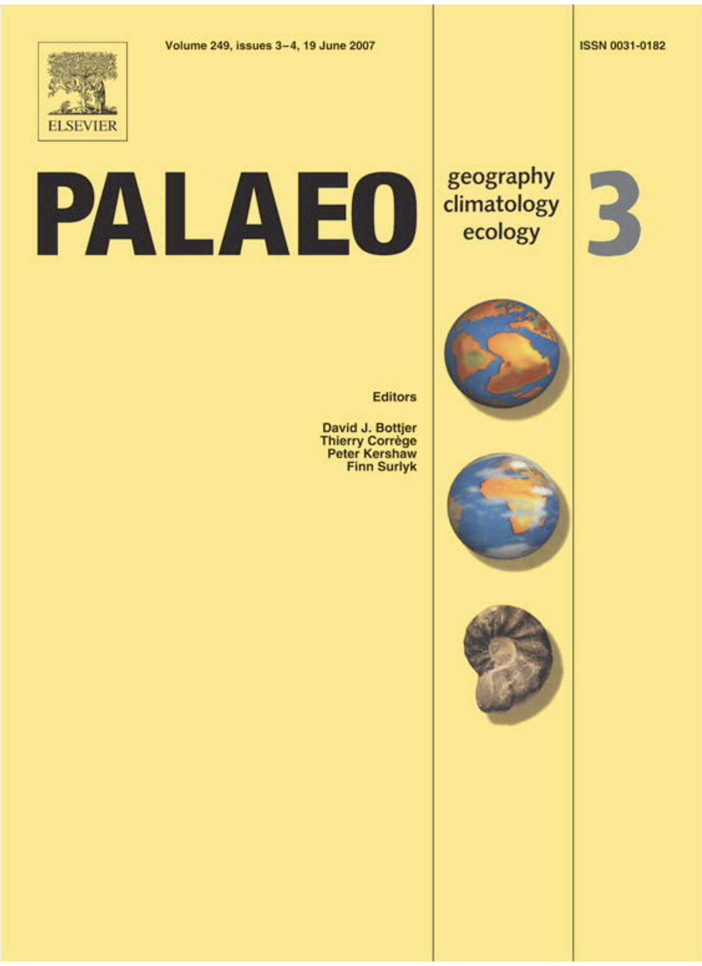
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Miocene salmon (*Oncorhynchus*) from Western North America: Gill Raker evolution correlated with plankton productivity in the Eastern Pacific

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Abstract

Miocene salmon were more specialized than modern salmon in their feeding apparatus. Computed tomography scans of two late Miocene Pacific salmon reveal unusually long, closely-spaced, and numerous gill rakers (plankton straining structures in the pharynx). Middle Miocene *Oncorhynchus rastrosus* also has more numerous and more finely spaced gill rakers than living species. The fossils described here, including one new species, appear to be related to modern Sockeye Salmon and Chum Salmon, differing most in the numbers and morphology of gill rakers. These structural adaptations to plankton feeding in a group of fish otherwise adapted to fish predation are concordant with oceanographic evidence for remarkably high plankton productivity in the North Pacific Ocean during the middle Miocene.

Keywords: fish fossils; Chalk Hills Formation; Salmon life history; Miocene temperature

1. Introduction

The five species of Pacific salmon (*Oncorhynchus*) in North America are fundamental parts of marine, freshwater, and forest ecosystems (Montgomery, 2000), but little is known about their evolutionary history. Two well-preserved forms of late Miocene (6–8 Ma) Pacific salmon (Figs. 1 and 2) have been recovered from freshwater sediments in the Chalk Hills Formation of the Western Snake River Plain, Oregon and Idaho (Smith, 1992). These specimens show unexpectedly long gill rakers and high gill raker numbers, features exhibited in extreme form by the Miocene Pacific tusk-tooth salmon, *Oncorhynchus* (*Smilodonichthys*) *rastrosus* (Cavender and Miller, 1972). Gill rakers are highly specialized, comb-like, anterior projections of bony gill arches in the pharynx, used to strain food and direct it back through the pharynx for ingestion. Because gill rakers play an important role in the feeding ecology of salmon, they may be indicators of evolutionary history and paleoecology. Numerous long, closely-spaced gill rakers are efficient at straining small plankton from the water column, whereas short, coarse gill rakers work to process larger food particles (Wankowski, 1979) such as fish. Long, fine gill rakers are associated with small teeth (e.g., *Oncorhynchus nerka*, Sockeye Salmon), whereas short, coarse gill rakers (e.g., *Oncorhynchus keta*, Chum

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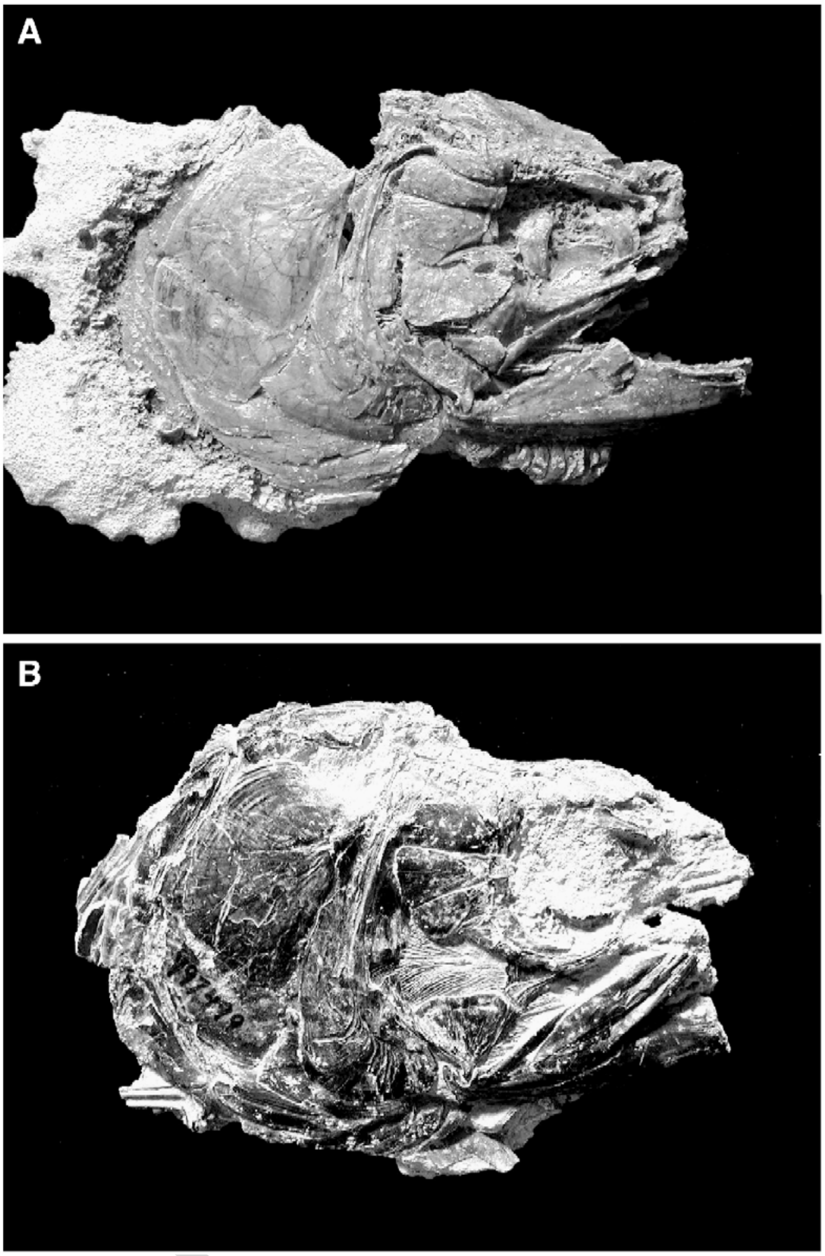

Fig. 1. Right lateral view of head of: A. *Oncorhynchus salax* (UMMP 62100, holotype, skull 132 mm long), B. *Oncorhynchus salax* (UMMP 97499, skull 137 mm long), specimen scanned in this study.

Salmon) are usually associated with large teeth used to catch larger prey (Table 1).

The two fossil forms from the Chalk Hills Formation were proposed by Smith (1992) to be relatives of modern Sockeye Salmon and Chum Salmon on the basis of small teeth and fine gill rakers in one form and large teeth and apparently coarse gill rakers in the other. The specimens were presumed to indicate diversification of Sockeye and Chum Salmons prior to 6 Ma. They are related to *O. rastrosus*, a large, anadromous (sea-run) salmon from the Miocene of Oregon, California, and Washington, that had more than 100 fine gill rakers on each arch (Cavender and Miller, 1972; Stearley and Smith, 1993; Smith et al., 2000). Middle Miocene (ca. 11–12 Ma) specimens of *O. rastrosus* from the Clarendonian Monterey Formation of California are the oldest known *Oncorhynchus* (Barnes, 1976). A dwarfed and land-locked form of this species, also presumed to have had planktivorous gill rakers, is found in the Miocene Chalk Hills lake beds of southwest Idaho (Smith et al., 1982). Phylogenetic analysis indicated that *O. rastrosus* is a

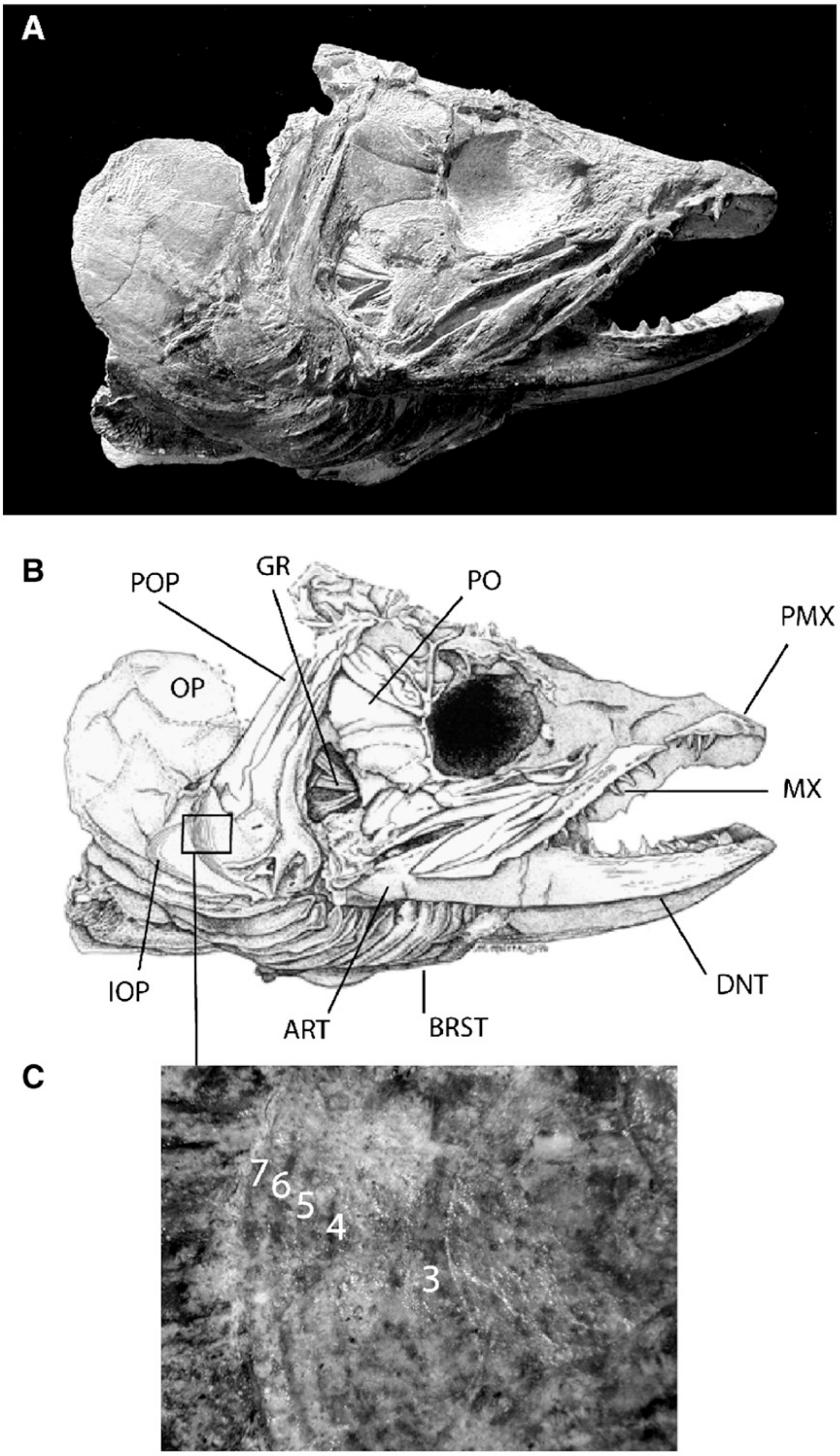

Fig. 2. A, *Oncorhynchus ketopsis* n. sp. (UMMP 97500, holotype, from the Chalk Hills Formation, skull 157 mm long); B, Abbreviations: ART, articular–angular; BRST, branchiostegal rays; DNT, dentary; GR, gill rakers; IOP, interopercle; MX, maxilla; OP, opercle; PMX, premaxilla; PO, post-orbital; POP, preopercle; C, outer edge of the preopercle of the type specimen, showing growth rings indicating an age of about 7 years.

relative of *O. nerka* (Sockeye Salmon), *Oncorhynchus gorbuscha* (Pink Salmon), and *O. keta* (Chum Salmon), with the cladistic relationships: (outgroup (*O. keta* (*O. gorbuscha* (*O. nerka*, *O. rastrosus*)))) (characters and cladogram in Stearley and Smith, 1993). If this relationship is correct, it implies diversification of

Table 1
Gill raker number and maximum length (at mid arch) on the first arch (and second arch in *O. keta* and *O. ketopsis*), and primary foods (in order of abundance) of Pacific salmon species

Species	Raker #	Lengths and %	Food in freshwater (Fw), in estuaries (Est), and in the Sea
O. kisutch	18–25	9.5–16 mm=17–32% ("short")	Fw: chironomid larvae, adult insects Est: copepods, amphipods, insects, small fish Sea: amphipods, euphausiids, fish
O. tshawytscha	16–26	8.3–16 mm=14–27% ("short")	Fw: aquatic insects, crustaceans Est: amphipods, copepods, small fish Sea: fish, euphausiids, squid
O. gorbuscha	24–35	8–13.5 mm=23–30% ("medium")	Fw: insect larvae, algae, copepods Est: copepods, cirripedia, cladocerans Sea: copepods, cirriped larvae, euphausiids, small fish
O. keta	16–26	3.5–11 mm=17–25% ("short") 6.5–6.6 mm=11–12%[a]	Fw: chironomids, cladocerans, amphipods Est: copepods, amphipods, insects, cladocerans Sea: copepods, amphipods, fish, euphausiids
O. nerka	29–44	9.9–14 mm=26–30% ("long")	Fw: copepods, cladocerans, chironomid larvae Est: adult diptera, chironomid larvae Sea: copepods, fish larvae, euphausiids, amphipods, cladocerans
O. nerka (kokanee, fw)	31–44	5.5–9.6 mm=26–36% ("long")	Fw: copepods, cladocerans, insect larvae
O. salax (Miocene)	50+	21 mm=36%	
O. ketopsis (Miocene)	ca 12–15, 40+[a]	13 mm=21%, 20 mm=32%[a]	

(From Higgs et al., 1995; Scott and Crossman, 1973). Gill raker lengths measured on museum specimens and reported as percentages of the greatest depth of the preopercle (because the elongation of jaw bones in breeding males makes the head lengths or standard lengths too variable). Qualitative designations of length of adult rakers from Scott and Crossman (1973). Gill rakers increase in length through sub-adult life. Low percentages are in adult individuals; high percentages are in sub-adults.

[a] Arch 2 of *O. keta* and *O. ketopsis*.

ancestors of modern species of *Oncorhynchus* in the middle Miocene.

The goal of this paper is to apply high resolution X-ray computed tomography (CT) to the study of gill rakers of Chalk Hills salmon in order to identify their relationships and place their evolution in the context of ecology of the Pacific Ocean and Pacific rim river drainages in the late Miocene. We present evidence of several late Miocene Pacific salmons with gill rakers more specialized and more numerous than their modern descendants, which suggests that they had richer sources of planktonic food than present today.

2. Geologic setting

The 6–8 Ma Chalk Hills Formation (Malde and Powers, 1962; Kimmel, 1982) contains fluvial and lacustrine sediments that represent an early record of a large lake system on the western Snake River Plain (Fig. 3). These beds unconformably overlie the Poison Creek Formation and Idavada Volcanics of the Idaho Group (Malde and Powers, 1962; Kimmel, 1982) and are unconformably overlaid by sediments of the Glenns Ferry Formation (Kimmel, 1982; Smith et al., 1982). Stratigraphic correlations and paleoecological reconstructions of fish faunas indicate that the Chalk Hills and Glenns Ferry Formations were deposited in a large lacustrine basin, with floodplain environments replacing lacustrine deposition at the lake margins and tops of sequences (Kimmel, 1982; Smith et al., 1982). Fish species diagnostic of the Chalk Hills Formation include minnows, *Mylocheilus inflexus*, *Mylocheilus copei*, char, *Salvelinus larsoni*, a dwarf form of *Oncorhynchus rastrosus*, and unique forms of catfish, trout, and sunfish (Smith et al., 1982).

Fossil Salmon on the Snake River Plain are restricted to the Chalk Hills Formation except for two small dentaries and a large premaxilla possibly related to Chinook Salmon, *Oncorhynchus tschawytscha*, found in the Davis Ranch sample from near the base of the Glenns Ferry Formation (Smith et al., 1982). The assignment of these salmon to the Glenns Ferry Formation is based on their co-occurrence with trout, minnows, lake suckers, catfish, sunfish, sculpins, and whitefish that do not occur in the Chalk Hills Formation (Smith et al., 1982). Distributional evidence from snails (Taylor, 1985) and fish (Smith et al., 1982, 2000) supports the geological conclusion of Wheeler and Cook (1954) that the large Miocene and Pliocene lakes of the Snake River Plain drained west to the Pacific through Oregon and California prior to stream capture

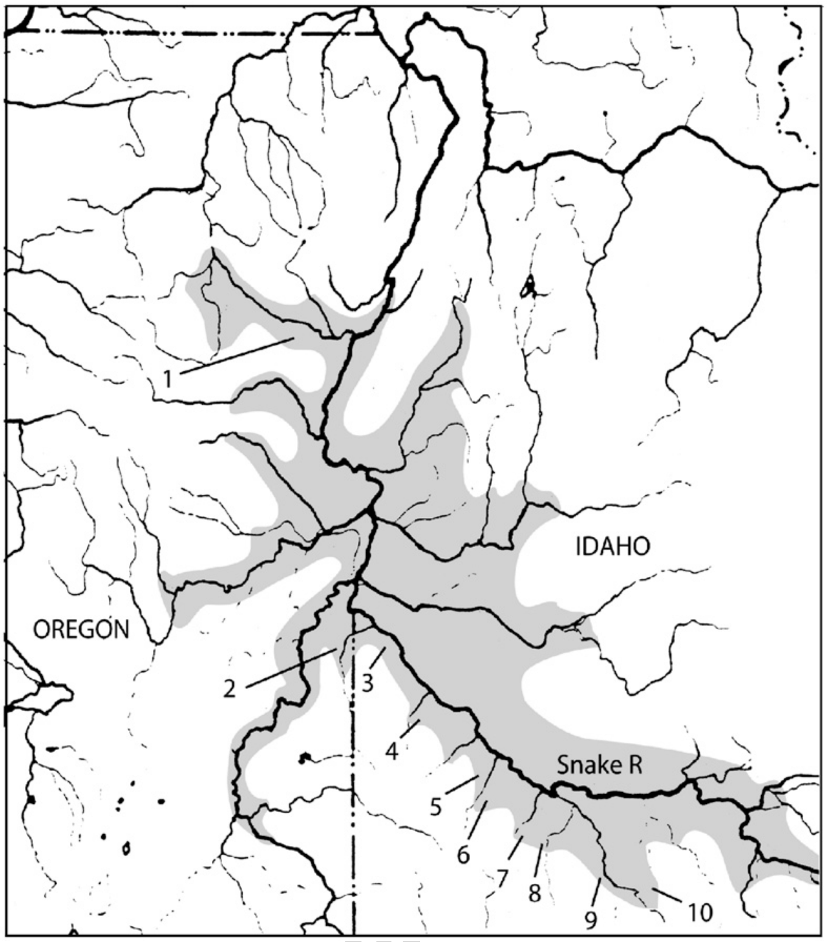

Fig. 3. Shaded area of Snake River Plain shows inferred lateral extent of sediments of Idaho Group (Malde and Powers, 1962; Smith et al., 1982) with Late Miocene Chalk Hills localities, Oregon and Idaho, indicated by numbers. 1, Possible Chalk Hills correlate, Powder River basin (Ledgerwood and Van Tassell, 2005); 2, Coyote Gulch near Tunnel Road, type locality of *Oncorhynchus ketopsis* n. sp. (Kimmel, 1982); 3 Cossel Ranch and 4, Reynolds Creek (Smith and Cossel, 2002); 5, Brown Creek; 6, Castle Creek; 7, Shoofly Creek (type locality of *O. salax*); 8, Chalk Hills; 9, Horse Hill; 10, East of Bruneau River (5–10 from Smith et al., 1982, Fig. 1 and Table 1).

through Hells Canyon to the Columbia River about 2 Ma (Malde, 1991; Smith et al., 2000).

3. Methods

All studied specimens are deposited in the University of Michigan Museum of Paleontology (UMMP) and the University of Michigan Museum of Zoology (UMMZ; see online Appendix for list of specimens examined, http://dx.doi.org/doi:10.1016/j.palaeo.2007.02.011). *Oncorhynchus salax* (UMMP 97499) and *Oncorhynchus ketopsis*, n. sp. (UMMP 97500) were scanned at the University of Texas High Resolution X-ray Computed Tomography (HRXCT) facility in October, 2004. HRXCT provides a means to study the internal anatomy of paleontological specimens nondestructively (Carlson et al., 2003). The fossil specimens were scanned antero-posteriorly along the coronal axis; the field of reconstruction for both images was 103 mm, and the interslice spacing was 0.22 mm. The interslice spacings along the horizontal and sagittal axes were 0.10 mm. The data for each specimen were then digitally resliced in the sagittal plane with an interslice spacing of 0.10 mm. The sagitally resliced data were made into image sequences using VG Studio Max 1.2 (Volume Graphics GmbH, Heidelberg, Germany) and Quicktime 7 Pro (Apple, Cupertino, California). Individual sagittal images were analyzed in Adobe Photoshop 7.0 (Adobe Systems Incorporated, San Jose, California). Gill rakers were colored according to their attachment arch: first arch, blue; second, orange; third, purple; fourth, red (see online Appendix for colored images, http://dx.doi.org/doi:10.1016/j.palaeo.2007.02.011) and re-colored in black and white for publication. The length of the rakers and number on each arch were then analyzed with colored images, and compared with raker morphology and number among extant salmonids. Pertinent salmon osteology is illustrated in Stearley and Smith (1993).

4. Results

4.1. Systematic paleontology

The fossil record of Salmonidae is relatively poor, with the earliest specimens known from the Eocene (Wilson and Li, 1999). Extant salmonid fishes are conventionally placed into three subfamilies: Coregoninae, Thymallinae, and Salmoninae. Five or more genera of Salmoninae are currently recognized (Stearley and Smith, 1993). The Salmoninae include *Brachymystax* (lenok), *Hucho* (huchen and taimen), *Salmo* (Atlantic salmon and trout), *Salvelinus* (char), and *Oncorhynchus* (Pacific salmon and trout). *Oncorhynchus* is usually recognized as the sister group to *Salmo* on the basis of morphology and life history (Stearley and Smith, 1993; Murata et al., 1996; Wilson and Li, 1999), although molecular phylogenies are inconsistent with this interpretation (Crespi and Fulton, 2004). The split between *Salmo* and *Oncorhynchus* occurred prior to 11–12 Ma and subsequent diversification of *Oncorhynchus* occurred before 6 Ma (Stearley and Smith, 1993; see discussion).

Oncorhynchus salax (Figs. 1, 4, and 4′) was discovered in sediments of the Chalk Hills Formation (originally misidentified as Glenns Ferry Formation) and described in Smith (1975). The species was recognized as a relative of *O. nerka* by its distinctive jaw suspension and jaw bones, small teeth, and numerous,

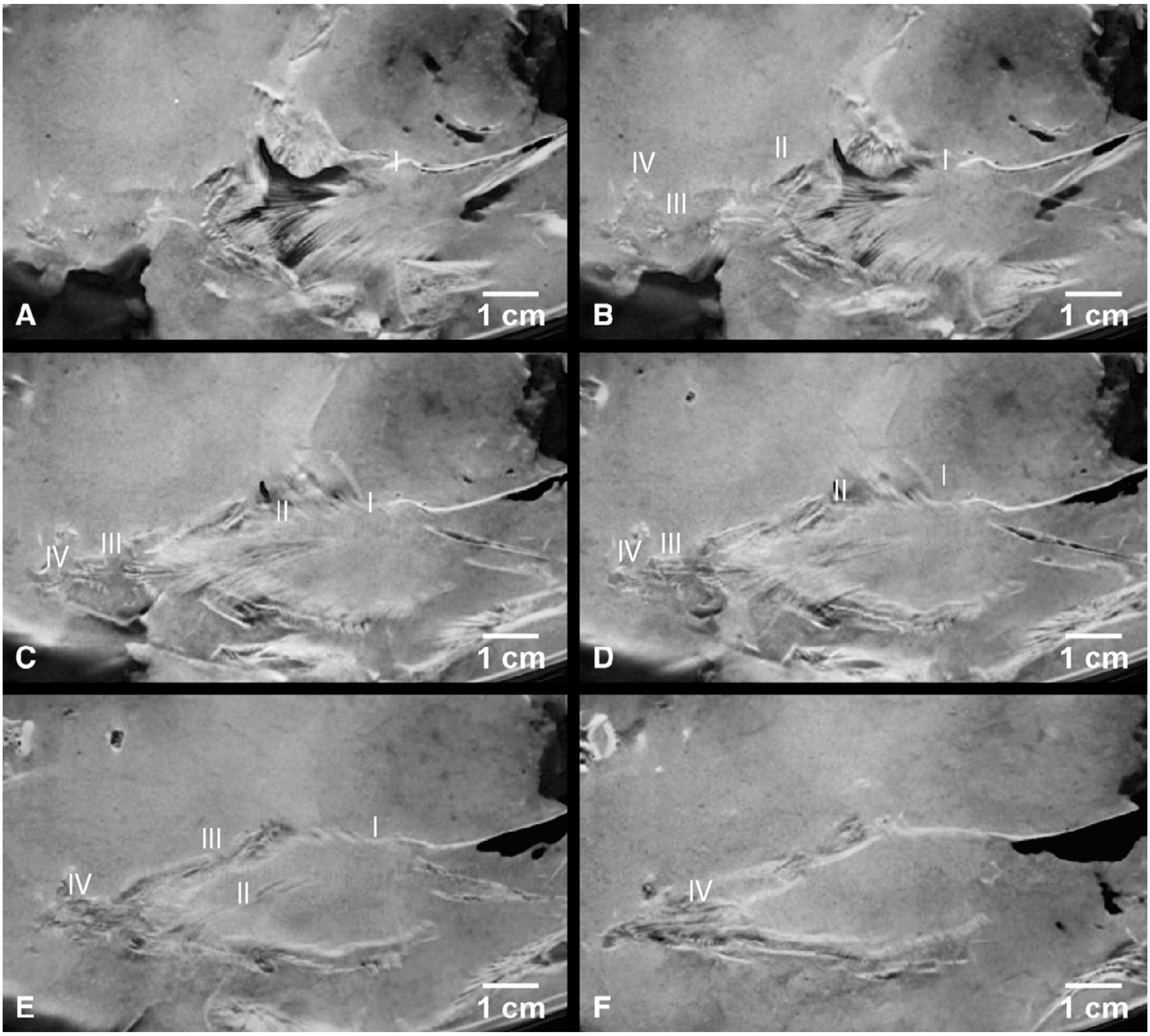

Fig. 4. Unmodified right lateral images of *Oncorhynchus salax* (UMMP 97499) scanned in this study: A, slice 60, showing gill rakers on arch I; B, slice 63; C, slice 69; D, slice 72; E, slice 79; B–E, showing gill rakers on arches I, II, III, and IV; F, slice 94, showing gill rakers on arch IV.

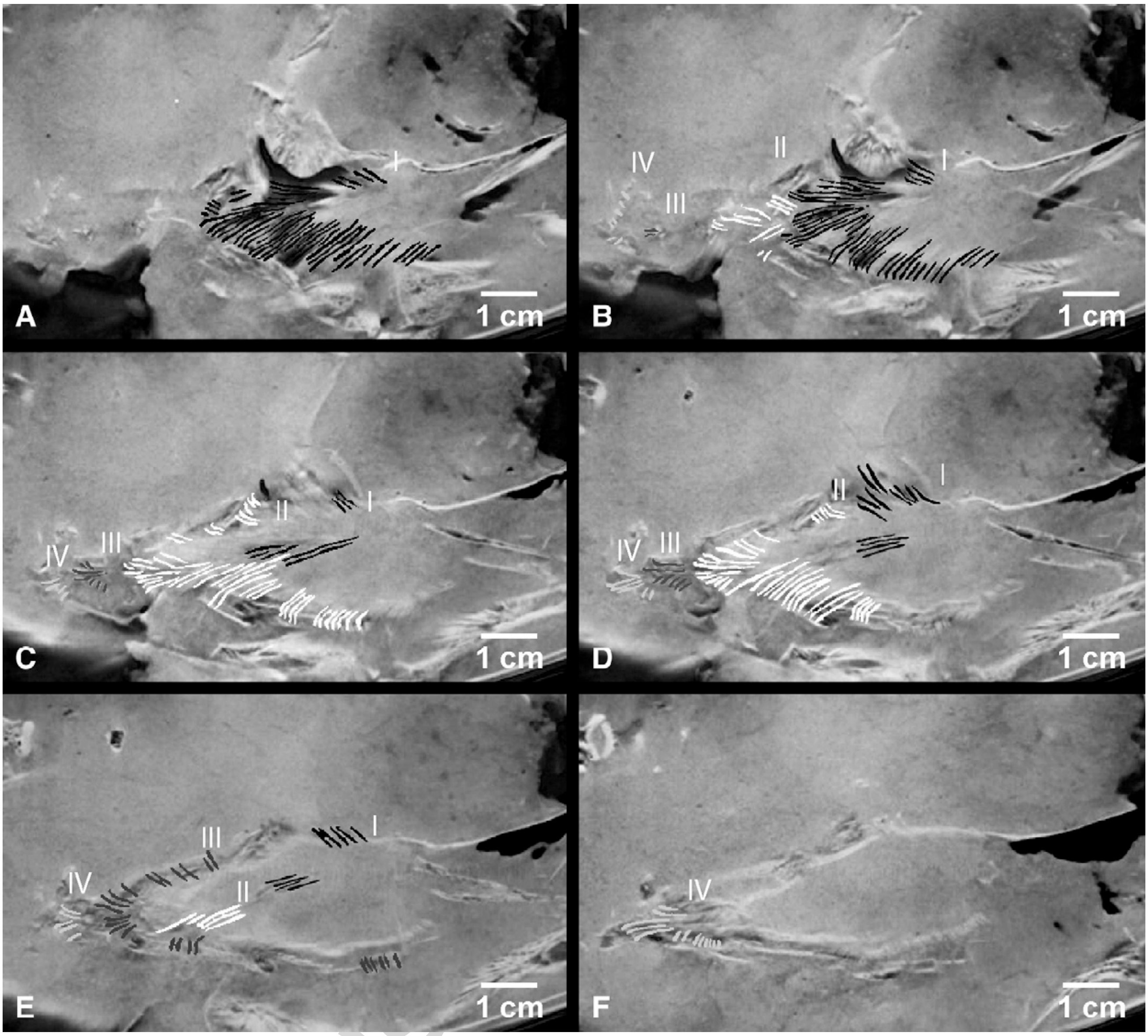

Fig. 4′. Right lateral images of *Oncorhynchus salax* (UMMP 97499) scanned in this study. Slices numbered as in Fig. 4. Rakers colored as follows: black, arch I; white, arch II; dark gray, arch III; light gray, arch IV.

long gill rakers. Its small size (body length about 600 mm) and the presence of three annuli after maturity (Smith, 1975; Fig. 2C), suggest that the species was land-locked in the lake rather than making the 600 km journey to the sea multiple times, but fossil salmon isotopic data are ambiguous (Zazzo et al., 2006). Later, a distinctive specimen of *Oncorhynchus* of similar size was discovered in beds of the Chalk Hills Formation in southeastern Oregon, but remained undescribed while a search for additional specimens was conducted (Kimmel, 1982; although the specimen was illustrated and commented upon by Smith, 1992). The opportunity to analyze the internal skull parts by CT now allows an examination of the remarkable gill rakers, with diagnosis and description of the new taxon.

Description of *Oncorhynchus ketopsis* new species. (Figs. 2A–C; 5A–F; 5′A–F; Appendix Figure 2A–F)

4.1.1. Holotype

UMMP 97500, a partial skull of a female (?) salmon, 157 mm long. The specimen was discovered by Gladys Swigert in about 1978 and donated to the University of Michigan Museum of Paleontology through Peter G. Kimmel.

4.1.2. Type locality and horizon

Fine, gray sands within the upper part of the late Miocene (Hemphillian) Chalk Hills Formation (“Tunnel Mountain Horizon” of Kimmel, 1982), in Coyote Gulch, Malheur County, T 22S, R 46E, Sec 21, Adrian

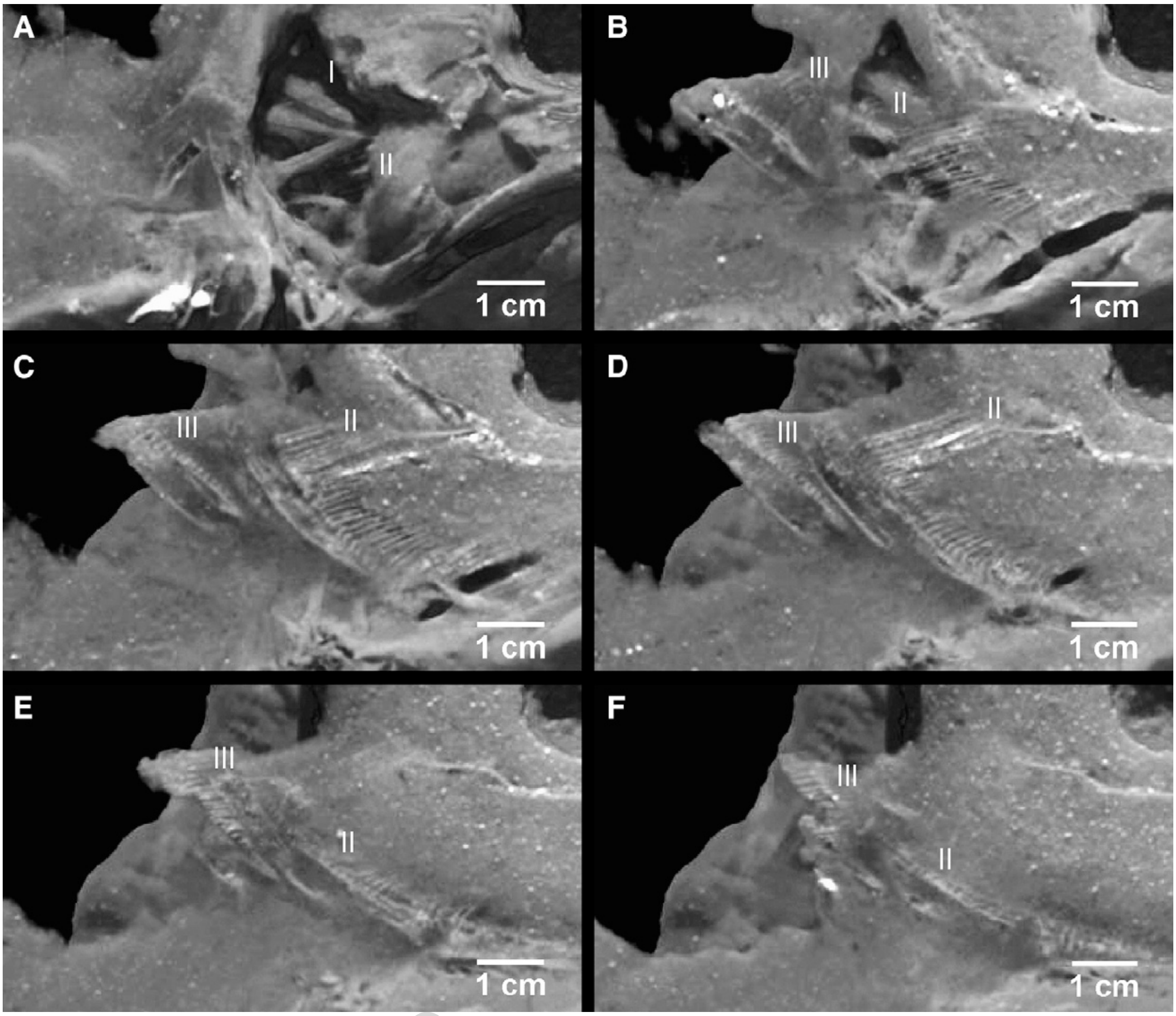

Fig. 5. Unmodified right lateral images of *Oncorhynchus ketopsis* n. sp. (UMMP 97500) scanned in this study: A, slice 51, showing flattened gill rakers on arch I and long rakers on arch II; B, slice 70; C, slice 77; D, slice 84; E, slice 92; F, slice 100; B–F, showing gill rakers on arch II and III.

quadrangle, Oregon. The Chalk Hills Formation consists of sands, silts, and tephra, ranging in age from about 8 to 6 Ma (Kimmel, 1982).

4.1.3. Diagnosis

A member of the genus *Oncorhynchus*, based on the following synapomorphy: length of the post-orbitals reach to within a few millimeters of upper limb of the preopercle. A member of the *O. keta*, *O. gorbuscha*, *O. nerka*, *O. rastrosus* clade, based on the following synapomorphy: nearly straight (not strongly decurved) maxilla. A sister species to *O. keta* based on the following synapomorphies: large maxillary, dentary, and premaxillary teeth, exceeding 5 mm long anteriorly, but not exhibiting secondary male enlargement; about 12–15 short, robust external gill rakers estimated on the first arch (only six preserved). Distinct from *O. keta* based on the following autapomorphy: over 40 long, fine gill rakers on internal arches. Diagnostic apomorphies from Stearley and Smith (1993) and this study.

Differs from *Oncorhynchus tshawytscha*, *Oncorhynchus kisutch*, *Oncorhynchus mykiss* and *Oncorhynchus clarki*, which have curved maxillae and fewer, shorter gill rakers; from *O. gorbuscha*, *O. nerka*, *O. salax*, and *O. rastrosus*, which have small, minute, or reduced maxillary and dentary teeth on the parts of jaw bones unmodified in sexually mature males, but similar to *O. gorbuscha* in possession of compressed jaw teeth. Preopercle with a moderate convex expansion on the posterior edge of its dorsal limb as in *O. nerka*, O. *rastrosus*, and *O. keta*; angles, proportions, and shape of the preopercle most like *O. nerka*. Dentary

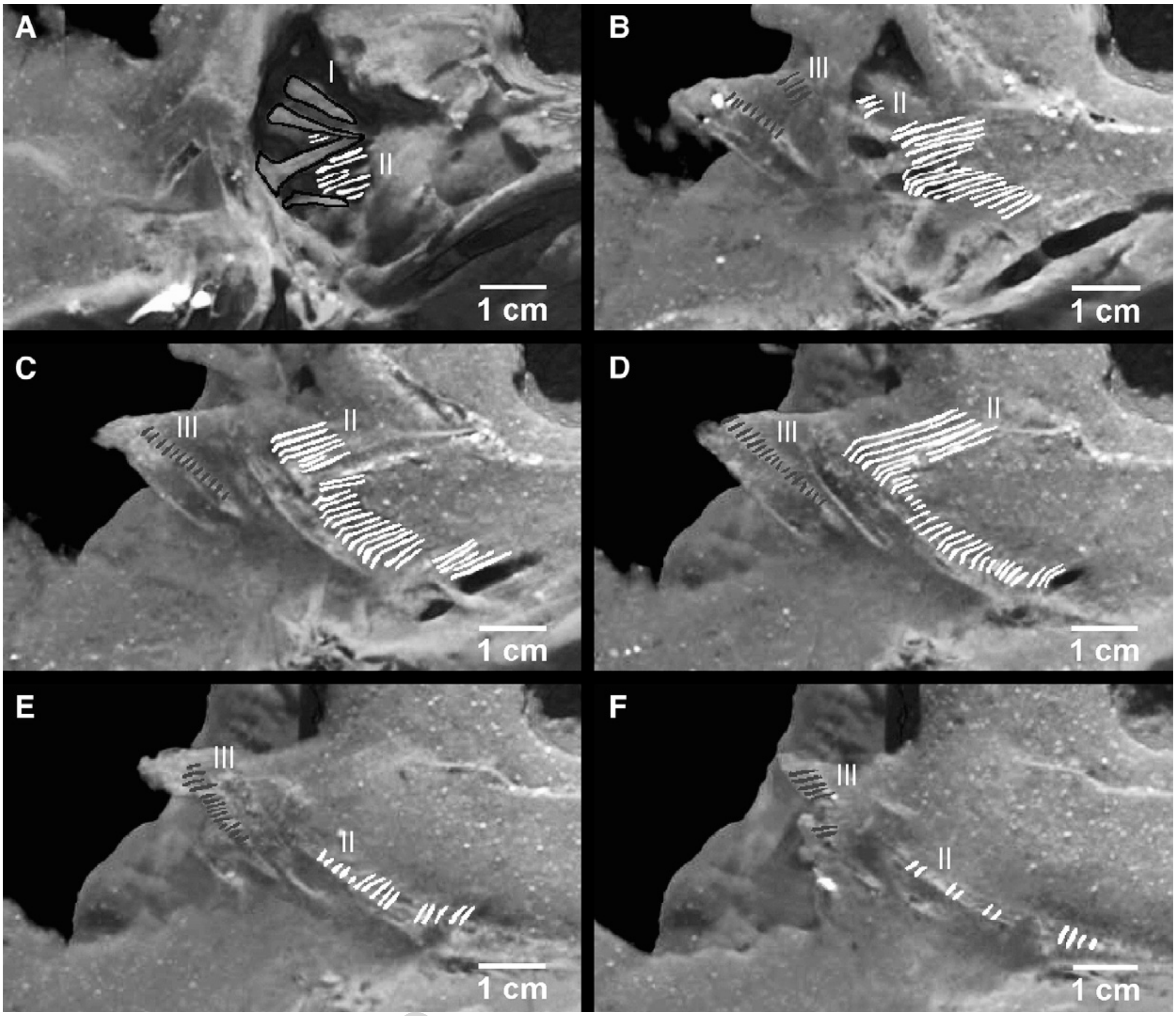

Fig. 5′. Right lateral images of *Oncorhynchus ketopsis* n. sp. (UMMP 97500, holotype) scanned in this study. Slices numbered as in Fig. 5. Rakers colored as in Fig. 4′.

with anterolateral edge flared laterally, and smooth, less striated laterally than modern salmon. Premaxillary lunate and uniformly convex dorsally, as in female *O. keta*, *O. nerka*, and *O. gorbuscha*.

4.1.4. Description

The holotype is a medium sized salmon, probably about 600 mm in total length, based on proportions of extant salmon specimens (University of Michigan Museum of Zoology). It is a mature female or possibly a post-spawning male with an undistorted dentary. The skull is 157 mm long, with a lower jaw 104 mm; maxilla 62 mm; supra-maxilla ovate and 32 mm; longest post-orbitals 33 mm; orbit 25 mm; preopercle 55 mm high. The longest gill rakers on the first arch are 13 mm long and robust at the base; longest gill rakers on the second arch are about 20 mm long and numerous. The dentary is slightly striated anteriorly and ventrally. The length of lower jaw is twice the length of the articular–angular from its posterior end to the antero-dorsal point of the coronoid process. The maxilla is straight, but with its anteroventral border slightly concave and posteroventral border slightly convex. The dermethmoid is incomplete, but similar to those of *O. nerka*, *O. keta*, and *O. gorbuscha*. There are 16 branchiostegal rays. Three or more narrow, external, growth rings on the interopercle appear to represent adult marks; extrapolation of up to seven growth rings on the preopercle (Fig. 2C) suggests that the fish may have been about 7 years old: modern mature *Oncorhynchus keta* migrate from the sea, spawn, and die, usually at age 4 (Quinn, 2005, Tables 12-1, 12-3). The presence of 3 years of minimal growth after maturity was reached implies that the fish was a repeat spawner. (Growth bands are wide in premature fish, but narrow after maturity, when energy is expended on gamete formation and reproduction rather than growth. Pacific salmon do not normally show narrow growth bands after maturity is reached, because of mortality [Quinn, 2005].) Repeat spawning as adults probably precludes secondary sexual enlargement of the jaw bones because the jaws must retain their trophic function in subsequent years.

4.1.5. Etymology

Keta is the original north Asian name applied by Walbaum (1792) to the Chum Salmon; *opsis* is Greek indicating likeness.

4.2. Computed tomography: Gill Raker number and anatomy

The results of the HRXCT scans of *Oncorhynchus salax* and *O. ketopsis* are included as six images in sequence from lateral to mesial in Figs. 4 and 4′ [and Appendix 1] for *O. salax*, and Figs. 5 and 5′ [and Appendix 2] for *O. ketopsis*. Supplementary photographs and movies tracing the rakers through successive sagittal slices can be found online (see online Appendix, http://dx.doi.org/doi:10.1016/j.palaeo.2007.02.011).

Figs. 4 and 4′ [and Appendix 1] show a sequence of six sagittal slices of the right side of the skull of *O. salax* passing medially through the skull. The gill rakers of the first arch are up to 21 mm long and number at least 50. The rakers from the second, third, and fourth arches appear in many of the same slices.

Rakers from three *O. ketopsis* gill arches are visible in the scans, Figs. 5 and 5′ [and Appendix 2]. Accounting for taphonomic effects and raker spacing, we estimate there were about 12–15 gill rakers attached to the first gill arch, reaching 13 mm in length. Rakers of the second gill arch are the best preserved and most readily apparent. We count 32 rakers on this arch. They are up to 20 mm long and closely-spaced. Gill rakers attached to the third arch are also visible. Numbering about 12, these rakers are typically thicker and shorter than those of the second arch. Inferring spacing of missing rakers on arches two and three, we estimate that the number on each internal arch exceeded 40.

5. Discussion

Anatomical preparations of intact gill arches of modern salmons provide clues about orientation of rakers of sequential arches. There are five pairs of gill arches, the first four consisting of a lower hypobranchial and ceratobranchial, and an upper epibranchial and dorsal pharyngobranchial. Rakers may be attached to all of the four branchial bones-on the anterior faces of the bones of the first arch and the anterior and posterior faces of the bones of arches two, three and four. Variations occur on the hypobranchials and pharyngobranchials of arch four. Arch five is modified to support pharyngeal teeth posteriorly, with rudimentary rakers on the anterior face. For practical purposes we deal with the first four arches, which have large rakers, especially on the two middle bones, the ceratobranchial and epibranchial. Individual rakers are tapered distally and broader near the base, with minute anterior teeth and a basal cross-bar for attachment to the branchial bones.

Recognizing distortion by taphonomic processes represents a challenge to satisfactory interpretation of the anatomy seen in the scans. The specimens were crushed to approximately one-fifth of their original width, juxtaposing some gill arches and rakers into the same plane although in life they had been adjacent. Some rakers became detached from their arch during decay. Assignment of gill rakers to their proper arch in the areas where multiple arches overlap requires cycling through successive slice images repeatedly, tracing rakers from their attachment to an arch to their termination in later CT slices, or by their position relative to other, more clearly defined rakers. In addition, the fossils are embedded in a matrix of fine-grained sandstone that incorporates some high-density rock fragments, which have a similar grayscale value to the fossil material and tend to obscure adjoining bones and gill rakers.

Oncorhynchus salax and *O. ketopsis* surpass their living relatives in the high numbers of gill rakers they possess, over 50 in the former and over 40 on the second arch of the latter (Table 1; Figs. 4 and 5). *O. salax* also has proportionally longer gill rakers than in any other known *Oncorhynchus* except landlocked kokanee, which are smaller (Table 1; Figs. 4 and 5). *Oncorhynchus ketopsis* has short, robust gill rakers on the first arch and numerous long gill rakers on the second arch. (Recent *Oncorhynchus keta* have successively shorter gill rakers on the second, third, and fourth arches, compared to the first arch.) *Oncorhynchus rastrosus* of middle Miocene age had more than 100 rakers (Cavender and Miller, 1972), about twice the number of any other salmon (cf. Scott and Crossman, 1973). The presence of gill raker numbers higher than living salmon in the only three Miocene species for which data are available suggests that either plankton feeding was far more important in the Miocene than at present, or that the intervening climate extremes of the

Pleistocene caused extirpation of salmon with high raker numbers.

5.1. Historical ecology and life history

The late Miocene was a time of dramatic climate change in Earth's history. Following a thermal maximum about 15 Ma, the late Miocene was marked by a 9 to 10 million year cooling episode. This cool period produced higher temperature gradients between polar and tropical regions, resulting in intense ocean circulation and enhanced upwelling along coastal regions (Kennett, 1982; Barron and Keller, 1983; Jacobs et al., 2004). This is postulated to have recycled nutrients (chiefly phosphates and nitrates) abundantly, reducing nutrient starvation as a limiting factor in plankton productivity. Consequently, during this late Miocene cooling episode, long intervals of high marine plankton productivity occurred in the Pacific and worldwide (Dickens and Owen, 1999; Lyle et al., 2000; Barron et al., 2002; Diester-Haass et al., 2002; Grant and Dickens, 2002; Gupta et al., 2004; see Fig. 6). Higher phytoplankton productivity could have caused high zooplankton abundance. Phytoplankton are the major food for zooplankton such as copepods, euphausiids, and amphipods, as well as larvae of other marine animals (Raymont, 1963). Zooplankton are a principal food during many life history stages of *Oncorhynchus* (Table 1), so salmon abundance would be expected to increase in response to high plankton productivity. Extant Pacific salmon show marked distributional responses to changes in temperature associated with variations in ocean currents, such as those occurring during El Niño events (Kaeriyama et al., 2004).

Hence, high marine plankton productivity and diversity during the middle to late Miocene may have promoted diversification of planktivorous salmon. *Oncorhynchus rastrosus*, *O. salax*, and *O. ketopsis* had long gill rakers, closely-spaced to function as efficient plankton strainers. *Oncorhynchus salax* had more gill rakers than any living salmon, and it likely consumed plankton during the middle to late Miocene stages of high plankton productivity. Reduced gill raker numbers in its apparent descendant, *O. nerka*, is consistent with observed lower post-Miocene plankton productivity and diversity. *Oncorhynchus ketopsis* shows raker morphology intermediate between planktivory and carnivory. Its coarse, thick external rakers and large teeth, synapomorphies with modern *O. keta*, possibly indicate a transition from planktivory to predation during later life history stages. The presence of many elongate rakers on arch two clearly functioned to strain plankton and have no counterpart in *O. keta.* No analog of the mixed raker morphology similar to *O. ketopsis* exists today, so it is difficult to hypothesize how such a system functioned. We suggest that *O. ketopsis* represents a mostly planktivorous form in the Miocene; recent *O. keta* is more piscivourous. The last record of *O. rastrosus*, the most extreme planktivore among salmon, is in the late Miocene (prior to 5.3 Ma) Ringold Formation of Washington (Smith et al., 2000), perhaps correlated with the end of the Miocene plankton peak in the north Pacific (Fig. 6). Supporting the hypothesized influence of plankton abundance on salmon evolution is the diversification of marine mammals during the middle and late Miocene, including cetaceans and pinnipeds (Lipps and Mitchell, 1976), and marine mollusks (E.A. Nesbitt, pers. comm., 2006). Lipps and Mitchell (1976) predict that marine mammals diversified in areas of intense upwelling and high productivity. Other data (L.G. Barnes, unpublished) suggest that marine mammals were diverse during periods with less abundant plankton in the Oligocene and Pliocene as well

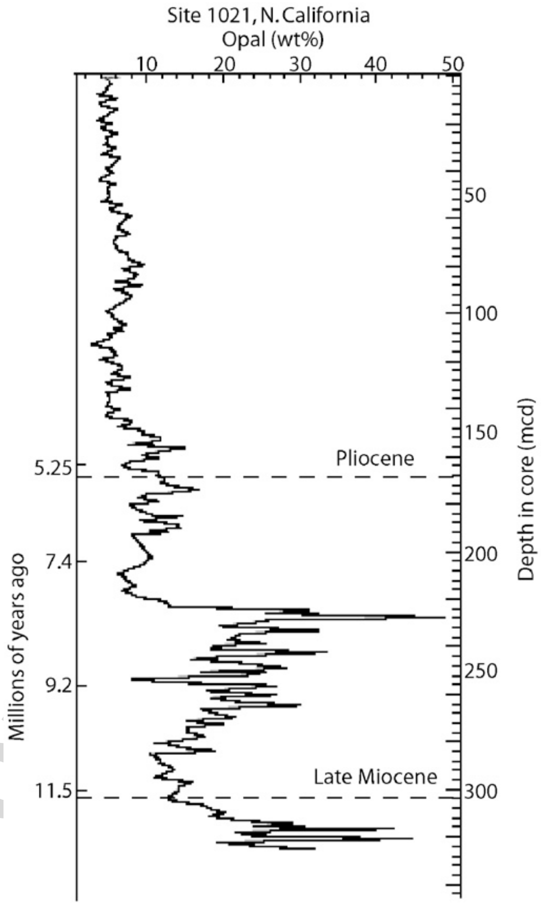

Fig. 6. Biogenic opal abundance in a North Pacific drill cores from ODP Leg 167 along the California margin (modified from Lyle et al., 2000, fig. 37).

as the Miocene; however, the diversification of various groups during periods of intense upwelling remains an important hypothesis.

We cannot be certain of the anadromous vs. freshwater life history of *O. salax* and *O. ketopsis*. Preliminary analysis of oxygen isotopes in apatite of Miocene salmon vertebrae from the Chalk Hills Formation suggests that the fish might have inhabited fresh water throughout life (W.P. Patterson, unpublished). Zazzo et al. (2006) found that oxygen isotopes in various tissues of fossil Sockeye Salmon show characteristic signatures of marine and fresh water, even if diagenesis had altered the isotopic ratios in some fossil apatite. The relatively small size of known adult specimens of *O. salax* and *O. ketopsis* is possibly consistent with landlocked life history. Landlocked Sockeye Salmon (nonanadromous kokanee) are smaller (adults less than 350 mm long) than migratory Sockeye Salmon (adults more than 450 mm long) (Quinn, 2005). Juvenile *Oncorhynchus* bones are known from the Chalk Hills Formation, but we are not certain whether these are trout or salmon fossils. In addition, the dwarf form of *O. rastrosus* in the Chalk Hills Formation is unlikely to be a migrant from the sea, given its small maximum size, ca 400 mm standard length, and representation by juvenile bones in the formation. If *O. salax* and *O. ketopsis* migrated from the sea, it was probably through the Klamath or Pit River drainages, or parts of both. If they spent their entire lives in the Chalk Hills lake, their late Miocene ancestors were ultimately of Miocene anadromous origin (Stearley, 1992). Their presence in the lake could also indicate regional climatic influences on plankton productivity in fresh waters as well as in the North Pacific Ocean. Several narrow external growth rings on the outer edge of bones of *O. salax* (Smith, 1975) and *O. ketopsis* (Fig. 2C) suggest that the salmon lived several years beyond the 4 years typical of modern Sockeye and Chum Salmon. The premaxilla of a large salmon (UMMP 67765) most similar to *O. tshawytscha*, from the base of the Glenns Ferry Formation (G.R. Smith, unpublished), is judged to be an anadromous migrant based on its large size (secondarily enlarged premaxilla 54 mm long, from a fish more than 1 m long).

6. Conclusions

Computed tomography allows a first glimpse into the internal anatomy of two Late Miocene fossil salmon. Gill raker morphology and spacing indicates likely planktivory in these, as in the other Miocene salmon. *Oncorhynchus rastrosus*, an extremely large planktivore (longer than 1.5 m) with more than 100 gill rakers, was apparently extirpated at the end of the Miocene. Most gill rakers of these salmon are numerous and long. These morphological attributes are consistent with the observed peak Pacific Ocean plankton productivity of the middle and late Miocene, suggesting that the gill raker numbers and lengths in Pacific salmons were driven by trophic ecology. The Miocene *O. ketopsis* had few short (carnivorous) gill rakers on the first arch and numerous, long (planktivorous) gill rakers on the second arch, compared to uniformly few, short, gill rakers in its modern relative, *O. keta*. *Oncorhynchus salax*, also a Miocene salmon, had longer and more numerous (planktivorous) gill rakers than its modern relative, *O. salax*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2007.02.011.

References

Barnes, L.G., 1976. Outline of eastern North Pacific Cetacean fossil assemblages. Systematic Zoology 25, 321–343.

Barron, J.A., Keller, G., 1983. Paleotemperature oscillations in the middle and late Miocene of the northeastern Pacific. Micropaleontology 29, 150–181.

Barron, J.A., Lyle, M., Koizumi, I., 2002. Late Miocene and early Pliocene biosiliceous sedimentation along the California margin. Revista Mexicana de Ciencias Geológicas 19, 161–169.

Carlson, W.D., Rowe, T., Ketcham, R.A., Colbert, M.W., 2003. Applications of high-resolution X-ray computed tomography in petrology, meteoritics, and palaeontology. In: Mees, F., Swennen, R., Van Geet, M., Jacobs, P. (Eds.), Applications of X-Ray Computed Tomography in the Geosciences. Geological Society, London, Special Publications, pp. 7–22.

Cavender, T.M., Miller, R.R., 1972. *Smilodonichthys rastrosus*, a new Pliocene salmonid fish from western United States. Bulletin of the Oregon Museum of Natural History 18, 1–44.

Crespi, B.J., Fulton, M.J., 2004. Molecular systematics of Salmonidae: combined nuclear data yields a robust phylogeny. Molecular Phylogenetics and Evolution 31, 658–679.

Dickens, G.R., Owen, R.M., 1999. The latest Miocene–early Pliocene biogenic bloom: a revised Indian Ocean perspective. Marine Geology 161, 75–91.

Diester-Haass, L., Meyers, P.A., Vidal, L., 2002. The late Miocene onset of high productivity in the Benguela Current upwelling system as part of a global pattern. Marine Geology 180, 87–103.

Grant, K.M., Dickens, G.R., 2002. Coupled productivity and carbon isotope records in the southwest Pacific Ocean during the late Miocene–early Pliocene biogenic bloom. Palaeogeography, Palaeoclimatology, Palaeoecology 187, 61–82.

Gupta, A.K., Singh, R.K., Joseph, S., Thomas, E., 2004. Indian Ocean high-productivity event (10–8 Ma): linked to global cooling or to the initiation of the Indian monsoons? Geology 32, 753–756.

Higgs, D.A., Macdonald, J.S., Levings, C.D., Dosanjh, B.S., 1995. Nutrition and feeding habits in relation to life history stage. In: Groot, C., Margolis, L., Clarke, W.C. (Eds.), Physiological Ecology of Pacific Salmon. U.B.C. Press, Vancouver, pp. 159–316.

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

Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V, Myers, K.W., 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography 13, 197–207.

Kennett, J.P., 1982. Marine Geology. Prentice Hall, Englewood Cliffs, New Jersey.

Kimmel, P.G., 1982. Stratigraphy, age, and tectonic setting of the Miocene–Pliocene lacustrine sediments of the western Snake River plain, Oregon and Idaho. In: Bonnichsen, B., Breckenridge, R.M. (Eds.), Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin, vol. 26, pp. 559–578.

Ledgerwood, R., Van Tassell, J., 2005. Stratigraphy and age of the late Miocene sediments and volcanic deposits along the Baker–Copperfield highway between Banta Road and the Love Ranch, Keating, Oregon. Eastern Oregon Geology 3, 1–17.

Lipps, J.H., Mitchell, E., 1976. Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. Paleobiology 2, 147–155.

Lyle, M., Koizumi, I., Delaney, M.L., Barron, J.A., 2000. Sedimentary record of the California current system, middle Miocene to Holocene: a synthesis of Leg 167 results. In: Lyle, M., Koizumi, I., Richter, C., Moore Jr., T.C. (Eds.), Proceedings of the Ocean Drilling Program. Scientific Results, vol. 167, pp. 341–376.

Malde, H.E., 1991. Quaternary geology and structural history of the Snake River Plain, Idaho and Oregon. In: Morrison, R.B. (Ed.), Quaternary nonglacial geology; conterminous U.S.: Boulder, CO, Geological Society of America. The Geology of North America, vol. K-2, pp. 252–281.

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

Montgomery, D.R., 2000. Coevolution of the Pacific salmon and Pacific Rim topography. Geology 28, 1107–1110.

Murata, S., Takasaki, N., Saitoh, M., Tachida, H., Okada, N., 1996. Details of retropositional genome dynamics that provide a rationale for a genetic division: the distinct branching of all the Pacific salmon and trout (*Oncorhynchus*) from the Atlantic salmon and trout (*Salmo*). Genetics 142, 915–926.

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

Raymont, J.E.G., 1963. Plankton and Productivity in the Oceans. Pergamon Press, Oxford.

Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, 1–966.

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., 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. Systematic Biology 41, 41–57.

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

Smith, G.R., Swirydczuk, K., Kimmel, P.G., Wilkinson, B.H., 1982. Fish biostratigraphy of late Miocene to Pleistocene sediments of the western Snake River plain, Idaho. In: Bonnichsen, B., Breckenridge, R.M. (Eds.), Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin, vol. 26, pp. 519–541.

Smith, G.R., Morgan, N., Gustafson, E., 2000. Fishes of the Mio-Pliocene Ringold Formation, Washington: Pliocene capture of the Snake River by the Columbia River. University of Michigan Museum of Paleontology Papers on Paleontology 32, 1–47.

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

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

Taylor, D.W., 1985. Late Cenozoic history of the Pacific Northwest: evolution of freshwater drainages and molluscs in western North America. In: Smiley, C.J. (Ed.), Late Cenozoic history of the Pacific Northwest. Pacific Division American Association for the Advancement of Science and the California Academy of Science, San Francisco, California, pp. 265–321.

Walbaum, J.J., 1792. Petri Artedi Sueci Genera piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis Speciebus 242 ad genera 52. Ichthyologiae, pars iii. Grypeswaldiae, pp. 1–723.

Wankowski, J.W.J., 1979. Morphological limitations, prey size selectivity, and growth response of the juvenile Atlantic Salmon, *Salmo salar*. Journal of Fish Biology 14, 89–100.

Wheeler, H.E., Cook, E.F., 1954. Structural and stratigraphic significance of the Snake River capture, Idaho–Oregon. Journal of Geology 62, 525–536.

Wilson, M.V.H., Li, G.-Q., 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.

Zazzo, A., Smith, G.R., Patterson, W.P., Dufour, E., 2006. Life history reconstruction of modern and fossil sockeye salmon (*Oncorhynchus nerka*) by oxygen isotopic analysis of otoliths, vertebrae, and teeth: implication for paleoenvironmental reconstruction. Earth and Planetary Science Letters 249, 200–215.