail *Fisherola* upstream from the Columbia River to the Snake River drainage basin. The nearly 1 mi. erosional depth of Hells Canyon is unmatched by any valley carved during any of the earlier late Miocene-Pliocene drainage connections that may have occurred in this region.

It is possible that a change in drainage direction in the Baker and Grande Ronde Valleys to Hells Canyon was triggered by faulting and tilting that occurred in the region after the deposition of the ~4.5 Ma Always Welcome Inn sequence and prior to the deposition of the ~3–2 Ma gravels that rest unconformably above the Always Welcome Inn and other late Pliocene sedimentary sequences in the region. This tectonic activity coincides with long-term changes in the tectonics of the Columbia Plateau area (Barrash et al., 1983). More research is needed to understand the relationship between tectonism, volcanism, climate, and the changes in regional drainages that occurred during the Pliocene and early Pleistocene.

SUMMARY

The Keating, Always Welcome Inn, and Imbler fish genera are a small part of a larger Pacific Northwest fauna that inhabited the region east of the Cascade Mountains, e.g., Ellensburg, Washington, south to the Pit and Klamath drainages, California, and east to the Oregon-Idaho Graben, Drewsey-Juntura Graben, and Western Snake River Plain in southwest Idaho and southeast Oregon (Fig. 1a, b; Table 1). Keating, Always Welcome Inn, and Imbler fish dispersed mostly from the Oregon-Idaho Graben, Drewsey-Juntura Graben, and Columbia drainage, probably about 10–8 Ma. Many Western Snake River Plain fishes probably dispersed there from the Sacramento and Klamath rivers to the Oregon-Idaho Graben and Drewsey-Juntura Graben, probably about 10–8 Ma. The Oregon-Idaho Graben (15.5–10.5 Ma; Cummings et al., 2000) and nearby Drewsey-Juntura Graben (Table 1) were the central pathways to regional patterns of dispersal. These were the source of colonization north to the Always Welcome Inn and east to the Western Snake River Plain, of fish that originally came from coastal drainages, including the Sacramento, Klamath, Deschutes, and Columbia rivers.

Ptychocheilus is the primary index fossil of the Pacific Northwest paleofauna. It was widespread, known from almost all Late Miocene paleodrainages and all paleofaunas except one (Table 1). Slightly later, *Ameiurus* (catfish), *Mylocheilus* (Peamouth Chub), and *Archoplites* (sunfish) were in the Columbia drainage Ellensburg formation (10.5–10.2) (Table 1). Absence of *Ameiurus*, *Mylocheilus*, and *Oncorhynchus* (salmon) in the Always Welcome Inn fauna is evidence favoring limited headwater transfers among the Imbler, Baker Valley, Western Snake River Plain (Powder River tributary to the Chalk Hills lake) and Baker Valley drainages in the Late Miocene. Of these taxa, only *Ameiurus* is in the Imbler paleofauna of the Grande Ronde Valley (3.8–3.7 Ma), sympatric with *Ptychocheilus, Archoplites*, and a whitefish, *Prosopium*).

Three additional genera of fishes support North–South hydrographic connections among the Oregon-Idaho Graben, Drewsey-Juntura Graben, Baker Valley, Western Snake River Plain, and the Columbia drainage about 10–9 Ma. *Catostomus* and *Archoplites* were in the Poison Creek formation (11–9 Ma WSRP), (Smith and Cossel, 2002) Oregon-Idaho Graben, Drewsey-Juntura Graben, and probably in streams in Baker Valley. *Ptychocheilus, Mystocheilus, Catostomus,* and *Archoplites* are shared by faunas from the Oregon-Idaho Graben, Drewsey-Juntura Graben, the Always Welcome Inn in Baker Valley, and the Ringold Formation. *Pantosteus* (Mountain Sucker) occurred in the Ellensburg, Drewsey, and Glenns Ferry formations and the Always Welcome Inn paleofauna (Table 1).

The *Cottus* preopercles of the Always Welcome Inn paleofauna may be distantly related to those of the rich *Cottus* diversity of modern sculpins of the Sacramento, Klamath, Pit, and Columbia-Snake drainages (Sigler and Zaroban, 2018) because they share well-developed stout, spines, but different orientations. Two of the modern Idaho *Cottus* are somewhat similar to the weak-spined fossil *C. calcatus* of the WSRP (compare figures of 10 preopercles of Idaho sculpins in Sigler and Zaroban, 2018, p. 189). There is evidence consistent with Livingston's proposed connection in the Telocaset area, but lack of extensive faunal exchange suggests that it was earlier than he supposed and not a through-flowing river, but a headwater stream capture. When it occurred it probably added fishes to drainages where they already existed.

The uniqueness of *Mystocheilus* and the Always Welcome Inn and Taunton *Archoplites molaris* and *A. langrellorum* suggests one or more million years of isolation of those aquatic habitats, perhaps dating from barriers in the Columbia drainage, as it was divided and filled by tectonics and eruptions of the Columbia River Basalts. The observed amount of morphological change between the Juntura and Ellensburg species and the Pliocene to modern Columbia fauna is minimal, suggesting that these genera existed in their modern form earlier than Middle Miocene, probably in coastal drainages, allowing slow, frequently interrupted, genetic differentiation. The similarities within the Always Welcome Inn and Drewsey-Juntura Graben imply late Miocene and early Pliocene connections.

ACKNOWLEDGMENTS

Special thanks go to Richard and Lynn Langrell, owners of the Always Welcome Inn, for giving us permission to collect and for their enthusiasm and support throughout the project. J. Platt Bradbury identified the diatoms from the Imbler wells that suggest a possible connection with the large late Miocene to Pliocene lakes on the western Snake River Plain. Les Hoxie collected the fish fossils from the Keating Valley and Terry Frest discovered the Always Welcome Inn fish fossils. Mark Ferns and Jason McClaughry suggested that the Columbia River was blocked during the early Pliocene migration of the voles. Many thanks go to the students, faculty and other people who helped us sample and identify the fossils from the Always Welcome Inn and other areas. Nate Carpenter supplied the age ranges in Table 1. Nate Carpenter, Mark Ferns, and John Lundberg reviewed the manuscript and made especially helpful suggestions regarding stratigraphy, tectonics, volcanism, and fossils.

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RECENT *MISCELLANEOUS PUBLICATIONS*

Smith, G. R., Martin, J.E., and Carpenter, N.E. 2018. Fossil fishes from the miocene Ellensburg formation, South Central Washinton. pp.1-19, figs. 11. *In*: Fishes of the Mio-Pliocene Western Snake River Plain and Vicinity. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 204, no. 4.

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