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***SALMO AUSTRALIS*, A NEW SPECIES OF FOSSIL SALMONID FROM SOUTHWESTERN MEXICO**

BY

TED M. CAVENDER¹ AND ROBERT RUSH MILLER²

Abstract.—A new species of salmonid fish is described from an unconsolidated sand deposit close to the present shoreline of Lake Chapala at Ajijic, Jalisco, Mexico. Because of the superficial nature of the deposit the age of the fossil is believed to be Pleistocene. Additional salmonid remains from the lake bottom at Ajijic are associated with Pleistocene mammalian fossils.

Osteological details of the fossil cranium indicate the new species is related to Western North American representatives of the genus *Salmo*. *Salmo australis* is morphologically differentiated from the known fossil and Recent species. The fossil extends the known range of Western North American Salmonidae about 400 km south to nearly 20° N latitude.

INTRODUCTION

The new species of Mexican salmonid described in this paper is of considerable zoogeographic interest because its occurrence near 20° N latitude is the southernmost record for native Salmonidae in North America. It is also one of a number of fossil discoveries over the last decade (Cavender and Miller, 1972; G. R. Smith, 1975; Kimmel, 1975) that call attention to the past diversity and evolutionary complexity of this family during late Cenozoic time in Western North America.

The history of the Salmonidae in Western North America is represented by usually fragmentary fossils that have been uncovered mainly in Miocene to Pleistocene deposits of intermontane basins or in fluvial sediments of the northwestern Pacific slope (Miller, 1965; G. R. Smith, 1981). The new fossil *Salmo* described below comes from probable Pleistocene deposits of the Lake Chapala basin, State of Jalisco, in southwestern Mexico. The morphological features of its cranial skeleton show that it was a species highly differentiated from any known member of the extant genera *Salmo* and *Oncorhynchus*, which are widely distributed along the margins of the North Pacific basin. The unusual circumstances surrounding the discovery of this fossil, its uncertain stratigraphic position, the complex geology of the Chapala basin, the lack of osteological information on Western North American *Oncorhynchus* and *Salmo* and the paucity of early field data on the distribution of the native trouts of the Mexican Pacific slope all presented problems that had to be dealt with before this study could be satisfactorily completed.

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FOSSIL OCCURRENCE

Bones representing parts of the neurocranium, jaws and vertebral column of a large salmonid were unearthed during the construction of a cellar foundation in Ajijic, a small community near the northwestern end of Lake Chapala. The name of the laborer who dug up the fossil and the exact date of the find are unknown to us. Mr. José Frances, foreman at the construction site, forwarded the fossil to Prof. Federico Solórzano of Guadalajara, who gave it to Dr. José Alvarez del Villar, Instituto Politécnico Nacional, Mexico City. The original material consisted of about a dozen disarticulated cranial elements and vertebrae. One associated bone, a hyomandibular, did not belong to the salmonid; it is assigned to an extinct species of *Micropterus* described earlier (M. L. Smith et al., 1975).

Examination of the salmonid remains showed that the interstices of the bone were filled with fine sand. Reconnaissance of the Ajijic area carried out in 1971 revealed that similar sand was found along the lake shore. For that reason, the cellar where the fossil was discovered is believed to be located along one of the southernmost streets (closest to the lake shore) in Ajijic. It is postulated that this sand layer is part of a former beach ridge or lake terrace. The fact that today Lake Chapala is a shallow, warm-water lake with no salmonids living within its boundaries or in the Río Lerma basin suggests that the fossil represents a Pliocene or Pleistocene faunal element which occupied the drainage area during a former cold climatic cycle—possibly during the Illinoian or Wisconsin ice age. This is consistent with the partial mineral replacement of the bone that has occurred in the fossilization process. The associated remains of a centrarchid and salmonid are unexpected, but not unknown from Pliocene and Pleistocene deposits in western United States. One such example is given by G. R. Smith (1975).

The field work of February, 1971, included an attempt to recover additional material belonging to the new species from fossil-bearing exposures near the west end of Lake Chapala. These deposits were described in M. L. Smith et al. (1975). No salmonid fishes were found then or have been taken since, despite intensive search for them. In the mid-1950's Mexican workers collected several vertebral centra and one cranial element along with a large assemblage of other fossils, including crayfish carapaces, from the lake bottom at Ajijic. As with most of these lake-bottom fossils, the salmonid vertebrae are permeated with black manganese salts. These vertebrae, as well as bones of other fossil fishes, are badly worn from wind or water abrasion. The lake-bottom occurrence of the salmonid fossil at Ajijic lends credence to both the age determination and locality of the type specimen. Most of the land mammalian fossils from the lake-bottom assemblage have been regarded as Pleistocene in age (Clements, 1963). Clements speculated that this fauna may have been derived from terrace deposits along the north shore of Lake Chapala. However, no such fossil-bearing deposits have been located or described unless those at Ajijic are placed in this category.

MATERIAL EXAMINED

Osteological preparations used in this study are listed below. Dry skeletons prepared by dermestids are designated by -S; cleared and stained material by -C&S. All are in The University of Michigan Museum of Zoology (UMMZ) unless otherwise noted.

Brachymystax lenok (Korea): 172489-S, 183 mm, Daidon R.; 172490-C&S, 132 mm, Tomán R., Kaineri.

Hucho perryi (Japan): 187612-S, 4, 140-317 mm, Bettogagawa, Hokkaido; 187613-S, ♀ 460 mm, Furengawa Catching Sta., Hokkaido.

- Oncorhynchus gorbusha*: 172444-S, ♂ 600 mm, King Cove, Alaska.
Oncorhynchus keta: 172452, 5 heads, N-central Pacific; 175915-S, ♂ skull, Taku Inlet, Alaska.
Oncorhynchus kisutch: 175912-S, head, Taku Inlet, Alaska; 186653-S, ♀ 690 mm, Bonneville Salmon Hatchery, Ore.; 186654-S, br. ♂ 672 mm, Westport, Wash.; 187925-S, 624 mm, Platte R., Mich.; 190382-S, head, near Petoskey, Mich.; 192595-S, ♀ 572 mm, Mich.; 192596-S, ♀, Mich.; 201705-S, 527 mm, Little Manistee R., Mich.
Oncorhynchus masou (Japan): 173829-C&S, Naka R., NE Tokyo; 173831-C&S, 112 mm, Ohata-mura, Aomori Pref.
Oncorhynchus nerka: 172453-S, 3 heads, N-central Pacific.
Oncorhynchus rhodurus: 187609-S, ♀ 343 mm, L. Biwa, Japan.
Oncorhynchus ishawytscha: 175914-S, ♂ skull, Taku Inlet, Alaska; 178987-S, 985 mm, Kalama R., Wash.; 201705-S, ♂ 889 and ♀ 798 mm, Little Manistee R., Mich.
Salmo a. aguabonita: 105568, 363 mm, ♂ skull with kype, Hidden Lakes, Mont.; 189880-S, 5, 156-196 mm, Cottonwood Lakes, Calif.
Salmo aguabonita ssp. (redband trout—see Miller, 1972; Gold, 1977): 188847-C&S, 150 mm, and 190815-S, 2, 134 and 166 mm, Shepheaven Cr., Calif.
Salmo apache (Ariz.): 162770-C&S, paratype, 67 mm, E. Fk. White R.; 189634-C&S, 131 mm, Ord Cr.; 189636-C&S, 98 mm, Squaw Cr.; 193314-S, 378 mm, ♂ skull with kype, Ord Cr.
Salmo chrysogaster: 188846-C&S, 99 mm, either headwaters of Río Verde, Durango, or Río Sinaloa, Chihuahua, Mexico.
Salmo clarki: 92426, 550 mm, ♂ skull with kype, Crescent L., Wash.; 136872-C&S, 150 mm, Snow Cr. trib. Summit L., Nev.; 179560, 4, 119-167 mm, La Junta Cr., N. Mex.; 181728-S, 3, 295-306 mm, Wall Cr., Nev.; 194655-S, 3, Hoback R., Wyo.
Salmo gairdneri: 61249-C&S, 2, 118 and 123 mm, Garberville, Calif. [Gilbert et al., VI:30-1898]; 101705-S, 800 mm, ♂ skull with kype, Manistee R., Mich.; 107988-S, 1, S. Br. Pine R., Mich.; 171042-S, 4, 233-455 mm, L. Superior, Mich.; 172468-S, 218 mm, Cherry Cr. Fish Hatchery, Mich.; 178976-S, 512 mm, Manistee R., Mich.; 183703-S, 277 mm, Presque Isle R., Mich.; 184344-S, 1, Columbia R. at Portland, Ore.; 186206-S, 660 mm, ♂ skull with kype, N. Fk. Alcea R., Ore.; 186300, 2, 640 and 642 mm, L. Michigan at Manistee R., Mich.; 186328-S, 1, Portland Fish Co., Ore.; 190915-S, 470 mm TL, skull, Platte R., Mich.; 194308-S, 365 mm, Grand Traverse Bay, Mich.; 198677-S, 525 mm, Au Sable R., Mich.; 201666-S, 1003 mm TL, L. Michigan, Mich.
Salmo gilae (N. Mex.): 137090-C&S, 60 mm, Diamond Cr.; 182405-S, 3, 258-305 mm, Glenwood Fish Hatchery (from Diamond Cr.).
Salmo ohridanus: 177293-C&S, 220 mm, Lake Ohrid, Yugoslavia.
Salmo salar: 195067-S, 477 mm, Au Sable R. at Mio Dam, Mich.
Salmo trutta: 172470-S, 413 mm, Bridge L., Mich.; 175169-S, ♂ 625 mm, Alice L., Mich.; 182489-S, 3, 328, 409, 542 mm, New Fork R. near Marbleton, Wyo.; 183694-S, 9, 434-513 mm, Montreal R., Mich.; 194318-S, ♂ 755 mm, Pentwater L., Mich.
Salmo sp. (Río Mayo trout): 209829, ♂ 269 mm, trib. Río Candameña above Cascada de Basaseachic, Chihuahua, Mexico.

SYSTEMATIC DESCRIPTION

Salmo australis n. sp.

Figs. 1-11

Salmo sp. Miller, 1972:417-418 (locality, possible age, vertebral characters).

Diagnosis.—A large salmonine, reaching nearly one meter in total length at breeding size, distinguished from other known fossil and Recent species by the following combination of characters: jaw teeth with enlarged, round osseus bases, which have vertical striations radially arranged on the surface of each tooth base; jaw teeth few in number (12 on the dentary) originating from deep sockets; cusps of the teeth relatively small in proportion to their bases; cusps originate from a lateral position on the tooth base and are curved inward; vomer possessing large, stoutly conical, socketed teeth that also have round osseous bases; the teeth

arranged in a long alternating series on the vomerine shaft, with those on the head positioned as lateral teeth, one on each side of a central socket; anterior process of vomer elongated, tapered to a blunt point and curved slightly upward, with a longitudinal indentation on its ventral surface; posterior portions of frontals with smooth dorsal surface; four long branches of the supraorbital canal radiating laterally from the bend of the canal, each branch enclosed in a slender bony tube and slightly elevated above the surface of the frontal; lateral surfaces of the anguloarticular (Nelson, 1973) mostly smooth, without well-developed rugosities or cancellous structure.

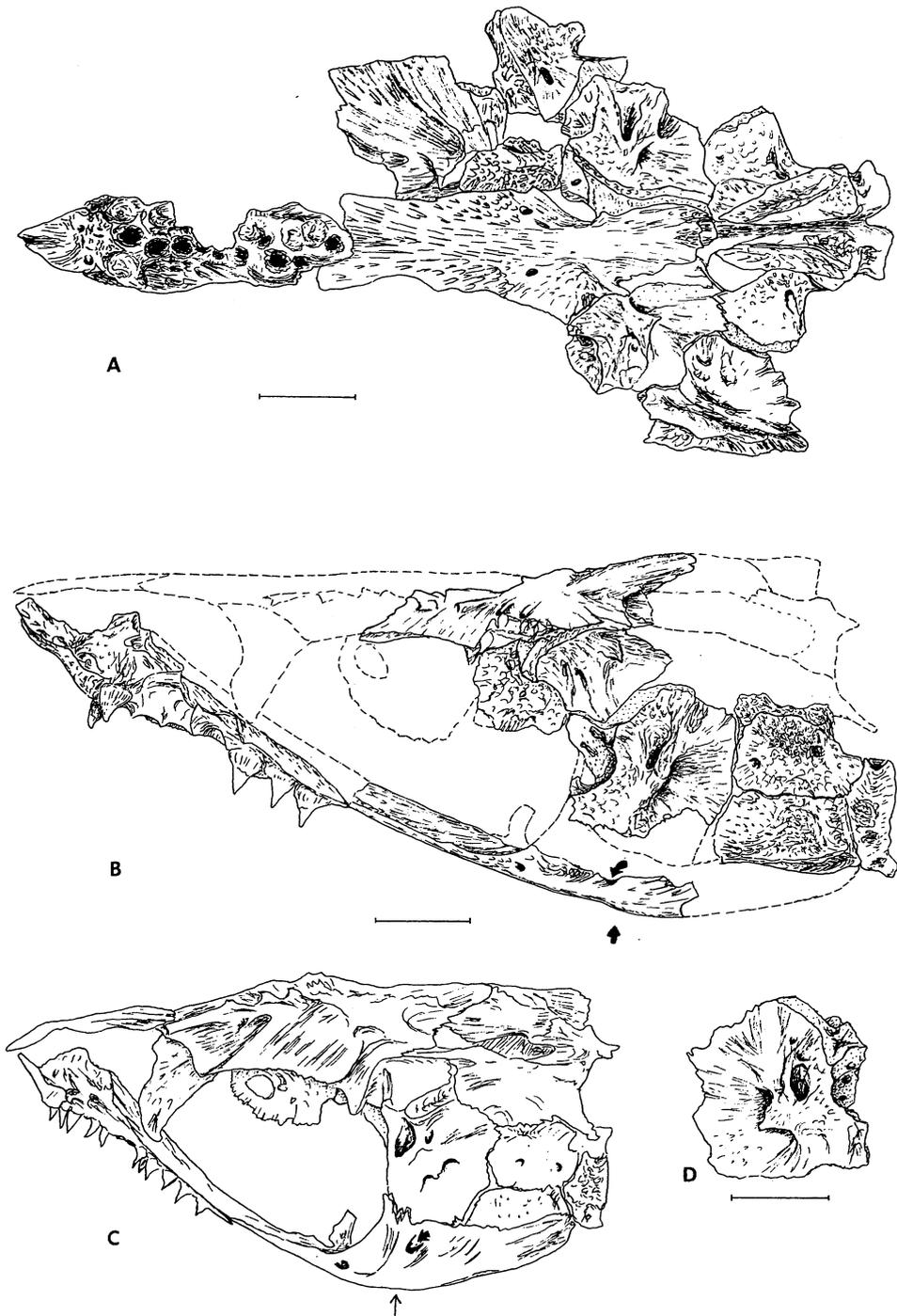
Description.—The holotype, UMMP V78900, consists of a partial neurocranium (95 mm long), jaws and associated skeletal elements. The ossified parts of the neurocranium were recovered in a disarticulated condition and reassembled for study (Fig. 1). The individual elements are listed below. They represent a breeding male between 900 and 1000 mm total length. Size estimation was based on comparison of the lower-jaw length and vertebral diameter. Severely-abraded fossil salmonid vertebrae from the lake bottom (possibly belonging to this species but not designated types—UMMP V78901) are of an even larger-sized fish well over 1000 mm total length.

Disarticulated elements of neurocranium: Complete basioccipital 16 mm long; atlas centrum partly fused to the basioccipital, right and left exoccipitals (left incomplete), right and left prootics; incomplete right pterotic, left sphenotic, left pterosphenoid; incomplete left frontal, posteromesial part of right frontal; incomplete parasphenoid; and nearly complete vomer 40 mm long.

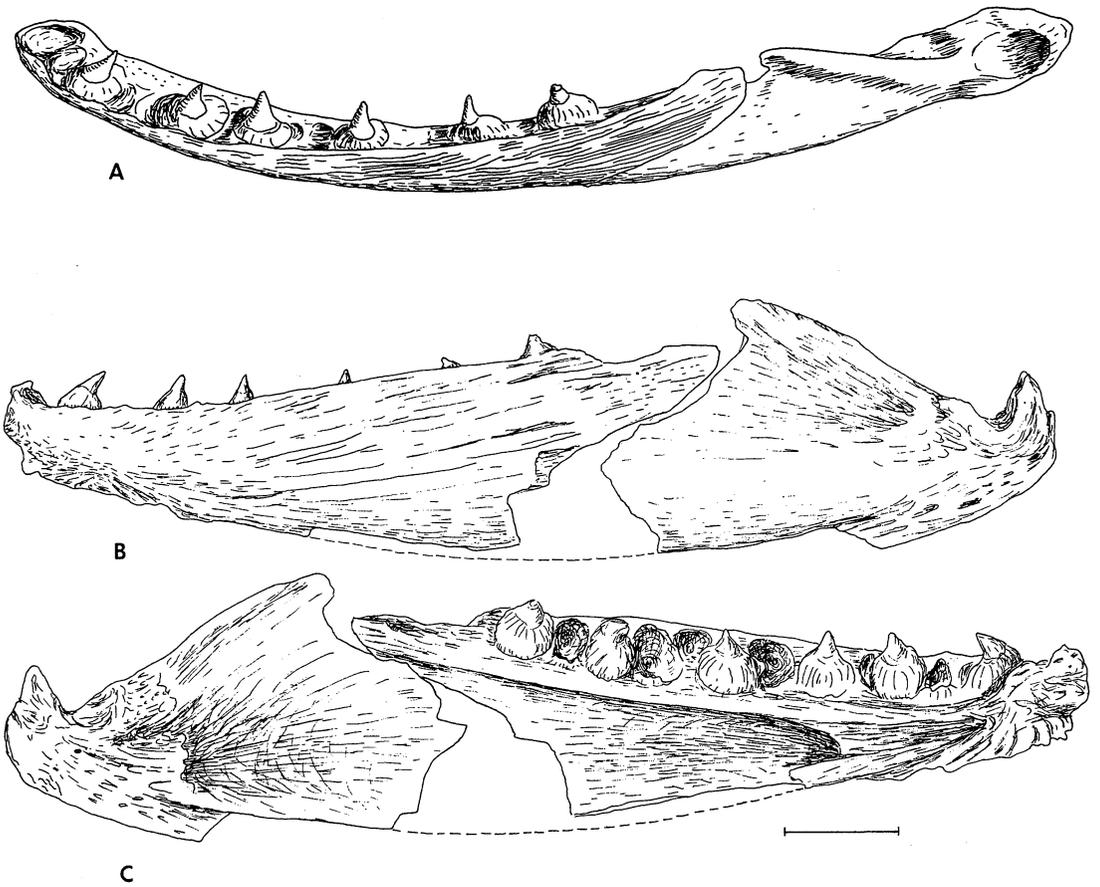
Branchiocranium: Incomplete right and left anguloarticulars (left one with retroarticular attached); incomplete left dentary (but with dentition complete); almost complete right maxilla 76 mm long (extreme distal end missing), anterior half of left maxilla; incomplete right and left hyoid bars with parts of both epihyal and ceratohyal preserved, the ceratohyal 32 mm long and 22 mm deep at its posterior end, the epihyal 22 mm long as measured along its dorsal border and 22 mm deep; middle portion of left preopercle; incomplete left and right pelvic bones; right symplectic; fragmentary right and left interopercles; left scapula; two incomplete epi- or ceratobranchials; a number of indeterminate fragments and scraps, including parts of the gill cover.

Five vertebral centra: One from the anterior precaudal region 11.9 mm in horizontal diameter and 10.0 mm in vertical diameter, one from the posterior precaudal region, and three from the caudal series.

The jaws are large and powerful with comparatively few, well-developed, firmly-socketed teeth. The left mandible, 104 mm long, is estimated to have been 27 mm deep at the coronoid process. The coronoid angle (Cavender and Miller, 1972) is 30°. The mandible has a pronounced mesial curvature in the horizontal plane (Fig. 2). This is most comparable to the condition in subgenera *Salmo* and *Rhabdofario*. The American *Oncorhynchus* have nearly straight mandibles that meet at an acute angle anteriorly. The fossil mandibles were joined at a horizontally elongated and interdigitated symphysial area that is positioned ventral to an expanded region at the dentary tip. The latter diverges from the midline and must have supported a protruding knob of soft tissue. The dentary possesses a wide tooth platform which extends along most of the inner dorsal margin. It seats all of the teeth, which have normal-sized cusps but unusually large bases. There are six teeth and six empty sockets positioned along the platform. One tooth and two sockets are crowded at the symphysial end but the anterior tooth is not greatly enlarged as in some *Oncorhynchus*, such as *O. keta*. The cusps of the teeth are supported by disproportionately large, bulblike bases which are ornamented with numerous fine, vertical striations radiating from the base of the cusp. Each cusp arises from a lateral position on the bulblike base rather



TEXT-FIG. 1 — Reconstructed neurocranium of *Salmo australis*, UMMP V78900, holotype; straight arrow shows point of deflection of parasphenoid and curved arrow location of internal carotid foramen. (A) dorsal view, (B) lateral view, (C) neurocranium of *Salmo gairdneri* for comparison, UMMZ 178976-S, 512 mm SL, Manistee R., Mich., (D) right prootic of *Salmo australis*, lateral view, anterior to right. Scale is one cm.

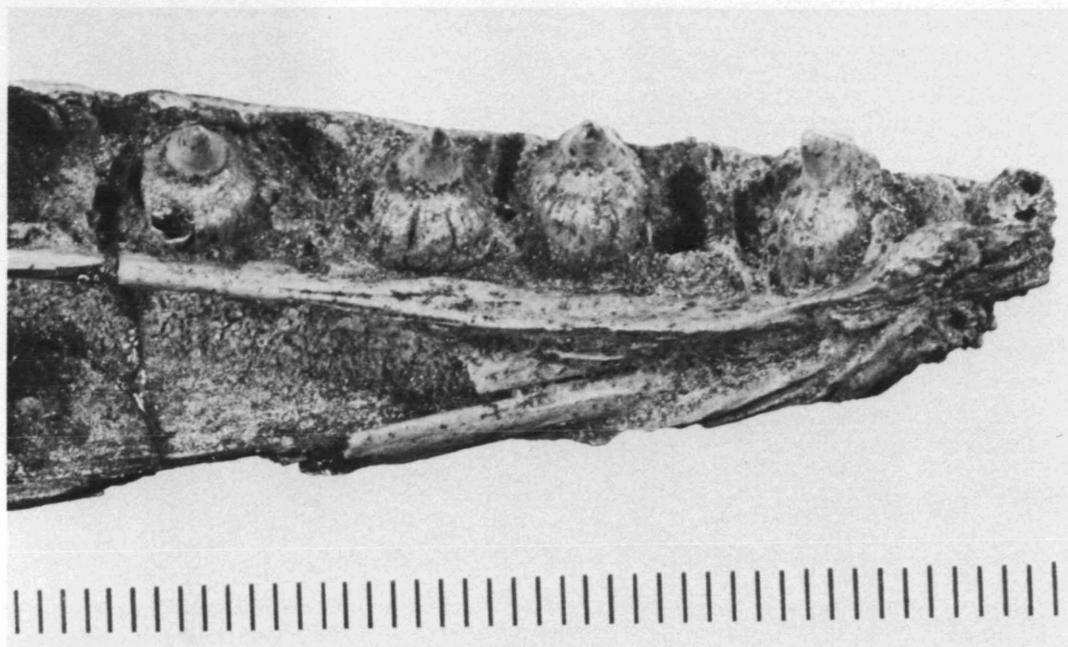


TEXT-FIG. 2 — Left mandible of *Salmo australis*, UMP V78900. (A) dorsal view, (B) lateral view, (C) mesial view. Scale one cm.

than from a central origin (Fig. 3). The cusps are directed mesially when the tooth platform is oriented in a horizontal position.

The lower margin of the mandible curves slightly upward toward the symphysis. The mandible is more robust than in North American *Oncorhynchus* but approximates those in the subgenera *Salmo* and *Rhabdofario*. The lateral surface of the dentary is ornamented with many longitudinal striations running nearly parallel to the length of the dorsal margin. The anguloarticular is smooth except for fine ridges on the area below and behind the articular facet. The posterior process is vertically oriented and thickened, without any lateral compression in the region below the facet or along its posterior margin, as in *Salmo*. The anguloarticular has a relatively high coronoid ramus as opposed to that in *Oncorhynchus*. Its lateral surface is concave in the region immediately below the ascending margin. This distinctive concavity corresponds to the area that was overlapped by the distal end of the maxilla.

The maxilla (Fig. 4) has a strong downward curvature and is recurved distally. The nearly complete right maxilla has seven teeth and eleven deep sockets. The teeth are similar in all respects to those on the dentary except that the bases are not as large. The first tooth is the largest of the maxillary series. In cross section the maxilla is ovate as in *Oncorhynchus*, subgenus *Rhabdofario*, and in large adults of subgenus *Parasalmo*. Only the distal, recurved portion of the

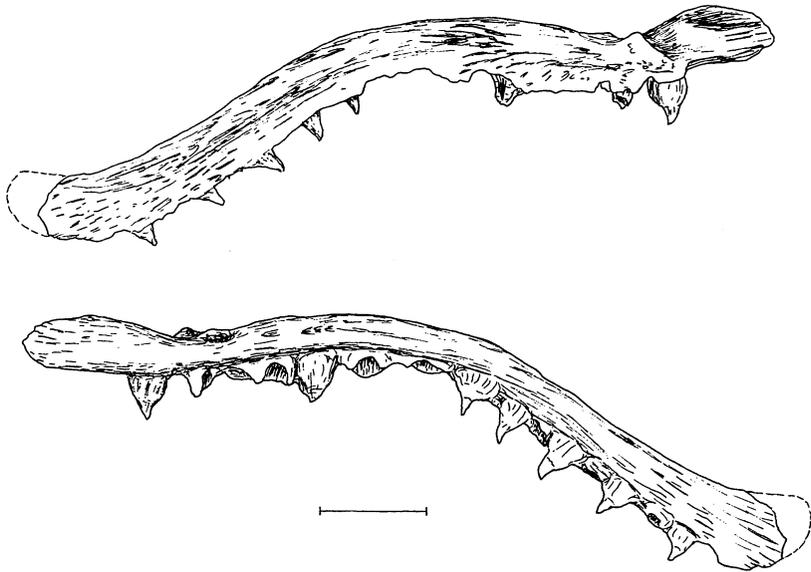


TEXT-FIG. 3 — Detail of tip of left mandible, UMMP V78900. Scale in mm.

alveolar shank is laterally compressed. The posterior one-third of the lateral surface is ornamented with fine pits and striations. There is a median longitudinal groove on the posterolateral surface, marking the place of attachment of the supramaxilla. The articulating process is subcylindrical, with slight lateral compression. There is a deep longitudinal groove below its dorsal margin. The process is oriented at a slight angle to the anterior part of the tooth platform and is raised above the main body of the maxilla. These characteristics of the articular process are unlike *Oncorhynchus* or subgenus *Rhabdofario* and more comparable to subgenus *Salmo*.

In horizontal profile the axis of the vomer (Fig. 1B) is nearly straight. The anterior process extending forward from the tooth platform is turned slightly upward. In ventral view (Fig. 1A) this process tapers to a blunt point with a deep groove at its apex. Fine longitudinal striations occur on its ventral surface. The ornamentation at the base of the process and anterior to the tooth sockets is composed of complex vermiform ridges. The elongated shaft of the vomer has an alternating series of teeth running along its center line. The teeth are well socketed and have swollen bases that show a striated ornamentation. The cusps protrude from a central position on the tooth bases. About six deep sockets are present along with five teeth. Two of the teeth are lateral in position on the head of the vomer. A moundlike cancellous ossification, located dorsal to the vomer head, probably represents an ossification of the ethmoid cartilage (ventral mesethmoid). The features of the fossil vomer resemble those of subgenus *Parasalmo*, differing markedly from those of subgenus *Rhabdofario*.

The parasphenoid (Fig. 1B) is characterized by a flexure located at the level of the internal carotid foramen. The posterior ("flexed") portion of the parasphenoid is broken off but its orientation with respect to the main part of the parasphenoid can be deduced from the articulating surfaces on the basioccipital. Lines drawn through the long axis of both the anterior



TEXT-FIG. 4 — Right maxilla of *Salmo australis*, UMMP V78900. Lateral view above, mesial view below. Scale one cm.

and posterior portions of the parasphenoid meet at an angle of 138° . The anterior end of the parasphenoid is indicated by the form of the vomer and points of attachment of both bones. That part of the parasphenoid in front of the ascending processes is relatively wide, with the foramina for the efferent pseudobranchial arteries placed well inside the lateral margins. This area is well ornamented with many distinct pits, indicating a cancellous bone structure.

The basioccipital (Fig. 1A,B) is rectangular in outline with its ventral edge flared laterally along the line of attachment with the parasphenoid. Ventral flanges extending down from the basioccipital for articulation with the parasphenoid are weakly developed. This feature correlates well with the narrow myodome canal. A narrow myodome canal through the basioccipital is found in some species of *Oncorhynchus*. *Smilodonichthys* has a very restricted posterior myodome whereas in *Salmo* the myodome canal is typically broad. The atlas vertebral centrum is partly fused to the basioccipital in *Salmo australis*.

The vertical dimension of the prootic in articulated position equals its horizontal dimensions (Fig. 1D), a characteristic that is typical of *Oncorhynchus* and such *Salmo* as *S. clarki*. A greater vertical than horizontal measurement is usually found in *S. gairdneri* (Fig. 1C) and *S. aguabonita*. In its anterior wall the fossil prootic contains a large unobstructed trigeminal-facial chamber that opens anterolaterally like that in some *Oncorhynchus*. The anteroventral portion of the lateral prootic wall is turned outward to meet the ascending process of the parasphenoid.

The sphenotic has a well-developed lateral process projecting beyond the frontal margin. There is a large foramen located in its anterolateral surface. A second but smaller process projects posterolaterally immediately in front of the pterotic-sphenotic contact. The pterosphenoic is a relatively thin, squarish bone with a deeply pitted surface. The orbitosphenoic was not recovered. An incomplete pterotic is present on the right side. It has a deeply concave dorsal surface of smooth bone with no ornamentation. Four pores of the cephalic lateralis canal are visible along the outer margin. The distal part of the pterotic process is broken off but the remaining portion indicates the process must have been well developed. It curves laterally and



TEXT-FIG. 5 — Incomplete left frontal of *Salmo australis*, UMMP V78900, in dorsal view; anterior to the left. Scale one cm.

has a deep sulcus mesial to its base. The form of the pterotic partly outlines a well-developed posttemporal fossa that extended forward to penetrate the posterolateral margin of the frontal.

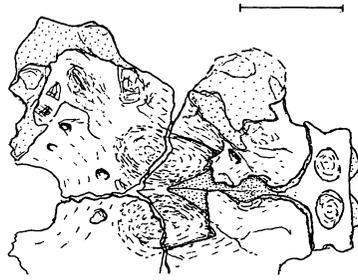
The frontal (Fig. 5) has a smooth posterior surface broken only by a few small foramina and very weak ridges. In that part of the frontal which extends over the orbit, the pattern of ridges and grooves is well developed. The supraorbital canal is evident from its system of long tubelike branches that radiate from the inner bend of the canal. Four of the branches are raised above the frontal surface and clearly delineated. The supraorbital canal and its branches are of small diameter. This is also true of the mandibular canal.

As in other salmonines, the exoccipital contributes with the basioccipital to the formation of the posterior half of the saccular recess. The posteromesial wall of the recess is formed by a long, tapered anterior process that fits neatly with a tapered pedicel on the basioccipital (Fig. 6). The exceptional forward extension of this exoccipital-basioccipital junction is variably developed within *Salmo* and *Oncorhynchus*. In general the saccular recess tends to be much better developed in certain *Oncorhynchus* such as *O. tshawytscha*, which correspondingly have a large sagittal otolith. The structure of the saccular recess and the contained otolith in salmonines may be of systematic value and probably deserves careful study.

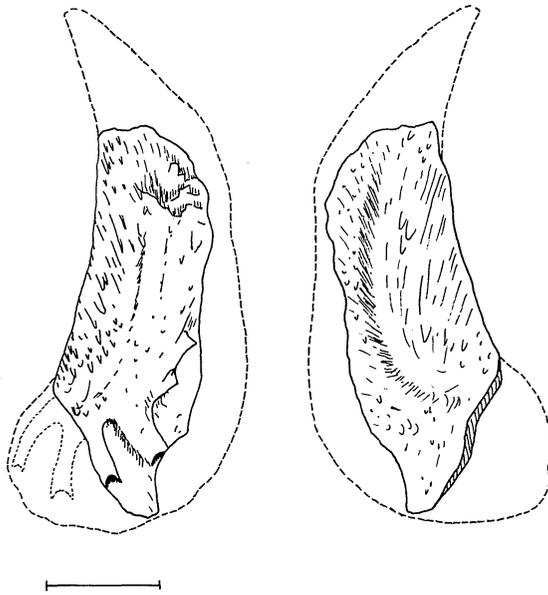
Two incomplete elements of the opercular series were recovered with the neurocranium. The broken preopercle (Fig. 7) consists of the anteromedial portion of the bone where the vertical and horizontal limbs come together. Two long, ventrally-directed branches of the preopercular canal are visible on the preserved posterior part of the horizontal limb. Except for fine striations, the lateral surface is fairly smooth and slightly convex in the area between the two limbs and the anterior margin. There is no groove or concavity. On the mesial surface a ridge follows the bend in the preopercle. There is a substantial area of membrane bone extending forward from the inner bend of this ridge. All these characteristics agree more with *Oncorhynchus* than with *Salmo*.

The right and left interopercles are too fragmentary to reveal much about their shape except that the posterior part was produced dorsally into a low to moderately well developed process. The lateral surface is smooth as in *Salmo*.

The hyoid bar (Fig. 8), with the ceratohyal and epihyal reassembled, agrees favorably in its proportions with the hyoid bar in North American *Oncorhynchus* and the steelhead, *Salmo gairdneri*. The dorsal margin of the bar is nearly straight with only slight concavity toward the middle of the ceratohyal. The ceratohyal is of stocky shape and has a maximum depth/length ratio of 2:3. The anterior three-fourths of its mesial face is well ornamented with grooves and



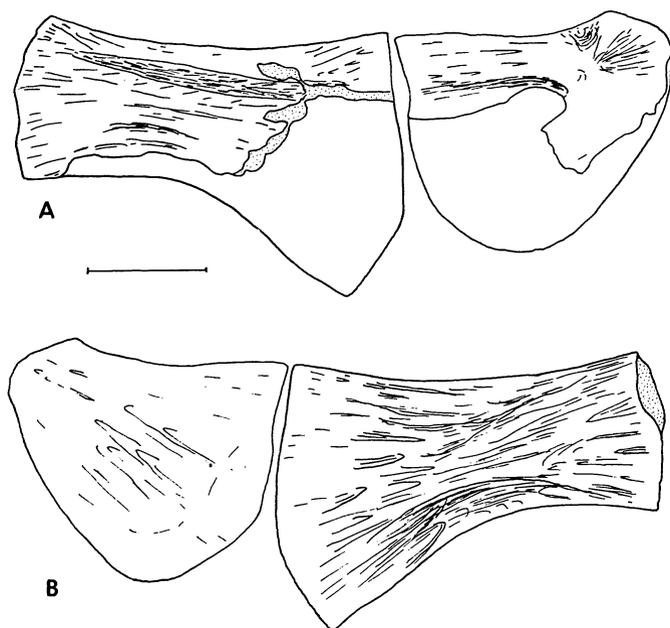
TEXT-FIG. 6 — Saccular recess of *Salmo australis*, UMP V78900, in dorsal view; anterior to left. Scale one cm.



TEXT-FIG. 7 — Incomplete left preopercle of *Salmo australis*; UMP V78900; lateral view on left, mesial view on right. Scale one cm.

pockets. The groove for the hyoidean artery is deeply incised on the lateral face of both the epihyal and ceratohyal, and the vertical surfaces (lateral and mesial) tend to be nearly parallel.

Both the precaudal and caudal vertebrae (Figs. 9 and 10) associated with the neurocranium have an ornamentation pattern on the walls of the centra that agrees in general with that found in most North American species of *Oncorhynchus*. This pattern consists of numerous uniform perforations sometimes overridden by fine longitudinal ridges. In the fossil species the pattern is somewhat complicated since the holes are irregular in size, ranging from relatively small but easily seen perforations to minute pits. The latter are positioned in the partitions dividing the larger holes. A count on one centrum from the anterior caudal series shows at least fifty holes penetrating its lateral surface. A second centrum from the caudal series shows a weak development of irregular horizontal ridges (Fig. 10A). Sufficient variation exists in the small



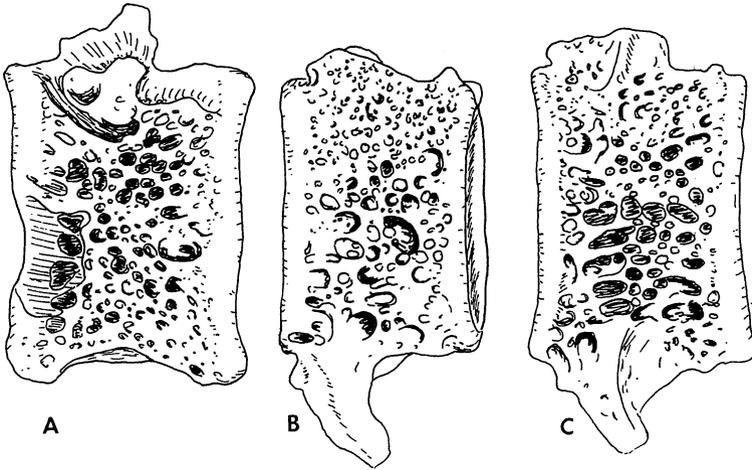
TEXT-FIG. 8 — Left hyoid bar (ceratohyal and epihyal) of *Salmo australis*, UMMP V78900. (A) lateral view, (B) reconstruction, mesial view. Scale one cm.

sample of vertebrae available to make it difficult to characterize the ornamentation. In lateral view the vertebrae of *S. australis* show considerable constriction of the centrum cylinder which accents their spoollike (amphicoelous) appearance.

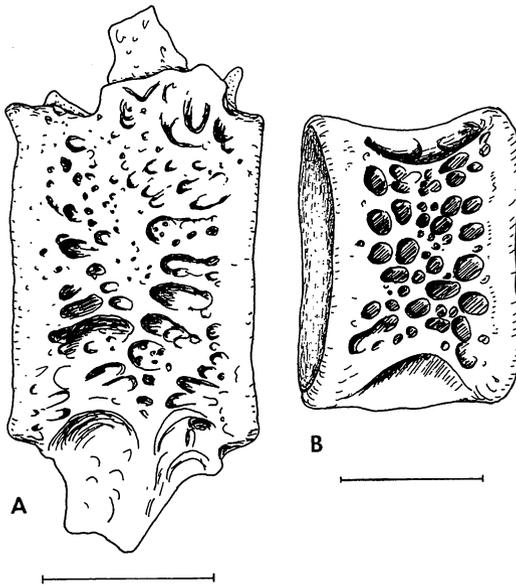
Additional Salmonid Material

UMMP V78901 is an incomplete left premaxilla (Fig. 11), 20 × 17 mm in maximum length and depth, collected from the bottom of Lake Chapala at Ajijic. This specimen was found among a collection of crayfish carapaces taken from the lake bottom during the low lake levels of the early and mid-1950's. The crayfish collection is in the possession of Dr. Federico Solórzano of Guadalajara. Several salmonid vertebrae were also found in this collection along with disarticulated cranial elements and vertebrae belonging to *Micropterus relictus* and *Ictalurus* sp. All the lake-bottom specimens are water-worn and black in appearance.

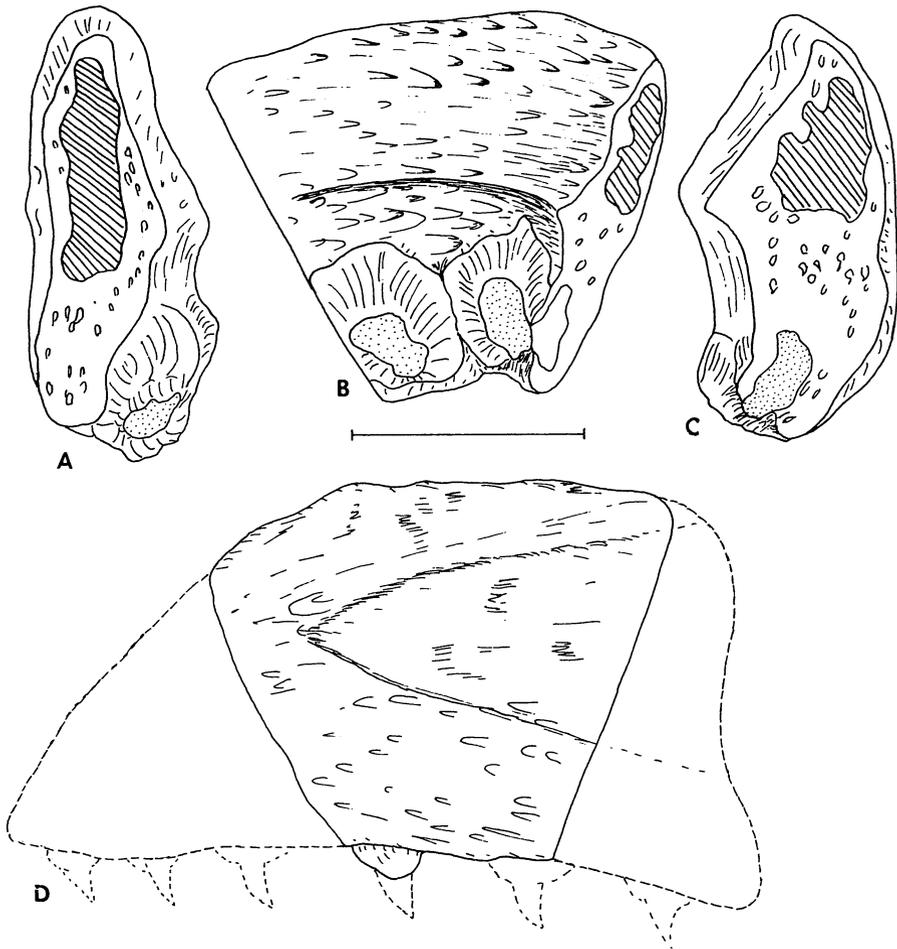
UMMP V78901 consists of the midportion of a premaxilla from a very large adult (at least the size of the holotype). Both the anterior and posterior ends are broken off, as well as the cusps of two teeth. The broken ends were ground smooth to reveal details of the bone structure. The bases of the teeth are enlarged and firmly socketed to the alveolar border. In cross section the tooth bases are slightly anteroposteriorly compressed as in *Oncorhynchus*. The lateral surface of the premaxilla is smooth except for a central, shallow, triangular depression with the apex of the triangle anteriorly directed. The dorsal outline of the bone is slightly convex. The mesial face has two angled surfaces that meet in a longitudinal ridge (Fig. 11B). The dorsal of the two surfaces forms a narrow, slightly concave articular surface for seating the premaxilla on the rostrum. Its characteristics resemble those found on the premaxillae of *Oncorhynchus* and indicate that the fossil individual may have possessed an azygous rostrum. In some respects such as the lateral



TEXT-FIG. 9 — Individual vertebrae of *Salmo australis*, UMMP V78900, in lateral view, anterior to left. (A) from posterior region of precaudal series, (B) from caudal series, (C) from caudal series. Scale 0.5 cm.



TEXT-FIG. 10 — Two vertebrae of *Salmo australis*, UMMP V78900, in lateral view, anterior to right. (A) from caudal series, (B) from anterior region of precaudal series. Scale 0.5 cm.



TEXT-FIG. 11 — Incomplete left premaxilla of *Oncorhynchus* sp., UMMP V78901. (A) cross-sectional view of posterior end, (B) mesial view, anterior to right, (C) cross-sectional view of anterior end, (D) lateral view, anterior to left. Scale one cm.

compression, depth, and surface indentation, the premaxilla is more comparable to that of subgenus *Parasalmo* and subgenus *Rhabdofario*. Internal bone structure is cancellous except for the tooth platform. At the anterior end there is a large sinus located internal to the mesial longitudinal ridge. The two mesial surfaces have a pitted ornamentation while the lateral surface is smooth above and below the indentation. The polished anterior end of the premaxilla (Fig. 11C) has exposed one of the teeth internally. The swollen tooth has a large pulp cavity agreeing closely with the structure of a breeding tooth in *Oncorhynchus*. Referral of this specimen to *Oncorhynchus* sp. rather than to *Salmo australis* is based on overall similarity to that genus.

DISCUSSION

Vladykov and Gruchy (1972) proposed that *Parahucho* Vladykov (type species *Salmo perryi* Brevoort), *Parasalmo* Vladykov (type species *Salmo clarki* Richardson), and *Rhabdofario* Cope (type species *Rhabdofario lacustris* Cope) be regarded as subgenera of *Salmo*, along with *Platysalmo* Behnke (type species *Salmo platycephalus* Behnke). Earlier, Uyeno and Miller (1963:12) synonymized *Rhabdofario* with *Salmo* and renamed the type species *Salmo copei*. Smith (1975:7) opposed this action, stating that *Rhabdofario* is readily separable from *Salmo* “. . . on the basis of the cylindrical rather than flattened maxilla.” We find that in large adults of *Parasalmo* (ca. 700–1,000 mm SL), and to a lesser extent in subgenus *Salmo* (e.g., *S. trutta*), the maxilla is cylindrical and hence that the shape of this bone does not sharply separate *Rhabdofario* from *Salmo*. Thus we adopt the subgeneric classification indicated above, with the realization that the phylogenetic history of *Salmo* (sensu lato) is still uncertain and that, on the basis of osteological characters, only *Oncorhynchus* appears to be definable by derived characters (items 1, 9, and 11, Table 1). However, these may not hold up when the osteology of the Japanese species currently placed in *Oncorhynchus* is thoroughly known.

The incomplete nature of the fossil specimen prohibits an adequate assessment of its relationships. Without the premaxilla, one of the most important characters (the zygous rostrum) which separates *Oncorhynchus* from other salmonines is lacking in our analysis (Table 1). The fragmentary premaxilla recovered from the lake bottom at Ajijic which we have tentatively assigned to *Oncorhynchus* may in fact belong to *Salmo australis*. The anterior end, the most diagnostic portion of the bone, is missing. The four derived characters we have listed for *S. australis* are shared between three generic or subgeneric salmonine groups (*Parasalmo*, *Rhabdofario*, and *Oncorhynchus*) native to the North Pacific basin. Only one character is shared with the subgenus *Salmo* of the North Atlantic and Mediterranean basins. These results suggest

TABLE 1 — Comparison of fossil with *Oncorhynchus* and subgenera of *Salmo*¹

Derived Character State	<i>S. australis</i>	<i>Parasalmo</i>	<i>Rhabdofario</i>	<i>Oncorhynchus</i>	<i>Salmo</i>
1. Breeding teeth without deep sockets	–	–	–	+	–
2. Breeding teeth of jaws with greatly enlarged bases	+	–	+	+	–
				(anterior teeth)	
3. Loss of lateral teeth on head of vomer	–	–	+	+	–
4. Reduction of alternating series of teeth on shaft of vomer	–	–	+	–	–
5. Anterior process of vomer elongated in large breeding males	+	+	+	+	–
6. Articulating process of maxilla oriented at an angle to alveolar shaft	+	+	–	–	+
7. Parasphenoid with median ridge at flexure	–	–	+	+	–
				(lacking in some species)	
8. Basioccipital with myodome canal narrowed posteriorly	+	–	–	+	–
9. Dermal cranial bones with abundant cancellous structure	–	–	–	+	–
10. Basihyal tooth plate usually tapered anteriorly to a narrow tip	unknown	–	+	+	–
11. Rostrum zygous	unknown	–	–	+	–

¹Information from Tchernavin (1938), Vladykov (1962), Kimmel (1975), and G. R. Smith (1975) was helpful in preparing this table.

an alignment of the fossil species, *S. australis*, with the Pacific forms, as expected from its geographic position. They also underline the need for a thorough study of salmonine interrelationships utilizing all the extant taxa, and suggest that our current use of the generic name *Salmo* may not be phyletic.

Salmo chrysogaster Needham and Gard (1964), the native salmonid geographically closest to the fossil locality, is considered to be not closely related to *Salmo australis* through disagreement on a number of important character states. *Salmo chrysogaster* has a relatively wide myodome, poorly developed pterotic and sphenotic processes, and the cephalic lateralis canals are of relatively large diameter with fewer pores and branches. The jaw, tooth and vomer characters are too difficult to assess because of the small individual sizes of our study material.

Salmo australis differs from the extinct Plio-Pleistocene *Oncorhynchus salax* and *Smilodonichthys* in the characters of its lower jaw and teeth. It can be distinguished from the two species *Salmo copei* and *S. carinatum*, belonging to the subgenus *Rhabdofario*, by the following set of characters: articulating process of maxilla oriented in a vertical plane and deflected dorsally at a slight angle to the alveolar shaft; cusps of dentary and maxillary teeth disproportionately small in comparison to their enlarged bases; head of vomer with transverse row of teeth; vomerine shaft with a fully extended alternating series of teeth; the myodome canal of the basioccipital narrowed posteriorly; and the parasphenoid without a median ridge located at its point of flexure.

Salmonid vertebrae mentioned by Miller (1972) from the San Marcos basin, immediately west of the Chapala basin, are the geographically closest known fossil salmonid remains. The total material (M. L. Smith, 1980, The evolutionary and ecological history of the fish fauna of the Río Lerma basin, Mexico. PhD dissertation, Univ. Mich., 191 pp.) consists of five caudal vertebrae, possibly all from one individual of about 400 mm SL, and an incomplete right anguloarticular of a specimen in the 500–600 mm size range. The vertebrae differ from those of *Salmo australis* in their well-developed series of irregular longitudinal ridges that cross the finely perforated centra walls. They do show some agreement in this character with *Oncorhynchus masou*. The anguloarticular differs from that of *Salmo australis* in several characteristics, including the absence of a concavity on the lateral surface below the ascending margin of the coronoid ramus; the strongly compressed posteroventral margin; the lower, more rounded and compressed posterior process; and in details of ornamentation. The San Marcos anguloarticular is more closely comparable to that of Recent *Oncorhynchus* than it is to *Salmo australis*. We conclude that the San Marcos material is referable to the genus *Oncorhynchus* and definitely represents a different species than *S. australis*. Further material is needed for specific determination.

With our present knowledge of the sedimentary geology and occurrence of fossils within the Chapala basin, it is difficult to reach a definite conclusion about the age of *Salmo australis*. The exact source of the Pleistocene fossils from the lake bottom at Ajijic is unknown. It has been pointed out by Downs (1958) that the fossil assemblage which yielded the salmonid premaxilla may be a mixture of both Late Pleistocene and Late Pliocene to Early Pleistocene mammalian taxa. He considered the majority of forms to be Late Pleistocene in age. The stratigraphic placement of the holotype of *Salmo australis* could not be determined from collection data accompanying the specimen. Its reported location places it at or near the top of the Chapala basin sedimentary section in a probably Pleistocene age sand terrace at Ajijic (Clements, 1963).

The occurrence of *Salmo australis* at the western edge of the high central plateau of Mexico places it within the drainage system of the Río Lerma-Santiago. This river runs westward from a 3700 m divide just east of Toluca to Lake Chapala. The water exits to the Pacific Ocean via the Río Grande de Santiago, a torrential river that has cut a deep gorge through the northwestern

edge of the plateau near Guadalajara. It is logical to assume that *Salmo australis* used the ancestral Río Lerma to reach the Chapala basin before or during a cold climatic maximum in the Pleistocene. The high, level terrain surrounding the basin would have provided a cooling effect on its waters; possibly even cold-water streams were present that would have been suitable for spawning during the winter months.

The presence of a large salmonine so far south suggests cold surface waters existed along the coast at least to the tip of Baja California. Upwelling of cold California currents occurs today along the Pacific coast of northern Baja California (Hubbs and Roden, 1964). These currents could have been pushed much farther south during times of maximum glaciation in the Pleistocene.

Evidence for a cooler and moister climate as far south as 20° N latitude during at least the Late Pleistocene is found in submerged tree trunks, cones and leaves off the Pacific coast of Mexico. These represent remnants of the evergreen forests that extended over areas now occupied by arid desert or thorn forest vegetation. The forest remains have been dated at 30,000 years B.P. (Dott and Batten, 1976:443). On a world scale, glaciers are known to have existed at 20° N latitude at elevations close to 3000 meters. The highest peaks surrounding the Chapala basin are 2240 to 2960 m at the west end and 1970 to 2430 m at the east end (see sheet F13-12, Guadalajara, Carta Topográfica, Estados Unidos Mexicanos 1:250,000, 1977).

Additional evidence for ice-age, surface-water cooling is found in radiolarian species now occurring in the cool waters off Washington, Oregon and northernmost California. These radiolarians extended their distribution at least 1000 km to the south in the California current about 18,000 years B.P. The southward shift of the frontal region associated with the California current resulted in a large temperature decrease off the coast of northern Mexico (McIntyre et al., 1976). One of the largest local differences of surface air temperature (present minus ice age) occurred in the area of 20° N to 25° N latitude in western Mexico where July surface air temperatures were calculated to lie between 5° and 6° C cooler at 18,000 B.P. (Gates, 1976).

Cooling of surface waters and lowering of surface air temperatures at the lower latitudes may have followed a similar pattern during pre-Wisconsinan glacial maxima.

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