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

I. SALMONID FISHES FROM MIO-PLIOCENE LAKE SEDIMENTS IN THE WESTERN SNAKE RIVER PLAIN AND THE GREAT BASIN

by

RALPH F. STEARLEY AND GERALD R. SMITH

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COVER PHOTOGRAPH—Oncorhynchus ketops, UMMP 97500.
SALMONID FISHES FROM MIO-PLIOCENE LAKE SEDIMENTS IN THE WESTERN SNAKE RIVER PLAIN AND THE GREAT BASIN

by

Ralph F. Stearley and Gerald R. Smith
ABSTRACT

Salmon are iconic fishes of the North Pacific Rim. The evolution of Pacific salmon, formerly thought to be an ice age phenomenon, is now known to date back at least to the middle Miocene. We report nine lineages of salmons, trouts, and chars from the late Miocene in drainages of the North Pacific in North America. The lacustrine fossil fish assemblage from the Late Miocene Chalk Hills Formation (8.7 to 6.3 Ma), southwest Idaho and southeast Oregon, exhibits the greatest salmonine diversity of any Cenozoic paleontological site known – five lineages. This fauna includes *Oncorhynchus ketopsis*, a small, landlocked relative of the modern chum salmon; *Oncorhynchus salax*, a landlocked planktivorous salmon about twice the size of a kokanee; and a 35 cm landlocked sister species to the 2.4 m Pacific planktivorous salmon, *Oncorhynchus rastrosus*. An abundant 1 m redband trout, *Oncorhynchus lacustris*, and a 1.4 m char, *Paleolox larsoni* were top predators in the lakes for several million years. Salmonids comprise five of 20 species of fishes in the Chalk Hills Lake sediments. At about 6 Ma the char and two of the salmon were locally missing from the record, owing to lack of sediments, but after 4.2 Ma a trout, two salmon, and two whitefish species invaded the deep Glens Ferry rift lake. Salmonids then comprised five of 32 species. No fossil Cutthroat Trout are known from the Western Snake River Plain. A modern analog is in Kootenay Lake, in the upper Columbia River drainage, British Columbia, which hosts a large redband trout, a kokanee, a char, and two whitefish among 17 fish species. The salmonids of the lakes on the Snake River Plain pose an important hydrographic puzzle because the Columbia River drainage has only scant evidence of Miocene and Pliocene salmonids at the time of their diverse presence in the Snake River drainage. Thousands of identified fish specimens in the White Bluffs and Taunton fish faunas of Washington's Ringgold Formation, on the banks of the Columbia River above the junction with the Snake River, lacked salmonids for most of its history, but produced one pair of large *Oncorhynchus rastrosus* dentaries from the base of the section. The late middle Miocene Ellensburg fish fauna of central Washington also lacks salmonids. Fishes of the Sacramento drainage show by far the greatest faunal similarity to the Western Snake River Plain, suggesting a former aquatic connection. Idaho Batholith-age muscovites in Klamath area deposits of late Miocene-early Pliocene age, as well as fish and mollusk fossils, suggest that the ancestral Snake River flowed west to the Klamath River. Geological evidence for the capture of the upper Snake River by a tributary to the Salmon and Columbia rivers at the oxbow, near the head of Hells Canyon, was thoroughly developed by Harry Wheeler and Earl Cook in 1954. Geologic and biogeographic evidence suggest capture 3.1 Ma, and drainage of the Glenss Ferry Lake through Hells Canyon in the late Pleistocene.
FISH PALEONTOLOGY OF THE WESTERN SNAKE RIVER PLAIN

Interest in the natural resources in uncharted terrain west of the Rocky Mountains was renewed at the conclusion of the American Civil War in 1865. A series of national exploratory surveys were initiated, funded by the U.S. Congress. These surveys amassed collections of rocks, minerals, ores, plant and animal specimens, and fossils. In several locations, including the Western Snake River Plain (WSRP), the survey geologists were profoundly impressed by broad regional exposures of laminated pale sediments containing fossils of aquatic organisms—the residuals of vanished ancient lakes. In the WSRP sediments, such fossils included those of freshwater mollusks, plants, diatoms, crayfish, freshwater fishes, turtles, frogs, and mammals, which would have lived in or adjacent to ancient lakes. The fossils were forwarded to natural scientists in New England. The naturalists John Strong Newberry, Edward Drinker Cope, and Joseph Leidy studied fossil fishes from these lakebeds during the 1870s (Leidy, 1870, 1873; Newberry, 1871; Cope, 1870, 1884a). Cope (1884b) recognized that Lake Idaho represented a new Pliocene deposit, and christened its sediments the "Idaho Formation" (Fig. 1). Collectively these scientists discerned a Snake River Plain fish fauna consisting of around 20 species in eight families (but two records—a loach, Cobitidae, and a ray, Rajidae—were misidentifications, Uyeno and Miller, 1963). Fish fossils from the WSRP sediments now include representatives from six ostichthyan families: Salmonidae (salmons, trouts and whitefishes), Cyprinidae (minnows), Catostomidae (suckers); Ictaluridae (catfishes); Centrarchidae (sunfishes); and Cottidae (sculpins) (Kimmel, 1975; Smith, 1975; Smith et al., 1982). The number of fish species from the two lakes recorded by the Chalk Hills Formation and the Glenns Ferry formation is currently about 37.

E. D. Cope (1870) was the first scientist to identify a fossil trout from these sediments, which he named Rhabdofario lacustris. Since Cope's time, hundreds of individual bones of R. lacustris clearly identify it as a Pacific trout, genus Oncorhynchus (Smith and Stearley, 1989; Stearley and Smith, 1993). Oncorhynchus lacustris is the first taxon of that genus discovered in the strata of the Western Snake River Plain.

During the early part of the 20th century, sporadic field investigations began to improve our understanding of the origination and history of the lakes occupying the WSRP (Russell, 1902; Kirkham, 1931; Malde and Powers, 1962). However, early 20th-century studies of the ancient biota of these lakes were typically focused on the fossil mammals, such as those spectacularly exposed at Hagerman, near the eastern margin of the ancient lake (summarized in Ruez, 2009a). Following early exploration by R.W. Wilson (1933) and C. Lewis Gazin (1936), intensive study of WSRP Neogene mammals and their paleoecology began in the late 1950s, under Claude Hibbard and associates from the University of Michigan. At Hibbard's suggestion, Robert Miller, Teruya Uyeno, and Gerald Smith began collecting and analyzing fish bones from the Snake River Plain (c.f. Uyeno, 1961; Uyeno and Miller, 1963; Miller and Smith, 1967; Lundberg, 1975; Smith, 1975, 1987; Kimmel, 1975; Smith et al., 1982; Smith and Cossel, 2002). Many thousands of fish and other fossils are now catalogued at the University of Michigan. Smaller collections reside at the Idaho Museum of Natural History, Pocatello, the Orma J. Smith Museum of Natural History at the College of Idaho, Caldwell, and the Museum of Natural and Cultural History Condon Fossil Collection, University of Oregon, Eugene. The fish-faunal assemblage of the WSRP Neogene lakes, and particularly those of the Pliocene Glenns Ferry Formation, demonstrate that this aquatic system was a focal point for western fish biodiversity.

This report addresses fossil salmonids of the Snake River Plain and its ancient fluvial and biogeographic connections. The fossils include representatives of two whitefishes, Coregoninae, and at least five salmon, trout, and char, Salmoninae, demonstrating that diversification of these taxa occurred earlier than 8 Ma, in contrast to proposals that postulated that advances and retreats of Pleistocene ice sheets generated diversity. The migratory salmonids of the Miocene and Pliocene lakes also provide key arguments for drainage connections to the Pacific Ocean, possibly through upper Klamath basin and Pit River tributaries to the Sacramento River, prior to the capture of the ancestral Snake River by the Columbia through Hell's Canyon (Wheeler and Cook, 1954). A prior outlet through the Columbia River, through the region of the current valley of the Powder River was suggested by Livingston (1928). This region was tectonically and volcanically active, the history was complex, and many lines of geologic and biogeographic evidence are currently being investigated (see discussion below, under “Geologic and Biogeographic Evidences for Past Drainage Connections to the Pacific Ocean” and Smith and Van Tassell, this volume).

GEOGRAPHY AND GEOLOGICAL HISTORY

Pale, loosely-consolidated Miocene and Pliocene silts, sands, and tephras are exposed across a large region of southwestern Idaho and southeastern Oregon, from near Hagerman, Idaho, to Vale and Adrian, Oregon, generally flanking the strike of the modern river (Fig. 1). Typically the beds dip gently toward the present valley center. Numerous incised gullies and canyons occupied by permanent or ephemeral streams expose eroding sediments with abundant fossils, especially south of the Snake River. Sediments are often interbedded with localized basalt flows (Jenks et al., 1998).

These laminated sediments were deposited in a subsiding, fault-bounded structural basin (Malde, 1991; Wood and
Clemens, 2002; Shervais et al., 2002). The faults trend N40°W and accord with similarly-oriented structures occurring through central Oregon and into southern Washington (Brothers Fault Zone; Eugene-Denio Fault Zone; Olympic-Wallowa Lineament) apparently symptomatic of zones of deep crustal weakness (Reidel et al., 1994; Orr and Orr, 2000; Wood and Clemens, 2002). Late Neogene local basalt eruptive centers within the WSRP also are aligned in several distinct belts trending NW-SE (Bonnichsen and Godchaux, 2002).

Seismic profiles and deep drill holes demonstrate that the basement below the lacustrine fill is intruded by mafic rock. Approximate 10% extension across the 60 km wide plain is accommodated by motion along the faults and the mafic intrusions (Warner, 1975). Several volcanic units bounding the north and south sides of the WSRP indicate onset of significant faulting between 11.8 and 11.0 Ma (Clemens and Wood, 1993; Godchaux and Bonnichsen, 2002; Wood and Clemens, 2002).
Surface sedimentary units occupying the WSRP basin are included within the Idaho Group, spanning the Miocene to Late Pleistocene; 11.0 to < 1.0 Ma. Lacustrine sediments form most of four accepted formations within the Idaho Group: the Poison Creek, Chalk Hills, Glenns Ferry, and Bruneau formations (Malde and Powers, 1962) (Table 1).

Poison Creek Formation

The Poison Creek Formation is poorly exposed and remains the least-understood formation within the WSRP Neogene basin. The two primary exposures (Fig. 1) are the type section on the south side of the basin southwest of Marsing (Buwalda, 1923), and sandstones beneath the Chalk Hills lake beds, east and west of Reynolds Creek Road (Fig. 2) and north of Chalky Butte (Carpenter and Smith, this volume). Malde and Powers (1962) also record it near Sinker Creek, south of Murphy, and Squaw Creek 2 mi east of highway 95 near the north end of the Owyhee mountains, where it lies on tilted and faulted Idavada volcanics (rhyolite). Near Homedale it is overlain by Glenns Ferry Formation. It overlies extensive rhyolite flows, including ignimbrites, that were emplaced ca. 11.7 to 11.1 Ma across the basin (Godchaux and Bonnichsen, 2002; Wood and Clemens, 2002). These flows demonstrate several classes of water-interactive features that testify to the presence of a lake in the WSRP prior to the formal beginning of the Poison Creek Formation (Godchaux and Bonnichsen, 2002). The Poison Creek Formation consists of a coarse delta deposit at the type section (Sander and Wood, 2005) – a widespread, coarse, reddish sand unit, fine-grained volcanic ash, and tuffaceous water-transported sediments, interbedded with thin arkosic sands (Warner, 1975, 1977; Wood and Clemens, 2002). It is locally overlain by a basalt unit, which was confusingly termed the Banbury Basalt in older literature. [The type of the Banbury Basalt is a Pliocene-aged tholeite near Banbury Hot Springs, which is inferred to lie between the Chalk Hills and Glenns Ferry Formations (Ruez, 2009b).] Large char vertebrae are among the fossils of 10 kinds of fishes known from the Poison Creek Formation north of Chalky Butte. The Poison Creek Formation also includes two species of bullhead catfish, *Ameiurus*; four minnows: *Ptychocheilus*, two *Mylocheilus*, and *Acrocheilus*; a sucker, *Catostomus*; and a sunfish, *Archoplites* (Smith and Cossel, 2002).

Chalk Hills Formation

The Chalk Hills Formation dips ~6° to the northeast; it unconformably overlies the much-disturbed Poison Creek Formation at Chalky Butte and east of Reynolds Creek Road (Fig. 2). The Chalk Hills Formation is approximately 100 meters thick and includes the Hot Creek limestone (Straccia et al., 1990), a reef-like microbialite unit that helps diagnose a balanced-filled, volcanically-mediated lake basin (Bohaea...
formation of opal-CT and zeolites, indicating a lake of low-to-moderate salinity, and a pH of 7-9. Dates on volcanic ash beds within the Chalk Hills Fm. range from 8.5 to 5.9 Ma (Kimmel, 1982; Perkins et al., 1998; Perkins and Nash, 2002; Carpenter and Smith, this volume). The Walcott Tuff, a prominent marker bed in the eastern Snake River Plain dated to 6.27 Ma, is present in the uppermost Chalk Hills Formation (Perkins et al., 1998; Morgan and McIntosh, 2005).

Three species of salmon, one species of trout, and one char are most common in deepwater and shoreface facies near Horse Hill and Browns Creek in Idaho, and the Vines Hill, Adrian, and Vale, areas in Oregon. They are not known from the shallow (warm) reef-like facies (Straccia et al., 1990; Bohacs, 2013: fig. 14) at the southeast end of the basin. Berenek et al., (2006) presented detrital zircon evidence that at the time of deposition of Chalk Hills sediments, the lake was isolated by thermal bulge of the Twin Falls volcanic field from Snake River drainage originating in the Idaho-Wyoming thrust belt.

### Glenns Ferry Formation

The Chalk Hills Formation, dipping 6° northeast, and the Glenns Ferry Formation, dipping 3° northeast, are separated by a low-angle unconformity (Fig. 3) east of Horse Hill. A floodplain mudstone is the base of the Glenns Ferry Formation locally; it underlies a widespread transgressive beach deposit.

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Table 1.— Stratigraphy (Malde & Powers, 1962) and numbers of salmonids through Neogene time on the Western Snake River Plain.

<table>
<thead>
<tr>
<th>AGE</th>
<th>ROCK UNIT</th>
<th>SALMONIDAE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1−</td>
<td>Black Mesa Gravel</td>
<td>Oncorhynchus lacustris</td>
</tr>
<tr>
<td>2−</td>
<td>Bruneau Formation</td>
<td></td>
</tr>
<tr>
<td>3−</td>
<td>Tuana Gravel</td>
<td>Prosopium prolixus</td>
</tr>
<tr>
<td>4−</td>
<td>Glenns Ferry Fm.</td>
<td>Prosopium sp.</td>
</tr>
<tr>
<td>5−</td>
<td>Glens Ferry Fm.</td>
<td>Oncorhynchus lacustris</td>
</tr>
<tr>
<td>6−</td>
<td>Glens Ferry Fm.</td>
<td>Oncorhynchus salax</td>
</tr>
<tr>
<td>7−</td>
<td>Chalk Hills Fm.</td>
<td>Oncorhynchus tshawytscha</td>
</tr>
<tr>
<td>8−</td>
<td>Chalk Hills Fm.</td>
<td>Paleolox larsoni</td>
</tr>
<tr>
<td>9−</td>
<td>Chalk Hills Fm.</td>
<td>Oncorhynchus lacustris</td>
</tr>
<tr>
<td>10−</td>
<td>Poison Creek Fm.</td>
<td>Paleolox larsoni ?</td>
</tr>
<tr>
<td>11−</td>
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</table>

Figure 3.— Angular unconformity between Chalk Hills Formation (lower) and Glenns Ferry Formation (upper), east of Horse Hill. Unconformity surface lies 5 feet above head of geologist Nathan Nelson, (USFS). Photo by R. Stearley.
fining upward from orange quartzite cobbles derived from the Jarbridge mountains at the head of the Bruneau River. Further north, the Shoofly Oolite (Swirydczuk et al., 1979, 1980) northwest of Horse Hill is interpreted as a transgressive beach deposit evidencing the return of the lake. On the east, the Glenns Ferry Formation directly overlies the Banbury Basalt, dated to 4.4 Ma (Armstrong et al., 1975; Ruez, 2009b). The maximum thickness of the Glenns Ferry Formation approaches 700 meters. It consists mostly of friable tan silts, very-fine gray sands, often micaceous, and numerous thin tephra laminae (Swirydczuk et al., 1982). Flood-plain sediments, occasional shale, and associated fossils are prominent in the Hagerman area. Glenns Ferry lake beds extend from Peters Gulch at the west end of the Hagerman beds to Blackjack Butte in Malheur County, Oregon (Kimmel, 1975).

Three species of salmonids – two salmon and the char – disappeared from the Snake River Plain during the hiatus between the Chalk Hills and Glenns Ferry lakes. *Oncorhynchus ketopsis* and *O. rastellus* (described below) die out, but *O. salax* and *lacustris* remain in the Glenns Ferry Lake. Presence of *O. salax* is evidence for continuation of lacustrine habitat in the basin. Rare fossils of migratory *O. tshawytscha* in the Glenns Ferry Formation indicate an occasional through-flowing outlet to the Pacific Ocean. A large whitefish in the genus *Prosopium* is common in Glenns Ferry sediments. A smaller species, represented by distinct maxillae and dentaries, is less common. Thirty-two species of fishes are recorded from Glenns Ferry sediments (Table 2). The fish fauna is dominated by minnows (Cyprinidae), sculpins (Cottidae), and suckers (Catostomidae). The Glenns Ferry Formation has produced 109 species of mollusks (D.W. Taylor in Malde and Powers, 1999) and many species of ostracods (Swain, 1986, 1999), and many species of diatoms.

**SALMONID FISHES OF THE WESTERN SNAKE RIVER PLAIN**

Salmonid systematists divide the group into three clades, variously considered families or subfamilies (Sanford, 2000): the whitefishes (subfamily Coregoninae); graylings (Thymalinae); and trouts, chars and salmon (Salmoninae) (Norden, Table 2.— Comparison of Chalk Hills and Glenns Ferry fish species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Chalk Hills Fm.</th>
<th>Glenns Ferry Fm.</th>
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<tbody>
<tr>
<td>Family Ictaluridae</td>
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</tr>
<tr>
<td><em>Ameiurus vespertinus</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Ameiurus peregrinus</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Family Cyprinidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Orthodon hadrognathus</em></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>* Ptychocheilus arciferus*</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>* Mylopharodon hagermanensis*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>* Mylocheilus robustus*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>* Mylocheilus kingi*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Mylocheilus inflexus*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Acrocheilus latus*</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>* Lavinia hibbardi*</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>* Gila (Klamathella) milleri*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Richardsonius durranui*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Rhinichthys osculus*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Family Catostomidae</td>
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</tr>
<tr>
<td><em>Deltistes shoshonensis</em></td>
<td>X?</td>
<td>X</td>
</tr>
<tr>
<td>* Deltistes wyhewee*</td>
<td>X?</td>
<td>X</td>
</tr>
<tr>
<td>* Chasmistes spatulifer*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Catostomus cristatus*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Pantosteus oromyzon*</td>
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<tr>
<td>Family Salmonidae</td>
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<tr>
<td><em>Prosopium prolirx</em></td>
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<tr>
<td>* Prosopium sp.*</td>
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<tr>
<td>* Paleolox larsoni*</td>
<td>X</td>
<td></td>
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<tr>
<td>* Oncorhynchus lacustris*</td>
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<td>* Oncorhynchus salax*</td>
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<td>* Oncorhynchus ketopsis*</td>
<td>X</td>
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<tr>
<td>* Oncorhynchus tshawytscha*</td>
<td>X</td>
<td></td>
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<tr>
<td>* Oncorhynchus rastellus*</td>
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<tr>
<td>Family Centrarchidae</td>
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<tr>
<td>* Archoplites taylori*</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>* Archoplites sp.*</td>
<td>X</td>
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<tr>
<td>Family Cottidae</td>
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<tr>
<td>* Cottus calcatus*</td>
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</tr>
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<td>* Cottus cf. bairdi*</td>
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<td>* Kerocottus hypocceras*</td>
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<td>* Kerocottus sp. 1*</td>
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<td>* Kerocottus sp. 2*</td>
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Figure 4a.— Fossil *Prosopium* dentaries from the Glenns Ferry Formation: a, *Prosopium* sp., UMMP V58270 pt, left dentary, mesial view; b-d, *Prosopium prolirx*, UMMP V58270, three dentaries, mesial view; e, above and left, *Prosopium prolirx*, UMMP V86641 pt, two right dentaries, mesial view; e, below, *Prosopium* sp., UMMP V86641 pt, right dentary, mesial view; f, *Prosopium prolirx*,UMMP V58270, 2 dentaries, lateral view; g, *Prosopium prolirx*, UMMP V59300, left dentary, mesial view; h, *Prosopium* sp., UMMP V62420, right dentary, mesial view; i, *Prosopium prolirx*, UMMP V 62030, biting edge of left dentary, dorsal view; j, *Prosopium prolirx*, UMMP V50633, left dentary, lateral view.
in features of the anterior articular surface, demonstrating presence of two species of Prosopium (Fig. 4a, 4b); analogous to the species flocks of Prosopium in Bear Lake, Utah and Idaho; and Coregonus (Leucichthys) in the Laurentian Great Lakes (Smith and Todd, 1984).

**SALMONINAE**

Salmonines exhibit many osteological characters that distinguish them from coregonines or thymallines. The frontals are expanded above the sphenotics and extend posteriorly, to form the anterior floor of the post-temporal fossa. The pterotic bears a long fossa for the articulation of the dorsal hyomandibular edge. The mesopterygoid overlaps the quadrate. A suprapercole is present. In the tail, the stegural (formed from uroneurals) is expanded into a pair of fan-shaped plates.

The oldest discovered fossil salmonine, *Eosalmo driftwoodensis*, is also the most plesiomorphic member of the clade (Wilson, 1977; Wilson and Li, 1999). It exhibits all of the synapomorphies listed above, but does not possess some shared derived features common to all extant or fossil salmonines, such as the separation of the pariets by posterior extension of the frontals.

A number of plesiomorphic salmonine taxa are extant today, occupying a belt of lakes and rivers extending from the Atlas Mountains and Europe, through the Balkans, Turkey, Armenia, and Siberia to Mongolia, Northern China, and Korea. The modern lenok, *Brachymystax lenok*, is the best understood of these; but it remains controversial. *Brachymystax* and the other plesiomorphic trouts exhibit small maxillae with a convex ventral edge bearing tiny teeth, much as in grayling and *Eosalmo*. The vomerine teeth are similarly small and form a simple arched row along the anterior edge of the bone and are thus unlike those of *Salvelinus*, *Salmo*, and *Oncorhynchus* (but oriented like the vomerine tooth row in *Hucho* and *Paleolox*). On the other hand, the modern genera *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus* all exhibit elongate maxillae, lacking a convex ventral edge, a metapterygoid not in broad contact with the symplectic, and other synapomorphies, leading Stearley and Smith (1993) to consider these fishes a derived sub-clade, the Eusalmonina. Stearley and Smith treated the more plesiomorphic trouts informally as “archaic trouts,” spanning the morphological gap between *Eosalmo* and the eusalmonines. Within their Eusalmonina, the Huchen (*Hucho*) plus chars (*Salvelinus*) are sister genera; the Atlantic salmon and trouts (*Salmo*) and the Pacific salmon and trouts (*Oncorhynchus*) are sisters.

**COREGONINAE**

Coregonine fishes are diagnosed by many osteological characters, including cranial characters (Norden, 1961; Cavender, 1970) which occur in fossils and in deposits of the Western Snake River Plain (Smith, 1975: p. 15, fig. 7). The coregonine maxilla is toothless. It is flat and bladelike with a convex lower margin, and terminates anteriorly in a distinctive rounded process for the connection to the premaxilla. The premaxilla is small; it and the anterior dentary bear a few vestigial teeth or none at all. The retroarticular process of the angular-articular extends to the posterior and is not bent dorsally, leaving an open angle for articulation with the quadrate. The parietals meet at the midline (in salmonines, the parietals are excluded from mutual contact by posterior extension of the frontals). Correspondingly, frontals have a square posterior border.

The genus *Prosopium* encompasses the round white-fishes. Osteological characters which uniquely characterize *Prosopium* within coregonines include long and slender dermethylene lacking a posterior notch; and high angles on the coronoid processes of the angular-articular and on the dentary, which, when articulated, yield a gap in the middle of the articular fit (Cavender, 1970).

Miller and Smith (1967) listed *Prosopium* among the taxa of Glenns Ferry Formation, but did not comment further. Smith (1975) diagnosed the species *Prosopium prolixus* based on characters of the dentary (Fig. 4a), maxilla (Fig. 4b), angular-articular, and hyomandibula (Smith, 1975: fig. 7). The maxillary length-to-depth ratio is extreme, averaging 4 to 5; the species name, *prolixus*, refers to this elongation. Small maxillae and dentaries from the Glenns Ferry Formation differ from all other extant or fossil salmonines. A number of plesiomorphic taxa are extant today, occupying a belt of lakes and rivers extending from the Atlas Mountains and Europe, through the Balkans, Turkey, Armenia, and Siberia to Mongolia, Northern China, and Korea. The modern lenok, *Brachymystax lenok*, is the best understood of these; but it remains controversial. *Brachymystax* and the other plesiomorphic trouts exhibit small maxillae with a convex ventral edge bearing tiny teeth, much as in grayling and *Eosalmo*. The vomerine teeth are similarly small and form a simple arched row along the anterior edge of the bone and are thus unlike those of *Salvelinus*, *Salmo*, and *Oncorhynchus* (but oriented like the vomerine tooth row in *Hucho* and *Paleolox*). On the other hand, the modern genera *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus* all exhibit elongate maxillae, lacking a convex ventral edge, a metapterygoid not in broad contact with the symplectic, and other synapomorphies, leading Stearley and Smith (1993) to consider these fishes a derived sub-clade, the Eusalmonina. Stearley and Smith treated the more plesiomorphic trouts informally as “archaic trouts,” spanning the morphological gap between *Eosalmo* and the eusalmonines. Within their Eusalmonina, the Huchen (*Hucho*) plus chars (*Salvelinus*) are sister genera; the Atlantic salmon and trouts (*Salmo*) and the Pacific salmon and trouts (*Oncorhynchus*) are sisters. Sanford (2000) included *Brachymystax* as a member of the huchen plus char clade, which collectively he termed the “Salvelini”; but did not examine the systematic position of the remainder of the archaic trouts. Wilson and Williams (2010) derived a different tree, in which *Brachymystax* is an archaic trout; *Hucho* is paraphyletic and hence split into two genera; and the odd endemic taxa *Acantholingua*, *Salmothymus*, and
Figure 5a.—Type specimen of *Paleolox larsoni*, UMMP 62222. Collected by Peter Kimmel, Tunnel Mountain Locality, Malheur County, Oregon. Top: right posterior jaw and suspensiorium. Bottom: Right view of posterior cranium. Symbols: Ang, Angular-articular; Atl, Atlas; Boc, Basioccipital; Cer, Ceratohyal; Den, Dentary; Dsp, Dermosphenotic; Fro, Frontal; Hyo, Hyomandibula; Max, Maxilla; Mpt, Metapterygoid; Oc, Ocular; = Sclerotic; Pop, Preopercle; Psp, Parasphenoid; Pto, Pterotic; Qua, Quadrade; SMax, Supramaxilla; So, Supraorbital; Sph, Sphenotic; Sym, Symplectic.

Figure 5b.—Type specimen of *Paleolox larsoni*, continued. Top: dorsal view of posterior cranium. Bottom: close-up of hyoid region. Ang, Angular; Br, Branchiostegal; Cer, Ceratohyal; Epi, Epiotic; Fro, Frontal; Hph, Hypohyal; Hyo, Hyomandibula; Par, Parietal; Pto, Pterotic.
Figure 6.— Laterally-compressed cranium and shoulder girdle of *Paleolox larsoni*, UMMP V22270, collected by Bruce Wilkinson from the Chalk Hills Formation, Browns Creek locality, Owyhee County, Idaho.

*Platysalmo*, which Stearley and Smith considered archaic trouts, are treated as plesiomorphic subgenera of *Salmo*, related to the European Brown Trout, *Salmo trutta*. Molecular data (Phillips and Oakley, 1997; Crespi and Fulton, 2003; Crete-Lafreniere, Weir and Bernatchez, 2012) suggest that *Oncorhynchus* is the sister clade to *Salvelinus*, rather than *Salmo*. This interpretation, based on a small number of genes, is inconsistent with extensive morphological studies (Stearley and Smith, 1993; Sanford, 2000; Wilson and Williams, 2010), which are presumably based on a much larger sampling of non-neutral genes responsible for development, morphology, and physiology, and more likely to reflect evolutionary history.

**FOSSIL ARCHAIC SALMONINES IN NORTH AMERICA**

Two clades of Salmoninae are represented in the Late Cenozoic fossil record in western United States--*Oncorhynchus*, the Pacific salmons and trouts; and the clade comprising *Hucho*, *Paleolox*, and *Salvelinus* (Fig. 5, 6, 7, 8, Table 2, 3). Each has many relatives in Asia and an inferred history of more than 30 million years prior to the occurrences reported here. The phylogeny of *Salvelinus* and its relatives is outlined in Figure 8. Within the *Oncorhynchus* clade of Pacific-basin trouts and salmons, the Cutthroat Trout group represent the most ancient branching event; next the Redband and Rainbow Trout lineage, and then the series of Pacific salmons (Stearley and Smith, 1993; Smith and Stearley, in prep.). The most derived extant Pacific salmons are those termed “Type A” by Hikita (1962): Chum Salmon, Pink Salmon, and Sockeye Salmon and their fossil relatives (Stearley and Smith, 1993, see discussion below). Late Miocene and Pliocene fossils do not clearly indicate vicariance (however, a prior Miocene vicariant separation between the lineages of Atlantic-basin trouts and salmon, genus *Salmo*, and Pacific-basin trouts and salmon, *Oncorhynchus*, is inferred [Stearley, 1992]). Here we report on the Late Miocene and Pliocene chars, trouts, and salmons known to us from the Western Snake River Plain and Great Basin.
Paleolox larsoni

Late Miocene sediments of the WSRP host a large predatory char-like salmonin. Kimmel (1975) described and named this taxon as a new genus, *Paleolox*, from sediments of the Chalk Hills Formation in Malheur County, Oregon, and Owyhee County, Idaho. The suffix “lox,” with various spellings, means salmon in numerous European languages. The early specimens were mistakenly attributed to the Deer Butte Formation and the Glenns Ferry Formation, respectively by Kimmel (1975) and Smith (1975), before the discovery of the broad extent of the Chalk Hills formation and the unconformity between it and the overlying Glenns Ferry Formation. The taxon was referred to *Salvelinus larsoni* by Stearley and Smith (1993: fig. 11, table 2). The WSRP material now includes a diversity of skulls, jaws and neurocrania previously listed under other genera (c.f. Kimmel, 1975; Smith, 1975; Smith et al., 1982; Stearley and
Smith, 1993; Smith et al., 2002). Smith and Cossel (2002) recorded *P. larsoni* in the Poison Creek Formation as well as the Chalk Hills Formation.

The type specimen of *Paleolox larsoni*, UMMP 62222, represents an individual longer than 1 m in standard length (Fig. 5a-b). It possesses a basioccipital: vertebral junction 21 mm in diameter. The Wilkinson specimen (discussed below), collected by Bruce Wilkinson from the Chalk Hills Formation (Fig. 6), represents an individual about 120 cm in standard length. The largest specimen, a neurocranium (UMMP 116957) collected by Ralph Stearley from Browns Creek, Owyhee County, Idaho, has a basioccipital condyle 29 mm in diameter, 38 percent larger than the holotype – possibly 138 cm in standard length or 1.7 m (5.6 ft) total length.

The holotype’s ceratohyal is long and slender, resembling that of *Hucho* or *Salvelinus*, unlike that of *Oncorhynchus*. The maxilla is flat, uniquely deep, and bladelike and the stout premaxillary process exits mesially at a high angle (Kimmel, 1975), as in modern *Salvelinus* and *Hucho*. The anterior and posterior borders of the quadrate form an obtuse angle where they intersect across the mandibular articulatory surface (condyle), a primitive character state, which is present in *Hucho* and some species of *Salvelinus* but not *Salmo* or *Oncorhynchus*. The anterior part of the dentary and the vomer are not present on the holotype, but are well represented on other specimens.

The Wilkinson specimen is a large, laterally-compressed cranium plus shoulder girdle from the Chalk Hills Formation at Browns Creek. This cranium (Fig. 6) exhibits all of the above characters, and with associated material from Browns Creek, provides many more particulars of the anatomy. Notably, the vomer (UMMP 69018 and 22269) demonstrates the combination of the transverse anterior tooth row characteristic of *Hucho*; and the antero-posterior row of teeth anchored on an elevated crest similar to *Salvelinus namaycush* (the teeth forming a “T”-shaped pattern) (Fig. 7). The vomer thus demonstrates morphological intermediacy between *Hucho* and derived *Salvelinus*, with flared posterolateral processes on the basal plate, which are unique. Because the fossil manifested the synapomorphy of the raised tooth crest, computer-calculated trees included this form within the genus *Salvelinus*, as the most primitive member of this clade (Stearley and Smith, 1993). The specimen apparently has five infraorbital bones. Reinvestigation of the cladogram, based on a review of all fossil material identifies *Paleolox larsoni* as a distinct branch more terminal than *Hucho* and near the base of the *Salvelinus* clade (Fig. 8).

During the past few decades, three or more mid-to-late western U.S. Miocene lakebeds have produced fossils assignable to *Salvelinus or Hucho*, or to an intermediate form. The Miocene Clarkia Lake (15.7 Ma, Geraghty et al., 2016) in northern Idaho contains a salmonid that Smith and Miller (1985) assigned to “probably” *Hucho* (the vomer of this fish is unknown) and Late Miocene localities in western Nevada have produced two distinct fossil chars (Fig. 9) (Cavender and Miller, this volume; Stearley and Cavender, in prep).
Table 3. — Node support for salmonine cladogram, Figure 8.

1. Eusalmonia:
   - Prootic foramen for exit of trigeminal-facial displaced postero-medially
   - Orbitosphenoid without anterior emargination
   - Metapterygoid not in broad contact with symplectic
   - Maxilla extends posterior to orbit
   - Maxilla straight to arched, without convex ventral edge
   - Coronoid process of dentary shallow

2. Salmonini:
   - Anterior transverse tooth row on vomer reduced
   - Vomer with anterior extension in breeding males
   - Maxillae ovate to round in cross-section
   - Ascending process of premaxilla posteriorly deflected and merged with body
   - 2nd infraorbital is tubular, not bladelike
   - Kype on dentary

3. Salvelini:
   - Sphenotic with stout anterior ramus and open lateral face
   - Supramaxilla long, slender, pointed and slightly sigmoid
   - Parasphenoid straight or nearly so in sagittal view
   - Basibranchial teeth and plate present (plesiomorphic)

4. Orbitosphenoid unknown in Clarkia form—see node 10 below
   - Presence/absence of pale spots unknown
   - BUT scales large—see node 13

5. Hucho:
   - Hyomandibula lateral face square
   - Pyloric caeca count high
   - Dentary deep anterior to Meckelian groove

6. H. perryi:
   - Ethmoid ossified
   - Small median denticles on basibranchial plate
   - Hyomandibula with curved, pointed extension on ventro-anterior corner

7. H. hucho + H. taimen:
   - > 67 vertebrae
   - No basibranchial tooth plate

8. H. hucho:
   - “hourglass”-shaped dermethmoid

9. H. taimen:
   - Posterior vomer constricted laterally
   - Caudal and anal fin red

10. Paleolox plus Salvelinus:
    - Orbitosphenoid oval in cross-section.
    - 5 infraorbitals (lacrimal, 2-5)

11. Clarkia form

12. P. larsoni:
    - Vomer tooth pattern unique, and vomer with paired posterior prongs
    - Numerous basibranchial teeth
    - Parasphenoid overlaps atlas ventrally

13. Salvelinus sensu strictu:
    - Scales small
    - Lateral line scales reduced
    - Coronoid height reduced; < .25 mandibular length
    - Pale spots
    - Prominent white leading edge on fins

14. S. alpinus + S. malma:
    - Dermethmoid spade-shaped, with prominent midlength constriction
    - Frontals do not form part of post-temporal fossa
    - Parasphenoid arched
    - Frontals gabled at midline sensu Cavender
    - Vertebral count > 61

15. S. fontinalis + S. leucomaeenis + S. namaycush + S. confluentus:
    - Hyomandibular face broad and dished (concave laterally)
    - Adductor ridge on hyomandibula reduced to near-absence or complete absence
    - Spotting pattern elaborated as vermiculations (absent in confluentus)

16. S. alpinus:
    - No morphologic apomorphies

17. S. malma:
    - Gill raker count high; > 25

18. S. namaycush + S. confluentus:
    - Metapterygoid extends extremely high, dorsally
    - Vertebrae > 61

19. S. fontinalis:
    - Extreme reduction of lower limb of preopercle
    - Basibranchial teeth frequently absent

20. S. leucomaeenis:
    - Numerous white spots

21. S. namaycush:
    - Pyloric caeca > 70
    - Nuptial tubercles present

22. S. confluentus:
    - Vermiculations absent
Figure 9.— cf. *Hucho* from the Clarkia Lake Beds, type section, locality P-33, St. Maries River valley, Idaho. Photograph by C. J. Smiley, reproduced in Smith and Miller, 1985.
fossils document a radiation of *Salvelinus* and *Hucho*-like forms in the Columbia-Great Basin region prior to 10 Ma.

Apomorphies that diagnose *Paleolox* include: “T”-shaped tooth pattern on the prevomer with 5-8 teeth in an anterior transverse row, preceded by a semicircular crest, 9 teeth in a midventral crest, two posterolateral prongs extending at a 35° angle (also in *Salvelinus namaycush*), deep maxilla with the anterior process at a high angle, uniquely deep dentary, a large pointed and winged basibranchial with over 47 teeth (Fig. 7); large scales, an “L”-shaped preopercle with a short lower limb, and no kype on the dentary. Posterior extension of the ventral processes of the basioccipital, and posterior flanges of the parasphenoid, overlap the entire ventral edge of the atlas (Fig. 7).

**FOSSIL PACIFIC SALMONS AND TROUTS**

*Oncorhynchus*

Salmonines belonging to the clade *Oncorhynchus* (Pacific-basin trouts and salmons) are diagnosed by the following characters: a prominent posterior notch in the dermethmoid; contact between the intercalar and the prootic; long postorbitals covering most to all of the hyomandibula; a tubular 2nd infraorbital; a greatly reduced lower limb of the preopercle; three epurals; the suture between the articular-angular and the retroarticular at a high angle; and the inflection of the premaxillary process of the maxilla directly mesial of the maxilla (i.e., not inflected dorsally), or even flat and inflected ventrally (Stearley and Smith, 1993).

Within *Oncorhynchus*, a clade consisting of the fossil taxon *Oncorhynchus lacustris* (see below), extant *Oncorhynchus mykiss* (Redband and Rainbow trouts) and all fossil and extant Pacific salmons can be diagnosed by characters including a "square" ceratohyal; a dermethmoid with expanded posterior margin, such that along with the posterior notch previously noted, the dermethmoid is distinctly “A”-shaped; frontals exhibiting a laterally-expanded shelf above the orbit; and lateral ethmoids square.
Figure 11.— Holotype *Oncorhynchus belli* n. sp., UMMP V74362. Top: complete specimen. Bottom: Closeup of cranium. Art, articular-angular; Clei, Cleithrum; Den, Dentary; Deth, dermethmoid; Ept, Epiphydroid; Fro, Frontal; Hyo, Hyomandibula; Iop, interopercle; Max, Maxilla; Mpt, Metapterygoid; Op, Opercle; Pmx, premaxilla; Pop, Preopercle; Psp, parasphenoid; Ptp, pterygoid; SMax, Supramaxilla.

Fossil Cutthroat-lineage trouts of the pre-Lahontan drainage basin.

To date, skeletal elements that can be identified as a cutthroat trout are significantly absent from this drainage. However, cutthroat trouts were present in adjacent basins. Because this biogeographic datum is significant for our current analysis, we here examine the fossil plesiomorphic (*O. clarkii*-series) trout from 10 Ma Truckee Formation of westernmost Nevada.

Laminated diatomites of Mid- to Late Miocene age are quarried extensively for industrial use in northeastern Lyon County, and adjacent Churchill County, Nevada, southeast of the town of Fernley (Moore, 1969; Houseman, 2004). Diatomites in several isolated basins parallel the course of the Truckee River, and are assigned to the Truckee Formation (King, 1878; Houseman, 2004). Five genera of fossil fishes (*Fundulus, Gasterosteus, Siphateles, Ameiurus, and Oncorhynchus*) as well as fossil shorebirds, snakes, a frog, and a salamander are known from these beds (Baumgartner, 1982; Bell, 1994; Smith et al., 2002). Michael Bell and associates have been intensively quarrying fossil sticklebacks, *Gasterosteus doryssus*, for the past 3 decades from these beds, at the Celite Quarry (Fig. 10). The stratigraphy and geologic context are well-established. The fossil fishes collected here, including the *Oncorhynchus* specimens, are from a vertical sequence spanning around 100,000 years, based on detailed varve counts, and dated by a contained ash at 10.2 Ma (Bell, 1994; Bell, personal communication).
Systematic Paleontology:

Teleostei
Salmoniformes
Salmonidae
Genus *Oncorhynchus* Richardson

*Oncorhynchus belli* new species

Type Locality.— Nevada, Lyon County, Truckee Formation, 39.526 N. Latitude, 119.04 W. Longitude, (Two Tips Quadrangle, Nevada 15-minute series topographic, USGS) in pale laminated diatomite. Varve counts within this sequence provide an approximately 100,000-yr. time span; a volcanic ash layer within this sequence is dated at 10.2 Ma.

Holotype.— Figure 11, UMMP V74362, a single, laterally-compressed fish, 22 cm long, with the left side exposed. A few vertebrae are missing in the thoracic region, but at least 28 caudal and 27 thoracic vertebrae can be discerned; total vertebral count is 59 or 60. Both pelvic fin plates are present; most of the dorsal fin is intact, with 12 rays, the anal fin is intact and bears 12 rays. Most of the branchiostegal rays are missing. Some cranial elements are intact; others are fragmental.

Paratypes.— Figure 12, UMMP 42380, a laterally-compressed juvenile, 10 cm long; as part and counterpart. Both parts contain partial sagittal sections of the skull roofing bones. The part provides internal view of right dentary, left and right preopercles; left lateral ethmoid; partial paraphephenoid, partial left cleithrum, folded left pectoral fin and interior view of right pectoral fin, with 12 rays. Counterpart includes interior view of left premaxilla; interior of left dentary; paraphephenoid; right supracleithrum. Dorsal fin with 12 rays; anal fin with 12 rays. Almost all of the branchiostegal rays are missing.

Diagnosis.— The taxon demonstrates numerous synapomorphies of the genus *Oncorhynchus*, including a palmate, ventrally-directed premaxillary process of the maxilla; a pre-opercle with reduced lower limb and rounded anterior margin of the lower limb; a deep subopercle, and three epurals. Within the genus *Oncorhynchus*, it is plesiomorphic, lacking many synapomorphies that diagnose the derived clade (*O. mykiss* +...
Pacific salmons). *Oncorhynchus belli* is sister to the extant Cutthroat Trout, *O. clarkii*, based on the shared synapomorphy of an expanded flange on the anterior post-temporal. The hyomandibula is apomorphic in *O. belli*: the anterior flange extending ventrally almost to the ventral border of the posterodorsal process.

**Description.**—Salmonine fish with fan-shaped stégural in the caudal skeleton and with three epurals; dentaries and maxillae stoutly toothed; short, oval supramaxilla; hyomandibula square (i.e., not dish-shaped) and apomorphic, as noted above. The cleithrum and urohyal, visible in the type specimen, are typical for salmonines. Metapterygoid with high dorsal flange, characteristic of eusalmonines. The trigemino-facial foramen of the prootic is expanded and in lateral position, a feature of eusalmonines. The parasphenoid is straight in profile, as viewed from the side. The maxilla is straight and not flattened side-to-side; not inflected nor flattened as occurs in *Salvelinus*. The premaxillary process of the maxilla is palmate and ventrally-directed, as in *Oncorhynchus* and not as in *Salvelinus, Paleolax, Hucho, or Salmo*. The premaxilla is a nearly-equilateral triangle in overall outline; the dorsal process is not strongly inflected to posterior (as is the case for Rainbow and Redband trouts and Pacific Salmons) and includes a median dorsally-directed rod-like buttress. The opercular bones demonstrate several features diagnostic of *Oncorhynchus*, including a reduced lower limb of preopercle with rounded anterior margin; inferred deep subopercle based on the positioning of the opercle relative to the preopercle. The anterior dentary possesses a stout median shelf. There are 12 anal fin rays, fewer than the 13+ possessed by Pacific Salmons. The frontals are intermediate in shape and ornament between modern *O. clarkii* and *O. mykiss* in that they exhibit more surficial rugosity and anterior edge convolution than in *O. clarkii*, but less development of an anterior shelf than in *O. mykiss*. The antero-dorsal edge of the post-temporal exhibits a flange like that of *O. clarkii*. The basihyoid demonstrates at least two tooth sockets on the dorsal side of the bone.

**Etymology.**—The species name, *belli*, honors Michael Bell for his extended program of paleontological research and discovery in the Truckee fauna, which yielded the type and paratype specimens as well as numerous major contributions to evolutionary biology.

**Discussion.**—Some scales are preserved; these are moderately small and ovate. The low vertebral count and the presence of some basihyal teeth, are concordant with a plesiomorphic member within the *Oncorhynchus* clade. The frontal does not possess a marked anterior shelf above the orbit, a feature shared by redband trouts (*O. mykiss*,...
O. lacustris) plus Pacific salmons. The lower limb of the preopercle, while reduced relative to the dorsal limb and possessing a rounded anterior margin, is not so reduced as in the Redband Trout and Rainbow Trouts and Pacific Salmons. The dentaries closely resemble those of modern Cutthroat Trout. The presence of a flange on the antero-dorsal edge of the post-temporal is a derived feature shared with extant Cutthroat Trouts. The parasphenoid is straight in lateral view; a character state shared with the Mexican Golden Trout, Oncorhynchus chrysogaster. Phylogenetically, this taxon is a primitive member within the Oncorhynchus clade, sharing traits with the most primitive extant members (c.f. Stearley and Smith, 1993), O. chrysogaster and O. clarkii.

Inferred life history.—These two trouts are the only specimens obtained from lacustrine diatomites that have been investigated by Michael Bell and his teams of paleontologists, and which have produced thousands of specimens of sticklebacks, Gasterosteus doryssus; and many Fundulus. The diatoms indicate a temperate lake, perhaps slightly saline. We conclude that these two specimens represent an ecologic complement, which mostly inhabited the colder tributary streams; perhaps entering the warm lacustrine waters to feed or after death.

Biogeography.—The Truckee diatomite lakes formed in a series of low-elevation transtensional basins along the western margin of the Mesozoic-Paleogene high plateau, the Nevadaplano, as it disassembled during the Neogene (c.f. Sonder and Jones, 1999; Wallace, 2003; DeCelles, 2004; Dickinson, 2006; Henry, 2008). Dated ash-filled paleovalleys which cross the current crest of the Sierra Nevada indicate that drainages linked the Walker Lane of western Nevada to the Great Valley and to the sea during the middle Cenozoic, while a major drainage divide existed further eastward in Nevada. Miocene drainage connections extended between the Lahontan Basin and Owens Valley, as well (Phillips, 2008). Sticklebacks and Fundulus cannot swim upstream against a strong gradient and are presumed to have colonized the warm diatom-rich lakes through low-gradient streams from coastal habitats lying to the west or southwest (Bell, 1994; Smith et al., 2002). While intermittent connections may have existed from the western Basin and Range province north to the Oregon-Idaho graben (and further north) during the middle Miocene, the absence of cutthroats such as O. belli from the Late Miocene-Pliocene salmonid community of the Western Snake River Plain (and the absence of Western Snake River Plain taxa from NW Nevada sites) indicates disjunction between the pre-Lahontan and Snake River drainages at that time.
Figure 15.— *Oncorhynchus salax*. **a**, Type specimen, UMMP V62100, collected by Beverly Smith, June, 1974; **b**, UMMP 97499 distal left dentary, mesial view, of breeding individual; **c**, UMMP V97499, dissected to display gill rakers.

**Fossil Redband-group trouts**

*Oncorhynchus lacustris*

The ancient trout, *Oncorhynchus lacustris* (Fig. 13) was first documented by E. D. Cope (1870) as *Rhabodofario lacustris*, based on an anterior cranium plus several isolated maxillae and one isolated dentary and palatine. Since that date, several more complete crania have been discovered, plus many hundreds of isolated cranial elements, in some cases with associated vertebrae. In 1975, Smith redescribed *O. lacustris* based on a better specimen, UMMP 59265, which included much of a cranium plus 20 vertebrae. Smith and Stearley (1989) demonstrated that this trout is a member of the genus that includes all Pacific-basin trouts and salmon, *Oncorhynchus*, and is anatomically similar to modern redband trout, *O. mykiss*, (Stearley and Smith, 1993). In life, individuals represented by these fossils would have ranged up to 60 cm or more in standard length.

The dentary, maxilla, premaxilla, and palatine of this trout are robust (Fig. 13, 14) but less so than *P. larsoni*. The premaxilla is wedge-shaped, tapering anteromesially, and lacking a pronounced ventrally-concave profile. The tapering
Figure 16.—a. *Oncorhynchus ketopsis*. Type specimen, UMMP 97500, Coyote Gulch, Malheur Co. Oregon. b. Premaxilla of *O. tshawytscha*, Late Pliocene Glenns Ferry Formation at small Butte 6 mi south of Grandview, Owyhee County, Idaho. Left, internal view, right external view. Length of bone 52 mm.

Profile is morphologically equivalent to the posterior deflection of the process for articulation with the dermethmoid; a derived character state typical of *Salmo* and *Oncorhynchus*, but unlike that in *Salvelinus*. The maxilla is long, extending posterior to the orbit, arched, with a round cross-section but laterally flattened over the posterior 1/6 of its extent. The premaxillary process of the maxilla extends in palmate fashion medially at a low angle with respect to the axis of the maxilla. The dentary has a blunt anterior edge, with a tooth-bearing shelf projecting anteriorly at the symphyseal margin, especially developed in larger specimens. The teeth in each of these three bones are conical, often striated, with robust bases well-anchored into sockets. They exhibit little to no inflection of the tooth tips as do some other *Oncorhynchus*. The dentary, maxillary, and premaxillary teeth are not crowded. The angular-articular includes a prominent, dorsally-directed process posterior to the surface for articulation with the quadrate. The vomer is similar to large *O. mykiss*, with a clump of anterior teeth, but no transverse row. The dermethmoid is “A-shaped” when viewed from above, with a posterior notch (c.f. Stearley and Smith, 1993: fig. 3). The postorbitals are long, extending back to the preopercle. The preopercle is arcuate rather than
approximating “L-shaped” (Smith and Stearley, 1989; Stearley and Smith, 1993; fig. 8), with a rounded anterior edge to the ventral ramus. The frontals extend laterally above the orbits. As in salmonines more derived than *Eosalmo*, the parietals do not meet at the midline; they do form the dorsal margin of the post-temporal fossae. The supraoccipital bears a posterior crest much as in other eusalmonines. Apomorphic characters for *O. lacustris* include the maxillary round in cross-section at midlength; the anterior dentary symphyseal shelf; and the presence of stout conical processes on the epiotics.
Kimmel (1975) described the Miocene form of *O. lacustris* as *Rhabdofario carinatum*, obtained from Chalk Hills Formation sediments in Malheur County, Oregon. The primary morphological differences between this taxon and *O. lacustris* lie in the premaxilla and maxilla. The latter bone bears a keel-like buttress on its dorsal surface. This taxon is currently considered a chronospecies, ancestral to *O. lacustris*; cladistic practice suggests that both forms be recognized under the older name.

**Pacific salmon**

*Oncorhynchus salax* Smith 1975

Smith (1975) figured and diagnosed a planktivorous salmon, *O. salax*, from the Chalk Hills Formation (confused with the Glenns Ferry Formation in Smith, 1975), Owyhee County, Idaho (Fig. 15). The type specimen, UMMP 62100, is clearly that of an *Oncorhynchus*. It exhibits the arcuate preopercle, long post-orbitals, and frontals expanded above the orbit typical of *Oncorhynchus* (c.f. Stearley and Smith, 1993). But the teeth are very small and poorly socketed; the coronoid angle on the angular-articular is very low; and the maxillae are straight rather than arched and smaller and more compressed than in *O. lacustris*. Additional specimens revealed that the premaxillary process of the maxilla is distinctive: it exits mesially at a very low angle, and is palmate. Apomorphic features diagnostic of this species include a cleithrum with a prominent lateral ridge at the edge of the anterior concavity.

Continued stratigraphic sampling established that the type locality is within the Chalk Hills Formation (Smith et al., 1982). There are, however, several smaller, kokanee-like maxillae, which we assign to *O. salax*, from localities within the Glenns Ferry Formation.

The gill rakers of *O. salax* are elongate and numerous—between 11 and 13 on the upper half of the arch and 37 to 40 on the lower half (Fig. 15) indicative of a planktivorous trophic style (Beacham, 1986). High-resolution X-ray computed tomography of a second cranium also demonstrated the large number, 50+, and elongate gill rakers on the first arch in *O. salax* (Eiting and Smith, 2007).

*Oncorhynchus salax* dentaries with breeding teeth are present in the Chalk Hills Formation (Fig. 15c). As in modern salmon, these breeding teeth are anchored to the dentary with late-developing bony cement, crowded, and with posteriorly-inflected tips. The dentary narrows anteriorly as seen in lateral profile (Fig. 15b), so that the tooth row descends toward the anterior. The second tooth is much larger than the others. These dentaries and teeth are similar to those of breeding individuals of modern *O. nerka*.

Smith (1975) and Eiting and Smith (2007) provided criteria for inferring that this taxon was landlocked and iteroparous: its maximal size was about 60 cm; and the opercle demonstrates three annuli after achieving adult size (Smith, 1975: Fig. 5). It appears to occupy a niche similar to that of modern Kokanee—landlocked planktivorous salmon.

*Oncorhynchus ketopsis* Eiting and Smith 2007

A fossil skull (Fig. 16a), which confirms the presence of a third *Oncorhynchus* species in the Chalk Hills Formation, was discovered by Gladys Swigert in Coyote Gulch, Oregon, in 1978, and donated to the University of Michigan Museum of Paleontology through Peter Kimmel. Eiting and Smith (2007), used computer-aided tomography of the gill rakers to diagnose and describe this as *O. ketopsis*, similar to modern *O. keta*.

The skull is clearly that of an *Oncorhynchus*. The maxilla extends posterior to the orbit, as is typical for eusalmonines. The lower limb of the preopercle is reduced and possesses a curved anterior margin; and the postorbitals contact the preopercle, as in *Oncorhynchus*. The antero-lateral edge of the frontal is expanded over the orbit; a synapomorphy of redband trouts plus Pacific salmonids. Further, the dorsal limb of the preopercle is expanded posteriorly, as occurs in Pacific salmonids (c.f., Stearley and Smith, 1993). In general the *ketopsis* bones are massive, with fewer pore spaces than in marine salmon.

Further, the maxilla of *O. ketopsis* is straight, as in *O. salax* and in modern Pink, Chum, and Sockeye Salmon—Hikita’s (1962) “Type A salmon.” The premaxillary process of the maxilla extends mesially at a low angle. The premaxilla is crescent-shaped and convex dorsally, also as in modern Pink, Chum, and Sockeye Salmon. The teeth, however, are much larger and more robust than those of *O. salax* and resemble those of modern chum salmon. The outer gill arch bears only 12-16 robust gill rakers (Fig. 16), unlike the condition seen in *O. salax*. Computed X-ray tomography scans of the inner gill arches reveal these to bear approximately 40 closely-spaced gill rakers (Eiting and Smith, 2007). Functionally, this taxon was a small, chum-like species that could include plankton in its diet (see discussion below under “Trophic Ecology”). The species grew to about 60 mm long.

*Oncorhynchus tshawytscha*.— A single premaxilla, 52 mm long (UMMP 67768, Fig. 16b), was collected from the Glenns Ferry Formation near a small butte 6 miles south of Grand View, Owyhee County, Idaho. The specimen is identified as *O. tshawytscha*, a Chinook Salmon, by its huge size, robust shape, texture, and six large breeding-fighting teeth. This individual evidently migrated to the Snake River Plain from the Pacific Ocean through the Sacramento, Klamath, or Columbia rivers. Absence of salmon from the Columbia River at this time (Smith et al., 2000; discussion below), suggests a Klamath -Sacramento migratory route of 600-1000 km. The salmon was about the size of the largest Chinook Salmon on record (see next section).

*Oncorhynchus rastrosus* Cavender and Miller 1972

In 1972, Cavender and Miller described a very large planktivorous Pacific salmon, which they christened *Smilodonichthys rastrosus*. The type specimen was a large cranium with gill arches in articulated position, collected by Mrs. George liames and Scott McKain in 1964, from the...
“Gateway” locality in Jefferson County, Oregon (Fig. 17). The taxon is now known from over a dozen more localities (Table 4, Fig. 18). This species migrated to the ancestral Columbia River in the late Miocene (Smith et al., 2000) and a small relative occurs in the Chalk Hills Formation (see Fig. 19). The widespread *O. rastrosus* was bizarre by any standard, reaching a total length of about 8 feet and weighing more than 430 pounds; it possessed over 100 gill rakers on the first arch and a single huge breeding tusk on each premaxillary. Biostratigraphic evidence (fossil mammals) and correlations set these fossils in the Clarendonian and Hemphillian NALMA, or approximately between 12 and 5 Ma. Stearley and Smith (1993) demonstrated that this form included numerous synapomorphies of *Oncorhynchus*, and further, within *Oncorhynchus*, of Hikita’s “Type A” (modern *O. nerka*, *gorbuscha*, and *keta*).

Synapomorphies link *O. rastrosus* to *O. nerka*: the straight maxilla; thin crest of the premaxilla; the contact of the frontals

![Table 4.— Localities from which *Oncorhynchus rastrosus* and the small form from the Snake River Plain have been collected.](image-url)
Figure 18.— Distribution map, fossil localities, for *Oncorhynchus rastrosus* and *O. rastellus*. Solid red dots: *O. rastrosus* (see Table 3). Red dots with white bulls-eyes: *O. rastellus*.
with epiotics in large individuals; the high gill raker count; and enlarged ventral limb of the preopercle were judged synapomorphies of *O. nerka* and *O. rastrosus*. Evolutionarily, this species demonstrates a marine planktivorous morphology and anadromous life history ancestral to that successfully exploited by Sockeye Salmon.

Eleven-million year old vertebrae of *O. rastrosus* in the Los Angeles County Museum (Table 4, locality 9) are 6 cm in diameter and 2.8 cm in length. Sockeye Salmon have 56-67 vertebrae. Assuming that *O. rastrosus* had 62 vertebrae, the body would have been 28 x 62 = 1736 mm long. Adding a 32% increment for the head length, 0.32 x 1736 mm = 2292 mm long; the head+body would be 2.29 m (7.5 ft) long. It is apparent that the total body length plus fork length of the tail reached about 7.9 feet long—about 1.5 times as long as recent large Chinook Salmon. If we assume that the *O. rastrosus* bodies were shaped for migration, like Chinook Salmon, the length-weight equations of Jasper and Evenson (2006) and Quinn and Deriso (1999) would estimate a weight of \( W = 1.44 \times 10^4 L^{1.32} = 439 \text{ lbs} \), where 1.44 is a constant and \( L \) is length (Fig. 20). Given the planktivorous diet and the rich Miocene productivity of the eastern Pacific (Behl, 1999; Barron et al., 2002; Jacobs et al., 2004; Eiting and Smith, 2007) the fish could have been heavier, depending on the girth. Salmon weights vary a great deal, depending on amount of fat and mass of eggs. A common formula for estimating the weight of a salmon is length x girth \( L \times W \) when length is measured (in inches) to the middle of the tail and girth is measured (in inches) at the fat part of the belly, ahead of the dorsal fin. We have no way of measuring the girth of these salmon, but a girth of 60" would be slender, as expected of a long-distance, anadromous salmon, and the fish would weigh about 450 lb; estimates based on a more sizeable girth reach 800 lbs. With this remarkable background, the discovery of a late Miocene small relative of *O. rastrosus*, landlocked in the Chalk Hills lake, probably 500 miles from the sea, is evolutionarily and ecologically interesting.

Chalk Hills fossils related to the giant *Oncorhynchus* ("Smilodonichthys") *rastrosus* (Cavender and Miller, 1972) (Sabertooth or Spiketooth Salmon) of coastal California and the Columbia drainage of Oregon and Washington are determined to be a landlocked, small species, not a juvenile, on the basis of presence of breeding teeth on the premaxilla and dentary and commonly four annular growth rings. Isolated bones of many individuals of the small species indicate sizes of 40-45 cm standard length. The concentration of remains in two small, restricted areas suggests remnants of spawning runs that usually died after spawning.

**Teleostei**  
Order Salmoniformes  
Family Salmonidae  
Genus *Oncorhynchus* Richardson  
*Oncorhynchus rastellus* new species  
Fig. 19

**Type Locality.**— Idaho, Owyhee County, lower Chalk Hills Formation, T. 5 S., R. 1 W., SE 1/4 Sec. 2, 3070 ft. elevation, in pale yellowish, ashy sands several meters below three separated black cinder layers.

**Holotype.**— Figure 19a, b. A distal fragment of a left dentary, UMMP 74156a, 32 mm long, 14 mm deep including distal tooth; distal (of two) tooth 6 mm long and 6 mm on greatest diameter of the base, slightly recurved; second tooth 4 mm long, 3.5 mm greatest diameter at the base, strongly recurved; dorsal edge of dentary sharp; lateral surface strongly striated, mesial surface smoothly striated; broken at sensory canal, sensory pores not countable.

**Paratypes.**— Figure 19c-t. UMMP 74156b, 69015, 69020, 42352, 47871, 47847 from the type locality: jaws with teeth, isolated teeth, pterygoids, distal fragment of a right dentary, angular-articular, anterior maxilla, urohyal, quadrate with attached angular-articular, basioccipital, sphenotic, parap Shenoid fragment with orbitosphenoid, hyomandibula, vertebrae, ceratohyals.

**Diagnosis.**— An *Oncorhynchus* similar to *O. rastrosus* (Cavender and Miller, 1972), but smaller, about 45-50 cm long, with a single, large tooth with a large bony base, on the premaxillar (Cavender and Miller, figs. 5, 6, 9); usually two, but up to four small teeth on the distal end of the dentary (Fig. 19a, b, g, h); maxilla apparently with two teeth (Fig. 19j), one maxilla shows two possible attachment surfaces for small teeth (in *O. rastrosus* the premaxillary teeth are similar in number and proportions, but the maxilla is toothless, and the dentary teeth are proportionally smaller, Cavender and Miller, figs. 5, 6). The dentary (Fig. 19a, b, g, h) is not as deep posteriorly, at the coronoid, as in *O. rastrosus* (Cavender and Miller, figs. 5, 6), but deeper and shorter than in *O. nerka*. The angular-articular condyle (Fig. 19i, l) is more open than in other *Oncohynchus* except *O. rastrosus*, suggesting a wider gape, possibly associated with planktivory.

**Description.**— A dwarf species of planktivorous salmon, more similar to *O. rastrosus* than to other salmon. The premaxilla bears a large bony base with one large tooth (Fig. 19c, d, e). The maxilla is reduced with 0, 1, or 2 teeth (Fig. 19j). The depth and proportions of the dentary are

Figure 19. — Elements of *O. rastellus*. 19a, b: Holotype, UMMP 74156a, distal left dentary; a, exterior view; b, mesial view; c-j, UMMP 74156b: c, d, e, premaxillae with breeding spike; f, Pterotic, ventral; g, anterior dentary; h, distal fragment, anterior right dentary; i, left angular-articular, mesial view; j, anterior maxilla; k, UMMP 69015, urohyal; l, UMMP 74156b, quadrate with attached angular-articular; m, UMMP 42352, basioccipital; n, UMMP 74156b, sphenotic; o, UMMP 47871, parap Shenoid fragment with orbitosphenoid; p, UMMP 42352, hyomandibula; q, UMMP 47847, two attached vertebrae; r, s, UMMP 69020a, vertebra; t, UMMP 69015, attached anterior and posterior ceratohyals.
intermediate between *O. nerka* and *O. rastrosus* (Fig. 19a, b, g, h). The dermal bones are cancellous and strongly striated externally (Fig. 19) as in *O. rastrosus*, *nerka*, *gorbuscha*, and other Pacific salmon; other salmonids are less striated the more distant they are from these, phylogenetically. This form of bony tissue is not seen in *Salmo* or *Salvelinus* (Cavender and Miller, 1972: 37). The prootic is flat, with the position of the VII foramen as in *O. rastrosus*, not concave as in *O. nerka*. The hyomandibula has a long articulation with the pterotic, a short articulation with the sphenotic, small condyle for the opercle, and a strong adductor ridge, as in *O. rastrosus*; these are divergent relative to *Salmo* or *Salvelinus*. Urohyal long (Fig. 19k) in *rastrosus*, *rastellus*, and *nerka*; not short like *Salvelinus* or *Salmo* (urohyal length is intermediate in *O. clarkii* and Redband Trout). Ceratohyals (Fig. 19t), anterior and posterior (epihyal) not deep in *rastellus*, compared to *nerka* (not well known in *O. rastrosus*). Lateral surfaces of vertebrae with fine longitudinal striations frequently connected with short transverse striations in *O. rastellus* (Figs. 19q, r, s), like *O. nerka*, and other *Onchorhynchus*, compared to coarse, sharp longitudinal striations (only) in *O. rastrosus* (Cavender and Miller, fig. 11), and coarse, rounded striations in *Salmo* and most *Salvelinus*.

**Etymology.**—The species name, *rastellus* (little rake, Latin) refers to the sister species, *Onchorhynchus* (“Smilodonichthys”) *rastrosus*, whose name refers to its gill rakers.

**Life History.**—These fish apparently died at the same time of life and season, at 4 years old, based on four growth rings and similar distances between the 4th annulus and the edge (Fig. 19r). The growth rate, entirely in fresh water, was therefore intermediate between *O. nerka* and kokanee and much lower than the marine *O. rastrosus* (Fig. 20).

**Associated fish species.**—*Ameiurus peregrinus*, *Ptychocheilus arciferus*, *Acrocheilus latus*, *Mylocheilus inflexus*, *Mylocheilus kingi*, *Catostomus cristatus*, *Catostomus
shoshonensis, Paleolox larsoni, Oncorhynchus lacustris, Archoplites taylori, indicative of the lower Chalk Hills Formation.

Material examined.—From Browns Creek, Owyhee County, Idaho, SE ¼, Sec. 3, TSS, R1W. Elevation 937 m (3075 ft). Miocene Chalk Hills Formation, Hemphillian NALMA: UMMP 42351, seven vertebrae 10.5-11 mm. UMMP 42352, fragments of two hyomandibulae 26-33 mm; four basioccipitals 11-19 mm, three vertebrae. UMMP 47847 part, 40 vertebrae 5-12 mm, eight associated. UMMP 47871 one fragment of parasphenoid 15 mm with orbitosphenoid fragment attached; one fragment of epiotic 14 mm. UMMP 69015, fragments of three parasphenoids 31-36 mm; one ceratohyal complex 19 mm. UMMP 69020, 37 vertebrae 9-11 mm. UMMP 74156a, Holotype partial left dentary 32 mm. UMMP 74156b, fragments of: one left maxilla, 32 mm; 26 premaxillae and fragments with one tooth each, 8-22 mm; 23 dentaries and fragment 10-38 mm; four articular-angulomers 17-31 mm; one hyomandibula, 32 mm; one parasphenoid 35 mm with prootic, one prootic 23 mm, one sphenotic 19 mm. UMMP 74156c, fragments of two maxillae 11-24 mm; one articular-angular-quadrate complex 38 mm. UMMP 69036, Idaho: Owyhee County, T5S, R1E, W ½, NE ¼ Sec. 18, 50 ft below oolite, five vertebrae 8.3-9 mm.

Identity and formation uncertain.—UMMP 71971, Idaho, Owyhee County, Castle Cr., T5S, R1E, Ctr, NE ¼, Sec. 31, three vertebrae, 12-13 mm.

DISCUSSION

TROPHIC ECOLOGY

The Chalk Hills ichthyofauna is currently known to include 20 species, from six families: Salmonidae, Cyprinidae, Catostomidae, Ictaluridae, Centrarchidae, and Cottidae. Salmonid species comprise five of these 20 taxa (Tables 1, 2). The Glenns Ferry ichthyofauna is more diverse, with 32 species; including five salmonid and nine cottid taxa. The Glenns Ferry sediments and the biota indicate a larger, deeper, and colder lake than the Chalk Hills Lake.

Modern analogs for trophic niche partitioning of salmonids of the native ichthyofauna of Kootenay Lake, British Columbia allow us to infer trophic roles among the WSRP salmonids. Following the retreat of Pleistocene ice-sheets, a linear lake filled the valley between the Selkirk Mountains and the Purcell Mountains. The lake depth averages 90+ meters with a maximum of 150 meters. The depth has been only moderately affected by recent dams. The native ichthyofauna includes a sturgeon (Acipenser transmontanus), Burbot (Lota lota), four cyprinids, two suckers and two sculpins, in addition to six salmonids, discussed below. The native lacustrine ichthyofauna was derived from a set of large proglacial lakes in Montana (Lake Missoula) as well as colonization upstream through the Columbia River. Northcote (1973) cites derivation of one species of sucker, three cyprinids, a sculpin and three salmonid taxa, from the Columbia River. (Two species of centrarchids, Lepomis gibbosus and Micropterus salmoides, were stocked in the Twentieth Century.) The environmental niches and in many cases the ecological actors are remarkably similar to those of the Miocene and Pliocene lakes occupying the Snake River Plain. For example, the Kootenay Lake cyprinids include the Peamouth, Mylocheilus, and a pikeminnow, Ptychocheilus. The sculpins occupy colder habitat and the sunfish thrive in the warmer shallows.

The Kootenay Lake native ichthyofauna is rich in salmonids: Rainbow Trout (Oncorhynchus mykiss), char (Salvelinus confluentus), Kokanee (O. nerka), Westslope Cutthroat Trout (O. clarkia lewisi), Mountain Whitefish (Prosopium williamsoni), and Pigmy Whitefish (P. couteri) (Northcote, 1973; McPhail, 2007). Northcote considers the Cutthroat Trout and the Pygmy Whitefish to be rare in this system and the others common. Within the Kootenay Lake salmonid community, there is pronounced trophic partitioning (c.f. Northcote, 1973). Prior to the artificial introduction of mysids, Mountain Whitefish focused on aquatic and terrestrial insects when small, and gradually to exclusive benthic insect feeding when large. Kokanee were and are the primary zooplanktivores on the lake. Prior to the introduction of mysid shrimp, they typically attained sizes of 30 cm; after the introduction of mysids, the mean size increased somewhat. Rainbow Trout include the large, endemic Gerrard stock; these feed heavily on insects at the lake surface when young, gradually adding fishes (including a significant percentage of Kokanee) to the diet with increasing size (Irvine, 1978; Andrusak and Parkinson, 1984). The Gerard Rainbow Trout live up to 8 years and achieve very large size, averaging 6 to 9 kg. Char in Kootenay Lake are exclusively piscivorous.

The analogous morphologies of the ichthyofauna of the WSRP lakes, including jaw sizes, teeth, and gill-raker morphology in the Chalk Hills Fm. and Glenns Ferry Formation salmonids argue that Kootenay Lake trophic roles were present in the Neogene WSRP lakes. Furthermore, the large areal extent and depth of these ancient lakes provided habitat, including seasonal refugia, as well as providing a greater diversity of prey items than available in Kootenay Lake. This was particularly the case during the history of the larger and deeper Glenns Ferry lake. Smith (1987), for example, suggested that nine species of sculpins were permitted to diversify in the Glenns Ferry lake through progressive colonization of colder and deeper benthic habitats with different zooplankton (Smith and Todd, 1984). The differences in gill-raker count and shape and tooth size between O. salax and O. ketopsis argue that the latter, while including a substantial portion of zooplankton in its diet, also foraged on smaller fishes and aquatic insects (c.f. Beacham, 1986). Extant Chum Salmon, O. keta, take significant numbers of large zooplankton while at sea,
gradually including more and more small fishes such as herring and smelt as they grow (Salo, 1991). Large-bodied and well-toothed *O. lacustris* and *P. larsoni* represented the top carnivores of the lacustrine system of the Snake River Plain, with diets largely of pelagic fishes as in the case of the Gerrard race of *O. mykiss* in Kootenay Lake.

The divergence in jaw shapes in the Glenns Ferry whitefish indicate dietary specialization as well. Notably, within Pleistocene and modern *Prosopium* in Lake Bonneville and Bear Lake, Utah and Idaho, four snout and gill-raker variant species (Stokes et al., 1965; Smith and Todd, 1984; Broughton et al., 2000; Wallace and Zaroban, 2013) are related to different trophic behaviors.

**COLONIZATION POTENTIAL FOR ANADROMOUS SALMONINES**

Many lines of geologic evidence argue for a middle Miocene warm period that has been termed the Mid-Miocene Climatic Optimum, extending between 17 and 14 Ma (Chapin, 2008). Global climate then cooled in the late Miocene, during which time we see the appearance of the first Neogene salmonids in western United States. Magnesium/calcium ratios in tandem with oxygen isotopic signatures in benthic foraminifera demonstrate that during a short interval of time around 14 Ma, the Southern Ocean cooled by 6 to 7 degrees Celsius, coupled with substantial Antarctic ice growth (Shevenell et al., 2004). Global ocean circulation

Figure 21.— Potential drainage connections, western Snake River Plain. Abbreviations: B, Bear River; Kla, Klamath drainage; OB, Oxbow; Pit, Pitt River; PL, Pyramid Lake; RRP, Red Rock Pass; R, Ringold Formation; UL, Utah Lake; WSRP, Western Snake River Plain; Y, Yellowstone.
patterns were in flux, but during this time the deep circulation system that characterizes our modern world was coming into being. Upwelling along coastal California during the middle Miocene increased, as evidenced by large accumulations of biosiliceous sediments like those of the Monterey Formation (Behl, 1999; Barron et al., 2002; Jacobs et al., 2004). These conditions of enhanced upwelling and planktonic productivity coincided with the development of the cool California current, especially after 11 Ma (Isaacs, 2001). The oldest salmonid fossils located in offshore facies sediments are in fact those of the large planktivore, *O. rastrosus*, known from several localities in central and southern California, from Monterey or Monterey-equivalent sediments (e.g., Barnes et al., 1985; Table 4). Because *O. rastrosus* represents a derived Pacific salmon, we infer that sea-run Pacific salmon were present along the coast during earlier intervals, but probably further to the north. A test of this inference will come from eventual discovery of early Miocene coastal *Oncorhynchus* from British Columbia, Alaska, or Kamchatka. Our observation here is that cool, high-productivity coastal environments were present and populated by salmonines in the middle to late Miocene. Dispersion along the coast and colonization upstream was a biogeographic option for in-shore chars as well as for far-ranging migratory *Oncorhynchus* (Stearley, 1992; Jacobs et al., 2004). We address the specific implications and scenarios for drainage evolution below.

Longer-lived lakes accumulate higher fish diversity through immigration and speciation. Deep rift lakes have exceptional numbers of fish habitats and species because of the creation and maintenance of multiple deep habitats via continued deepening of the lake by subsidence (Smith and Todd, 1984). Stability of habitats as illustrated by the continuity within lakes (Table 2) is conferred when rift lakes are seasonally cool enough to be oxygenated to the bottom, as is apparent from the bioturbated, non-organic benthic sediments of the Chalk Hills and Glenns Ferry lakes.

Axelrod (1968) interpreted succession of lowland hardwoods, lower elevations, and thicker sediments in the Western Snake River Plain in the middle Miocene to indicate valley elevations of about 300 m with flanking uplands 300 m higher. Rifting continued to widen and deepen the lakes and uplift the margins as volcanics intermittently blocked connections to the west, creating the Chalk Hills lake in later Miocene. The first inland salmonine, *Paleolox*, first appears in the Poison Creek Formation, followed by an influx of salmon, trout, and large minnows and suckers from the west into the Chalk Hills Lake (Carpenter and Smith, this volume). Following a low point in lacustrine deposition, connections to the north allowed colonization of the Glenns Ferry lake by coldwater sculpins and whitefish (Table 2) about 4.3 Ma (Smith et al., 1982; Carpenter and Smith, this volume), about 1.1 m.y. before inception of drainage through Hells Canyon (Smith et al., 2000; Wood and Clemens, 2002).

**GEOLOGIC AND BIOGEOGRAPHIC EVIDENCES FOR PAST DRAINAGE CONNECTIONS TO THE PACIFIC OCEAN**

Original colonization routes to lakes of the Snake River Plain.

The first lacustrine fishes to occupy the Miocene Western Snake River Plain were *Amiurus* catfish, *Catostomus* suckers, and *Archoplites* sunfish, in the Poison Creek lake (Smith and Cossel, 2002) and the Pickett Creek lake (Buechler and Smith, this volume). These lived with a relative of *Paleolox* and several minnows (Cyprinidae). Middle Miocene relatives of these fishes were in west-central Nevada (Baumgartner, 1982; Stearley and Cavender, in prep), Clarkia, Idaho (Smith and Miller, 1985), the Sacramento Valley, California (Spencer et al., 2008), and southeastern Oregon (Carpenter and Smith, this volume). At this time, the Western Snake River Plain and Western Nevada were separated from the Eastern Snake River Plain and eastern Nevada by a drainage divide (Beranek et al., 2006; Henry, 2008). Aquatic connections were primarily west and southwest until the end of the Miocene (Fig. 21).

Livingston (1928) hypothesized that a prior outlet of the WSRP Miocene-Pliocene lakes drained to the northwest across valleys now occupied by the Burnt or Powder Rivers, Oregon, and thence through the Grand Ronde River valley to the ancestral Salmon River and ultimately into the Miocene-Pliocene Columbia River. Harry Wheeler and Earl Cook (1954) detailed several lines of evidence, including abandoned river terraces and barbed tributaries, that indicated that prior drainage of the WSRP Miocene-Pliocene lakes was southwest to the Sacramento River, possibly through the course of what is now the lower Owyhee River (but possibly later than Livingston’s proposed connection to the Columbia). In their proposal, the capture of the WSRP waters to the Salmon-Columbia was accomplished at an elevation of ~1006 m (3300 ft) through the Oxbow, south of Homestead, Oregon. Wood and Clemens (2002) supported Wheeler and Cook’s proposal, but proposed a site of spillover further upstream, near the confluence of the Burnt and Snake rivers. Geologic data can be marshaled to support the track of a paleo-outlet from the western Snake River graben lakes either northwestward to the Columbia or southward to the Klamath/Sacramento Rivers. Stephen Reidel, Terry Tolan, and co-workers have developed a variant of the Livingston proposal for an ancestral drainage route to the Columbia, via the valley of the Burnt River to the Umatilla Basin and thence to the lower Columbia (Reidel et al., 1994; Reidel and Tolan, 2013 and references therein). In their view, this was a long-standing connection during the Miocene; the paleochannel being deflected back and forth in response to intervals of Columbia River Flood Basalt extrusion but providing a consistently functional outlet to the lower Columbia. A late Middle Miocene connection between the Columbia and Snake rivers, prior to the Late Miocene -
Pliocene disruption, is supported by the generic relationships of the fish faunas.

The biogeography of extant and fossil aquatic organisms strongly supports the thesis that the Western Snake River Plain Neogene lakes were connected, at least periodically, to the Klamath and/or Sacramento drainages. The earliest systematic collection of fishes in the lakes of the SE Oregon desert and their tributary streams, undertaken by J. O. Snyder, revealed that several fish species were shared uniquely between SE Oregon and the Klamath drainages, and yet others shared uniquely between the SE Oregon desert lakes and the Sacramento and its tributaries (Snyder, 1908). Dwight Taylor (1966, 1985) amassed molluscan distributional evidences for a freshwater connection from the late Tertiary of the Snake River Plain southwest through southern Oregon, largely following the trend of the current terminal lakes occupying the Malheur and Harney basins, to the upper Klamath river and possibly the Pit River, thence to the Sacramento River. For example the freshwater clam, *Pisidium ultramontanum*, today resident in the upper Klamath and Pit Rivers, is documented in Neogene sediments of the Snake River Plain as well as those of the lake basins in south-central Oregon (Taylor, 1960). Miocene and Pliocene fish evidence (Smith, 1975; Kimmel, 1975; Smith et al., 1982; Smith et al., 2000; Spencer et al., 2008) identified taxa shared between the ancient Idaho lakes and the current Sacramento and Klamath rivers – the centarchid, *Archoplites*, and cyprinids, *Lavinia*, *Orthodon*, *Mylopharodon*, and *Mylocheilus*, and catostomids, *Deltistes* and *Chasmistes*. Additionally, Taylor and Smith (1981) demonstrated that late Tertiary fossil fishes and mollusks from northeastern California resembled those of the Glenns Ferry Formation.

Ken Aalto and co-workers (1998) supplied evidence—$^{40}$Ar/$^{39}$Ar dates on micas as well as K-feldspar content—for the Miocene-Pleistocene Wildcat Group in northwestern California that favor a source of Wildcat Group sediments from the Idaho Batholith. Aalto (2006) further demonstrated that the modern Klamath Mountain topography was achieved post-Miocene. During the time in which the Miocene and Pliocene lakes of the Snake River Plain were deepening, the present Klamath region was a low coastal peneplain and would not have served as a drainage barrier for a stream flowing across southern Oregon/northwestern California to the sea. In addition, Idaho Batholith-derived materials are present in the Eocene Great Valley forearc basin sediments, leading Dumitru and colleagues (2013) to postulate an Eocene “Princeton River” which flowed southwestward across southern Oregon, passing east of the Klamath block and flowing into marine waters at the northern end of the Great Valley. Thus, sedimentology supports the hypothesis that a river connection extended from southwestern Idaho to southwestern Oregon and northern California, the Pit, Klamath, Snake River corridor, at several intervals during the Cenozoic Era.

Additional late Neogene fossil fish faunas from south-central Washington, and the Grand Ronde Valley, Oregon, further clarify the timetable for the initiation of a linkage between the WSRP and the Columbia River. The Ringold Formation (Smith et al., 2000) was deposited by Late Miocene and Pliocene rivers and lakes in the Pasco Basin of south-central Washington. Two large dentaries of *Oncorhynchus rastrosus* and some associated fragments, but no other salmonid remains, have been obtained from the base of this horizon. During the remainder of Ringold deposition through the Pliocene, no salmonid skeletal elements were incorporated among thousands of bones of low elevation fishes. If during this Pliocene interval the Columbia River traversed the lower Yakima basin, near where salmonids had been absent in the Ellensburg Formation several million years earlier (Martin et al., this volume), the absence of salmonid evidence of a connection to the sea is significant. The abundance of large catfish and large sunfish and absence of sculpins, whitefish, and salmonines (with the exception of the three elements previously referred to) in the Ringold and Ellensburg sediments indicate that these basins lay at a low elevation with a warm climate.

Timing of the draining of the Glenns Ferry lake and capture of the upper Snake River through Hells Canyon is indicated by the appearance of the Glenns Ferry cyprinids, *Lavinia*, *Acrocheilus*, and *Klamathella*, at about 3.1-3.0 Ma in the Taunton Fauna of the Ringold Formation, following their absence from among the thousands of older fish bones in that Formation (Smith et al., 2000).

Fish fossils recovered from Pliocene sediments ca. 3 Ma near Imbler, Oregon, in the Grand Ronde Valley, include a pikeminnow (*Ptychocheilus* sp.), a catfish (*Amiarius* c.f. *reticulatus*), a sunfish (*Archoplites* sp.), a sculpin (*Cottus* sp.) and a whitefish (*Prosopium* sp.) (Van Tassell et al., 2001; Smith and Van Tassell, this volume). The catfish is distinctly like that found in the Ringold Formation, *Amiarius reticulatus*, rather than the Glenns Ferry catfish, *A. vespertinus*. Overall, the Imbler fauna resembles that of the Ringold Formation rather than that of the WSRP, with the exception of the whitefish. Thus, biogeographic evidence suggests that a connection from the WSRP through northeastern Oregon via the Grand Ronde Valley to the Columbia probably did not exist during late Miocene or Pliocene.

If colonization of the Chalk Hills Lake by anadromous salmon from the ancestral Sacramento or Klamath occurred, it was not through a single migration of six genera. Most of the WSRP minnows, sunfish, and Spiketooth Salmon are shared with the Sacramento; the suckers and salmonids, are shared with the Klamath River. *Oncorhynchus rastrosus* fossils are recorded from the Columbia, the Sacramento, and sediments, formerly assigned to the Yonna Formation, near Klamath Lake, Oregon (Newcomb, 1958; Cavender and Miller, 1972; Pickthorn and Sherrod, 1990; Sherrod and Pickthorn, 1992: Table 2). A salmonid population migrating from the sea at that time could have advanced upstream, ultimately colonizing the WSRP during Chalk Hills time.
Several hundred salmonine fossils have now been located from Neogene deposits in the Snake River Plain, including many skull and jaw bones and hundreds of isolated or clustered vertebrae. Five salmonine taxa are represented in this assemblage. None of the skulls resembles that of a Cutthroat Trout. In western Nevada, however, the Truckee Trout, *O. bellii*, is a primitive Cutthroat Trout. The other members of the ichthyofaunal assemblage from the Truckee Formation likewise do not support a biogeographical connection between the Truckee and the Western Snake River Plain during Miocene, although *Ptychocheilus*, *Mylocheilus*, and *Mylopharodon* support an older, indirect, western Nevada-WSRP connection (Smith et al., 2002). Exclusion of Cutthroat Trout from the WSRP may also indicate competitive exclusion or introgressive elimination by its close competitor, the Redband Trout, *O. lacustris*, abundant in the WSRP during late Miocene and Pliocene.

**ANTIQUITY AND EVOLUTION OF PACIFIC TROUTS AND SALMONS**

Numerous discoveries of fossil salmonids from fluvial, lacustrine, and nearshore marine sediments in western North America document the great diversity of taxa present during late Miocene and Pliocene time (e.g., Barnes et al., 1981; Barnes, 1985; Cavender and Miller, 1972; Smith, 1975; Smith and Miller, 1985; Smith, 1992; Stearley, 1992; Smith et al., 2002; Eiting and Smith, 2007; Waples et al., 2008). We now recognize that a radiation of inland *Salvelinus* had begun by at least mid-Miocene time (Cavender and Miller, this volume; Stearley and Cavender, in prep.) Within *Oncorhynchus*, cutthroat trout had diverged from more derived lineages during or prior to that same interval. For yet more-derived semelparous *Oncorhynchus*, the late Miocene presence of at least four species of “Type A” Pacific salmon (Hikita, 1962; Stearley and Smith, 1993) – *O. rastrosus*, *O. rastellus*, *O. ketopsis*, and *O. salax* – argues that profound diversification had begun some time before. These data refute notions that all or most of the species-level diversification within *Oncorhynchus* must have taken place during the Pleistocene (e.g., Neave, 1958; Behnke, 1992). While Pleistocene glaciation contributed to the isolation, extinction, and genetic divergence of stocks (c.f. Beacham et al., 2006), many of the generic and specific divergences began more than 10 million years ago.

Because climate was cooling during the late Miocene when the current Pacific circulation regime was being established, we hypothesize that a significant amount of the diversification of sea-run salmon would have occurred along coastlines to the north of current geographic distributional limits. Their occurrence inland during warm Miocene times required large, deep lakes, oxygenated to the bottom, and fed by high-altitude streams.

The biogeographical history of the suite of Western North American inland forms of *Oncorhynchus mykiss*, as well as the status of various named subspecies, has been debated (c.f. Needham and Gard, 1959; Schreck and Behnke, 1971; Gold, 1977; Behnke, 1981, 1992; Berg, 1987; Nielsen et al., 1999; Currens et al., 2009). Behnke (1992) summarized the nomenclatural history for these fishes, extending back to the work of D. S. Jordan in the 1880’s. Microsatellite DNA evidence supports the proposal (Schreck and Behnke, 1971; Behnke, 1992) that inland rainbow trouts now isolated along tributary rivers to the San Joaquin and Sacramento rivers, California (as well as the Rio Santo Domingo, Baja California, trout) are closely-related (Nielsen et al., 1999). Behnke’s argument that these populations formed a continuum during a cooler period of the Pleistocene is uncontroversial; in fact, a large Pleistocene member of the Rainbow-Redband clade, *Oncorhynchus lacustris*, is documented from lacustrine sediments from Jalisco province, Mexico, much further to the south (Cavender and Miller, 1982; Stearley and Smith, 1993). Behnke’s conclusion that “the ultimate origins of Redband and Rainbow trout lay near the Gulf of California” is not supported by the salmonid fossil record, or genetic evidence from Redband Trout stocks in south-central Oregon (Currens et al., 1990, 2009).

The *Oncorhynchus mykiss* group in the late Miocene-Pliocene Western Snake River Plain documents the presence of an ancestral inland Redband Trout, with a migratory life history connected to the Sacramento in the Miocene, Upper Klamath in the Pliocene, and the Columbia in the Pleistocene. An analysis of enzyme coding loci from inland Redband Trout from the southern Oregon Great Basin lakes supports the historical role of the WSRP lakes in the historical biology of inland Redband Trout (Currens et al., 1990, 2009). These genetic data suggest that extant Redband Trouts occupying the Goose Lake, Warner Valley and Chewaucan basins are related to the Sacramento redband trout, *O. mykiss stonei*, while Harney Basin redband trout share traits with Columbia River Redband Trout, *O. mykiss gairdneri*. On the other hand, Upper Klamath Lake Rainbow Trout included the recognized Klamath River subspecies, *O. mykiss newberryi*, plus a previously unrecognized (Sacramento River) group. These genetic associations and abundant fossil trout mark complex drainage connections, including stream captures, between the Mio-Pliocene Snake River Plain to the Sacramento and Upper Klamath drainages. In the Plio-Pleistocene Fort Rock area paleolakes were connected to the Deschutes River and the Columbia (Currens et al., 1990, 2009). Later connection of Fort Rock Lakes to the Snake River would have occurred through the Harney-Malheur Basin after the capture of the Glens Ferry Lake by the Salmon River at about 3.1 Ma to form Hells Canyon of the Snake River.

The dynamics of homing and straying in extant migratory salmonids, and implications for colonization of new habitat are well understood (Groot and Margulis, 1991; Hendry et al., 2004; Quinn, 2005; Augerot, 2005; Schtickzelle and Quinn,
Similarly, the eusalmonine tendency to evolve adfluvial or lacustrine populations from sea-run ones is thoroughly documented (e.g., Kwain, 1981, 1982; Carl, 1982; Burgner, 1991; Kato, 1991; Waples et al., 2001; Quinn, 2005; McPhee et al., 2007). The salmonid community of the WSRP lakes reveal that alternative life-history dynamics existed well before the late Miocene.

Extant sockeye salmon (Oncorhynchus nerka) exemplify the ability of Pacific salmon, in particular, planktivorous salmon, to occupy new lacustrine habitats and evolve forms reliant on significant lake residence, or abandonment of a sea-going phase (i.e., resident Kokanee) (Nelson, 1968; Burgner, 1991). Wood and colleagues (2008, p. 207) provide a strong case for what they term the “recurrent evolution hypothesis”, which claims that “the sea/river ecotype is an ancestral, straying form with poorly differentiated metapopulation structure, and that highly structured populations of lake-type sockeye and kokanee have evolved repeatedly in parallel adaptive radiations between recurrent glaciations of the Pleistocene epoch.” Wood et al. (2008) further noted a correlate of this metapopulation structure—frequent extinction of locally adapted and isolated lacustrine stocks. The parallel lacustrine adaptation demonstrated by the small Spiketooth Salmon, O. rastellus, and the sockeye-like planktivore, O. salax—and their extinction through the loss of lacustrine habitat—implies that selective (Wrightian) landscapes similar to those that favor the labile life histories for modern sockeye have been existence long prior to the Pleistocene. We interpret these life histories as highly adapted metapopulation phenomena, initially framed by a tectonically active landscape in which lakes emerged, disappeared, and changed drainage allegiances at a mesoscale timetable.

Oncorhynchus lacustris exhibits a different trophic role from O. salax or O. rastellus, and a different face to salmonid adaptive plasticity. Many specimens, including several more-or-less complete crania, of this WSRP lacustrine trout have been located (Fig. 14). Many of these are the remains of large (>60 cm) individuals; the bones of these are massive, the orbit is large, and the teeth are stout and firmly attached. Deterioration of bones, which would evidence a long migration from the sea have never been noted. We interpret this taxon as a large predator with an adfluvial life history similar to that of large Gerrard strain of rainbow trout in Kootenay Lake, previously discussed. These are opportunistic predators, focusing on insects early and transforming to increasing reliance on larger prey items, primarily pelagic fishes. The large, open-water adult form of the WSRP Mio-Pliocene lakes was seasonally silvery, like lacustrine Steelhead and Lahontan Cutthroat. Oncorhynchus lacustris exhibited the plasticity present in current O. mykiss: the ability for modest stream-resident “redband” forms to fill the adaptive niche of a large open-water predator opportunistically (Keeley et al., 2005 and references therein).

The metapopulation dynamics of migratory salmonids and ecological plasticity such as described above, are well-documented for many extant populations around the world, such as in Arctic Char, Brook Trout, Cherry Salmon, and Rainbow Trout, and may be correlated to the salmonid tetraploid karyotype (Waples et al., 2008). The Neogene tectonic environments of the North Pacific Rim, together with the spatial isolating mechanisms in the North American Basin-and-Range province and a global climatic cooling trend, have provided a phenomenal scope for the exercise of these adaptive proclivities and promotion of salmonid differentiation (Minckley et al., 1986; Stearley, 1992; Montgomery, 2000; Jacobs et al., 2004; Spencer et al., 2008; Waples et al., 2008).

SUMMARY AND CONCLUSIONS

1. The Miocene Chalk Hills and the Pliocene Glenns Ferry lakes of the Western Snake River Plain are the richest fish localities known in the Late Cenozoic of Pacific drainage Western North America. These lakes were the stable centers and sources of Western Neogene aquatic biodiversity, including salmonid fishes.

2. The lineages of Pacific salmon and trout were diversified prior to the late Miocene, 14-10 Ma.

3. The waters of the Western Snake River Plain were connected to the Sacramento drainage possibly in the Late Miocene and the Klamath drainage possibly in the Pliocene, according to fish distributions and Idaho Batholith sediments in the Klamath Peninsula (Aalto, 1998, 2006).

4. Salmonines diverged into planktivorous and carnivorous species by the Middle Miocene during a time of Eastern Pacific upwelling and rich primary productivity.

5. Inland forms of Cutthroat Trout and Redband Trout were present in the Great Basin and Snake River Plain, respectively, along with large chars, by 10 Ma.

6. Comparison of Snake River salmonines with Eocene Eosalmo from British Columbia and Washington imply change and diversification from large Grayling-like forms to trout and salmon during the Oligocene and early Miocene.

7. Evolutionary stasis of salmonids and other fishes in rift lakes of the Western Snake River Plain contrasts with the rapid divergence reported for African rift lake cichlids. Large cold-water fish in seasonal environments may be genetically and ecologically constrained in their diversification, compared to smaller tropical species in less seasonal environments.
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