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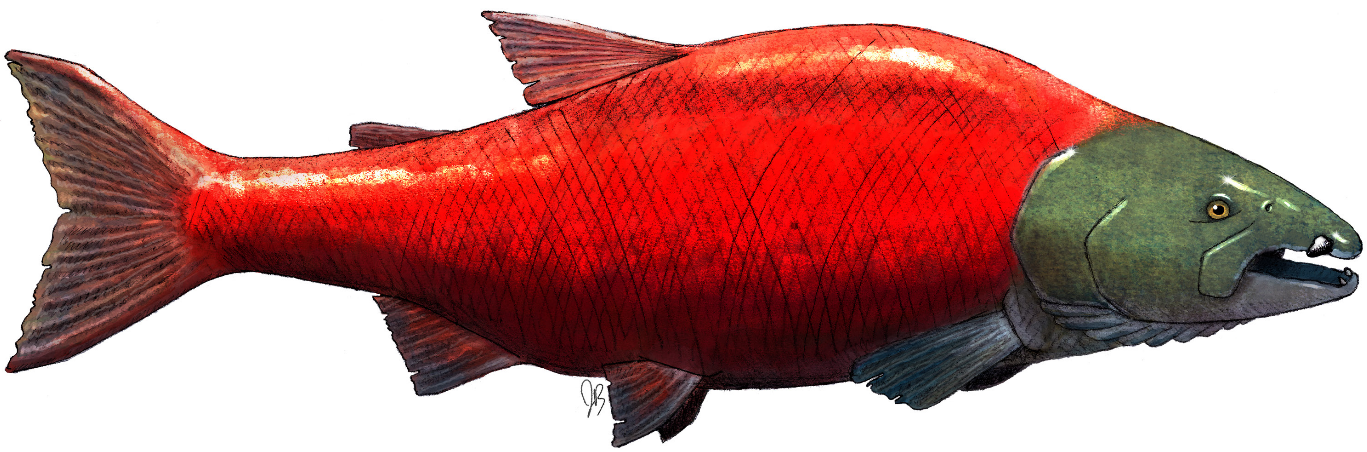

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**Cover photo**: Reconstruction of *Oncorhynchus rastrosus* by Jacob Biewer, 2015

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# The giant, spike-toothed salmon, *Oncorhynchus rastrosus* and the "Proto-Tuolumne River" (early Pliocene) of Central California

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*Oncorhynchus rastrosus* was a very large, spike-toothed, Pacific Salmon from the mid-Miocene to early Pliocene of the Pacific Northwest (California to Washington). It had two large premaxillary (breeding-fighting) teeth that stuck out laterally from the snout like spikes. It migrated from the Pacific Ocean to inland rivers to spawn, as extant Pacific salmon do today. It was planktivorous, based on numerous, long, over-lapping gill-rakers, and few, small teeth. There are gaps in our knowledge about this interesting salmon. First, one of the localities where many of the paratype specimens were collected (Turlock Lake, California), was not described geologically in the original paper beyond, 'from the Mehrten Formation'. Here we describe these deposits as cross-bedded sands, gravels and large, rounded cobbles indicative of a fast-flowing, river, which we coin here as the "proto-Tuolumne River," that periodically overflowed its banks. Paleocurrent directions indicate the river flowed to the southwest, where it joined the San Joaquin River in the Central Valley and flowed southward at this time (~5 Ma), emptying into a marine embayment near Bakersfield. Thus, the Turlock Lake *O. rastrosus* specimens would have migrated up from this embayment. Second, we investigated whether *O. rastrosus* developmentally changed before migration upriver to spawn, as extant Pacific salmon do today, by comparing premaxillary teeth from freshwater and coastal marine deposits in California. We found that the largest teeth (with the largest osseous tooth bases) were from freshwater deposits, and that these specimens had the most worn and blunt tooth tips. We propose that this was due to use in territorial defense during spawning and redd (nesting site) construction.

***Keywords:*** Turlock Lake, Mehrten Formation, migration, spawning

## INTRODUCTION

*Oncorhynchus rastrosus* (Cavender and Miller) Stearley and Smith, 1993 was a large, spike-toothed Pacific salmon from the mid-Miocene to early Pliocene of California, Oregon, and Washington (Fig. 1). Specifically, specimens have been collected from the Clarendonian to Hemphillian North American Land Mammal Age (NALMA), ~ 12–5 Ma (Cavender and Miller 1972, Stearley and Smith 2016). It was a large salmon, approximately 1.9 meters in length (based on proportions of the opercle to skull length to full body length; Cavender and Miller 1972) and weighed approximately 177 kg (based on the relationship between vertebral width and weight; Casteel 1974). Even larger dimensions and weights ("8 feet; 430 lbs.") were recently estimated by Stearley and Smith (2016). Other unusual characteristics include: (a) approximately 100 gill-rakers, (b) a pair of distinctive breeding teeth (premaxillary teeth), and (c) few other teeth. Most distinctive are the single, large, premaxillary (breeding) teeth (2–3 cm long; one tooth/side), which were probably used for breeding-territorial display and fighting (Cavender and Miller 1972, Stearley and Smith 2016). Originally, it was named *Smilodonichthys rastrosus* by Cavender and Miller (1972), the "sabertooth salmon", due to these large

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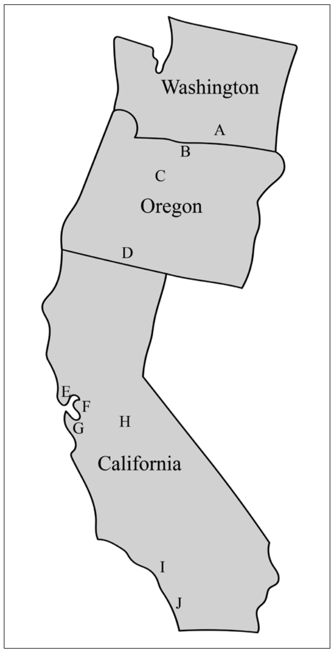


**Figure 1. A–I**. Map of distribution of *O. rastrosus* in California, Oregon, and Washington (Cavender and Miller 1972, Stearley and Smith 2016). **A.** Ringold Formation**. B.** Arlington**. C.** Gateway. **D.** Worden. **E.** Drakes Bay Formation. **F.** Pinole Tuff Formation. **G.** Santa Margarita Formation; Purisima Formation. **H.** Turlock Lake, Mehrten Formation. **I.** El Toro Trabuco; Monterey Formation; Mission Viejo; Marblehead; Aliso Creek; Laguna Niguel; Capistrano Formation. **J.** San Mateo Formation.

teeth and their belief that the species was different enough from *Oncorhynchus* to warrant a distinct genus. However, Stearley and Smith (1993) analyzed salmonids cladistically and moved the sabre-toothed salmon to *Oncorhynchus,* the genus that includes extant Pacific salmon such as the sockeye salmon. Recently discovered skulls that contain in-place premaxillary teeth show that these were actually oriented laterally, not downward as originally thought, and appear more like spikes not sabers (Claeson et al. 2016). It is now referred to as the "spike-toothed salmon" (Smith and Stearley 2015, Stearley and Smith 2016), and it may have used these teeth for making nesting sites (redds) in the river gravels during spawning (Claeson et al. 2016). We have discovered that teeth from freshwater specimens are larger with blunter tips compared to pre-maxillary teeth from coastal marine specimens, which supports this idea.

Fossils of *O. rastrosus* are found in both coastal marine and freshwater deposits in California. However, the Oregon and Washington localities are all freshwater deposits (Cavender and Miller 1972, Smith et al. 2000). Koch et al. (1992) determined from Sr isotope analysis that *O. rastrosus* was anadromous (i.e., it migrated from the ocean to rivers to spawn), like extant Pacific salmon. *Oncorhynchus rastrosus* was also planktivorous, based on the presence of numerous, long, closely-spaced, and overlapping gill rakers, but only a few, small teeth. This specialization is correlated with an increase in zooplankton in the Pacific Ocean caused by upwelling during the mid-Miocene to early Pliocene. The extinction of *O. rastrosus* may be related to the end of this zooplankton abundance (Cavender and Miller 1972, Eiting and Smith 2007, Stearley and Smith 2016).

The paleoecology of *O. rastrosus* is not yet well understood; questions about this interesting salmon remain, especially related to possible developmental changes prior to spawning. For example, extant large, male Pacific Salmon develop a kype (an expanded and hooked lower jaw that forms in Pacific male salmon during the spawning stage). In addition, their upper jaw curves down and is hooked at the tip as a result of bone and soft tissue growth (Morton 1965). There are other morphological transformations that occur in Pacific salmons before migration upriver to spawn: (a) they change in color and size and (b) they develop breeding teeth (often pigmented) (Fig. 2). These features are important for display and fighting over females and territory (Cavender and Miller 1972).

Did *O. rastrosus* also developmentally change prior to migration upriver to spawn? According to Cavender and Miller (1972) and Claeson et al. (2016), there is no evidence for a kype in the lower jaw of *O. rastrosus*. However, did other developmental changes occur in the spawning *O. rastrosus*, such as an increase in size of their large, premaxillary (breeding) teeth as in other Pacific Salmon? If so, these differences could be detected by comparing premaxillary teeth from coastal marine specimens (i.e., non-spawning) to freshwater specimens (i.e. spawning). This study investigates this question by comparing *O. rastrosus* specimens from coastal marine and freshwater deposits in California. Our working hypothesis was that the premaxillary teeth from coastal marine deposits should be smaller (i.e., from non-spawning fish) than those from freshwater deposits (i.e., from spawning fish). Our results supported this hypothesis. We found that: (a) coastal marine premaxillary teeth were smaller, had more sharply pointed tips, and had smaller osseous tooth bases and (b) freshwater specimens were larger, with rounder/blunter

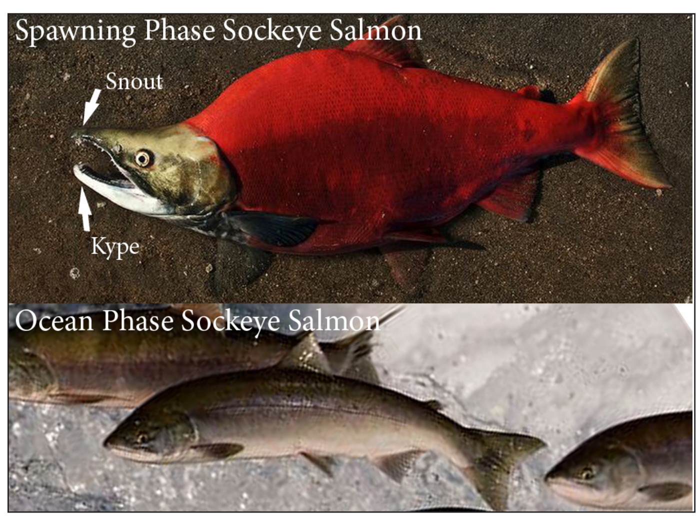


**Figure 2**. Physical differences in marine vs freshwater (spawning) stages of extant Sockeye salmon, the closest living relative of *O. rastrosus* (photos from www.arkive.com).

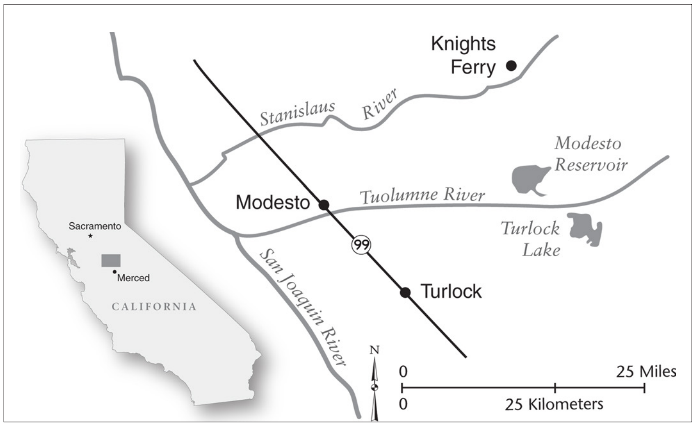


**Figure 3**. Map of California showing the location of Turlock Lake in relation to nearby cities, towns, and landmarks.

tips, and had more massive/robust osseous tooth bases. We interpret this to mean that *O. rastrosus* went through developmental changes prior to migration upriver to spawn, just as extant Pacific Salmon do today. In particular, *O. rastrosus* underwent enlargement of the 'spike' tooth and its osseous base, for display and fighting, and that during spawning activities, these teeth were worn down. Interestingly, all freshwater *O. rastrosus* specimens have been collected from deposits with sands, gravels, and cobbles representing large and, at times, fast flowing rivers. We suggest that the larger spike teeth would have been used not only for display and fighting, but also possibly for digging gravel for their redds.

In the original description of *O. rastrosus*, Cavender and Miller (1972) noted that many of the paratype specimens were collected from a Turlock Lake site (upper Mehrten Formation; Stanislaus Co., California; Fig. 3). However, beyond a geographic description, there were no descriptions or photographs of the fossil site, the sedimentary deposits, the depositional environments, or stratigraphic context. Owing to this, mis-understandings about this site occur in subsequent publications (i.e., Axelrod 1980). We remedy this situation in this paper. We: (a) re-located and confirmed the location of the site with the original collector, Mr. Dennis Garber; (b) documented the site with GPS and photographs; and (c) described the deposits in more detail and measured and described a stratigraphic section through them.

The Turlock Lake salmon site deposits are fluvial in character and diagnose a large, fast-flowing river. We refer to this Miocene-Pliocene river as the 'proto-Tuolumne River. We recognize these deposits by: (a) a sharp, erosional unconformity between the underlying fine-grained floodplain deposits and the overlying channel fill deposits and (b) channel fill deposits containing large, rip-up clasts of siltstone; large, rounded, basaltic cobbles; and steeply dipping cross-beds of sands and gravels. Paleocurrent directions indicate flow was to the southwest. We have mapped the distribution of these deposits in two major areas in Turlock Lake. Wagner (1981) and Marchand and Wagner (1980) noted and mapped these deposits, but did not describe or discuss them in detail. We do this in this paper.

## GEOLOGIC SETTING

Most of the freshwater specimens examined in this study are from the uppermost Mehrten Formation exposed at Turlock Lake (a man-made reservoir), Stanislaus County, California (Fig. 3). These specimens (teeth, skull bones, and vertebrae) were collected by Dennis Garber from 1957 to approximately 1964 (Cavender and Miller 1972). The fossils were surface finds from a beach exposed on the southeastern shore of Turlock Lake. With Mr. Garber's assistance, we have re-visited and re-examined this locality (described below). This locality is important for several reasons: (1) it is one of only two localities in California (in addition to the Pinole Tuff Formation), that has produced *O. rastrosus* from freshwater deposits; (2) it represents the only record of *O. rastrosus* from the Central Valley of California; and (3) it demonstrates that *O. rastrosus* migrated up large and at times, fast-flowing rivers like the "proto-Tuolumne River."

The Mehrten Formation is exposed in the low foothills of the Sierra Nevada Mountains, along the eastern margin of the San Joaquin Valley, from Sacramento to Merced (Fig. 3). It consists of andesitic sedimentary and volcaniclastic deposits that are late Miocene to early Pliocene in age (Wagner 1981). The Mehrten Formation interfingers with volcanic deposits that originated from the Walker Lane caldera near the California/Nevada border (Fig. 4). Basalts (specifically, latites) and lahars (volcanic mud flows) flowed down paleochannels of the Stanislaus and other rivers and into the eastern side the Central Valley of California; these are referred to as the Stanislaus Group (Fig. 5) (Wagner 1981; Busby et al., 2016). The sedimentary deposits of the Mehrten Formation range from fine-grained, tuffaceous siltstones, medium to coarse grained sandstones, breccias, and conglomerates, and were deposited in various environments within an alluvial fan and floodplain. In the northeastern San Joaquin valley, the Mehrten Formation was deposited by southwestern-trending streams (Bartow 1991).

The stratigraphy of the Mehrten Formation was extensively examined by Wagner (1981), who focused on correlating the outcrops between Knights Ferry and Turlock Lake. Wagner subdivided the Mehrten Formation into four members, and we follow this stratigraphy here (Fig. 5). The Modesto Reservoir member is within the uppermost Mehrten, and is primarily exposed at Modesto Reservoir and Turlock Lake. Hundreds of vertebrate fossils were collected from the


**Figure 4**. Early Pliocene (~5 Ma) reconstruction of California showing the modern locations of the Tuolumne River, Turlock Lake, latite flows of the Stanislaus Group, the Little Walker Caldera, the path of the "proto-Tuolumne River", and the shallow marine embayment near Bakersfield. Based on Blakey and Ranney 2008.

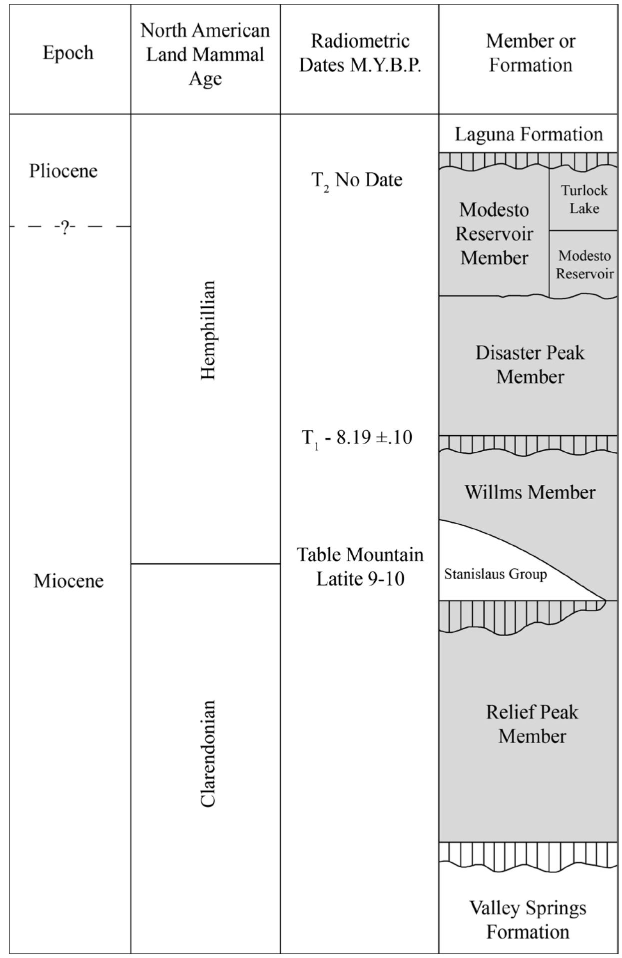


**Figure 5**. Generalized stratigraphy of the Mehrten Formation highlighted in grey. Modified from Wagner 1981.

Modesto Reservoir member exposed in and around Turlock Lake and the Modesto Reservoir by Mr. Dennis Garber and others starting in approximately 1957. Mr. Garber donated his collection to the University of California Berkeley Museum of Paleontology (UCMP) and the Natural History Museum of Los Angeles County (LACM). Mammal remains include those of horses, camels, antelope, giant ground sloth, mastodon, carnivores, rodents, and others. Wagner identified and described these mammals in detail, documented all of the fossil localities on a topographic map, and placed the localities within his 38 meter composite stratigraphic section (Wagner 1976, 1981; Fig. 6). The Modesto Reservoir Member contains mammals characteristic of the Hemphillian NALMA, and is quite similar in faunal composition to the Pinole Tuff Formation (~17 miles north of Oakland, CA; Contra Costa County; Stirton 1939, 1951, Wagner 1976, 1981, Tedford et al. 1987, Bell et al. 2004). The Pinole Tuff was dated at approximately 5.2 Ma (Evernden et al. 1964, Sarna-Wojcicki 1976). Thus, based on faunal similarity, the Modesto Reservoir Member is approximately 5 Ma (Wagner 1981). There is also an undated, water-laid tuff in the upper Modesto Reservoir Member at Turlock Lake ($T_2$ of Wagner 1981; Figs. 5, 6). We have sampled this tuff in various locations at Turlock Lake and sent it to two labs (Oregon State University and MIT) for dating, but neither lab was able to successfully date it. Better dating of the Modesto Reservoir member is needed.

There are various paleoenvironments represented in the Modesto Reservoir Member including floodplains with paleosols, rivers, and even a short-lived lake high in the section. Numerous plant fossils were collected from these lacustrine units, and include sycamore, oak, and other trees and shrubs, representing a riparian biome (Axelrod 1980). Based on the plants, the paleoclimate of this area ~ 5 Ma was wetter and milder than today. Annual rainfall totaled ~635 mm (25 inches), approximately double what it is today. Temperatures were milder, with less severe summers and winters. Average July temperature was ~22 degrees C (72.5 degrees F) and average January temperature was ~ 9 degrees C (48.5 degrees F; Axelrod 1980). The presence of the giant

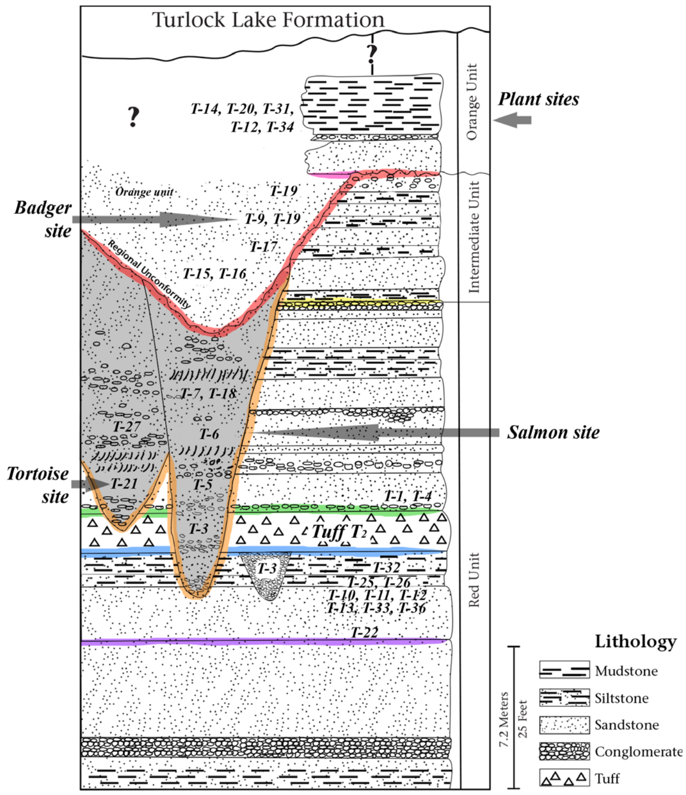


**Figure 6**. Stratigraphy of the upper Mehrten Formation (Modesto Reservoir member) at Turlock Lake. Modified from Wagner, 1981. Important and published fossil localities are indicated by arrows. Badger locality (Wagner 1976); Tortoise locality (Biewer et al. 2016); Plant localities (Axelrod 1980). The two highlighted, deep channels are what we refer to as the "proto-Tuolumne River" deposits.

tortoise *Hesperotestudo orthopygia* Hay, 1908 (Biewer et al. 2016) supports these paleoclimatic interpretations as giant tortoises would likely not have tolerated hard frosts. The more mild climate and higher rainfall correlate to the absence (or considerably smaller size) of the Coast Range, which today causes a rain shadow effect in the Central Valley. Uplift of the Coast Range started approximately 3–4 Ma due to convergence between the Pacific and North American Plates (Harden 1998).

The paleotopography of this area ~ 5 Ma was a relatively flat floodplain, based on four lines of evidence: (1) the presence (and abundance) in the lacustrine beds (uppermost Mehrten) of teeth from *Orthodon* Ayres, 1854, the Sacramento Blackfish, which avoids fast moving rapids (Casteel and Hutchinson 1973, Moyle 2002); (2) the plants in the lacustrine beds that are related to extant species found on or near river floodplains (Axelrod 1980); (3) the upper Mehrten deposits are typically flat-lying and laterally continuous, indicating deposition within a near base-level floodplain; and (4) paleosols, with numerous root casts, and occasionally large tree root casts are present, also indicators of a floodplain environment.

## MATERIALS AND METHODS

Field work at Turlock Lake to examine the fish and other fossil localities and the stratigraphy was accomplished via kayak from 2014–2016. Because there are no known field descriptions of the Turlock Lake fossil localities, we re-located and re-documented the localities in the following way: First, we identified the original sites on topographic maps with fossil localities indicated from the databases of the University of California Berkeley Museum of Paleontology (UCMP) and the Natural History Museum of Los Angeles County (LACM). Next, we revisited the areas, and took photographs of each general area. Then we showed the photographs to Mr. Dennis Garber, the original collector, who pointed out the exact location of each locality. Finally, we returned to each locality, took further photographs, recorded the GPS coordinates, and made lithologic descriptions. In addition, the locality numbers assigned by Mr. Garber, UCMP, and LACM were all linked in order to ease communication (Table 1). The photographs, GPS coordinates, lithologic descriptions, locality numbers, and other information gathered through interviews with Mr. Garber were compiled into a document, and given to UCMP and LACM to supplement their fossil collections from Turlock Lake.

The salmon locality at Turlock Lake is located within the "proto-Tuolumne" river deposits, within the upper Mehrten Formation. In order to document the distribution of these deposits in the area, we examined all outcrops of the upper Mehrten exposed in and around Turlock Lake. We then mapped the location of all these "proto-Tuolumne River" deposits and determined paleo-flow directions from cross-bedded sands and imbricated cobbles following Boggs (2012) (Fig. 7).

In order to determine whether *O. rastrosus* developmentally changed prior to migration upriver to spawn, we examined all *O. rastrosus* specimens from fresh water and coastal marine units in the Natural History Museum of Los Angeles County (LACM) and the University of California Museum of Paleontology Berkeley (UCMP). Detailed locality information is available upon request from the curators at those institutions. Specimens were measured with a digital calipers and were photographed with a Nikon Coolpix digital camera. Measurement dimensions are shown in Figure 9.

## RESULTS AND DISCUSSION

### Turlock Lake Salmon Locality

Although some of the paratype specimens of *O. rastrosus* are from Turlock Lake, California, there were no descriptions of the fossil locality, deposits, and geologic context in

**Table 1.** All Turlock Lake localities, their UCMP, LACM, and Dennis Garber locality numbers, and brief lithologic descriptions. Dashes represent either sites without equivalencies at differing institutions, or localities that we were not able to visit.

| Dennis Garber Number | LACM Number | UCMP Number | Description |
|---|---|---|---|
| **T-1** | 3904 | - | - |
| **T-2** | 3905 | - | - |
| **T-3** | 3906 | V5404 | Cobble sized conglomerate above sharp unconformity and siltstone. |
| **T-4** | 3907 | - | Cobble sized conglomerate above sharp unconformity and siltstone. |
| **T-5** | 3908 | V81248 | Silt/mudstone overlain by sharp unconformity and cobble size conglomerate. |
| **T-6** | 3909 | V5405 | Reworked sand/gravel. Underlies cliff of cross-bedded sandstone |
| **T-7** | 3910 | V90007 | Reworked sand/gravel washed down beach by wave action |
| **T-8** | 3911 | - | Reworked sand/gravel. Underlies cliff of cross-bedded sandstone |
| **T-9** | 3912 | - | Massive tan mud/siltstone |
| **T-10** | 3913 | - | Massive tan mud/siltstone |
| **T-11** | 3914 | - | Massive tan mud/siltstone |
| **T-12** | 3915 | V6874 | Siltstone exposed due to calving by wave action |
| **T-13** | 3916 | V80042 | Gray massive silt/fine sandstone |
| **T-14** | 3917 | V6878, PA616 | Strongly bedded shale |
| **T-15** | 3918 | V5837 | Silt/mudstone |
| **T-16** | 3919 | V82047 | Silt/mudstone with layers of fine sand |
| **T-17** | 3920 | - | Gravel sized conglomerate |
| **T-18** | 3921 | - | silt/sand |
| **T-19** | 3922 | V5836 | silt/sand |
| **T-20** | 3923 | PA616 | Repeating layers of bedded silt, mudstone, and fine sand |
| **T-21** | 3924 | V71137 | Medium cross-bedded sands, silty mudstones, and gravels |
| **T-22** | 3925 | - | Silt and fine sand |
| **T-23** | 3926 | - | Cross-bedded sands and some gravel |
| **T-24** | 3927 | - | Silt/mudstone underlying sharp unconformity and cobbles |
| **T-25** | 3928 | - | silt/mudstone |
| **T-26** | 3929 | - | Mudstone |
| **T-27** | 3930 | - | - |
| **T-28** | 3931 | - | Sand |
| **T-29** | 3932 | - | - |
| **T-30** | 3933 | - | - |
| **T-31** | 3934 | V68134 | - |
| **T-32** | 3935 (3937) | V68135 | Waterlain tuff above brown silt/mudstone |
| **T-33** | 3936 | - | - |
| **T-34** | 3937 (3935) | V68135 | Waterlain tuff above brown silt/mudstone |
| **T-35** | 3938 | - | - |
| **T-36** | 3939 | - | - |
| **T-37** | 3940 | - | - |
| **T-38** | 3941 | - | - |
| - | 3950 | V65711 | (General Turlock Lake locality –specific locality not known) |

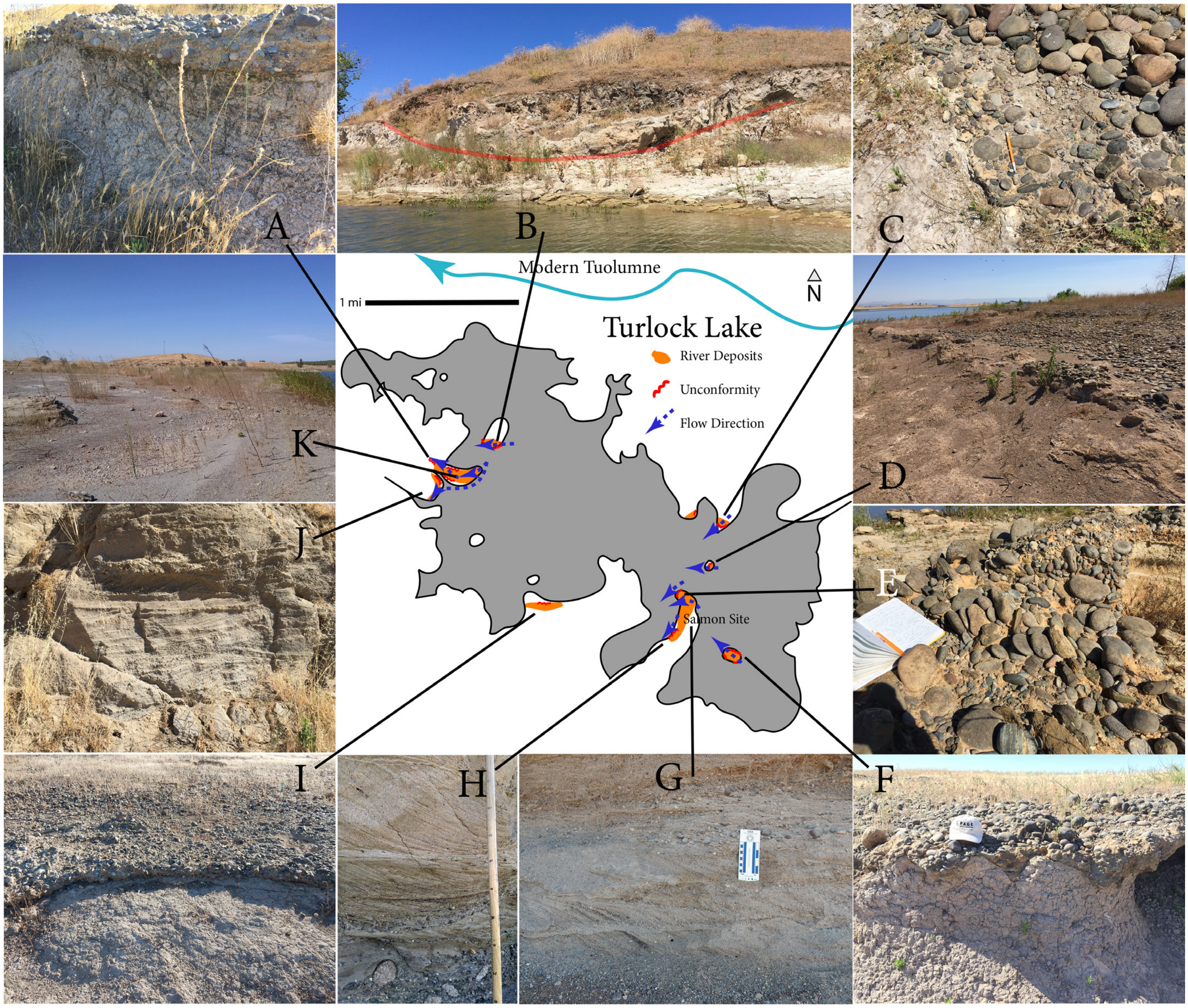


**Figure 7**. **A–K**. "Proto-Tuolumne River" deposits exposed at Turlock Lake indicated by orange on inset map. Arrows indicate observed flow directions. **A**. Unconformity exposed northwest of T-24. **B**. Channel cross-section visible at T-21. **C**. Unconformity exposed far north of salmon locality. **D**. Unconformity exposed on 'unmapped' island. **E**. Cobbles above unconformity at T-5 showing clear imbrication toward the left (southwest direction). **F**. Sharp, wavy unconformity on T-3/T-4 island. **G**. Cross-bedded sand of cliff face overlying salmon locality. **H**. Steep cross-beds and silt rip-up clasts exposed at cliff overlooking T-8. **I**. Unconformity exposed between T-15 and T-14. **J**. Cross-beds located southwest of T-24. **K**. Beach composed of cross-bedded sand and gravel at T-23.

the original paper, beyond that they were from the Mehrten Formation at Turlock Lake (Cavender and Miller 1972). Later, Marchand and Wagner (1980) described and mapped the Mehrten and other formations in and around Turlock Lake, and Wagner (1981) described the stratigraphy of the Mehrten, placing all the known fossil localities within this stratigraphy (Fig. 6). In this paper, we remedy this situation by: (1) describing the site and deposits, along with a stratigraphic section and (2) describing and documenting these "proto-Tuolumne River" deposits exposed in and around Turlock Lake.

The Turlock Lake fossil locality that produced the *O. rastrosus* specimens is UCMP V5405 (=LACM 3909). This locality was found and collected by Mr. Dennis Garber, and his original collection number is T-6. Jake Biewer interviewed Mr. Garber several times from 2015 to 2016 in order to re-document this and other Turlock Lake fossil localities that Mr. Garber had found and collected (Table 1). According

**Table 2.** Measurements of *O. rastrosus* premaxillary (breeding) teeth from UCMP and LACM.

| | | | | | | Osseous base of tooth | | | Tooth | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Specimen No.** | **Locality No.** | **Formation** | **Age** | **Freshwater** | **Marine** | **Base-Max width (Fig. 10.E)** | **Base-Max Height (Fig. 10.D)** | **Base-Max Length (Fig. 10.A)** | **Tooth Max width (Fig. 10.F)** | **Tooth-Max height** | **Tooth-Max length (Fig. 10.B)** | **Total Height of Specimen (base + tooth); Fig. 10.C** |
| 158730<br>147601 | LACM<br>5563 | Capistrano | Hemphillian | | x<br>x | 11.2<br>19.6 | 13.6<br>19.3 | 19.7<br>30.1 | 8.3<br>8.7 | 17.6<br>17.3 | 13.5<br>16.6 | 31.2<br>36.6 |
| 128775 | LACM<br>3820 | Capistrano | Hemphillian | | x | 8.9 | 7.3 | 10.2 | 6 | 8.5 | 5.7 | 15.8 |
| 115971<br>115972<br>115973 | LACM<br>4436 | Capistrano | Hemphillian | | x<br>x<br>x | 26.3<br>14.8<br>20.2 | 19.7<br>14.5<br>14.3 | 30.4<br>32.8<br>27.1 | 17.1<br>13.3<br>13.6 | 17.6<br>12.3<br>23.4 | 22.5<br>24.9<br>22.9 | 37.3<br>27.8<br>37.9 |
| 143828 | LACM<br>3186 | Capistrano | Hemphillian | | x | - | - | - | 6.03 | - | 10.3 | - |
| 147597<br>158729 | LACM<br>5563 | Capistrano | Hemphillian | | x<br>x | 23<br>- | 17.3<br>- | 36.3<br>- | 11.4<br>8.5 | 24.5<br>- | 21.5<br>14.5 | 41.8<br>- |
| 147673 | " | Capistrano | Hemphillian | | x | 16.5 | 20.8 | 24.2 | 6.7 | 8.5 | 12.3 | 29.3 |
| 147636 | LACM<br>5563 | Capistrano | Hemphillian | | x | 11.1 | 11.1 | 19.8 | 6.6 | 5.3 | 13.4 | 16.4 |
| 143827 | LACM<br>3186 | Capistrano | Hemphillian | | x | - | - | - | 8.3 | - | 12.2 | - |
| 147688 | LACM<br>5563 | Capistrano | Hemphillian | | x | 17.4 | 25.7 | 46 | 10.7 | 1.7 | 20.1 | 27.5 |
| 143819 | LACM<br>3186 | Capistrano | Hemphillian | | x | 15.1 | 14.9 | 21.9 | 8.8 | 4.8 | 11.4 | 19.7 |
| 123258 | LACM<br>6902 | Monterey | Clarendonian | | x | - | - | - | 3.9 | - | 5.7 | - |
| 58915 | LACM<br>1945 | Monterey | Clarendonian | | x | 11.2 | 7.8 | 13.1 | 5.9 | 12.6 | 10 | 20.4 |
| 135704 | LACM<br>4940 | Santa Margarita | Clarendonian | | x | 7.3 | 9.1 | 19.3 | 4.9 | 9.2 | 10.5 | 18.3 |
| 135697 | " | Santa Margarita | Clarendonian | | x | 18.9 | 21.3 | 27.2 | 9.5 | 13.8 | 11.2 | 35.1 |
| 88651 | UCMP<br>68145 | San Mateo | Hemphillian | | x | 30 | 26.7 | 43.5 | - | - | - | - |
| 61951<br>61952 | LACM<br>3909 | Mehrten | Hemphillian | x<br>x | | 38.7<br>35.1 | 44.2<br>29.5 | 55.5<br>46.7 | -<br>19 | -<br>8.3 | -<br>31.8 | 44.2<br>37.9 |
| 136029 | UCMP<br>5405 | Mehrten | Hemphillian | x | | 23.5 | 17.2 | 52.6 | 12.6 | 26.2 | 24 | 43.4 |
| 93181 | " | Mehrten | Hemphillian | x | | 30.7 | 24.5 | 39.6 | 15.3 | 15.6 | 25.8 | 44.4 |
| 93176 | " | Mehrten | Hemphillian | x | | 32.2 | 31.2 | 49.9 | 18.9 | 3.4 | 32.8 | 34.6 |
| 93179 | " | Mehrten | Hemphillian | x | | 25.3 | 22.8 | 41.5 | 10.5 | 18.2 | 19.3 | 41 |
| 93178 | " | Mehrten | Hemphillian | x | | 40.1 | 42.1 | 61.4 | 19.4 | 12.3 | 31.5 | 54.4 |
| 93184 | " | Mehrten | Hemphillian | x | | 34.1 | 29.3 | 40.3 | 19.4 | 17 | 28.7 | 46.3 |
| 93187 | " | Mehrten | Hemphillian | x | | 14.2 | 18.9 | 22.2 | 9.6 | 16.5 | 17.4 | 35.4 |
| 93182 | " | Mehrten | Hemphillian | x | | 32.5 | 25.4 | 45 | 21.2 | 25.5 | 29.2 | 50.9 |
| 93177 | " | Mehrten | Hemphillian | x | | 24 | 20.4 | 51.5 | - | - | - | 20.4 |
| 93183 | " | Mehrten | Hemphillian | x | | 27.9 | 22 | 57.1 | 18.6 | 29.4 | 32.2 | 51.4 |
| 93180 | " | Mehrten | Hemphillian | x | | 19 | 14.5 | 27.8 | 12.6 | 19.8 | 21.5 | 34.3 |
| 65630 | UCMP<br>2572 | Pinole Tuff | Hemphillian | x | | 26 | 26.7 | 36 | 14.4 | - | 22.2 | 44.6 |
| 37584 | UCMP<br>3425 | Pinole Tuff | Hemphillian | x | | 35 | 33.7 | 42.5 | 11.4 | 18.9 | 19.8 | 52.6 |
| 61550 | " | Pinole Tuff | Hemphillian | x | | 21.5 | 18 | 22.8 | 12.8 | - | 19.2 | 35.3 |
| 61554 | " | Pinole Tuff | Hemphillian | x | | 20.4 | 22.5 | 32.1 | 12 | 31.7 | 21 | 54.2 |


**Figure 8.** Map showing locations of all California specimens examined/measured in this study. Blue circles indicate marine deposits while orange indicates freshwater.

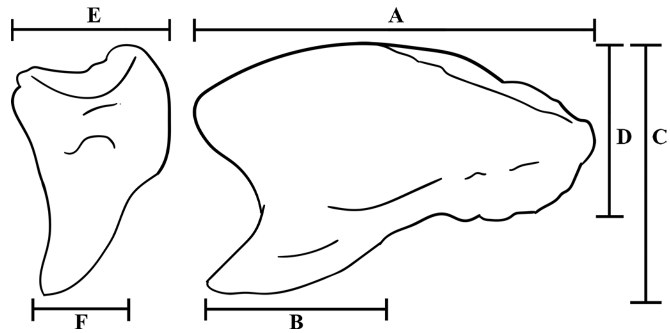


**Figure 9. A–F.** Measurements taken of *O. rastrosus* premaxillary teeth. **A.** Greatest length of the osseous base. **B.** Greatest length of the tooth cusp. **C.** Greatest height of the tooth cusp and osseous base. **D.** Greatest height of the osseous base. **E.** Greatest width of the osseous base. **F.** Greatest width of the tooth cusp.

to Mr. Garber, T-6 includes the entire beach below a short vertical cliff between two nearby localities, T-5 and T-7 (Fig. 10A, Table 1). Fossils have not been found in the sands of the cliff face, only as float and in-situ in the beach. The T-6 'beach' consists of medium to coarse sands and gravel with a water-lain tuff ('T2') exposed in one area (Fig. 10B). This is the only confirmed site at Turlock Lake where fossils of *O. rastrosus* have been found. Numerous horse and camel teeth and other mammal fossils also came from this site.

### "Proto-Tuolumne River" deposits

We returned to the T-6 area several times from 2014–2016 to re-document the site and to describe the deposits (Fig. 11). We describe and discuss the three main characteristics here, starting from the base of the channel deposits. First, there is a distinctive and sharp erosional unconformity between the underlying, fine-grained, pink to grey, tuffaceous siltstone representing floodplain deposits and the overlying channel fill deposits (Fig. 10C). Second, the thick channel fill deposits contain: (a) cross-bedded, medium to coarse sands and pebbles (Fig. 7G, H); (b) occasional large, rip-up clasts of siltstone (Fig. 7H); and (c) deposits of large, rounded, clast-supported cobbles (of volcanic and metamorphic composition) (example, T-5 (Table 2; Figs.7E; 10D). Based on the size of the cobbles, (of volcanic and metamorphic composition) (example, T-5 (Table 2; Figs. 7E, 10D) and that they are clast-supported and in places imbricated, we interpret these as gravel bar deposits within the "proto-Tuolumne River" (Fig. 7G, H). Current directions are predominantly to the southwest (Fig. 7).

Marchand and Wagner (1980) mapped this area as "Tmo" (Tertiary Mehrten O), which includes "brown sandstone, siltstone, and local conglomerate unconformably overlying Tmi and Tmr; fine-grained beds near top contain some biotite and abundant quartz and feldspar; abundant bone fragments (in the coarser beds), and a few leaf impressions (in the siltstones and mudstones)."

The "proto-Tuolumne River" deposits in outcrop are recognized by the following: (1) sharp, erosional contact at the base of the sequence; and (2) channel fill deposit with (a) large, rip-up clasts of siltstone; (b) large, rounded cobbles; and (c) cross-bedded sands and gravels. We have mapped its distribution in several locations in and around Turlock Lake (Fig. 7). Exposures can be divided into two areas, possibly representing two separate channels or a fork in the main channel (Fig. 7). The first area is in the southeast corner of the lake and includes the salmon locality. Flow directions from cross-bedded sands examined at T-6, T-7, and T-8 are generally to the southwest (Fig. 7 G, H). Imbricated cobbles at T-5, just to the north, also give a southwest flow direction (Fig. 7E). Further north there are more areas, one of which is a small, unmapped island, where the contact and cobbles are exposed (Fig. 7 C, D). At T-3/T-4, another small island to the southeast of the salmon locality, there is very sharp unconformity and imbricated cobbles (Table 1; Fig. 7F).

The second area of exposures of the "proto-Tuolumne River" deposits is on the northwest side of the lake (Fig. 7). Most notable of these is at T-21 (Table 1), known as 'Tortoise

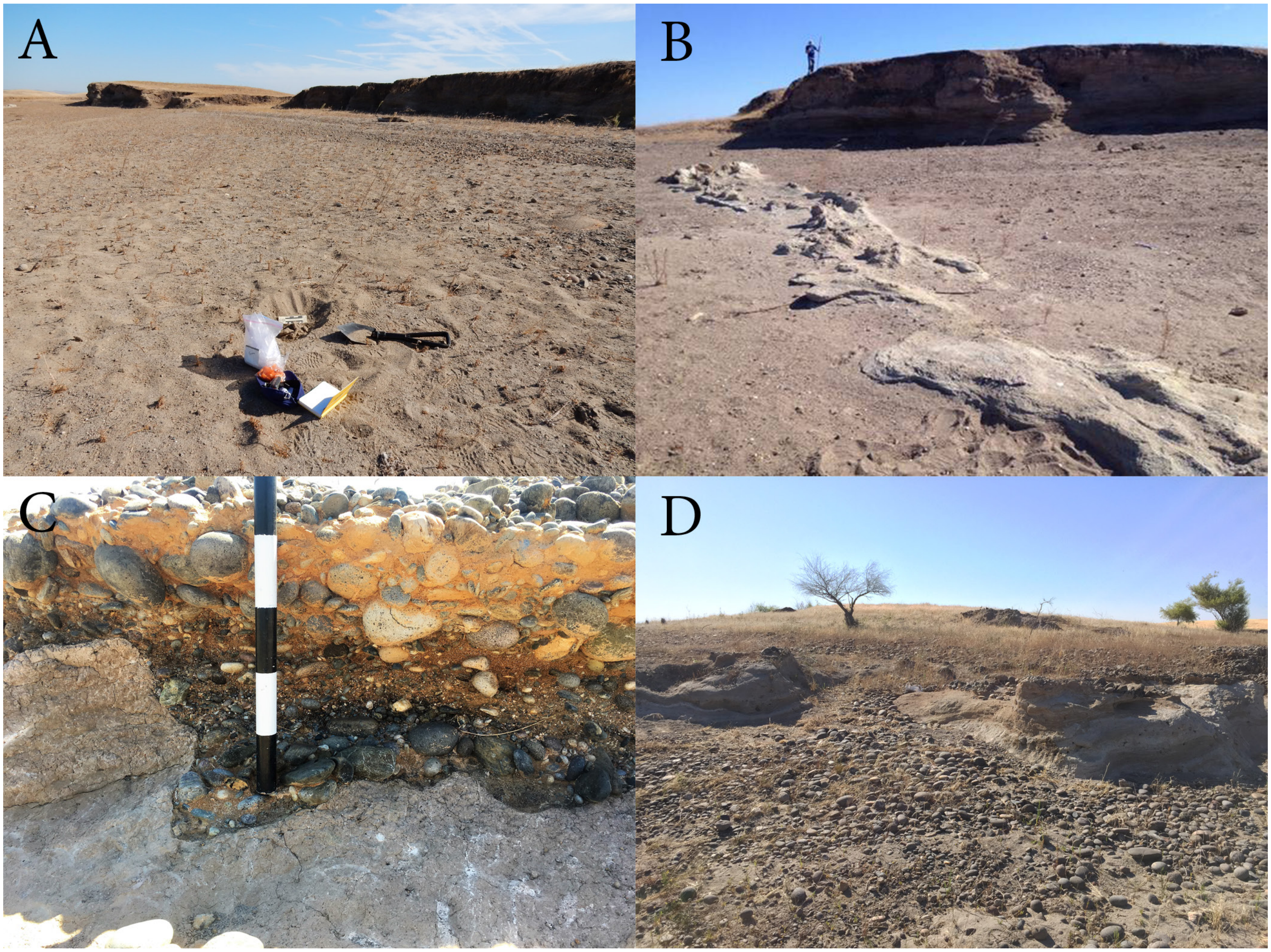

**Figure 10. A.** Photograph of fossil salmon locality, T-6, showing beach and overlying cliff. Specimens were collected from the surface of the beach area from ~1957–1964. **B.** Photograph taken at salmon locality, T-6, showing exposed water-lain tuff within the sands. **C.** Photograph of sharp unconformity underlying salmon locality. Below the unconformity is pink/tan tuffaceous silt. **D.** Photograph of T-5, a nearby site to T-6, with the sharp unconformity and large, rounded cobbles.

Island' owning to the many large tortoise fossils found there (Biewer et al. 2016). There, an excellent cross section of a channel is visible on the southeast corner of the island (Fig. 7B), with the unconformity that cuts into strongly laminated lacustrine beds, and with overlying gravels. Flow direction, indicated by cross-beds and the channel cross section, is to the west. Southwest of this island is a distinct promontory containing the T-23 and T-24 fossil localities (Table 1; Fig. 7A, K, J). The area primarily contains cross-bedded sands (Fig. 7 J, K); however, the sharp unconformity and cobbles are exposed only in a few areas along the southwestern shore (Fig. 7A). Many flow directions were taken from cross-beds in the area, and together show a general southwest direction (Fig. 7). In addition, there is a single outlier site located in between the two major areas, just south of one of the lacustrine plant localities, T-14 (Table 1, Fig. 7I). Here, there is a large area with cobbles and the erosional contact can be seen in a few places. Flow direction could not be gathered from this site.

We interpret the deposits as representing a large fast-flowing river that migrated laterally cutting into the floodplain and at times flooding. Wagner (1981) also noted channel deposits within the Modesto Reservoir member, and stated that in places these channels are “entrenched up to 12 meters,” with two of these channel deposits of sandstone and conglomerate composed of “50% andesite and most of the remainder metamorphic rocks.” However, he did not describe the unconformity or the channel deposits in detail, and there are no photographs or documentation of sites where he observed them.

As the “proto-Tuolumne River” cut across the floodplain,

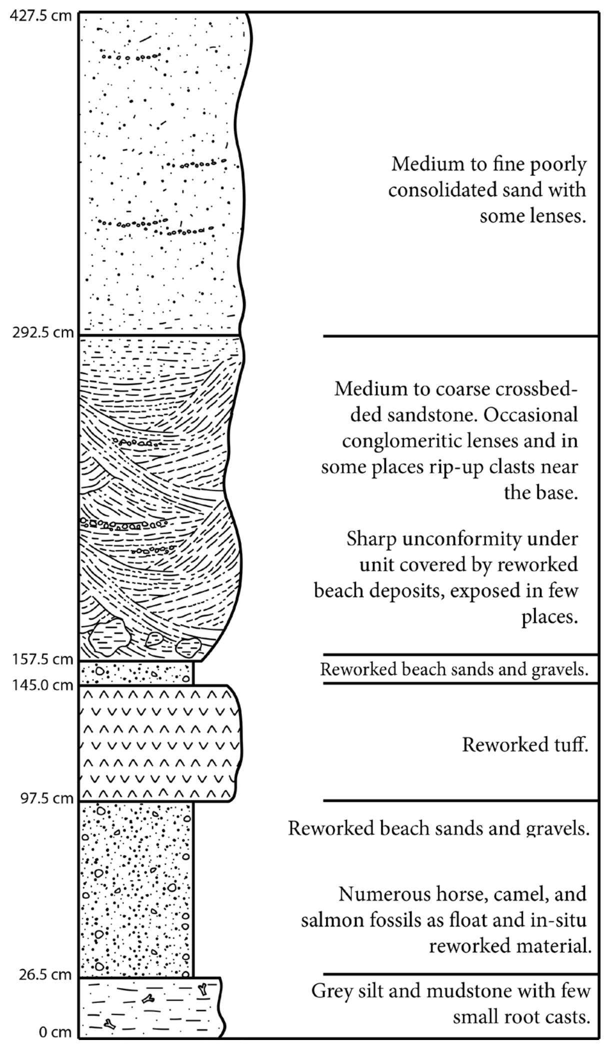


**Figure 11.** Stratigraphic section through the T-6 fossil locality (measured/described by Francisco Palacios and Jacob Biewer in October, 2015).

it deposited thick fluvial beds some of which contained numerous vertebrate fossils, including all the specimens of *O. rastrosus*. Based on paleo-current analysis of cross-beds, the river flowed predominantly to the southwest, which Bartow (1991) observed for other paleorivers in the northeast San Joaquin Valley, in contrast to today's rivers which flow to the west (Fig. 7). The position of the "proto-Tuolumne" River ~ 5 Ma was ~ 5 km to the south of and ~ 50 m higher than the modern Tuolumne River, which is deeply incised.

The type locality for *O. rastrosus*, the Gateway locality (Deschutes Formation) in Oregon, is also that of a large, fast-moving river and Shotwell informally referred to it as the "Torrential Beds" (Cavender and Miller 1972). The lithology of the Gateway locality is described as coarse gravel and boulders, and images of the locality in Cavender and Miller (1972) clearly show steeply dipping cross-bedded sands (Figs. 1, 2). We envision these massive, spike-toothed salmon migrating up large, fast-flowing rivers during the Miocene to early Pliocene, as extant salmon do today. These giant salmon would have spawned and died (as most spawning salmon do today), and their carcasses would have washed downstream during flooding events. We do not know how far down river these particular bones and teeth were moved prior to deposition at the Turlock Lake locality. The massive premaxillary teeth (and bases) would be the most durable parts of the body, and the most likely parts to survive transport. It is thus not anomalous that these teeth and also large centra and several robust skull bones are what have been found from the Turlock Lake locality.

We do not know how far upriver *O. rastrosus* migrated nor do we know how far east the "proto-Tuolumne River" extended. Current understanding is that it did not extend further east than the drainage divide of the present Sierra Nevada (Huber 1990). However, this is in contrast to the San Joaquin River, which extended further to the east and into Nevada until ~3.2 million years ago, when it was diverted by a volcanic lava flow (Huber 1981). Huber (1990) partially reconstructed the location of the "proto-Tuolumne River" of approximately 10 Ma based on volcanic flows that filled, dammed, and diverted part of the upper river channel (Fig. 4). Its flow at the time was approximately east to west, starting near where the crest of the current Sierra Nevada occurs today (near Mt. Dana). (At the time, a line of hills of moderate relief occupied this area.) In Huber's 1990 study the remnants of the "proto-Tuolumne River" channel could not be traced further west than 6.5 km northeast of Groveland, thus Huber's study does not shed light on the location of the river downstream (and closer to Turlock Lake) from this location. Huber cites Lindgren (1911) that the river may have flowed on to Chinese Camp and then to the south (Fig. 4); however the location of this ~10 Ma "proto-Tuolumne River" channel downriver from Chinese Camp is not documented in Huber (1990) or in other literature. However, we do know that once it reached the axis of the Central Valley, it (and other rivers) then flowed south to enter the shallow marine embayment that existed in the Coalinga/Kettleman Hills area (southern San Joaquin Valley) during this time (Fig. 4). By ~5 Ma, the outlet to the ocean was a narrow inlet or strait located near Monterey (Harden 1998). This shallow marine embayment/basin continued until late Pliocene, but ended approximately 3.0 to 2.5 Ma when the outlet was closed due to uplift of the Coast Range in this area (Bartow 1981, Harden 1998).

Today, rivers like the Merced, Tuolumne, and Stanislaus flow west, down from the Sierras, and enter the San Joaquin Valley, where they then join the San Joaquin River, which flows to the north. The San Joaquin River joins the

**Figure 12.** Freshwater specimens of *O. rastrosus* premaxillary teeth from the Mehrten Formation (Turlock Lake, CA; UCMP V5405). All are lateral views. **A.** Left tooth (UCMP 93181). **B.** Left tooth (UCMP 93183). **C.** Right tooth (UCMP 136029). **D.** Right tooth (UCMP 93179). **E.** Right tooth (UCMP 93184). **F.** Left tooth (UCMP 61951).

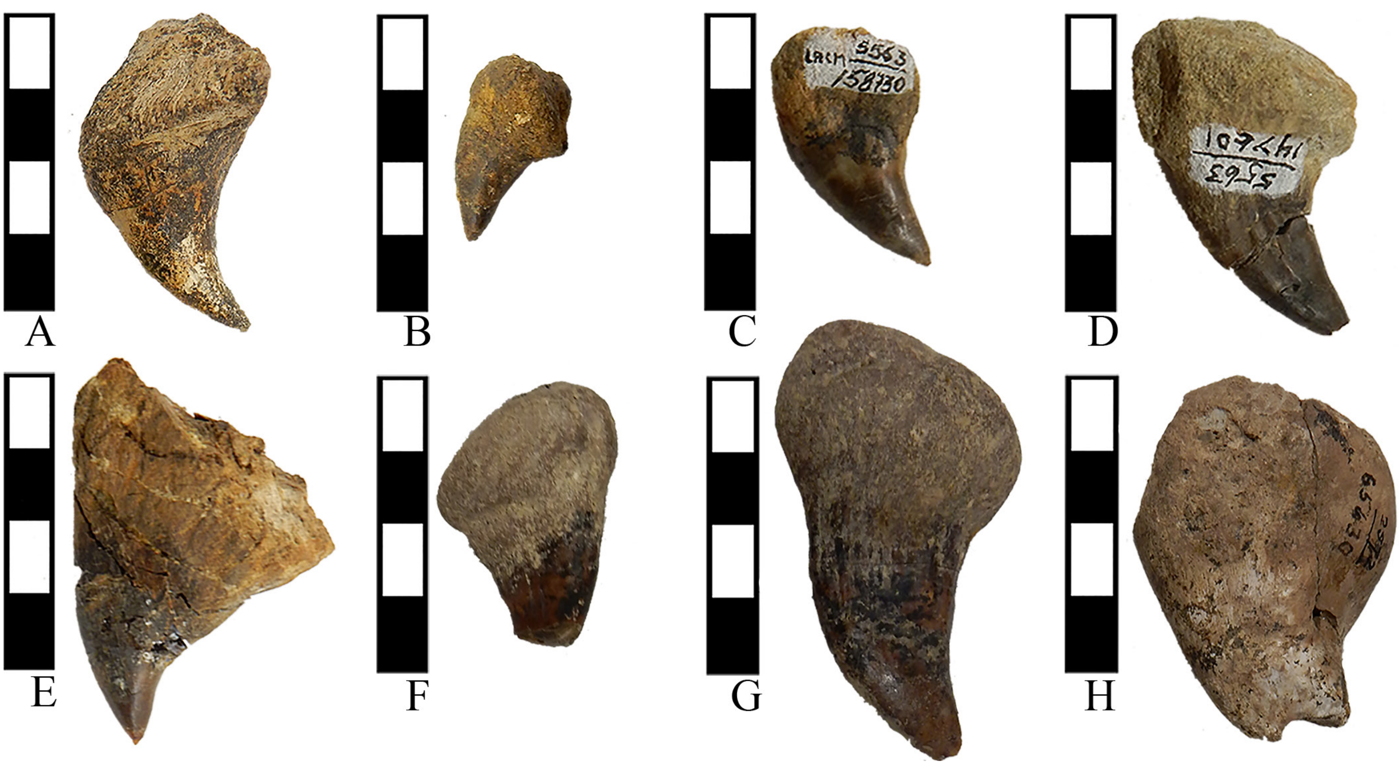

**Figure 13.** Coastal marine specimens of *O. rastrosus* premaxillary teeth from the Santa Margarita Formation, Monterey Formation, and Capistrano Formation. **A.** LACM 135697. **B.** LACM 58915. **C.** LACM 158730. **D.** LACM 147601. **E.** LACM 147597. Freshwater specimens from *O. rastrosus* from the Pinole Tuff Formation. **F.** UCMP 61550. **G.** UCMP 61554. **H.** UCMP 65630. All are lateral views.

Sacramento River in Stockton, and from there flows west into the San Francisco Bay. When did the San Joaquin begin flowing to the north? This timing can be approximated from various sources. First, the Corcoran Clay was deposited in a large, shallow lake (Lake Clyde) that existed in the San Joaquin and southern Sacramento Valleys from ~758,000 to ~665,000 B.P. Thus, there was no outlet for these rivers during this time. Second, 400,000 year-old sediments south of San Francisco contain minerals and rocks from the Sierra Nevada; this demonstrates there was a connection between the Central Valley and the Bay Area by this time. It is thought that Lake Clyde may have overflowed and drained into the Bay Area during a period of glacial melting. Thus, the San Joaquin was flowing to the north and into the Bay by ~400,000 years ago (Harden 1998).

The paleo-drainages of the "proto-Tuolumne River" and other rivers in this area were directly affected by uplift of the Sierra Nevada. Clearly, deposits from a large, fast-flowing "proto-Tuolumne River" in the Turlock Lake area indicate relief to the east. How high this was is not well known. Current understanding is that the southern and northern Sierra Nevada had different uplift histories, and that ~5-10 Ma, the northern Sierras were low (<200 m), the southern Sierras were high (>1000 m), and the Central Sierras were intermediate (~ 400 m) (Wakabayashi and Sawyer 2001).

### Did *O. rastrosus* developmentally change before migrating and spawning?

Extant Pacific salmon exhibit morphological and physiological transformations prior to and during migration up rivers to spawn (Groot and Margulis 1991; Fig. 2). These changes include growth and development of soft tissue and bone in their jaws. Did *O. rastrosus* also developmentally change prior to migration and spawning? No specimens of *O. rastrosus* demonstrate a significant development of a kype (Cavender and Miller 1972, Claeson et al. 2016). However, because the large, premaxillary teeth in *O. rastrosus* have been interpreted as important for display and fighting during spawning, we would expect to see differences in these teeth between the marine and freshwater stages, as in extant Pacific Salmon. In particular, we would expect to see larger pre-maxillary teeth in the freshwater specimens.

In order to determine whether *O. rastrosus* underwent developmental changes prior to spawning (i.e. between their marine and freshwater stages), as extant Pacific salmon today, we compared freshwater and marine premaxillary teeth from California (Fig. 8). All specimens are from the UCMP and LACM.

Freshwater specimens are from the Mehrten Formation (Turlock Lake; Stanislaus Co.; Fig. 12A–F; Table 2) and the Pinole Tuff Formation (Contra Costa Co.; Fig. 13F–H; Table

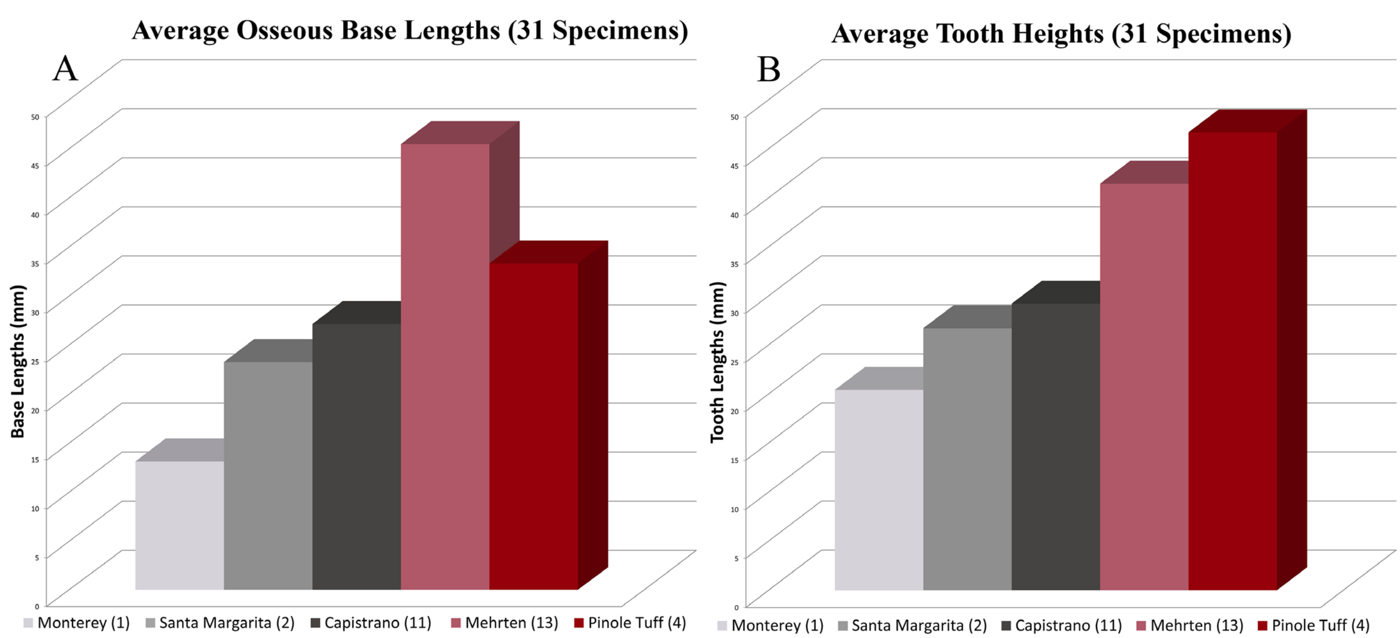


**Figure 14. A, B.** Measurements of *O. rastrosus* premaxillary teeth (31 specimens total), freshwater (pink/red) vs. coastal marine (grey/black). **A.** Average lengths of osseous bases. **B.** Average lengths of tooth cusps. Freshwater specimens are from the Mehrten Formation (pink) and Pinole Formation (red). Coastal marine specimens are from the Monterey, Santa Margarita, and Capistrano formations. How measurements were taken is shown in Fig. 10).

2). The Pinole Tuff is Hemphillian in age and contains an ash dated at 5.2 Ma, as previously discussed (Stirton 1939, Evernden et al. 1964, Bell et al. 2004). The coastal marine specimens (Fig. 13A–E; Table 2) examined in this study are from several mid-Miocene to early Pliocene geologic units. They are briefly described here, from oldest to youngest. The Monterey Formation is a mid-late Miocene (Clarendonian NALMA) in age, and occurs from northern to southern California. It consists of mudstone, shale, diatomite, and chert, deposited in offshore marine basins. Numerous fossil vertebrates from the Monterey Formation include fish and marine mammals such as dolphins, whales, and desmostylians. The Santa Margarita Formation overlies the Monterey Formation, is mid-late Miocene (Clarendonian NALMA) to early Pliocene (Hemphillian NALMA) in age, and occurs in central and southern California. It consists of coarse-grained sandstone, siltstone, and mudstone, and has produced many vertebrate fossils. Depositional environments represented include tidal-dominated shallow subtidal to outer shelf (Phillips 1983). The Capistrano Formation is late Miocene to mid Pliocene in age (Hemphillian NALMA), and occurs in southern California. It contains mudstone, siltstone, and conglomerates, and represents deep shelf, basin slope, and submarine fan deposits. Numerous marine vertebrates include fish, shark, whale, dolphin, pinniped, sea cow, and birds. The Oso Sand Member of the Capistrano is one of the most productive fossil producing units in Orange County (Babilonia et al. 2013). The San Mateo Formation is late Miocene-early Pliocene in age (Hemphillian NALMA), and occurs in southern California (Barnes et al. 1981).

We observed interesting differences between the freshwater and coastal marine specimens of *O. rastrosus*. In the Mehrten and Pinole Tuff specimens (freshwater) (Fig. 12): (1) the osseous tooth bases are considerably larger, more robust, and appear to be better fused to the tooth cusp and (2) tooth cusps are shorter, with tips more rounded and blunt. In contrast, in the coastal marine specimens (Fig. 13A–E): (1) the osseous tooth bases are considerably smaller; (2) tooth cusps are longer, with sharper tips.

We made six measurements on each complete premaxillary tooth examined, a total of 31 specimens (Table 2). Figure 10 illustrates how tooth measurements were made. Important measurements are the greatest length of osseous base (A), and the greatest height of the osseous base and tooth cusp combined (C). Figure 14A is a bar graph showing the averages of the two parameters A and C between freshwater and coastal marine specimens. This illustrates that the osseous bases in freshwater specimens (Mehrten and Pinole formations, shown in pink and red, respectively) were considerably bigger than those from the coastal marine specimens (shown as shades of grey). Figure 14B is a bar graph showing the averages of C between freshwater and coastal marine specimens. Freshwater specimens were also considerably larger than coastal marine specimens in this dimension.

Clearly, *O. rastrosus* premaxillary tooth shape and size differ between freshwater and coastal marine specimens, demonstrating that they did developmentally change over the transformation from ocean-resident to upstream migrant forms, as extant Pacific salmon do today. The most obvious difference between the freshwater and coastal marine specimens was the development of the massive osseous tooth base. This is especially obvious in the Mehrten specimens, from the furthest inland locality. This helped the tooth stay 'rooted' in the skull, especially during the freshwater, spawning stage of its life when there was intense fighting and even possibly digging in gravel to form redds. Stearley and Smith (2016) note that the breeding teeth of extant salmons are "anchored to the dentary with late-developing boney cement", and we think this occurred in *O. rastrosus* also.

The other significant difference we observed between the freshwater and coastal marine specimens was in the nature of the premaxillary tooth cusp. In the freshwater specimens, the premaxillary tooth cusp was smaller, with a rounder, blunt tooth tip. In contrast, the coastal marine tooth cusps were longer, with a sharper tip. We hypothesize that the freshwater specimens reflect much greater tooth wear that resulted from activities during spawning. In addition, this observation supports the idea that *O. rastrosus* may have used these spike teeth to assist in excavating redds in stream gravels.

## CONCLUSIONS

1. The original description of *O. rastrosus* included paratypes from the Mehrten Formation, Turlock Lake, Stanislaus County, California. However, there were no descriptions of the fossil site, including geologic context. We provide these here.

2. The Turlock Lake salmon locality is in deposits we refer to as the "proto-Tuolumne River". We describe these deposits in detail and map their distribution around Turlock Lake. Paleocurrent directions indicate this river flowed to the southwest. It would have joined the "proto-San Joaquin River", which at this time flowed south, and then entered a shallow marine embayment. In contrast, today's modern Tuolumne River flows directly west, joins the San Joaquin River, which now flows north, and eventually empties into the San Francisco Bay. This change in flow occurred ~400,000 years ago. Thus, the ~5 Ma *O. rastrosus* from Turlock Lake predates this, and they would have migrated up (i.e. north) in the "proto-San Joaquin River" from the marine embayment

near Bakersfield. They then would have entered the "proto-Tuolumne River" (and other rivers) and continued their migration upriver to the east to spawn. How far up river and to the east they migrated, we do not know.

3. Large, extant Pacific salmon undergo profound physiological and morphological transformations prior to and during migration inland to spawn. Previous work indicated that *O. rastrosus* and other Pacific Salmon grow limited lower-jaw kypes. However, their large premaxillary teeth were important for display and fighting, and it would be expected that these would be larger in freshwater specimens. Indeed, freshwater specimens (premaxillary teeth) of *O. rastrosus* were considerably more massive than coastal marine specimens, especially their osseous bases, just as in other Pacific Salmon. The tooth cusps from freshwater specimens were considerably more worn. This supports the idea that *O. rastrosus* used their large premaxillary teeth for fighting and display, but also potentially for assisting in excavating redds in the stream gravels.

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