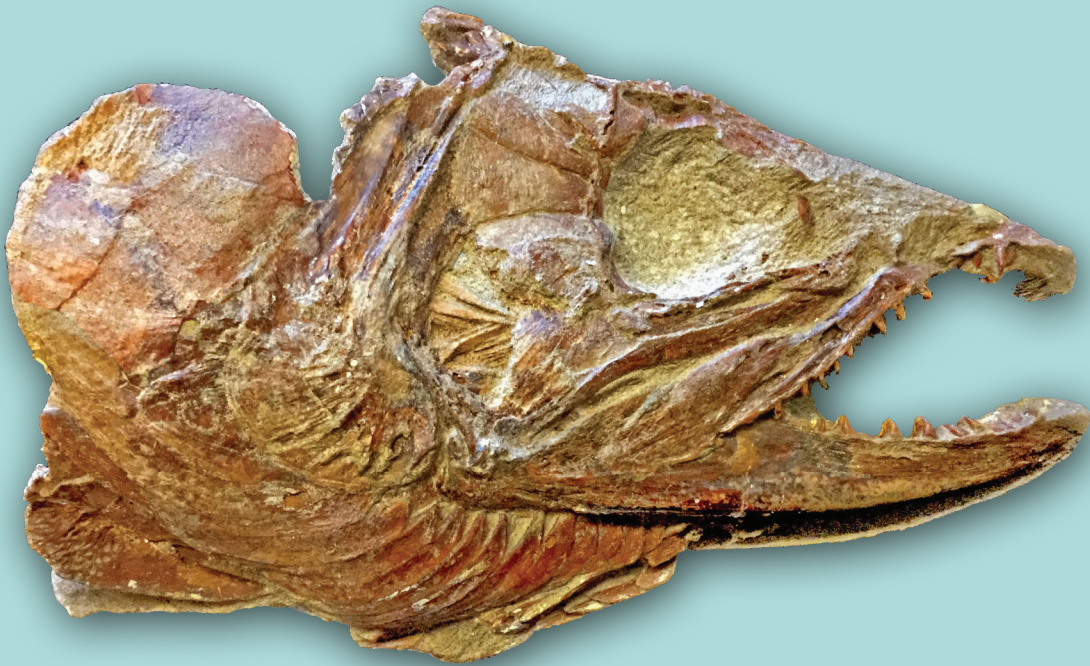# FISHES OF THE MIO-PLIOCENE WESTERN SNAKE RIVER PLAIN AND VICINITY

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

The publications of the Museum of Zoology, The University of Michigan, consist primarily of two series—the *Miscellaneous Publications* and the *Occasional Papers*. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb. Occasionally the Museum publishes contributions outside of these series. Beginning in 1990 these are titled *Special Publications* and *Circulars* and each are sequentially numbered. All submitted manuscripts to any of the Museum's publications receive external peer review.

The *Occasional Papers*, begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The *Miscellaneous Publications*, initiated in 1916, include monographic studies, papers on field and museum techniques, and other contributions not within the scope of the *Occasional Papers*, and are published separately. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Mammals, Birds, Reptiles and Amphibians, Fishes, Insects, Mollusks, and other topics is available. Address inquiries to Publications, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109–1079.

RECENT *MISCELLANEOUS PUBLICATIONS*

Stearley, R. F. and G. R. Smith, 2016. Salmonid fishes from Mio-Pliocene lake sediments in the Western Snake River Plain and the Great Basin. pp. 1-43, 17 figs., 4 tables, 3 maps. *In*: Fishes of the Mio-Pliocene Western Snake River Plain and Vicinity. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 204.

Cohn, T. J., D. R. Swanson, P. Fontana. 2013. Dichopetala and New Related North American Genera: A Study in Genitalic Similarity in sympatry and Genitalic Differences in Allopatry (Tettigoniidae: Phaneropterinae: Odonturini). *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 203, pp. *i-vi*, 1-175, 11 maps, 5 tables, 5 appendices.

Talbot, M. 2012. The natural history of the ants of Michigan's E. S. George Reserve: A 26 year study. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 202, pp. *i-v*, 1-219, 161 maps, 7 tables, 2 appendices.

Rainboth, W.J., C. Vidthayanon & M.D. Yen. 2012. Fishes of the Greater Mekong ecosystem with species list and photographic atlas. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 201, pp. *i-xvi*, 1-294, 2576 figs.

Campbell, J.A., E.N. Smith, J. Streicher, M.E. Acevedo & E.D. Brodie, Jr. 2010. New salamanders (Caudata: Plethodontidae) from Guatemala, with miscellaneous notes on known species. *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 200, pp. *i-vi*, 1-60, 42 figs., 4 tables, 3 appendices.

RECENT *OCCASIONAL PAPERS*

Kraus, Fred. 2015. A new species of the miniaturized frog genus *Paedophryne* (Anura: Microhylidae) from Papua New Guinea. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 745, pp. 1-11, 2 figs., 1 table, 1 map.

Wilkinson, M., A. O'Connor, R.A. Nussbaum. 2013. Taxonomic status of the neotropical Caeciliam genera *Brasilotyphlus* Taylor, 1968, *Microcaeilia* Taylor, 1968 and *Parvicaecilia* Taylor, 1968 (Amphibia: Gymnophiona: Siphonopidae) *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 744, pp. 1-10, 2 figs., 1 table.

Smith, G.R., J.D. Stewart & N.E. Carpenter. 2013. Fossil and Recent mountain suckers, *Pantosteus*, and significance of introgression in catostomin fishes of the western United States. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 743, pp. 1-59, 12 figs., 2 appendices, supplementary material.

Lindsay, A.R. & S.C.G. Haas. 2013. DNA from feces and museum specimens confirms a first state record bird. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 742, pp. 1-10, 4 figs., 1 table.

Oldfield, R.G. 2009. Captive breeding observations support the validity of a recently described cichlid species in Lake Apoyo, Nicaragua. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 741, pp. 1-14, 6 figs., 3 tables.

COVER PHOTOGRAPH— *Oncorhynchus ketopsis*, 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

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

By

Ralph F. Stearley[1] and Gerald R. Smith[2]

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 Glenns 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 Ringold 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 Glenns Ferry Lake through Hells Canyon in the late Pleistocene.

[1]Calvin College, Grand Rapids, MI 49546 (rstearle@calvin.edu)
[2]University of Michigan, Ann Arbor, MI 48109 (grsmith@umich.edu)

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 osteichthyan 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
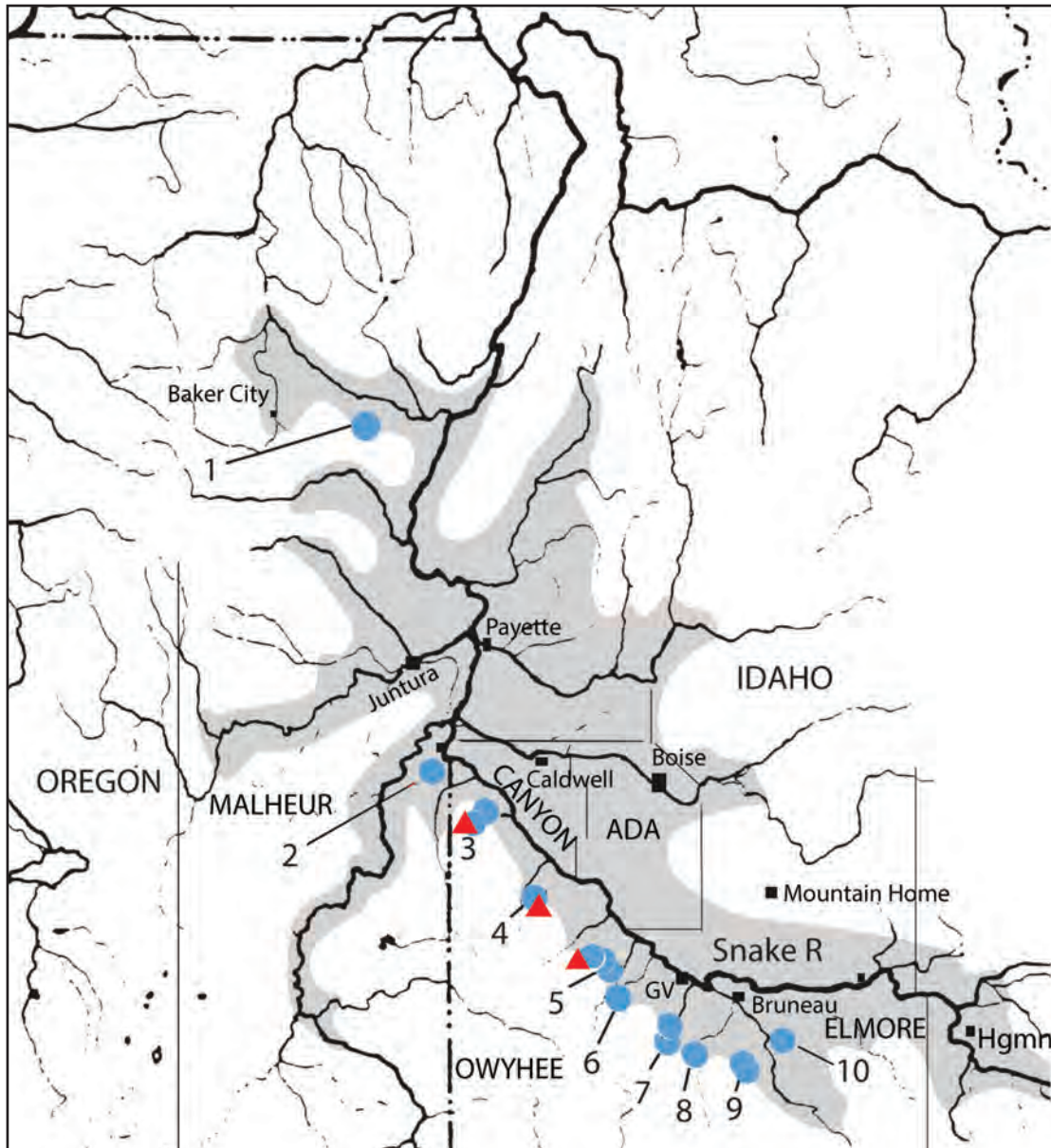
Figure 1.— Map of western Snake River region, Baker County, Oregon (locality 1), Malheur County, Oregon (locality 2), and Owyhee County, Idaho (localities 3-10). Shaded region = recorded extent of Idaho Group sediments. Red triangles refer to the Poison Creek Formation; blue circles the Chalk Hills Formation. Numbered fossil localities: **1**, Powder River Valley; **2**, Tunnel Mountain and Coyote Gulch, Malheur County, Oregon; **3**, Type locality of Poison Creek Formation, SW of Marsing, Idaho; **4**, Reynolds Creek; **5**, Pickett Creek and Browns Creek; **6**, Birch Creek and Castle Creek; **7**, Shoofly Creek; **8**, Chalk Hills; **9**, Horse Hill; **10**, Hot Springs Road.

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 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 (Bohacs

Figure 2.— Angular unconformity between Poison Creek Formation (orientation indicated by red line) and overlying Chalk Hills Formation (orientation indicated by blue line), near Reynolds Creek. Photo by G. R. Smith.

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

AGE		ROCK UNIT	SALMONIDAE
1– 2–	Pleist.	Black Mesa Gravel Bruneau Formation Tuana Gravel	*Oncorhynchus lacustris*
3– 4-- 5– 6–	Pliocene	Glenns Ferry Fm.	*Prosopium prolixus* *Prosopium* sp. *Oncorhynchus lacustris* *Oncorhynchus salax* *Oncorhynchus tshawytscha*
7– 8– 9–	Miocene	Chalk Hills Fm.	*Paleolox larsoni* *Oncorhynchus lacustris* *Oncorhynchus salax* *Oncorhychus ketopsis* *Oncorhynchus rastellus*
10– 11--		Poison Creek Fm. RHYOLITE	*Paleolox larsoni ?*

et al., 2013), with large amounts of mudstone and siltstone, alternating with vitric tuffs, some of which are 2 m or more thick. Sheppard (1991) examined the diagenetic alteration of the tuffaceous material and reported small-scale, localized 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

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.
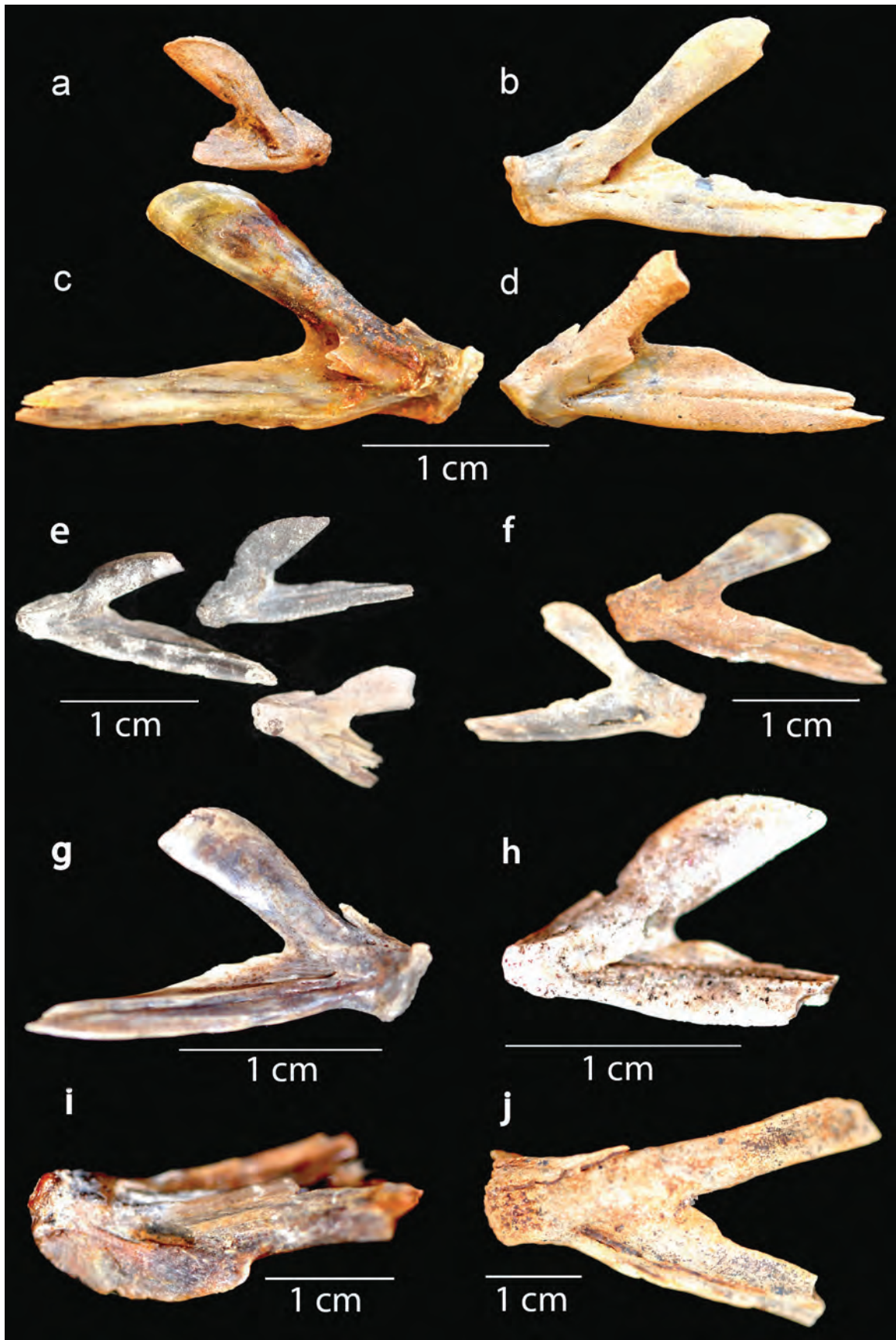
fining upward from orange quartzite cobbles derived from the Jarbidge mountains at the head of the Bruneau River. Farther north, the Shoofly Oolite (Swirydczuk et al., 1979, 1980) northwest of Horse Hill is interpreted as a transgressive beach deposit evidencing the return of the lake. On the east, the 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, 1962), about 125 species of ostracods (Swain, 1986, 1999), and many species of diatoms.
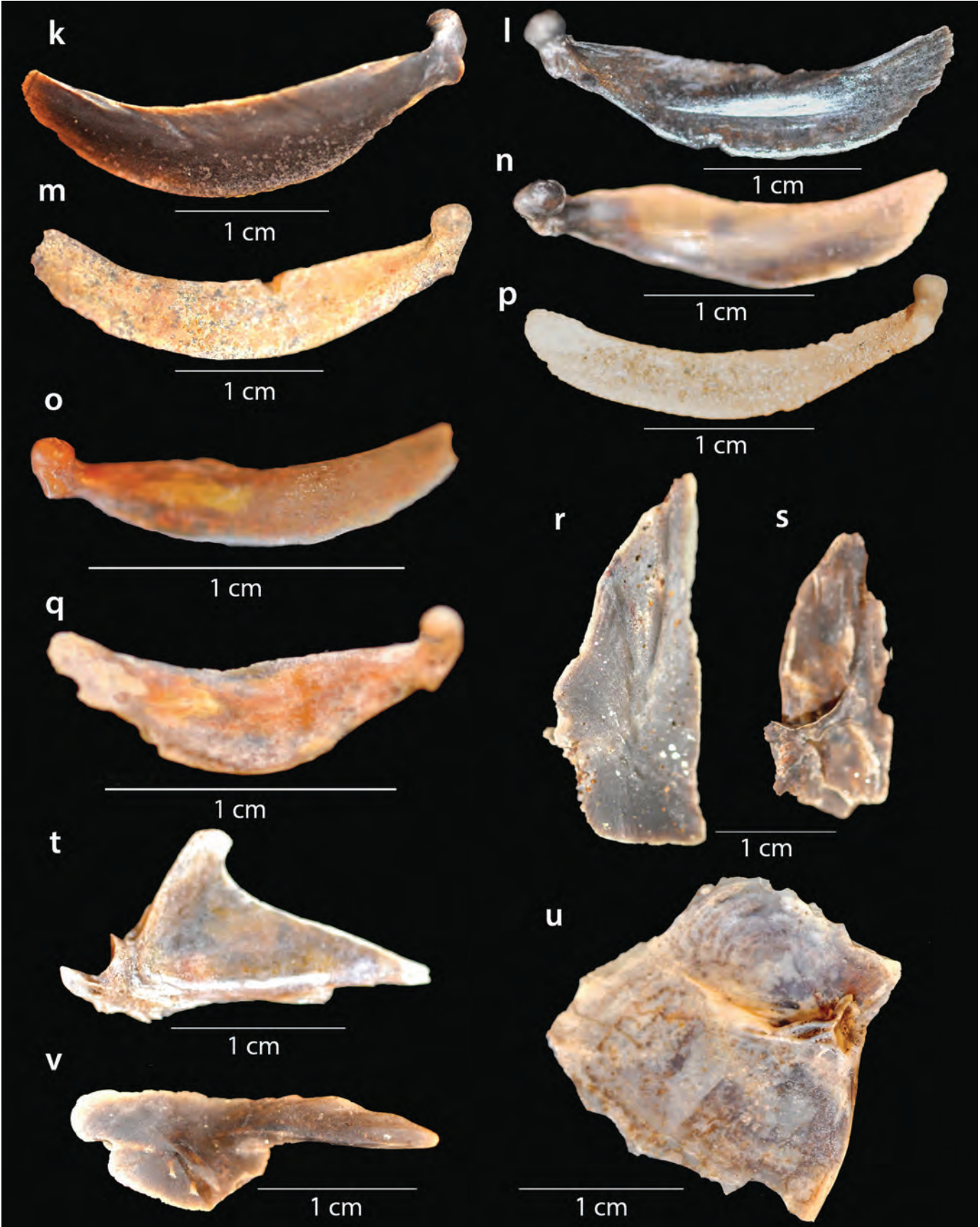
SALMONID FISHES OF THE WESTERN SNAKE RIVER PLAIN

Salmonid systematists divide the group into three clades, variously considered families or subfamilies (Sanford, 2000): the whitefishes (subfamily Coregoninae); graylings (Thymallinae); and trouts, chars and salmon (Salmoninae) (Norden,

Figure 4a.— Fossil *Prosopium* dentaries from the Glenns Ferry Formation: **a**, *Prosopium* sp., UMMP V58270 pt, left dentary, mesial view; **b-d**, *Prosopium prolixus*, UMMP V58270, three dentaries, mesial view; **e**, above and left, *Prosopium prolixus*, UMMP V86641 pt, two right dentaries, mesial view; **e**, below, *Prosopium* sp., UMMP V86641 pt, right dentary, mesial view; **f**, *Prosopium prolixus,* UMMP V58270, 2 dentaries, lateral view; **g**, *Prosopium prolixus*, UMMP V59300, left dentary, mesial view; **h**, *Prosopium* sp., UMMP V62420, right dentary, mesial view; **i**, *Prosopium prolixus,* UMMP V 62030, biting edge of left dentary, dorsal view; **j**, *Prosopium prolixus,* UMMP V50633, left dentary, lateral view.

Table 2.— Comparison of Chalk Hills and Glenns Ferry fish species.

Species	Chalk Hills Fm.	Glenns Ferry Fm.
Family Ictaluridae		
Ameiurus vespertinus	X	X
Ameiurus peregrinus	X	X
Family Cyprinidae		
Orthodon hadrognathus	X	X
Ptychocheilus arciferus	X	X
Mylopharodon hagermanensis		X
Mylocheilus robustus		X
Mylocheilus kingi	X	
Mylocheilus inflexus	X	
Acrocheilus latus	X	X
Lavinia hibbardi	X	X
Gila (Klamathella) milleri	X?	X
Richardsonius durranti		X
Rhinichthys osculus		X
Family Catostomidae		
Deltistes shoshonensis	X?	X
Deltistes owyhee	X?	X
Chasmistes spatulifer	X	X
Catostomus cristatus	X	X
Pantosteus oromyzon		X
Family Salmonidae		
Prosopium prolixus		X
Prosopium sp.		X
Paleolox larsoni	X	
Oncorhynchus lacustris	X	X
Oncorhynchus salax	X	X
Oncorhynchus ketopsis	X	
Oncorhynchus tshawytscha		X
Oncorhynchus rastellus	X	
Family Centrarchidae		
Archoplites taylori	X	X
Archoplites sp.		X
Family Cottidae		
Cottus calcatus	X	X
Cottus cf. *bairdi*		X
Myoxocephalus idahoensis		X
Myoxocephalus antiquus		X
Kerocottus divaricatus		X
Kerocottus pontifex		X
Kerocottus hypoceras		X
Kerocottus sp. 1		X
Kerocottus sp. 2		X

1961; Dorofeyeva et al., 1980; Kendall and Behnke, 1984; Stearley and Smith, 1993; Nelson, 2006). The coregonines are the sister group to (thymallines plus salmonines) according to morphological analyses. The salmoniform tree of Wilson and Williams (2010) also replicates this cladistic pattern, although Wilson and Williams do not supply taxonomic ranks. Macqueen and Johnston (2014), after correcting for duplicated DNA elements, found a sister-pair relationship joining the Coregoninae and Thymallinae, but the duplication supporting this relationship is earlier than (plesiomorphic to) the divergence of the three subfamilies.

COREGONINAE

Coregonine fishes are diagnosed by many osteological characters, including cranial characters (Norden, 1961; Cavender, 1970) which occur in fossils 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 anteriorially 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 dermethmoids 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 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 suprapreopercle 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 parietals 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 salmons and trouts (*Salmo*) and the Pacific salmons 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 4b.— Fossil *Prosopium* bones from the Glenns Ferry Formation: **k**, **m**, **p**, *Prosopium prolixus,* UMMP V86641, 62448, 58432, maxillae, mesial view; **q**, *Prosopium* sp., UMMP V27038, maxilla, mesial view; **l**, **n**, **o**, *Prosopium prolixus*, UMMP V62420, 62755, 62803, maxillae*,* mesial view; **r**, *Prosopium prolixus*, UMMP V62420, left frontal, dorsal view; **s**, *Prosopium prolixus,* UMMP V62420, right frontal, mesial view; **t**, *Prosopium prolixus*, UMMP V62755, right articular-angular, lateral view; **u**, *Prosopium prolixus,* UMMP V86641, left opercle, mesial view; **v**, *Prosopium prolixus*, UMMP V 86641, left supracleithrum, dorsal view.
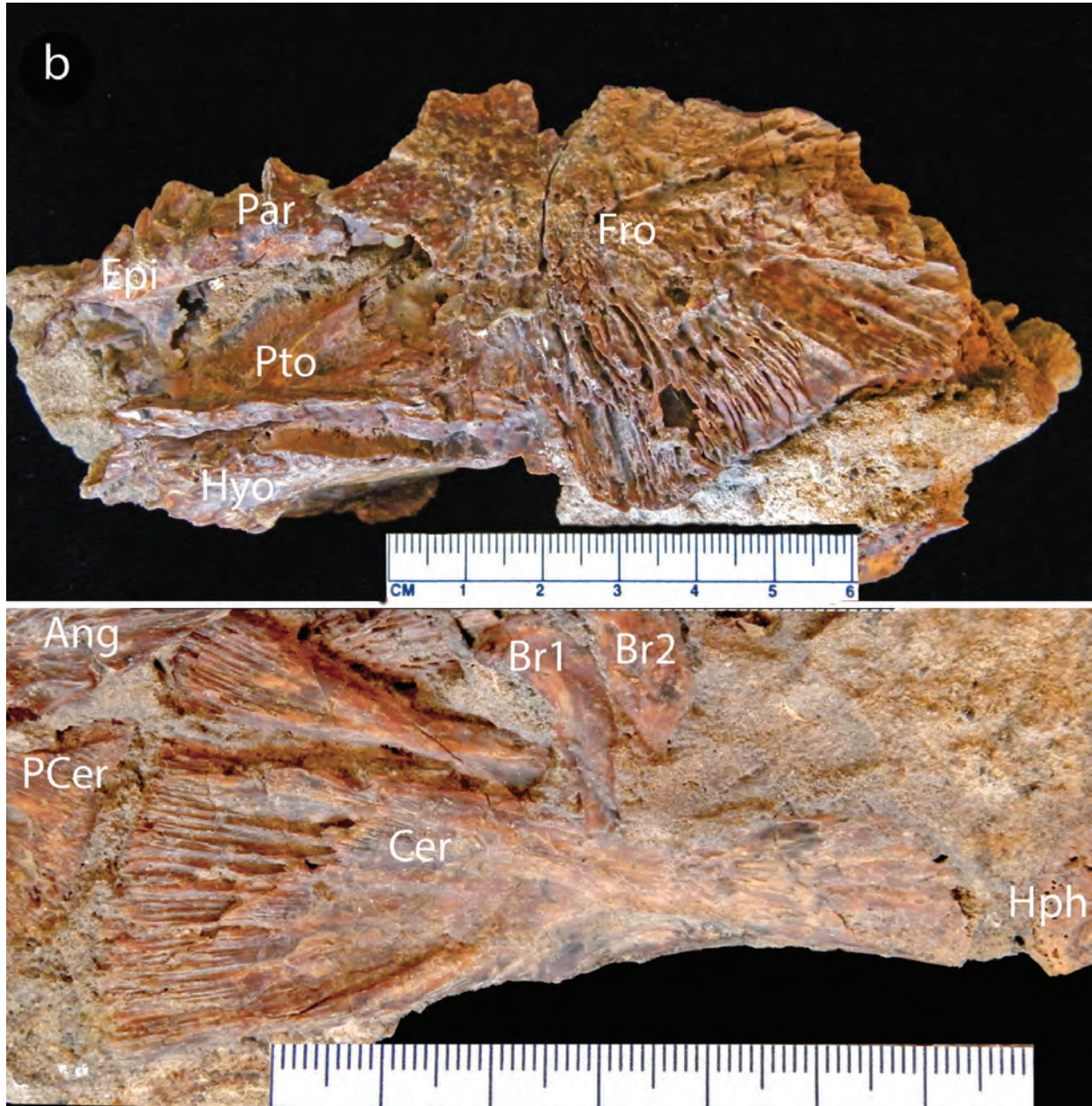
Figure 5a.—Type specimen of *Paleolox larsoni*, UMMP 62222. Collected by Peter Kimmel, Tunnel Mountain Locality, Malheur County, Oregon. Top: right posterior jaw and suspensiorium. Bottom: Right view of posterior cranium. Symbols: **Ang,** Angular-articular; **Atl,** Atlas; **Boc**; Basioccipital; **Cer**, Ceratohyal; **Den,** Dentary; **Dsp,** Dermosphenotic; **Fro,** Frontal; **Hyo,** Hyomandibula; **Max**, Maxilla; **Mpt**, Metapterygoid; **Oc**, Ocular; = Sclerotic; **Pop**, Preopercle; **Psp**, Parasphenoid; **Pto**, Pterotic; **Qua**, Quadrate; **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.
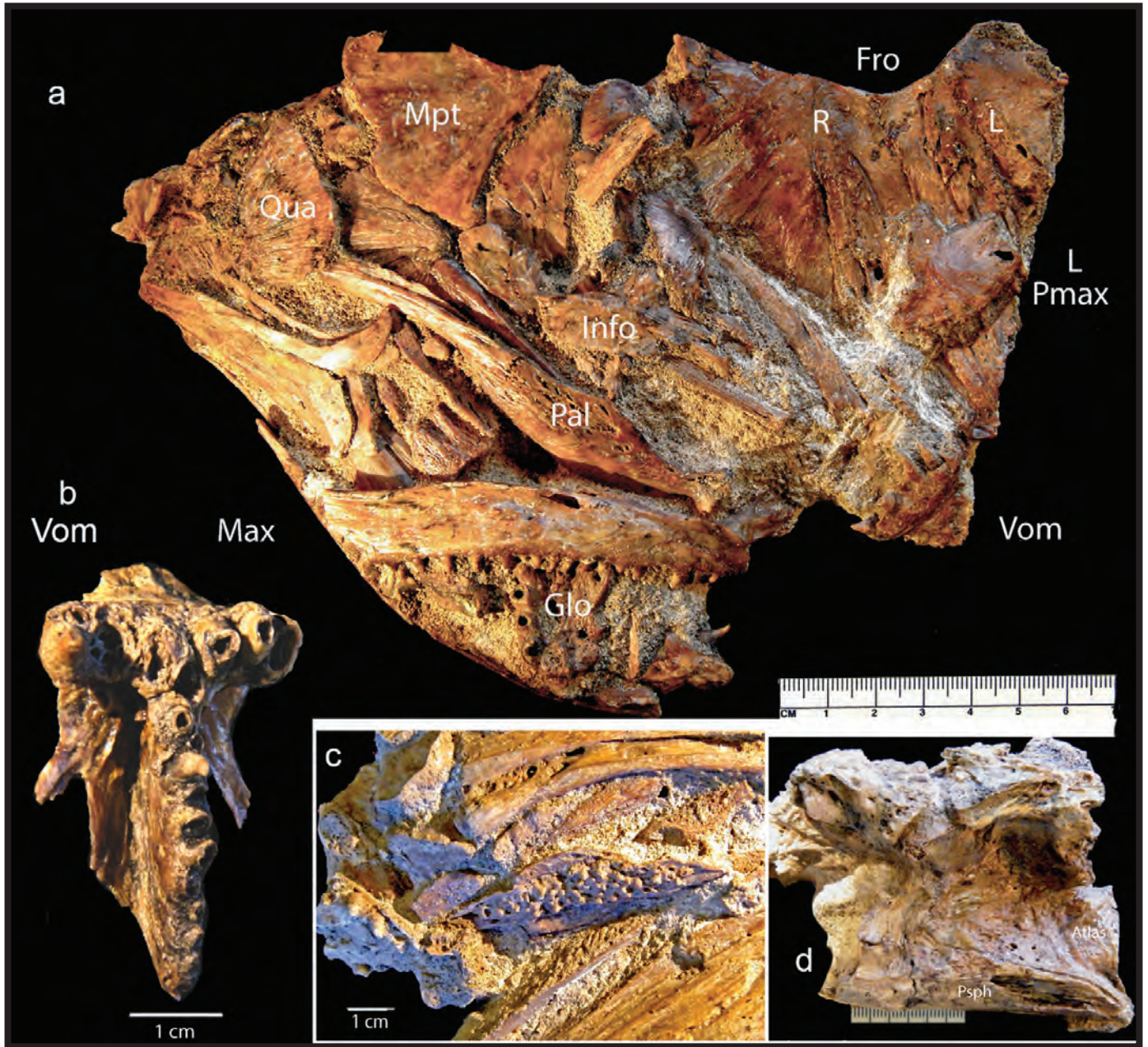
Figure 7.— **a**: UMMP specimen V42382, right anterior cranium plus anterior skull roof and left premaxilla. **Fro**, Frontal; **Glo**, Glossohyal; **Info**, Infraorbital; **Max**, Maxilla; **Mpt**, Metapterygoid; **Pal**, Palatine; **Pmax**, Premaxilla; **Qua**, Quadrate; **Vom**, Vomer. **b**: vomer, UMMP 69018. **c**: closeup of basibranchial tooth plate, Wilkinson specimen. **d**: UMMP 116957, neurocranium, left view, anterior to left. **Atlas**, Atlas; **Psph**, Parasphenoid.

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
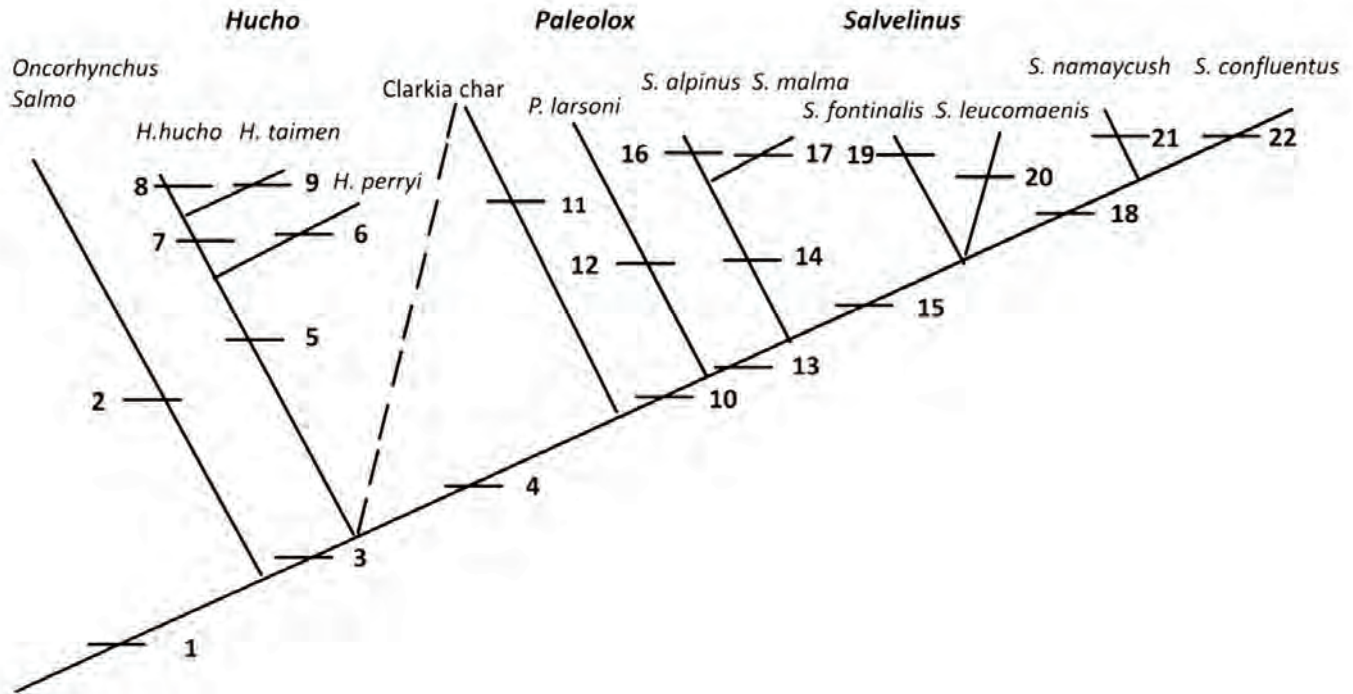
Figure 8.— Cladogram of char-huchen clade, including the Clarkia taxon c.f. *Hucho*, and *Paleolox larsoni*.

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). These

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 caecae 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-termporal fossa
    Parasphenoid arched
    Frontals gabled at midline *sensu* Cavender
    Vertebral count > 61

15. *S. fontinalis + S. leucomaenis + 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. leucomaenis*:
    Numerous white spots

21. *S. namaycush*:
    Pyloric caecae > 70
    Nuptial tubercles present

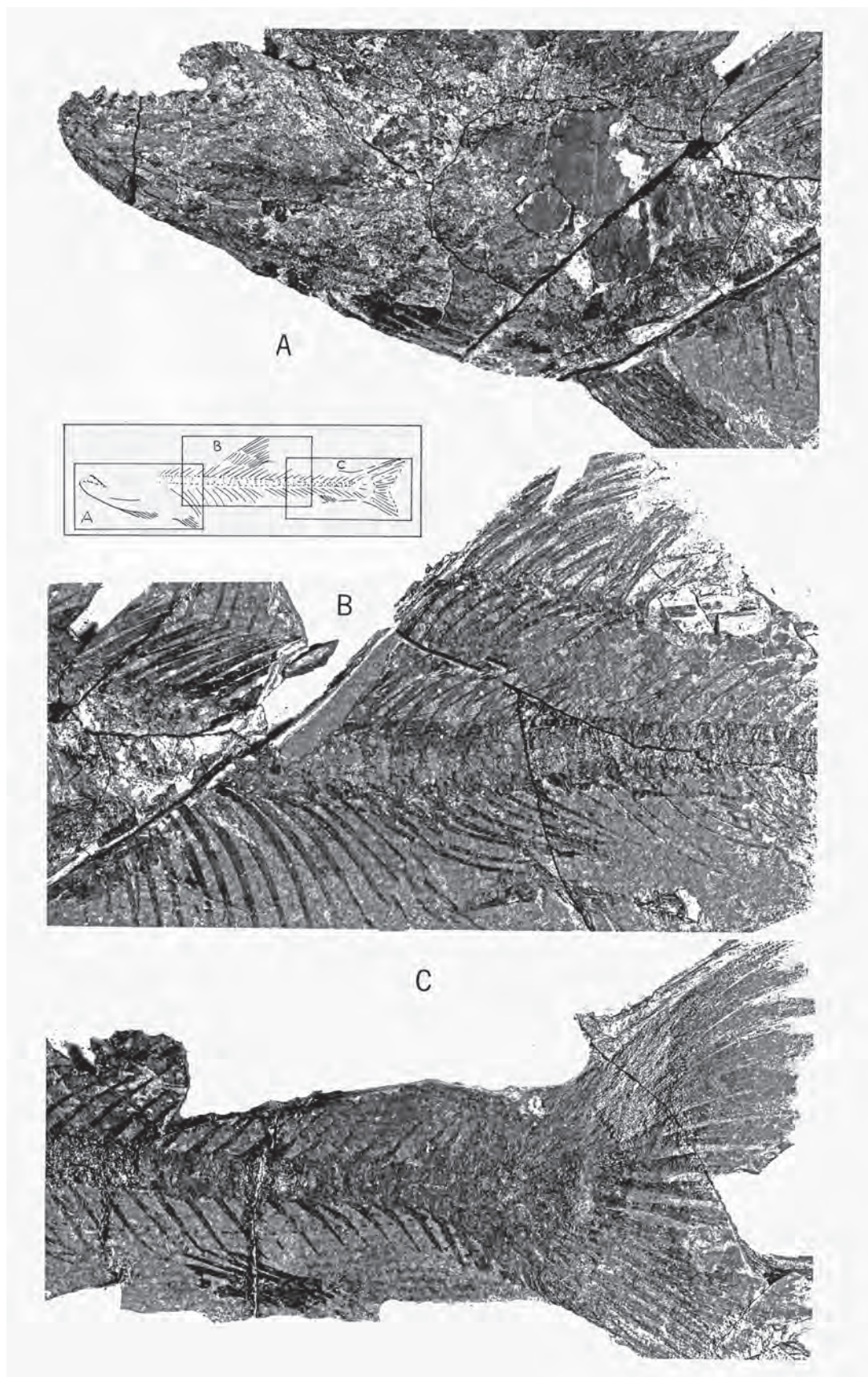22. *S. confluentus*:
    Vermiculations absent

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.

Figure 10.— Michael Bell at the Truckee Formation diatomites, Fernley, Nevada, August 5, 2009. Photo by R. Stearley.

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.
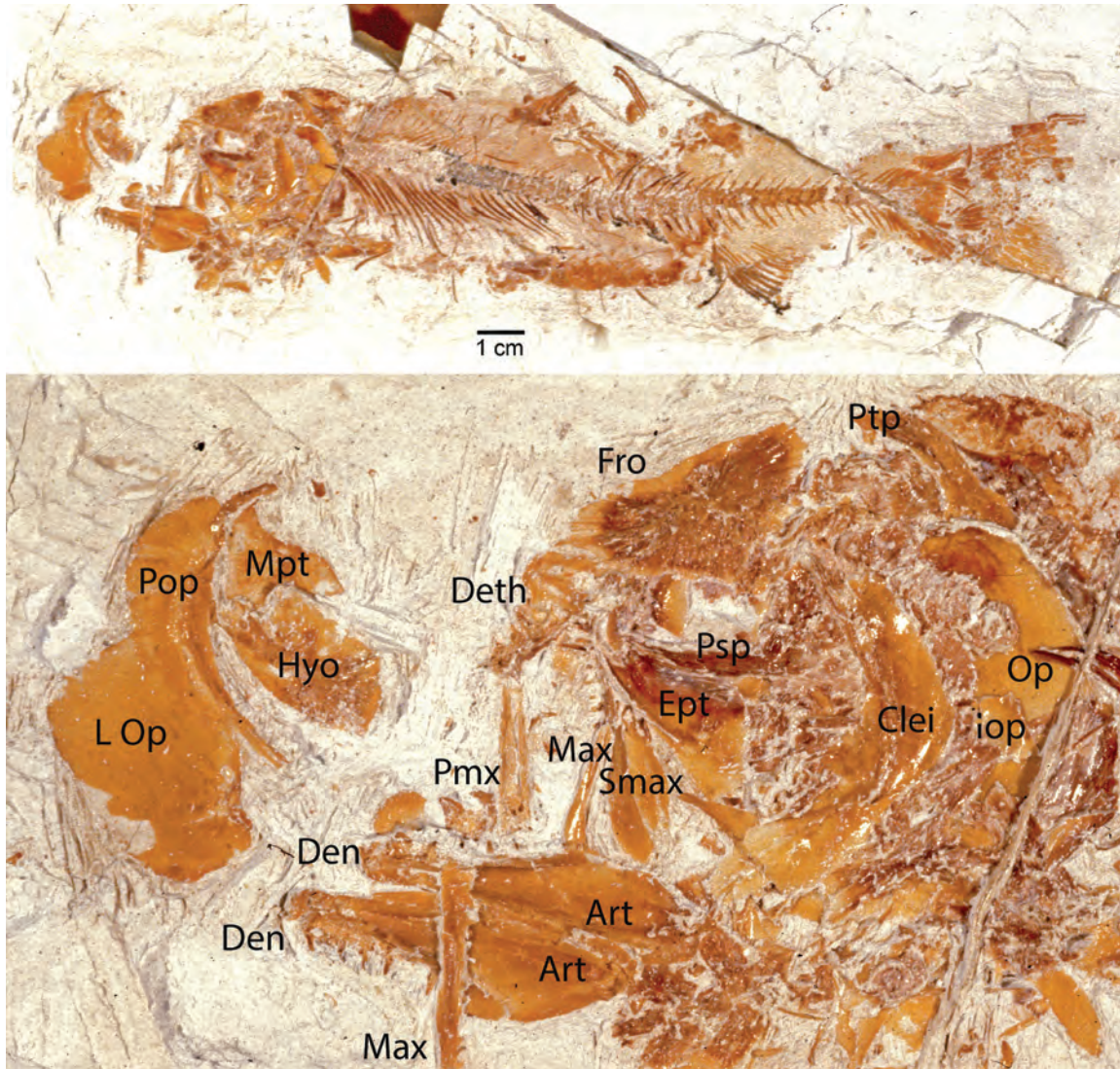
Figure 11.— Holotype *Oncorhynchus belli* n. sp., UMMP V74362. Top: complete specimen. Bottom: Closeup of cranium. **Art**, articular-angular; **Clei**, Cleithrum; **Den**, Dentary; **Deth**, dermethmoid; **Ept**, Epipterygoid; **Fro**, Frontal; **Hyo**, Hyomandibula; **iop**, interopercle; **Max**, 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).
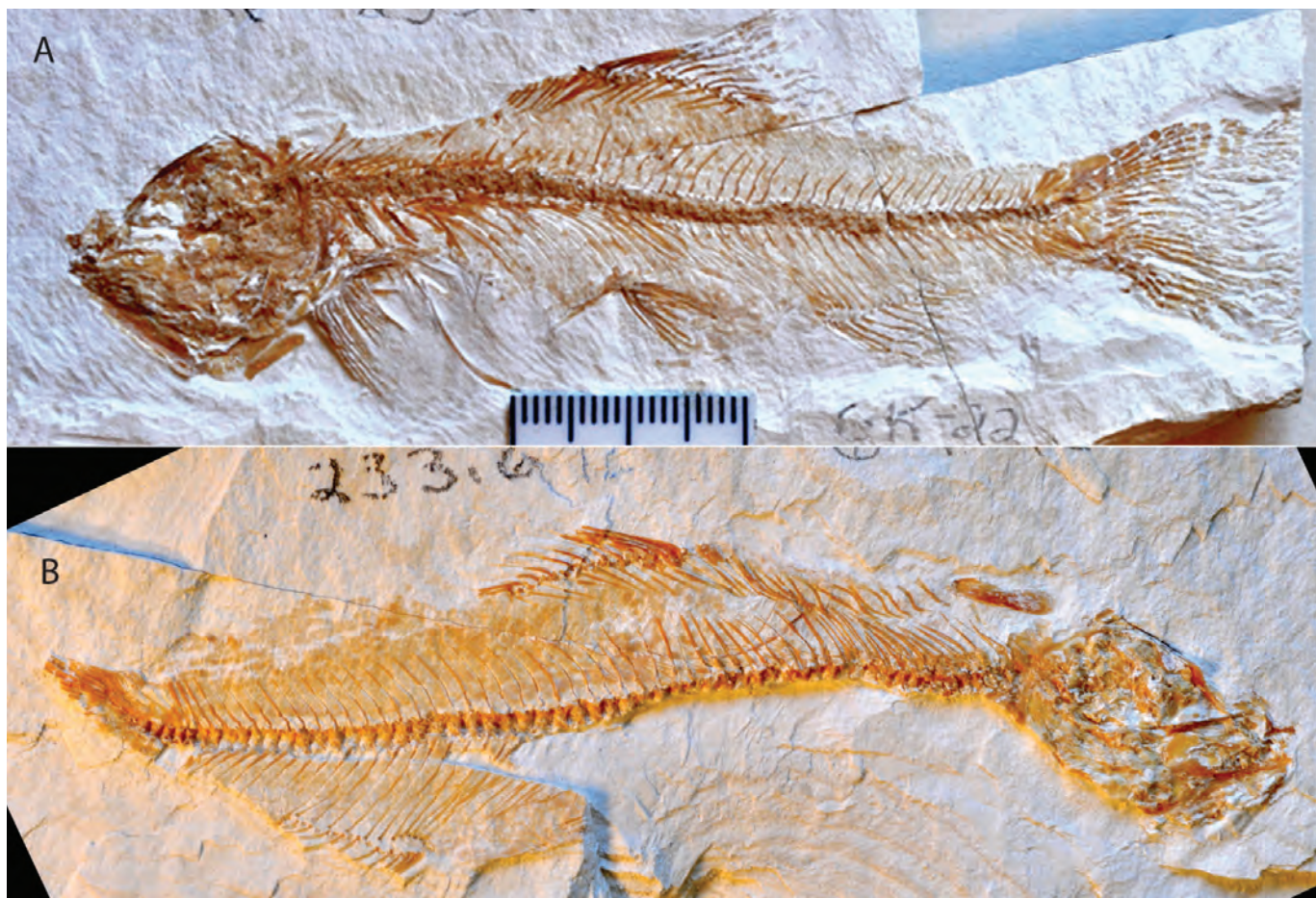
Figure 12.— Paratype of *O. belli*, UMMP 42380, part and counterpart.

Systematic Paleontology:

Teleostei
Salmoniformes
Salmonidae
Genus *Oncorhynchus* Richardson
***Oncorhynchus belli* new species**
Fig. 11, 12

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 parasphenoid, 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; parasphenoid; 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 preopercle 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* +

Figure 13.— *Oncorhynchus lacustris*. E. D. Cope's type specimen, USNM 13652.

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 postero-ventral process.

Description.— Salmonine fish with fan-shaped stegural 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*, *Paleolox*, *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*,

Figure 14.— *Oncorhynchus lacustris* cranium, UMMP V50302, specimen collected by R. Stearley, June 1987, from Browns Creek locality, Owyhee County, Idaho.

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 anterio-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.
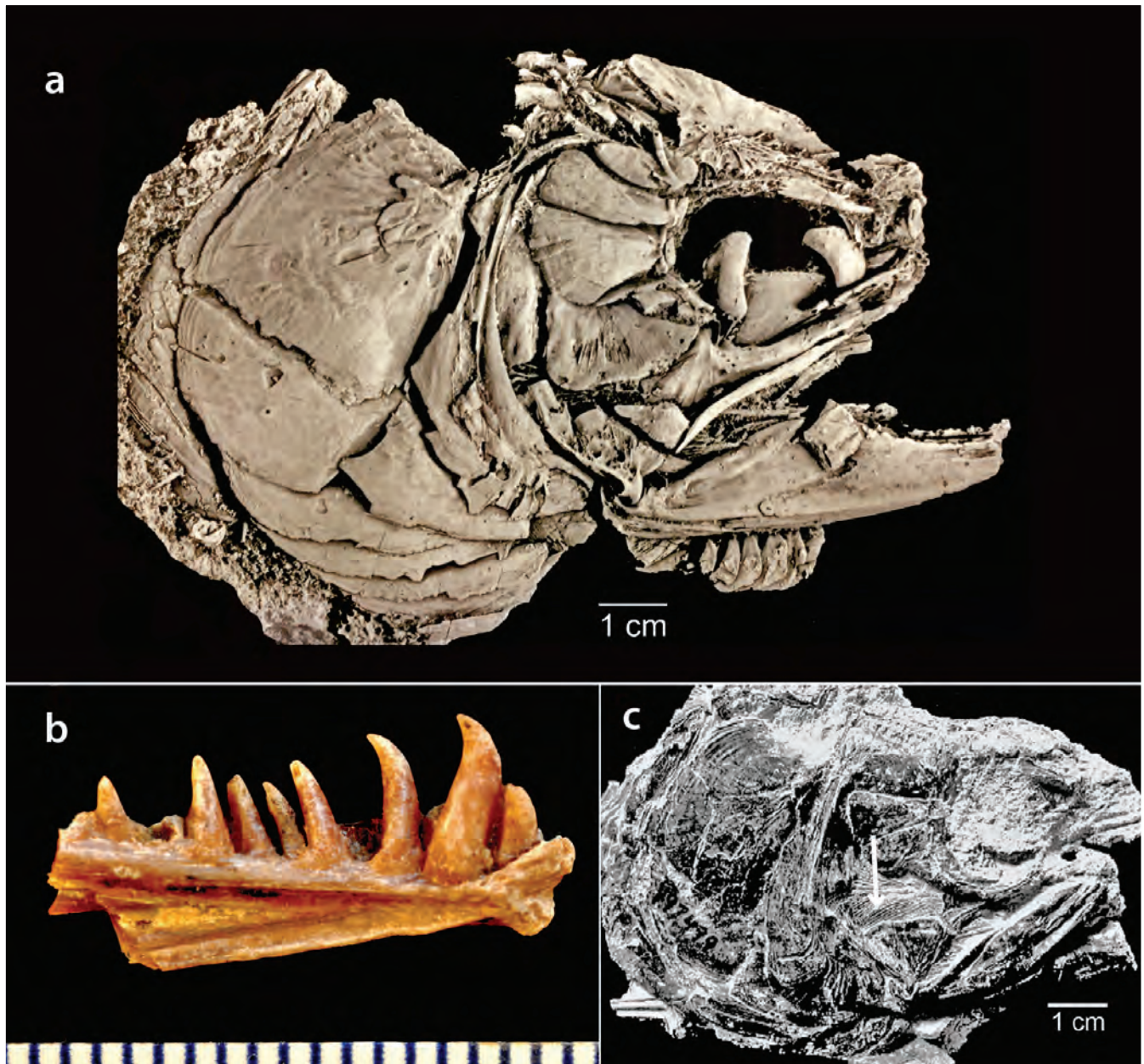
Figure 15.— *Oncorhynchus salax*. **a**, Type specimen, UMMP V62100, collected by Beverly Smith, June, 1974; **b**, UMMP 97499 distal left dentary, mesial view, of breeding individual; **c**, UMMP V97499, dissected to display gill rakers.

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
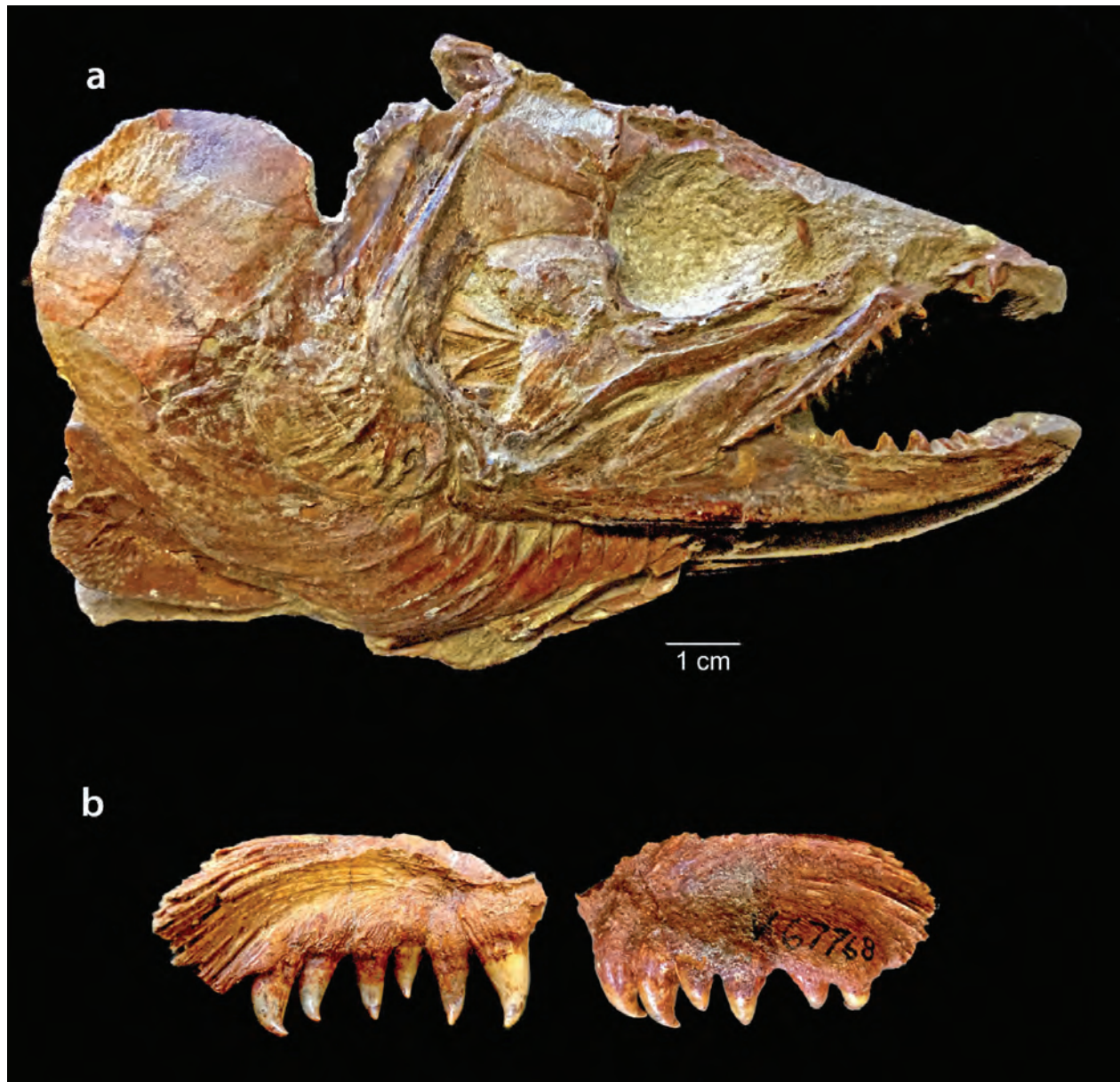
Figure 16.— **a**. *Oncorhynchus ketopsis*. Type specimen, UMMP 97500, Coyote Gulch, Malheur Co. Oregon. **b**. Premaxilla of *O. tshawytscha*, Late Pliocene Glenns Ferry Formation at small Butte 6 mi south of Grandview, Owyhee County, Idaho. Left, internal view, right external view. Length of bone 52 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 anteriorally 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
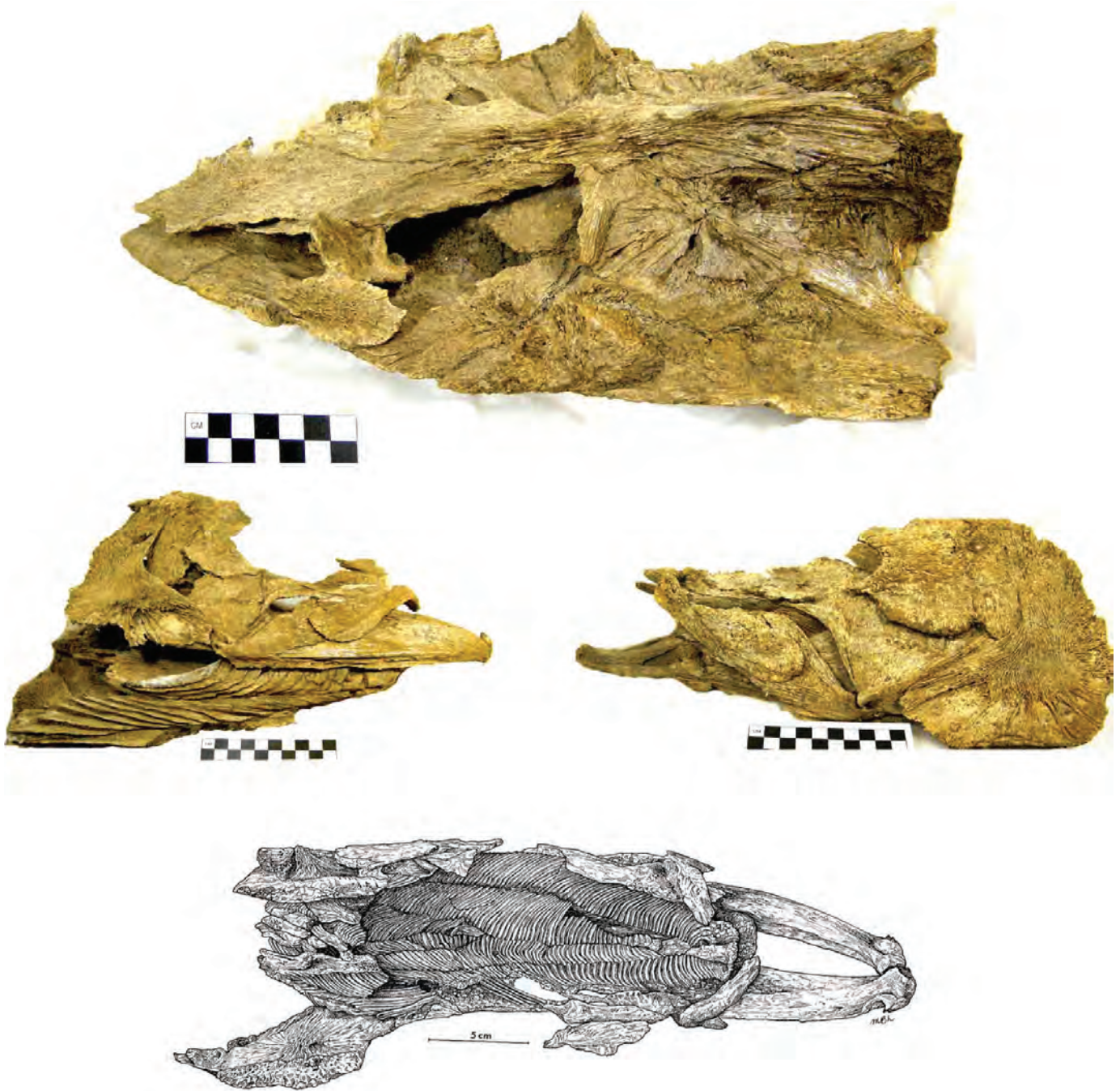
Figure 17.— Holotype, *Oncorhynchus rastrosus*; Gateway Locality, Oregon. UO 26799. Top: ventral view of neurocranium; anterior of neurocranium to left. Middle left: Right jaws, suspensorium, preopercle, and branchiostegals. Middle right: left jaws, palate, quadrate, preopercle. Bottom: dorsal view of orobranchial chamber, showing gill rakers in place. Photos by R. Stearley; figure at bottom reproduced from Cavender and Miller, Univ. Oregon Bulletin 18.

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 salmons, these breeding teeth are anchored to the dentary with late-developing bony cement, crowded, and with posteriorally-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 salmons.

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 salmons. Further, the dorsal limb of the preopercle is expanded posteriorly, as occurs in Pacific salmons (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 salmons." 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 Iiames and Scott McKain in 1964, from the

Table 4.— Localities from which *Oncorhynchus rastrosus* and the small form from the Snake River Plain have been collected.

Locality	Stratigraphic Unit	*Age
1. Gateway, Jefferson Co., OR (UO 2250), multiple collections	Deschutes Fm.	Early Hemphillian
2. Worden, Klamath Co., OR , multiple collections	"Yonna" Fm.	Late Hemphillian
3. Pinole, Contra Cost Co., CA (UCMP 2572, 3425, 3837)	Pinole Tuff	Late Hemphillian
4. Turlock Lake, Stanislaus Co., CA (UCMP 5405)	Mehrten Fm.	Late Hemphillian
5. Laguna Niguel district, Orange Co., CA (LACM 6902)	Monterey Fm.	Hemphillian or Late Clarendonian
6. Oceanside, San Diego Co., CA (LACM 4297; San Luis Rey L.F.)	Capistrano Fm.	Early Hemphillian
7. Oceanside, San Diego Co., CA (LACM 4301, Lawrence Canyon L.F.)	Capistrano Fm.	Late Hemphillian
8. Studio City, Los Angeles, CA (LACM 1229)	Modelo Fm.	Middle Clarendonian
9. El Toro, Los Angeles, CA (LACM 1945) [source of the two largest vertebrae]	Monterey Fm.	Hemphillian
10. Freeway cut, San Diego Co., CA (LACM 1267)	Modelo Fm.	Middle Clarendonian
11. Mission Viejo, Orange Co., CA (LACM 3186)	Capistrano Fm.	Late Hemphillian
12. Drake's Bay, Marin County, CA (UCMP 136028)	Purissima Fm.	Late Hemphillian
13. River Road, Franklin County, WA (UWBM CO479)	Ringold Fm.	Late Hemphillian

*North American Land Mammal Age Equivalent

"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
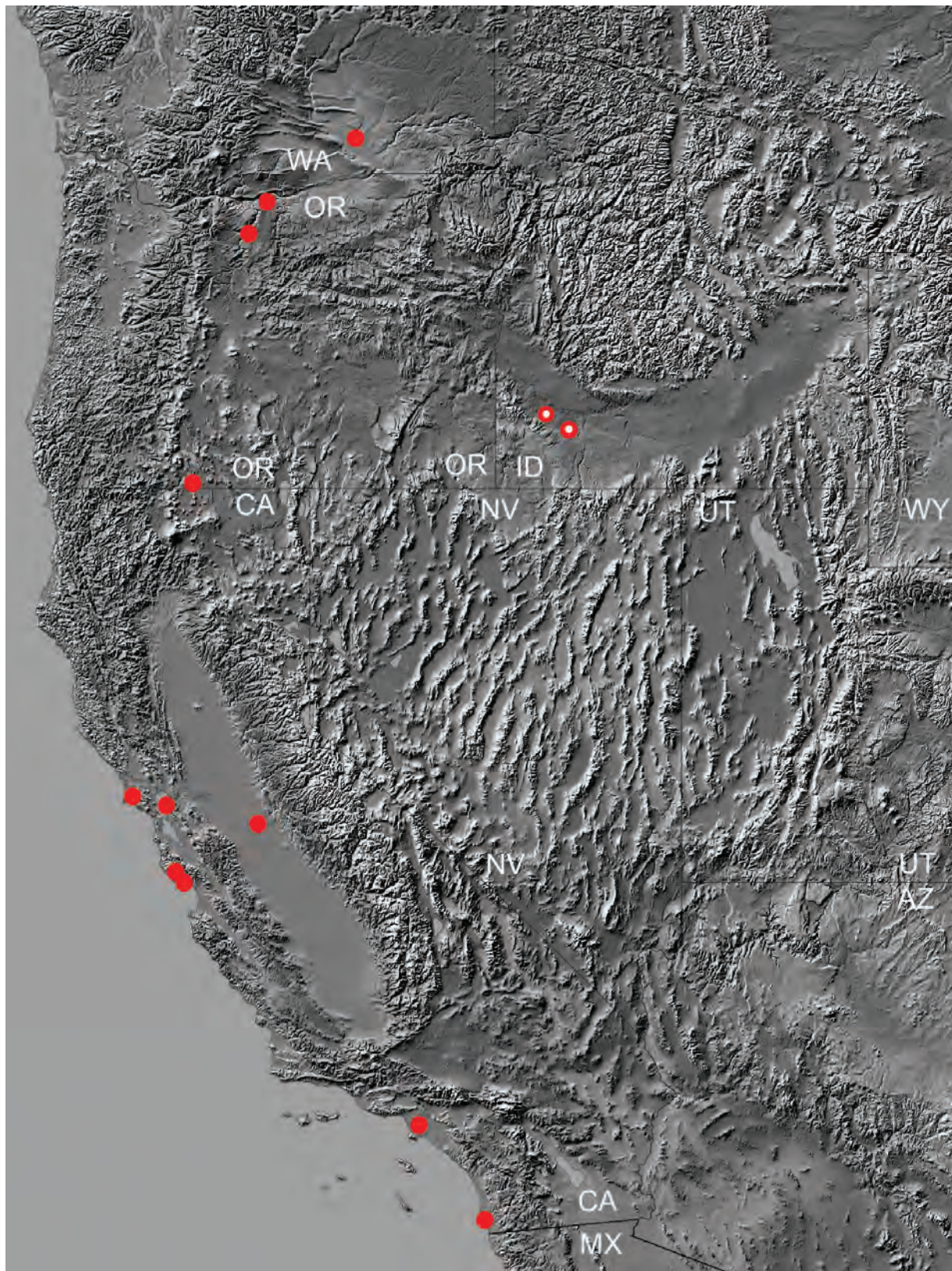
Figure 18.— Distribution map, fossil localities, for *Oncorhynchus rastrosus* and *O. rastellus*. Solid red dots: *O. rastrosus* (see Table 3). Red dots with white bulls-eyes: *O. rastellus*.

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 $W = 1.44$ x 10^{-8} $L^{3.12}$ = 439 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^2 / 740 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, parasphenoid 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 premaxillary (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 *Oncorhynchus* 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, parasphenoid 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.
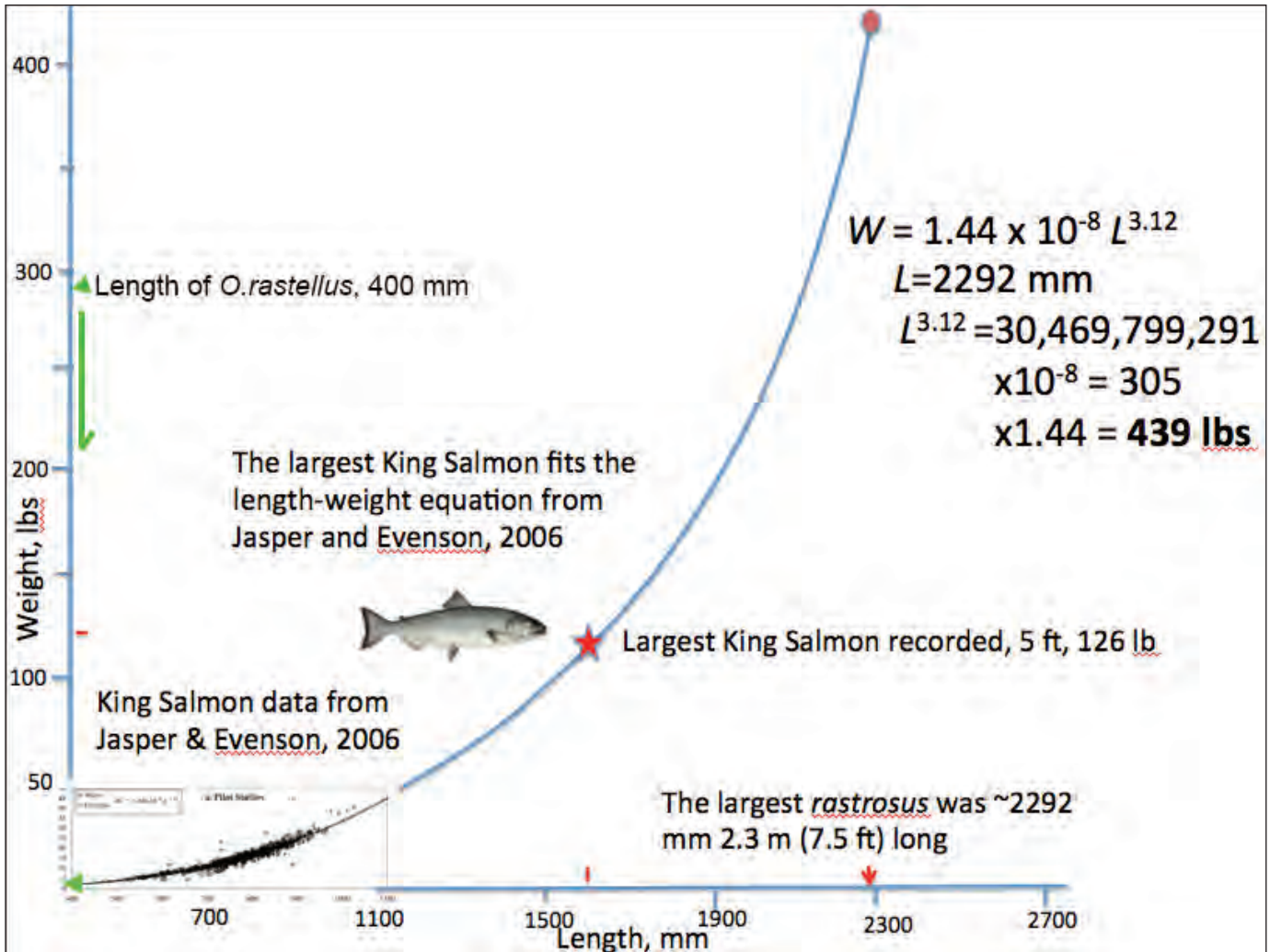
Figure 20.— Regression and calculation of size for *O. rastrosus* and *O. rastellus*.

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 *Oncorhynchus,* 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, *Oncorhynchus* (*"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, T5S, 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 45 mm, 13 miscellaneous skull roof bones. 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 fragmentd10-38 mm; four articular-angulars 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. coulteri*) (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 graduated 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,
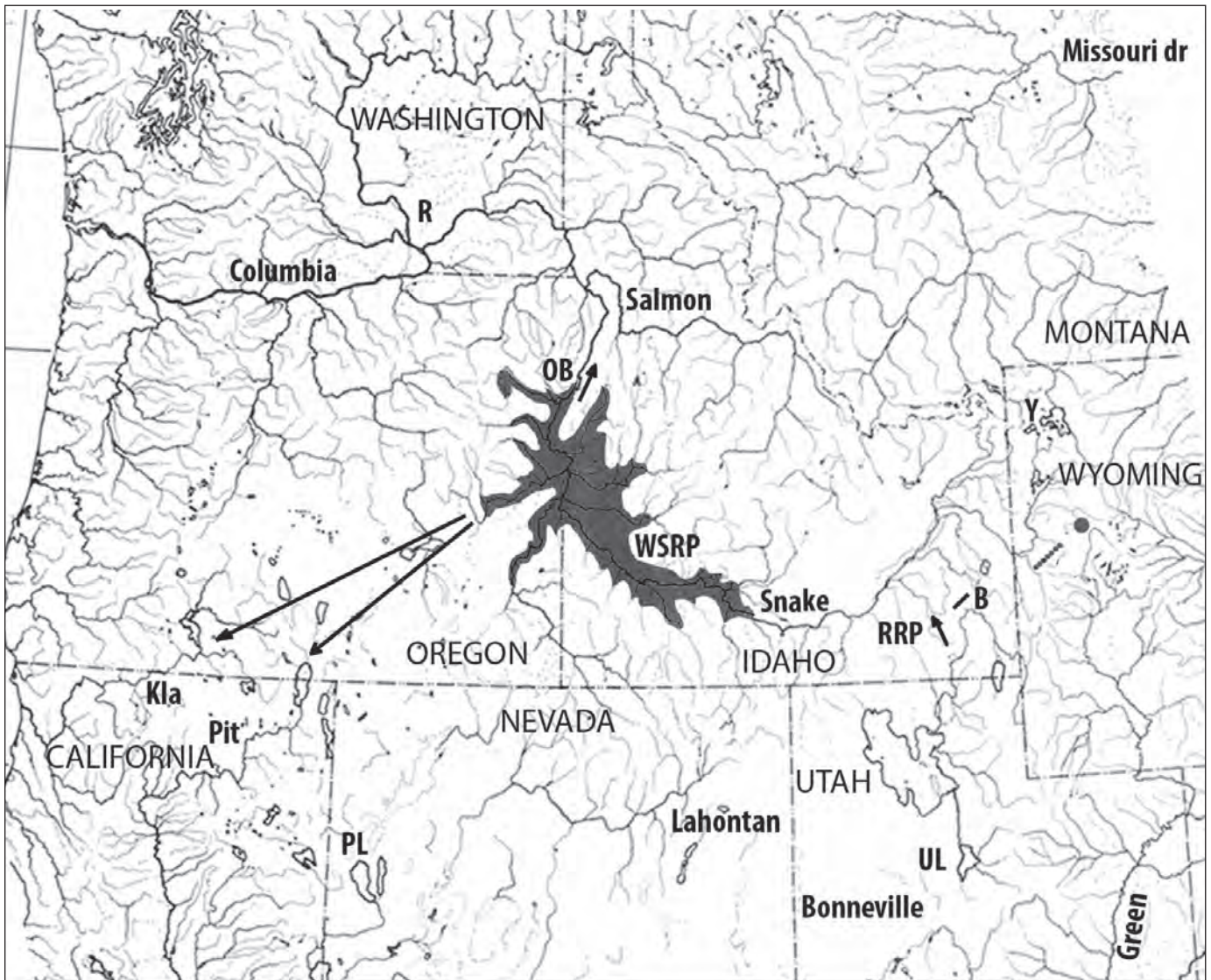
Figure 21.— Potential drainage connections, western Snake River Plain. Abbreviations: **B**, Bear River; **Kla**, Klamath drainage; **OB**, Oxbow; **Pit**, Pitt River; **PL**, Pyramid Lake; **RRP**, Red Rock Pass; **R**, Ringold Formation; **UL**, Utah Lake; **WSRP**, Western Snake River Plain; **Y**, Yellowstone.

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

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 11Ma (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 salmons 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 salmons, 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 *Ameiurus* 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 southwestward 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 centrarchid, *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 southwestwardly 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 (*Ameiurus* 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, *Ameiurus 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 salmons 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. belli*, 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 biogeographic 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 Glenns 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,

2007; Waples et al., 2008; Pess et al., 2014). 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 Peneplain (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.

ACKNOWLEDGEMENTS

LITERATURE CITED

Aalto, K. R. 2006. The Klamath peneplain: a review of J.S. Diller's classic erosion surface. Pp. 451-463 *In*: A. W. Snoke and C. G. Barnes, eds., Geological Studies in the Klamath Mountains Province, California and Oregon: A Volume in Honor of William P. Irwin. Boulder, Colorado, Geological Society of America Special Paper 410.

Aalto, K. R., W. D. Sharp, and P. R. Renne. 1998. $^{40}AR/^{39}Ar$ dating of detrital micas from Oligocene-Pleistocene sandstones of the Olympic Peninsula, Klamath Mountains and northern California Coast Ranges: Provenance and paleodrainage patterns. Canadian Journal of Earth Sciences 35:735-745.

Andrusak, H. and E. Parkinson. 1984. Food Habits of Gerrard Stock Rainbow Trout in Kootenay Lake, British Columbia. Vancouver, Province of British Columbia Fisheries Technical Circular No. 60.

Armstrong, R. L., W. P. Leeman, and H. E. Malde. 1975. K.Ar dating Quaternary and Neogene volcanic rocks of the Snake River Plain, Idaho. American J. Science. 273: 225-251.

Augerot, X. 2005. Atlas of Pacific Salmon. Berkeley, University of California Press.

Axelrod, D. I. 1968. Tertiary floras and topographic history of the Snake River basin, Idaho. Geological Society of America Bulletin 79: 17-34.

Barnes, L. G. 1981. A late Miocene marine vertebrate assemblage from southern California. National Geographic Society Research Reports 21:13-20.

Barnes, L. G., H. Howard, J. H. Hutchinson, and B. J. Welton. 1985. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. *In*: P. L. Abbott and S. O'Dunn, eds., Geologic Investigations of the San Diego Coastal Plain, San Diego Association of Geologists, San Diego, April, 1981.

Barron, J. A., M. Lyle, and I. Koizumi. 2002. Late Miocene and Pliocene biosiliceous sedimentation along the California margin. Revista Mexicana de Cincias Geologicas 19 (3): 161-169.

Baumgartner, J. V. 1982. A new fossil ictalurid catfish from the Miocene Middle Member of the Truckee Formation, Nevada. Copeia 1982 (1): 38-46.

Beacham, T. D. 1986. Type, quantity and food of Pacific salmon (*Oncorhynchus*) in the Strait of San Juan de Fuca, British Columbia. Fishery Bulletin of the National Marine Fisheries Service 84 (1): 77-89.

Beacham, T. D., B. McIntosh, C. MacConnachie, K. M. Miller, R. E. Withler, and N. Varnavskaya. 2006. Pacific rim population structure of sockey salmon as determined from microsatellite analysis. Transactions of the American Fisheries Society 135: 174-187.

Behl, R. J. 1999. Since Bramlette (1946): The Miocene Monterey Formation of California revisited. *In*: E. M. Moores, D. Sloan, and D. L. Stout, eds., Classic Cordilleran Concepts: A View from California. Boulder, Colorado, Geological Society of America Special Paper 338.

Behnke, R. J. 1981. Systematic and zoogeographic interpretation of Great Basin trouts. Pp. 95-124 *In*: R. J. Naiman and D. L. Soltz, eds., Fishes in North American Deserts. New York, John Wiley.

Behnke, R. J. 1992. Native Trout of Western North America. Bethesda, Maryland, American Fisheries Society Monograph 6.

Bell, M. A. 1994. Palaeobiology and evolution of threespine stickleback. Chapter 15, pp. 438-471 *In*: M. A. Bell and S. A. Foster, eds., The Evolutionary Biology of the Threespine Stickleback. Oxford, U.K., Oxford University Press.

Beranek, L. P., P. K. Link, and C. M. Fanning. 2006. Miocene to Holocene landscape evolution of the western Snake River Plain region, Idaho: Using the SHRIMP detrital zircon provenance record to track eastward migration of the Yellowstone hotspot. Geological Society of America Bulletin 118: 1027-1050.

Berg, W. J. 1987. Evolutionary genetics of rainbow trout, *Parasalmo gairdnerii* (Richardson). Ph.D. Dissertation, University of California, Davis.

Bohacs, K. M., K. Lamb-Wozniak, T. M. Demko, J. Eleson, O. McLaughlin, C. Lash, D. M. Cleveland, and S. Kaczmarek. 2013. Vertical and lateral distribution of

lacustrine carbonate lithofacies at the parasequence scale in the Miocene Hot Spring Limestone, Idaho: An analog addressing reservoir presence and quality. American Association of Petroleum Geologists Bulletin, v. 97, no. 11 (November 2013), pp. 1967–1995.

Bonnichsen, B. and M. M. Godchaux. 2002. Late Miocene, Pliocene and Pleistocene geology of southwestern Idaho with emphasis on basalts in the Bruneau-Jarbidge, Twin Falls, and western Snake River Plain regions. Pp. 233-312 *In*: B. Bonnichsen, C. M. White, and M. McCurry, eds., Tectonic and Magmatic Evolution of the Snake River Plain Volcanic Province. Moscow, Idaho, Idaho Geological Survey Bulletin 30.

Broughton, J. M., D. B. Madsen, J. Quade. 2000. Fish Re-mains from Homestead Cave and Lake Levels of the Past 13,000 Years in the Bonneville Basin. Quaternary Re-search, 53: 393-401.

Buechler, W. and G. R. Smith, this volume. Fishes of the Miocene Pickett Creek Diatomite *In* W. L. Fink and Nathan Carpenter, eds, Fishes of the Mio-Pliocene Western Snake River Plain and vicinity, University of Michigan Museum of Zoology, Miscellaneous Publication 204.

Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pp. 3-117 *In*: C. Groot and L. Margolis, eds., Pacific Salmon Life Histories. Vancouver, University of British Columbia Press.

Buwalda, J. P. 1923. A preliminary reconnaissance of the oil and gas possibilities of southwestern and south-central Idaho: Idaho Bureau of Mines and Geology Pamphlet 5, 10 pp.

Carl, L. M. 1982. Natural reproduction of coho salmon and chinook salmon in some Michigan streams. North American Journal of Fisheries Management 4: 375-380.

Carpenter, N. E., and G. R. Smith, this volume. Mio-Pliocene stratigraphy and fishes of the Western Snake River Plain, Oregon-Idaho Graben, and vicinity, *In* W. L. Fink and Nathan Carpenter, eds, Fishes of the Mio-Pliocene Western Snake River Plain and vicinity, University of Michigan Museum of Zoology, Miscellaneous Publication 204.

Cavender, T. M. 1970. A comparison of coregonines and other salmonids with the earliest known teleostean fishes. Pp. 1-32 *In*: C. C. Lindsey and C. S. Woods, eds., Biology of Coregonid Fishes. Winnipeg, University of Manitoba Press.

Cavender T. M., and R. R. Miller. 1972. *Smilodonichthys rastrosus*: a new Pliocene salmonid fish from western United States. Eugene, Oregon, University of Oregon Museum of Natural History Bulletin 18, pp. 1-44.

Cavender T. M. and R. R. Miller, 1982. *Salmo australis*, a new species of fossil salmonid from southwestern Mexico. Contributions from the Museum of Paleontology, University of Michigan 26 (1): 1-17.

Cavender T. M. and R. R. Milller. This volume, A new fossil species of *Salvelinus* from western North America, *In* W. L. Fink and Nathan Carpenter, eds, Fishes of the Mio-Pliocene Western Snake River Plain and vicinity, University of Michigan Museum of Zoology, Miscellaneous Publication 204.

Chapin, C. E. 2008. Interplay of oceanographic and paleocli-mate events with tectonism during middle to late Miocene sedimentation across the southwestern USA. Geosphere 4 (6): 976-991.

Clemens, D. M. and S. H. Wood. 1993. Radiometric dating, volcanic stratigraphy, and sedimentation in the Boise Foothills, northeastern margin of the western Snake River Plain, Ada County, Idaho. Isochron/West 59: 3-10.

Cope, E. D. 1870. On the fishes of a fresh water Tertiary in Idaho, discovered by Capt. Clarence King. Proceedings of the American Philosophical Society 11: 538-547.

Cope, E. D. 1884a. On the fishes of the Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake. Proceedings of the Academy of Natural Sciences of Philadelphia 35: 134-167.

Cope, E. D. 1884b. A new Pliocene formation in the Snake River Valley. American Naturalist, 17: 867-868.

Crespi, B. J. and M. J. Fulton. 2003. Molecular systematics of Salmonidae: Combined nuclear data yields a robust phylogeny. Molecular Phylogenetics and Evolution 31(2): 658-679.

Crete-Lafreniere, A., L. K. Wier, and L. Bernatchez. 2012. Framing the Salmonidae family phylogenetic portrait: a more complete picture from increased taxon sampling. PLOS ONE 7 (10): 1-19.

Currens, K. P., C. B. Schreck, and H. W. Li. 1990. Allozyme and morphological divergence of rainbow trout (*Oncorhynchus mykiss*) above and below waterfalls in the Deschutes River, Oregon. Copeia, 1990 (3): 730-746.

Currens, K. P., C. B. Schreck and H. W. Li. 2009. Evolutionary ecology of redband trout. Transactions of the American Fisheries Society 138 (4): 797-817.

DeCelles, P. F. 2004. Late Jurassic to Eocene evolution of the Cordilleran thrust belt and foreland basin system, western U.S. American Journal of Science 304: 105-168.

Dickinson, W. R. 2006. Geotectonic evolution of the Great Basin. Geosphere 2 (7): 353-368.

Dorofeyeva, Ye. A., Ye. A. Zinov'yev, V. A. Klyukanov, Yu. S. Reshetnikov, K. A. Savvaitova and G. Kh. Shaposhnikova. 1980. The present state of research into the phylogeny and classification of Salmonoidei. Journal of Ichthyology 20 (5): 1-20.

Dumitru, T. A., W. F. Ernst, J. E. Wright, J. L. Wooden, R. E. Wells, L. P. Farmer, A. J. R. Kent, and S. A. Graham. 2013. Eocene extension in Idaho generated massive sediment floods into the Franciscan trench and into the Tyee, Great Valley, and Green River basins. Geology 41: 187-190.

Eiting, T. P. and G. R. Smith. 2007. Miocene salmon (*Oncorhynchus*) from western North America: Gill raker evolution correlated with plankton productivity in the Eastern Pacific. Palaeogeography, Palaeoclimatology, Palaeoecology 249: 412-424.

Gazin, C. L. 1936. A study of the fossil horse remains from the upper Pliocene of Idaho: U.S. National Museum Proceedings, v. 83, p. 281–320.

Geraghty, Cassie S.; J. A. Wolff; D. R. Gaylord; O. K. Neil; W. C. Rember. 2016. Tephrochronology of Mid-Miocene Clarkia Lake: Better Constraining the Lake's Age and Insight Into Mid-Miocene Lacustrine Depositional Processes (Poster Presentation). Geological Society of America, Rocky Mountain Section, Moscow, Idaho, 18 May.

Godchaux, M. M. and B. Bonnichsen. 2002. Syneruptive magma-water and posteruptive lava-water interactions in the western Snake River Plain, Idaho, during the past 12 million years. Pp. 387-434 *In*: B. Bonnichsen, C. M. White, and M. McCurry, eds., Tectonic and Magmatic Evolution of the Snake River Plain Volcanic Province. Moscow, Idaho, Idaho Geological Survey Bulletin 30.

Gold, J. R. 1977. Systematics of western North American trout (*Salmo*), with notes on the redband trout of Sheepheaven Creek, California. Canadian Journal of Zoology 55: 1858-1873.

Groot, C. and L. Margolis, 1991 eds., Pacific Salmon Life Histories. Vancouver, University of British Columbia Press.

Hendry, A. P., V. Castric, M. T. Kinnison, and T. P. Quinn. 2004. The evolution of philopatry and dispersal: Homing versus straying in salmonids. Pp. 52-91 *In*: a. P. Hendry and S. C. Stearns, eds., Evolution Illuminated: Salmon and their Relatives. Oxford, UK, Oxford University Press.

Henry, C. D. 2008. Ash-flow tuffs and paleovalleys in northeastern Nevada: implications for Eocene paleogeography and extension in the Sevier hinterland, northern Great Basin. Geosphere 4: 1-35.

Hikita, T. 1962. Ecological and morphological studies of the genus *Oncorhynchus* (Salmonidae) with particular consideration on phylogeny. Scientific Reports of the Hokkaido Salmon Hatchery 17: 1-97.

Houseman, M. D. 2004. Late Miocene diatomite formation near Fernley, Nevada. Pp. 142-152 *In*: S. B. Castor, K. G. Papke, and R. O. Meeuwig, eds., Betting on Industrial Minerals: Proceedings of the 39th Forum on the Geology of Industrial Minerals. Reno, Nevada Bureau of Mines and Geology Special Publication 33.

Irvine, J. R. 1978. The Gerrard rainbow trout of Kootenay Lake, British Columbia—a discussion of their life history with management, research and enhancement recommendations. Vancouver, Province of British Columbia Fisheries Management Reports No. 72.

Isaacs, C. M. 2001. Depositional framework of the Monterey Formation, California, pp. 1-30 *In*: C. M. Isaacs and J. Rullkoetter, eds., The Monterey Formation: From Rocks to Molecules. New York, Columbia University Press.

Jacobs, D. K., T. A. Haney, and K. D. Louie. 2004. Genes, diversity, and geologic processes on the Pacific coast. Annual Review of Earth and Planetary Sciences 32: 601-652.

Jasper, J. R. and D. F. Evenson. 2006. Length-girth, length-weight, and fecundity of Yukon River Chinook Salmon *Oncorhynchus tshawytscha*. Alaska Department of Fish and Game Fishery Data Series No. 06-70, 27 pp.

Jenks, M. D., B. Bonnichsen, and M. M. Godchaux. 1998. Geologic map of the Grand View-Bruneau area, Owyhee County, Idaho: Idaho Geological Survey Technical Report 9801, scale 1:100,000, 3 sheets.

Kato, F. 1991. Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodorus*), pp. 447-522 *In*: C. Groot and L. Margolis, eds., Pacific Salmon Life Histories. Vancouver, University of British Columbia Press.

Keeley, E. R., E. A. Parkinson, and E. B. Taylor. 2005. Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 62:1523-1539.

Kendall, A. W. and R. J. Behnke. 1984. Salmonidae: development and relationships, pp. 142-149 *In*: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. American Society of Ichthyologists and Herpetologists Special Publication 1. Lawrence, Kansas, Allen Press.

Kimmel, P. 1975. Fishes of the Miocene-Pliocene Deer Butte Formation, southeast Oregon. University of Michigan Papers on Paleontology 14: 69-87.

Kimmel, P. 1982. Stratigraphy, age, and tectonic setting of the Miocene-Pliocene lacustrine sediments of the western Snake River Plain, Oregon and Idaho, pp. 559-578 *In*: B. Bonnichsen and R. M. Breckinridge, eds., Cenozoic Geology of Idaho. Moscow, Idaho, Idaho Bureau of Mines and Geology Bulletin 26.

King, C. 1878. Systematic geology. Washington, D. C., Report of the U. S. Geol. Expl. 40th Parallel, Vol. 1.

Kirkham, V. R. D. 1931. Revision of the Payette and Idaho Formations. Journal of Geology, 39 (3): 193-239.

Kwain, W. H. 1981. Pink salmon in the Great Lakes. Fisheries 6 (2): 2-6.

Kwain, W. H. 1982. Spawning behavior and early life history of pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 39: 1353-1360.

Leidy, J. 1870. [... on new fossil fishes from the Rocky Mountain Region] Proc. Academy of Natural Sciences of Philadelphia, 22: 69-71.

Leidy, J. 1873. Contributions to the extinct vertebrate fauna of the western Territories. Rept. U.S.. Geographic Survey Territories 1: 1-358.

Livingston, D. C. 1928. Certain topographic features of northeastern Oregon and their relation to faulting. Journal of Geology 36: 694-708.

Lundberg, J. G. 1975. The Fossil Catfishes of North America. University of Michigan Papers on Paleontology, 11.

Macqueen, D. J. and I. A. Johnston. 2014. A well-constrained estimate for the timing of the salmonid whole genome duplication reveals major decoupling from species diversification, Proc. R. Soc. B: 281; DOI: 10.1098/rspb.2013.2881.

Malde, H. E. 1991. Quaternary geology and structural history of the Snake River Plain, Idaho and Oregon, pp. 251-281 *In*: R. B. Morrison, ed., Quaternary Nonglacial Geology: Conterminous U.S. Boulder, Colorado, Geological Society of America, The Geology of North America, K-2.

Malde, H. E. and H. A. Powers. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. Geological Society of America Bulletin 73: 1197-1220.

Martin, J., G.R. Smith, N. E. Carpenter, This Volume. Fishes from the Late Miocene Ellensburg Formation. *In* W. L. Fink and N. E. Carpenter, Fishes of the Western Snake River Plain and Vicinity. University of Michigan Museum of Zoology Miscellaneous Publication 204.

McPhail, J. D. 2007. The Freshwater Fishes of British Columbia. Edmonton, Alberta, University of Alberta Press.

McPhee, M. V., F. Utter, J. A. Stanford, K. V. Kuzishchin, K. A. Savvaitova, D. S. Pavlov, and F. W. Allendorf. 2007. Population structure and partial anadromy in *Onchorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecology of Freshwater Fish 16: 539-547.

Miller, R. R. and G. R. Smith. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occasional Papers of the Museum of Zoology, University of Michigan, No. 654.

Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relation to intracontinental tectonism, pp. 56-613 *In*: C. H. Hocutt and E. O. Wiley, eds., Zoogeography of North American Freshwater Fishes. New York, Wiley.

Montgomery, D. 2000. Coevolution of the Pacific salmon and Pacific Rim topography. Geology 28 (12): 1107-1110.

Moore, J. G. 1969. Geology and Mineral Deposits of Lyon, Douglas, and Ormsby Counties, Nevada, with a section on Industrial Mineral Deposits, by N. L. Archbold. Reno, Nevada Bureau of Mines and Geology Bulletin 75.

Morgan, L. A. and W. C. McIntosh. 2005. Timing and development of the Heise Volcanic field, Snake River Plain, Idaho western USA. Geological Society of America Bulletin 117 (3-4): 288-306.

Neave, F. 1958. The origin and speciation of *Oncorhynchus*. Transactions of the Royal Society of Canada, Vol. VII, Series III, Section Five. Pp. 25-39.

Needham, P. R. and R. Gard. 1959. Rainbow trout in Mexico and California with notes on the cutthroat series. University of California Publications in Zoology 67: 1-124.

Nelson, J. S. 1968. Distribution and nomenclature of North American kokanee, *Oncorhynchus nerka*. Journal of the Fisheries Research Board of Canada 25(2): 409-414.

Nelson, J. S. 2006. Fishes of the World, 4th ed. New Jersey, John Wiley and Sons.

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

Newcomb, R. C. 1958. Yonna Formation of the Klamath River Basin, Oregon. Northwest Science 32(2): 41-48.

Nielsen, J. L., K. D. Crow and M. C. Fountain. 1999. Microsatellite diversity and conservation of a relic trout population: McCloud River redband trout. Molecular Ecology 8: S129-S142.

Norden, C. R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny. Journal of the Fisheries Research Board of Canada 18 (5): 679-791.

Northcote, T. G. 1973. Some impacts of man on Kootenay lake and its salmonoids. Ann Arbor, Michigan, Great Lakes Fishery Commission Technical Report No. 25.

Orr, E. L. and W. N. Orr. 2000. Geology of Oregon, 5th ed. Dubuque, Iowa, Kendall-Hunt Publishers.

Perkins, M. E., F. H. Brown, W. P. Nash, W. McIntosh, and S. K. Williams. 1998. Sequence, age and source of silicic fallout tuffs in middle to late Miocene basins of the northern Basin and Range province. Geological Society of America Bulletin 110: 344-360.

Perkins, M. E. and B. P. Nash. 2002. Explosive silicic volcanism of the Yellowstone hotspot: The ash fall tuff record: Geological Society of America Bulletin, v. 114: 367-381.

Pess, R. G., T. P. Quinn, S. R. Gephard, and R. Saunders. 2014. Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal. Review of Fish Biology and Fisheries 24: 881-900.

Phillips, F. M. 2008. Geological and hydrological history of the paleo-Owens River drainage since the late Miocene, pp. 115-150 *In*: M. C. Reheis, R. Hershler, and D. M. Miller, eds., Late Cenozoic Drainage History of the Southwestern Great Basin and Lower Colorado River Region: Geologic

and Biotic Perspectives. Boulder, Colorado, Geological Society of America Special Paper 439.

Phillips, R. B. and T. Oakley. 1997. Phylogenetic relationships among the Salmoninae based on nuclear and mitochondrial DNA sequences pp. 145-162 *In*: T. D. Kocher and C. A. Stepien, eds., Molecular Systematics of Fishes. Elsevier Publishers.

Pickthorn, L. B. G. and D. R. Sherrod. 1990. Potassium-argon ages from Klamath Falls area, south-central Oregon. Isochron/West 55: 13-17.

Quinn, T. P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. Seattle, University of Washington Press.

Quinn, T. P. and R. B. Deriso. 1999. Quantitative Fish Dynamics. New York, Oxford University Press.

Reidel, S. P., N. P. Campbell, K. R. Fecht, and K. A. Lindsey. 1994. Late Cenozoic structure and stratigraphy of south-central Washington, pp. 159-180 *In*: R. Lasmanis and E. Cheney, eds., Regional Geology of Washington State. Olympia, Washington, Washington Division of Geology and Earth Resources Bulletin 80.

Reidel, S. P. and T. L. Tolan. 2013. The late Cenozoic evolution of the Columbia River system in the Columbia River flood basalt province, pp. 201-230 *In*: S. Reidel, V. E. Camp, M. E. Ross, J. A. Wolff, B. S. Martin, T. L. Tolan and R. E. Wells, eds., The Columbia River Flood Basalt Province. Boulder, Colorado, Geological Society of America Special Paper 497.

Ruez, D. R., Jr. 2009a. Revision of the Blancan (Pliocene) mammals from Hagerman Fossil Beds National Monument, Idaho. Journal of the Idaho Academy of Sciences 45 (1): 1-143.

Ruez, D. R., Jr. 2009b. Framework for stratigraphic analysis of Pliocene fossiliferous deposits at Hagerman Fossil Beds National Monument, Idaho. Rocky Mountain Geology 44 (1): 33-70.

Russell, I. C. 1902. Geology and Water Resources of the Snake River Plains of Idaho. Washington, U.S. Geological Survey Bulletin 199: 1-192.

Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pp. 231-310 *In*: C. Groot and L. Margulis, eds., Pacific Salmon Life Histories. Vancouver, University of British Columbia Press.

Sander, K. T. and S. H Wood. 2005. The Poison Creek Formation, a coarse fan-delta facies in the Miocene Chalk Hills Formation of the western Snake River Plain, Idaho. Rocky Mountain and Cordilleran GSA Abstracts, 2004.

Sanford, C. P. J. 2000. Salmonoid fish osteology and phylogeny (Teleostei: Salmonidei). Theses Zoologicae, Volume 33. Lichtenstein, A. R. F. Gantner Verlag KG.

Schreck, C. B., and R. J. Behnke. 1971. Trouts of the Upper Kern River Basin, California, with reference to systematics and evolution of North American *Salmo*. Journal of the Fisheries Research Board of Canada 28:987-998.

Schtickzelle, N. and T. P. Quinn. 2007. A metapopulation perspective for salmon and other anadromous fish. Fish and Fisheries, 8:297-314.

Sheppard, R. A. 1991. Zeolitic diagenesis of tuffs in the Miocene Chalk Hills Formation, western Snake River Plain, Idaho. Washington, U.S. Geological Survey Bulletin 1963.

Sherrod, D. R. and L. B. G. Pickthorn. 1992. Geologic Map of the West Half of the Klamath Falls 1⁰ by 2⁰ Quadrangle, South-Central Oregon. U.S. Geological Survey Miscellaneous Investigatons Map I-2182.

Shervais, J. W., G. Shroff, S. K. Vetter, S. Matthews, B. B. Hanan, J. J. McGee. 2002. Origin and evolution of the western Snake River Plain: implications from stratigraphy, faulting, and the geochemistry of basalts near Mountain Home, Idaho. *In*: B. Bonnichsen, C. M. White, and M. McCurry, eds., Tectonic and Magmatic Evolution of the Snake River Plain Volcanic Province. Moscow, Idaho, Idaho Geological Survey Bulletin 30.

Shevenell, A., J. P. Kennett, and D. W. Lea. 2004. Middle Miocene southern ocean cooling and Antarctic cryosphere expansion. Science, 305: 1766-1770.

Smith, G. R. 1975. Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho. University of Michigan Papers on Paleontology 14: 1-68.

Smith, G. R. 1987. Fish speciation in a North American Pliocene rift lake. Palaios 2: 436-445.

Smith, G. R. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. Systematic Biology, 41: 41-57.

Smith, G. R., J. Chow, P. J. Unmack, D. F. Markle, and T. E. Dowling. This volume. Evolution of the R*hinichthys osculus* complex (Teleostei, Cyprinidae) in Western North America, *In* W. L. Fink and Nathan Carpenter, eds, Fishes of the Mio-Pliocene Western Snake River Plain and vicinity, University of Michigan Museum of Zoology, Miscellaneous Publication 204.

Smith, G. R. and J. Cossel, Jr. 2002. Fishes from the late Miocene Poison Creek and Chalk Hills Formations, Owyhee County, Idaho. pp. 23-35 *In*: W. A. Akersten, M. E. Thompson, D. J. Meldrum, R. A. Rapp, and H. G. McDonald, eds., And Whereas…Papers on Vertebrate Paleontology of Idaho Honoring John A. White, Volume 2. Pocatello, Idaho Museum of Natural History Occasional Paper 37.

Smith, G. R., T. E. Dowling, K. W. Gobalet, T. Lugaski, D. K. Shiozawa, and R. P. Evans. 2002. Biogeography and Timing of Evolutionary Events among Great Basin Fishes, pp. 175-234 *In*: R. B. Hershler, D. B. Madsen, and D. R. Currey, eds., Great Basin Aquatic Systems History. Washington, D. C., Smithsonian Contributions to the Earth Sciences 33.

Smith, G. R. and R. R. Miller. 1985. Taxonomy of fishes from Miocene Clarkia Lake beds, Idaho, pp. 75-83 *In*: C. J. Smiley, ed., Late Cenozoic History of the Pacific Northwest. San Francisco, California, Pacific Division of the American Association for the Advancement of Science.

Smith, G. R., N. Morgan, and E. Gustafson. 2000. Fishes of the Mio-Pliocene Ringold Formation, Washington: Pliocene Capture of the Snake River by the Columbia River. University of Michigan Papers on Paleontology No. 32.

Smith, G. R. and R. F. Stearley. 1989. The classification and scientific names of rainbow and cutthroat trout. Fisheries 14(1): 4-10.

Smith, G. R. and R. F. Stearley, in prep. The fossil record of Cutthroat Trout, in P. Trotter and P. Bisson, eds., American Fisheries Society Symposium on Cutthroat Trout Evolution and Taxonomy. American Fisheries Society, Bethesda, Md.

Smith, G. R., Stokes, W. L., and K. F. Horn. 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968: 807-816.

Smith, G. R., K. Swirydczuk, P. G. Kimmel, and B. H. Wilkinson. 1982. Fish biostratigraphy of late Miocene to Pleistocene sediments of the western Snake River Plain, Idaho, pp. 519-541 *In*: Bonnichsen, B., and R. M. Breckenridge, eds., Cenozoic Geology of Idaho. Moscow, Idaho, Idaho Bureau of Mines and Geology Bulletin 26.

Smith, G. R. and T. N Todd. 1984. Evolution of species flocks of fishes in north temperate lakes, pp. 45-68 *In* A.A. Echelle and I. Kornfield (eds.) Evolution of Fish Species Flocks. University of Maine at Orono Press.

Smith, G. R. and J. Van Tassel, in prep. Fishes of the Pliocene Always Welcome Inn local Fauna, Baker County, Oregon, *In* W. L. Fink and Nathan Carpenter, eds, Fishes of the Mio-Pliocene Western Snake River Plain and Vicinity. University Michigan Museum of Zoology, Miscellaneous Publication 204.

Snyder, J. O. 1908. Relationships of the fish fauna of the lakes of southeastern Oregon. Bulletin of the U.S. Bureau of Fisheries 27 (636): 69-102.

Sonder, L. J. and C. H. Jones. 1999. Western United States extension: how the West was widened. Annual Review of Earth and Planetary Sciences 27: 417-462.

Spencer, J. E., G. R. Smith, and T. E. Dowling. 2008. Middle to late Cenozoic geology, hydrography, and fish evolution in the American Southwest, pp. 279-300 *In*: M. C. Reheis, R. Hershler, and D. M. Miller, eds., Late Cenozoic Drainage History of the Southwestern Great Basin and Lower Colorado River Region: Geologic and Biotic Perspectives. Boulder, Colorado, Geological Society of America Special Paper 439.

Stearley, R. F. 1992. Historical ecology of salmoninae, with special reference to *Oncorhynchus*, pp. 622-658 *In*: R. L. Mayden, ed., Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford, Stanford University Press

Stearley, R. F. and T. M. Cavender. In prep. A new fossil species of *Salvelinus* from Stewart Valley, Nevada.

Stearley, R. F. and G. R. Smith. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society, 122: 1-33.

Straccia, F. G., B. H. Wilkinson, and G. R. Smith. 1990. Miocene lacustrine algal reef – southwestern Snake River Plain, Idaho. Sedimentary Geology, 67: 7-23.

Swain, F. M., Jr. 1986. Lacustrine Ostracod Biostratigraphy in Neogene Rocks of Basin and Range Province, Western United States. A.A.P.G. Abstract. Atlanta.

Swain, F. M., Jr. 1999. Fossil Non-marine Ostracoda of the United States. Developments in Paleontology and Stratigraphy 16, Elsevier.

Swirydczuk, K. 1980. The Pliocene Glenns Ferry Oolite II: Sedimentology of oolitic lacustrine terrace deposits. Journal of Sedimentary Petrology 50(4): 1237-1248.

Swirydczuk, K., G. P. Larson, and G. R. Smith. 1982. Volcanic ash beds as stratigraphic markers in the Glenns Ferry and Chalk Hills Formations from Adrian, Oregon to Bruneau, Idaho. *In*: Bonnichsen, B., and Breckenridge, R. M., eds., Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin 26, pp. 543-558.

Swirydczuk, K., B. H. Wilkinson, and G. R. Smith. 1979. The Pliocene Glenns Ferry oolite: lake-margin carbonate deposition in the southwestern Snake River Plain. Journal of Sedimentary Petrology 49: 995-1004.

Taylor, D. W. 1960. Distribution of the freshwater clam, *Pisidium ultramontanum*; a zoogeographic inquiry. American Journal of Science, 258A: 325-334.

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

Taylor, D. W. 1985. Evolution of freshwater drainages and molluscs of western North America, pp. 265-321 *In*: C. J. Smiley, ed., Late Cenozoic History of the Pacific Northwest. San Francisco, California, Pacific Division of the American Association for the Advancement of Science.

Taylor, D. W. and G. R. Smith. 1981. Pliocene molluscs and fishes from northeastern California and northwestern Nevada. University of Michigan Contributions from the Museum of Paleontology 25(18): 339-413.

Uyeno, T. 1961. Late Cenozoic cyprinid fishes from Idaho with notes on other fossil minnows in North America. Papers of the Michigan Academy of Sciences, Arts and Letters 46: 329-344.

Uyeno, T. and R. R. Miller. 1963. Summary of Late Cenozoic freshwater fish records for North America. Occasional Papers of the Museum of Zoology, University of Michigan 631: 1-34.

Van Tassell, J., M. Ferns, V. McConnell, and G. R. Smith. 2001. The Mid-Pliocene Imbler fish fossils, Grand Ronde Valley, Union County, Oregon, and the connection between

Lake Idaho and the Columbia River. Oregon Geology 63 (3):77-84, 89-96.

Wallace, A. R. 2003. Regional Geologic Setting of Late Cenozoic Lacustrine Diatomite Deposits, Great Basin and Surrounding Region: Overview and Plans for Investigation. Washington, D. C., U.S. Geological Survey Bulletin 2209-B

Wallace, R. L. and D. Zaroban. 2013. Native Fishes of Idaho. American Fisheries Society, Bethesda, Maryland.

Waples, R. S., R. G. Gustafson, and 14 others. 2001. Characterizing diversity in salmon from the Pacific Northwest. Journal of Fish Biology 59 (Supplement A): 1-41.

Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1: 189-206.

Warner, M. M. 1975. Special aspects of Cenozoic History of Southern Idaho and their geothermal implications. United Nations Second Sympoisium of Geothermal Resources, pp. 653-663.

Warner, M. M. 1977. The Cenozoic of the Snake River Plain of Idaho. Rocky Mountain Thrust Belt Geology and Resources, 29th Annual Field Conference Guidebook, Wyoming Geological Association, pp. 313-326.

Wheeler, H. E. and E. F. Cook. 1954. Structural and stratigraphic significance of the Snake River capture, Idaho-Oregon. The Journal of Geology 62(6): 525-536.

Wilson, M. V. H. 1977. Middle Eocene Freshwater Fishes from British Columbia. Royal Ontario Museum Life Sciences Contributions No. 113.

Wilson, M. V. H., and G. Q. Li. 1999. Osteology and systematic position of the Eocene salmonid *Eosalmo driftwoodensis* Wilson from western North America. Zoological Journal of the Linnean Society, 125: 279-311.

Wilson, M. V. H., and R. R. G. Williams. 2010. Salmoniform fishes: key fossils, supertree, and possible morphological synapomorphies, pp. 379-409 *In*: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds., Origin and Phylogenetic Interrelationships of Teleosts. Muenchen, Germany, Verlag Dr. Friedrich Pfeil.

Wilson, R. W. 1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. Carnegie Institution of Washington, 440:119-135.

Wood, C. C., J. H. Bickham, R. J. Nelson, C. J. Foote and J. C. Patton. 2008. Recurrent evolution of life history ecotypes in sockeye salmon: implications for conservation and future evolution. Evolutionary Applications 1: 207-221.

Wood, S. H., and D. M. Clemens. 2002. Geologic and tectonic history of the western Snake River Plain, Idaho and Oregon, pp. 69-103 *In*: B. Bonnichsen, C. M. White, and M. McCurry, eds., Tectonic and Magmatic Evolution of the Snake River Plain Volcanic Province. Moscow, Idaho, Idaho Geological Survey Bulletin 30.