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# SMILODONICHTHYS *RASTROSUS*, A NEW PLIOCENE SALMONID FISH FROM WESTERN UNITED STATES

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## INTRODUCTION

In western North America, the family Salmonidae is comprised of a diverse number of species (upwards of 30) belonging to seven genera assigned to three subfamilies (Norden, 1961). Though more than half of these species are endemic to the area, an astonishingly few fossil specimens have been discovered which can help document the evolution that has taken place in this group. An exception is the one described in this paper which adds importantly to our understanding of the past life of these fishes.

Materials of this fossil salmonid were collected over a period of fifty years from Pliocene, Pacific-slope localities in California and Oregon. As early as 1917, vertebrae, teeth and skull fragments of an extremely large but unfamiliar type of fish were unearthed, along with mammalian remains, at Pinole, Contra Costa County, California. Only within recent years, however, has it been possible to identify these with certainty as being the remains of an extinct form of salmonid that once was distributed in the coastal regions of the Pacific Northwest, probably much the way that Pacific salmon (*Oncorhynchus*) are today. In 1950 and again in 1964, more complete specimens were discovered of this unusual species from a Pliocene gravel pit in northcentral Oregon. The last find consisted of a large skull which is outstanding for its completeness and detail of preservation. It is a description of this skull that forms the

main context of the present paper and which has allowed fruitful comparison to be made with living salmonids.

The name *Smilodonichthys rastrosus* is proposed for this previously undescribed species. Because of its high degree of morphological distinction from other members of the Salmonidae, this species is made the type of a new genus. A number of its osteological features indicate a phyletic relationship closest to *Oncorhynchus*, yet none of the extant species of that genus approaches the fossil in the specialization of its feeding mechanism.

## ACKNOWLEDGMENTS

Cooperation from many sources has enabled the completion of this study. We are particularly indebted to J. Arnold Shotwell of the University of Oregon Museum of Natural History, who loaned the material that has provided the basis for distinguishing the new genus. For the loan and gift of other specimens we thank Donald E. Savage of the University of California Museum of Paleontology, C. A. Reppenning of the U.S. Geological Survey, and Norman V. Peterson of the Oregon State Department of Geology and Mineral Industries. W. I. Follett provided information leading to study of the Turlock material and Dennis Garber made available the specimens from Turlock Lake. James O. Berkland collected material and provided information on the Worden fossils. H. A.

Vibbert donated material from Gateway, as did Phil F. Brogan. C. H. Ellis and H. A. Demorest of the Washington State Department of Fisheries generously donated a large breeding male Chinook salmon for skeletal preparation. Elizabeth S. Wing loaned a large tarpon skeleton. Richard L. Wilson provided technical help. The carefully executed drawings of the type specimen are the work of Martha B. Lackey, staff artist of The University of Michigan Museum of Zoology, and Louis P. Martonyi took the photograph of the large vertebra. Financial support from the National Science Foundation, GB-4854X and GB-14871 (to R. R. Miller), including publication subsidy, is gratefully acknowledged.

#### MATERIAL

Institutional abbreviations are: University of Oregon Museum of Natural History (UO), University of California Museum of Paleontology (UCMP), University of Michigan Museum of Paleontology (UMMP), and University of Michigan Museum of Zoology (UMMZ).

The following material is all from Oregon.

Holotype, UO 26799, Gateway Locality, collected by Mrs. George Iames and Scott McKain, summer 1964: skull with jaws and anterior gill arches in articulated condition; opercles and subopercles missing (see Figs. 3-6, 10).

Paratype, UO F3335, Gateway Locality, collected by J. A. Shotwell and first discovered by Miss Ann Brownhill about 1950; associated parts from a single individual of very large size (somewhat larger than holotype) are listed as follows: badly crushed neurocranium showing posterior portion of parasphenoid, basioccipital, both exoccipitals and prootics; flattened on top of these bones are portions of the frontal, parietal, epiotic and pterotic (all of the left side), plus part of the supraoccipital; complete right and left mandibles and premaxillae, to each of which is firmly attached an extremely large breeding tooth (Fig. 9) with ossified base; left maxilla; right and left quadrate; right hyomandibular; right ceratohyal; por-

tions of three branchiostegal rays; part of the right preopercle; posterior part of the right cleithrum; complete right posttemporal and incomplete left posttemporal; miscellaneous fragments including parts of opercle, pectoral fin, basihyal plate, neural and hemal spines, branchial arches; approximately 40 vertebrae, both from the caudal and precaudal series; left epihyal; left interopercle; left lacrimal; right supraorbital.

UMMP V58061, about 20 vertebrae probably belonging to the paratype, Gateway Locality, R. R. Miller and field party, 1961.

UMMP V58062, five vertebrae probably belonging to the paratype, Gateway Locality, P. F. Brogan, Bend, Oregon, about 1950.

UMMP V58063, left hyomandibular possibly from the paratype, Gateway Locality, H. A. Vibbert, Madras, Oregon.

UMMP V58064, anterior portion of right dentary (Fig. 13) from a juvenile, Worden Locality, Norman V. Peterson, 1968.

Listed below is the material from California.

UCMP 65630, broken premaxillary tooth, Pinole Locality, C. Stock, 1917.

UCMP 22560, water-worn precaudal centrum, Pinole Locality, C. Stock, 1917.

UCMP 34566, central part of left preopercle and seven vertebral centra (some broken or crushed), Pinole Locality, WPA field party, 1938.

UCMP 37584, left premaxilla and tooth, Pinole Locality, WPA field party, 1940.

UCMP 65629, fragments of one vertebral centrum, Pinole Locality, C. Hotton, 1960.

UCMP 58570, incomplete, precaudal vertebral centrum, Pinole Locality, D. Savage and field party, 1961.

UCMP 61554, water-worn premaxillary tooth, Pinole Locality, Preston Ritter, 1962.

UCMP 61039, broken premaxillary tooth, Pinole Locality, Jean Firby, 1962.

UCMP 64100, parts of three vertebral centra, Pinole Locality.

UCMP 61550, right premaxillary tooth with tip missing, Pinole Locality, Melvin Washington.

UCMP 48657, part of vertical limb of left preopercle and part of sensory canal bone, Turlock Locality.

UCMP 44668, right frontal and 2 vertebral centra, Turlock Locality, 1954.

The following California material was collected at the Turlock Locality by Dennis Garber of Modesto, California, from 1957 to about 1964.

UCMP 93170, anterior end of right dentary.

UCMP 93171, articular fossa of right opercle.

UCMP 93172, portion of left frontal.

UCMP 93173-75, three large fragments interpreted as parts of the vertical limbs of preopercles.

UCMP 93176, fragmentary right premaxilla with osseous base of large tooth, in 2 pieces.

UCMP 93177, water-worn left premaxilla with tooth base.

UCMP 93178, right premaxilla with tooth base.

UCMP 93179, complete right premaxilla and tooth.

UCMP 93180, left premaxilla with complete tooth, most of enamel present, anterior portion of premaxilla broken off.

UCMP 93181-83, three left premaxillae with teeth, enamel portions mostly broken off, osseous bases complete.

UCMP 93184, complete right premaxilla and tooth, enamel portion worn.

UCMP 93185, eight vertebral centra (4 complete), largest 40 mm diameter, smallest 30 mm.

UCMP 93186, four bone fragments.

UCMP 93187, one tooth fragment.

#### LOCATION AND AGE

Fossils referable to *Smilodonichthys* have been found at four main localities, two in California and two in Oregon, plus additional minor sites along the Columbia River of Oregon. In two of the four localities, mammalian fossils have been recovered along with the fish remains and have supplied the valuable mammalian-age determinations.

A. Gateway Locality—UO loc 2250. Collected from a coarse boulder and gravel facies in the "Torrential Beds" (Shotwell's informal name) of the Madras Formation, near the town of Gateway, Jefferson County, Oregon; elev. ca. 2,250 ft. (Figs. 1-2). This unit consists of a mass of boulders, tree fragments, chunks of sediment from the underlying formation of Barstovian (Late Miocene) age, and numerous small sand lenses. Large salmonid vertebrae and, less frequently, teeth have been found along the bottom of these lenses.

The age of the "Torrential" unit is not definitely established. It contains reworked Barstovian vertebrates. According to Shotwell (pers. comm.), the age can be no older than Barstovian nor younger than Hemphillian (Middle Pliocene). There is a strong possibility that the Torrential Unit is of Hemphillian age. *Smilodonichthys* vertebrae have been recovered from Early Pliocene to Late Middle Pliocene deposits along the Columbia River in the vicinity of Arlington, Oregon, and twenty miles to the east.

B. Worden Locality—Abandoned railroad cut near Worden, Klamath County, Oregon, located in the Klamath Falls Quadrangle, collected by Norman Peterson, Oregon State Department of Geology and Mineral Industries, April 15, 1968. This locality consists of a 20-foot deep exposure of tuffaceous sandstone dipping 10 degrees to the northeast which is truncated at the east and west edges of the railroad cut by basaltic intrusions. The sandstone in places is cross-bedded and moderately well cemented. It may belong to the Yonna Formation which is Pliocene (Newcomb, 1958). Bones, including those of land mammals, found at the site were disarticulated and haphazardly assembled during deposition of the sand. Other fish remains that are associated with the salmonids belong to the families Cyprinidae and Catostomidae.

C. Pinole Locality—Pinole Tuff at Pinole, Contra Costa County, California, about 17 miles north of Oakland; UC loc V2572, V3425 and V3837. The locality has yielded a frag-



**Figure 1.** Gateway Locality, showing exposure of the "Torrential beds" of the Madras Formation, at gravel pit near Gateway, Oregon, 1961.

mentary mammalian fauna (Stirton, 1939). There is a potassium argon date of 5.2 million years (Evernden *et al.*, 1964) for the Pinole Tuff.

D. Turlock Locality—This locality consists of exposures of the Mehrten Formation which outcrop at the edge of Turlock Lake, Stanislaus County, California, 22 miles east of Modesto. UCMP loc V5405 lies in the NW of SE 1/4 of Sec. 8, T4S, R13E, Turlock Lake Quadrangle (USGS 1953). This site has also yielded a fragmentary land mammalian fauna.

The Turlock Lake and Pinole Localities are chronologically very closely related in terms of the land-mammal fossils which, according to D. E. Savage (pers. comm.), are judged to be a Late Hemphillian (Late Middle Pliocene) river-border fauna.

## SYSTEMATICS

### ORDER SALMONIFORMES

### FAMILY SALMONIDAE

### *SMILODONICHTHYS*, new genus

TYPE SPECIES: *Smilodonichthys rastrosus*, new species

(Figs. 3-13)

DIAGNOSIS: Distinguished from all known salmonid species by its numerous gill rakers, over 100 on the first branchial arch in the adult. Jaws and palate without feeding teeth; lower jaw very deep at coronoid process (greatest depth 3 times in length), without tooth-bearing region except an abbreviated shelf adjacent to the symphysis; maxilla toothless, apparently no teeth on palate and tongue; gill rakers and basibranchials toothless. Teeth of breeding in-



**Figure 2.** Detail of the horizon (sand lens being worked) which yielded the paratype of *Smilodonichthys rastrosus* at Gateway, 1961.

dividuals consist of one massive tooth on each premaxilla and much smaller teeth on the dentaries, usually one at each side of the mandibular symphysis. Supramaxilla exceptionally large, attaining 80% of length of oral border of maxilla. Posterior (basicranial) part of parasphenoid strongly compressed in the form of a keel. Posttemporal fossa very shallow and of small area; dermal part of pterotic lateral to posttemporal fossa, relatively wide. Interopercle with pronounced dorsal extension. Vomer diamond-shaped, with no tooth-bearing platform on shaft. Urohyal  $\frac{1}{5}$  as long as lower jaw. Ornamentation of vertebral centra consisting of many fine, elevated ridges running longitudinally.

**MEASUREMENTS:** The length of the neurocranium from the anterior tip of the supraethmoid

to the posterior end of the supraoccipital measures 307 mm. Ventrally the length measured from the anterior tip of the vomer to the posterior end of the basioccipital is 316 mm. Interorbital width about 157 mm; width at the attachment of the nasals 103 mm, and width at the frontal-supraethmoid junction 77 mm. Width between the sphenotic processes is 170 mm, between the pterotics 166 mm. Greatest posterior width of parasphenoid (at the ascending wings) 89 mm, greatest anterior width 67 mm. Depth of the neurocranium is markedly distorted due to the dorsoventral compression and loss of cartilage during fossilization.

In the branchiocranium, the distance on the right side between the anterior end of the mandible and the posterior border of the preopercle is 385 mm. The vertical distance on the right side from the horizontal line formed by the

ventral border of the **interopercle** to the dorsal border of the hyomandibular is 240 mm.

The right mandible measures 264 mm in length and 87 mm in depth at the coronoid process. The maxilla, with supramaxilla in place, measures 150 mm in length and 47 mm in greatest depth. The supramaxilla is 104 mm in length and 32 mm in greatest depth.

The right **preopercle**, with ventral border broken, measures about 200 mm in height.

The right premaxilla is 76 mm long; the osseous base of the single large tooth on the right premaxilla is 35 mm in greatest width and about 50 mm in greatest length.

The basioccipital condyle is about 45 mm wide (somewhat distorted due to dorsoventral compression). A precaudal centrum, taken from the paratype, is 35 mm in greatest diameter and 25.5 mm in anterior-posterior length (the largest vertebra of *Smilodonichthys* examined, UCMZ 44668, from Turlock Lake, measures 48 mm greatest diameter and 28.5 mm long).

In order to obtain some idea of overall size of the holotype, we have made corresponding measurements on skulls of two *Oncorhynchus tshawytscha*: UMMZ 178987-S, 985 mm S.L., 39½ lbs., male, and UMMZ 186299-S, 845 mm S.L., 28½ lbs., female. In that species the length of the **opercle** averages about 20 percent of head length. Using this proportion, the head length of the fossil (opercle missing) is estimated to be 462 mm. Through a linear progression taken from the proportion of head length to standard length, the fossil is calculated to have had a standard length of 1900 mm.

**CRANIAL MUSCULATURE:** A number of the individual characteristics of the skull bones in *Smilodonichthys* are associated with places of muscle and ligamentous attachment. In order to interpret more accurately some of these structures, comparisons are made between the fossil and a living salmonid, *Oncorhynchus kisutch*, in the areas of the lower jaw and suspensorium.

The adductor mandibulae is divided by an aponeurosis into an anterior (mandibular)

part housed in the meckelian fossa of the lower jaw and a posterior part covering a large area of the cheek between the **preopercle** and eye (Greene and Greene, 1914). In addition, the posterior part is split into three poorly defined divisions ( $A_1$ ,  $A_2$ , and  $A_3$  of Allis, 1897) which are best delineated where the muscle takes its origin. The longest division,  $A_1$ , has its origin dorsally on the well developed adductor ridge of the hyomandibular. It runs downward behind the eye to the aponeurosis situated at the coronoid margin of the articular. The second and largest division,  $A_2$ , originates principally on the anterior edge of the preopercle and adductor ridge but fibers are also attached to the quadrate and symplectic. The  $A_3$  division runs underneath and obliquely to the first two. It originates on the lateral face of the ascending wing of the metapterygoid. The mandibular portion of the adductor muscle inserts on the strong ledge that runs along the ventromesial part of the dentary. This ledge is a prominent feature on the dentary of *Smilodonichthys*. The extent of the meckelian fossa which provides room for the expansion of the adductor muscle during contraction is greater in *Smilodonichthys* than in *Oncorhynchus*. Also, in the former, the adductor ridge presumably serving as the area of origin for the  $A_1$  and  $A_2$  divisions is more pronounced and may exclude part of the upper limb of the preopercle as a place of muscle attachment.

Two muscles that operate the suspensorium are the adductor and levator arcus palatini. The former **originates** on the lateral face of the ascending process of the parasphenoid and on the anterior rim of the prootic. It inserts on the posteromesial extension of the endopterygoid. Both of these areas are developed to a greater degree in *Smilodonichthys* than in *Oncorhynchus*. A ridge transversely crosses the **endopterygoid** beneath the orbit of *Smilodonichthys*, possibly marking the anterior limit of insertion of the adductor arcus palatini. The levator has two major divisions. The anterior (outer) division inserts on the mesial side of the ascending wing of the metapterygoid. The innermost posterior division inserts on the lateral surface of

the hyomandibular head. The levator origin is on the sphenotic process and the pterotic. The opposite (mesial) side of the hyomandibular head forms a large area for insertion of the hyomandibulae muscle that takes its origin principally from the prootic. In *Oncorhynchus kisutch*, this muscle is subdivided into an anterior and posterior part at its insertion. In both *Smilodonichthys* and *Oncorhynchus*, the head of the hyomandibular is exceptionally broad.

On the back of the braincase at each side of the foramen magnum are shallow fossae for insertion of anterior trunk musculature. These muscles pass forward between the vertebral column and pectoral girdle to their place of attachment (Gosline, 1969). The posterior processes of the pterotics lie lateral to them and apparently form a support for the pectoral girdle at the point where the posttemporal is expanded ventrally. They also serve as a place of origin for part of the levator operculi. The fossae at each side of the foramen magnum appear to be in line with the row of anterior epineural ribs. Even when taking into consideration significant depression of the braincase during preservation, the depth of the rear wall of the braincase is greater in *Oncorhynchus* than it is in *Smilodonichthys*. The former also has much larger posttemporal fossae for insertion of the more dorsal portions of the anterior trunk muscles. The difference pointed out in rear skull proportions and body muscle attachment may indicate that *Oncorhynchus* has a greater body depth than was present in *Smilodonichthys*.

**ETYMOLOGY:** Named *Smilodonichthys*, from the fossil genus of sabre-toothed cat, in reference to the pair of large teeth at the anterior end of the upper jaw, and *rastrosus*, from the Latin word for raker, in reference to the numerous gill rakers.

## DESCRIPTION

**NEUROCRANIUM:** The neurocranium was disarticulated from the rest of the skull to enable careful study and illustration. Preservation was virtually complete, but some lateral distortion and depression (especially in the *orbita*

*sphenoid-pterosphenoid* region) occurred in fossilization.

**Cranial Roof .—**The most striking characteristics of the cranial roof (Fig. 3) are: (1) the overall size and elongate shape; (2) the heavily ossified construction of the component bones, especially the frontals; (3) the completeness of the bone-roofing posteriorly and the shallow posttemporal fossae; (4) the *supraoccipital* separating the parietals; (5) the frontals not entirely meeting over part of their midline; and (6) the triangular-shaped supraethmoid.

In area covered, the frontals are the major bones of the cranial roof. An incomplete right frontal, UCMP 44668, showing the central and lateral portions of the bone where it articulates with the sphenotic, is thick and massive in appearance. It indicates that the frontals were very strong where they form a low arch between the sphenotics. The oblique ridge on the lower frontal surface that unites with the sphenotic is exceptionally well developed. It lies under the heaviest part of the frontal. As in Recent *Oncorhynchus*, the fit between the frontal and sphenotic is so close that the line of junction is barely perceptible. Mesially, the frontals are very thin. They meet in the *midline* where they overlap the supraoccipital, near the middle of the cranium between the sphenotics, and probably also at their anterior ends where they contact the supraethmoid. Two large spaces in the midline, one ahead and one behind the zone of frontal contact in the area between the *sphenotics*, indicate regions occupied by cartilage. A similar separation of the frontals by cartilage occurs in Recent *Oncorhynchus*. The frontals are very long bones with most of the trabeculae running longitudinally. The trabeculae can be traced by ridges on the surface of the *bone*. Structurally, the frontals form strong bracing beams *between* the pterotics at the rear of the cranial roof and the supraethmoid in front.

The pattern of the surface ridges in the central portion of the frontals, where they bridge between the sphenotics, indicates that they meet compressional stresses from the sides probably set up by the suspensorium.

The anterior part of the cranial roof tapers to a point through the triangular shape of the median *supraethmoid*. The posterior extensions of this bone overlap the frontals on each side. The posterior limits of the supraethmoid are not clear. However, there may be a notch in the posterior border. In outline, the supraethmoid is similar to that of *Oncorhynchus kisutch* and *O. masou* (Vladykov, 1962: Figs. 28-29). It differs in its sturdier construction. Norden (1961) found that within the salmonines, the supraethmoid has the greatest taxonomic significance of all the dorsal roofing bones. *Nasals* are present, fastened to the lateral edges of the frontals just behind the supraethmoid.

One of the obvious differences in the cranial roof between the fossil and *Oncorhynchus* is the very limited development of the posttemporal fossae. There may be some distortion, due to partial flattening of the neurocranium, but even accounting for this, the fossae are shallow and short. The floor of the fossa, formed by the frontal, epiotic and pterotic, is apparently a continuous covering of bone. There is no cartilaginous interspace as in Recent salmonines.

*Ventral Bones of the Neurocranium.*—When viewed from below, the general appearance of the neurocranium (Fig. 4) again is that of an *Oncorhynchus*. The *parasphenoid* is very broad anteriorly. With the vomer attached, it dominates the whole lower surface. In addition to its anterior breadth and total length, this bone is distinctive in the form of its posterior extension and in the length of its ascending wings. The posterior extension forms the bottom of the eye-muscle canal or posterior myodome and meets the basioccipital and prootics. Instead of being broadly rounded, allowing the myodome to have a substantial opening to the posterior as in *Oncorhynchus*, it is laterally compressed to a point where the myodome is a narrow channel. Thus the parasphenoid is markedly keel-shaped. The closest comparison among the Salmonidae can be found in *Coregonus*, in which the posterior part of the parasphenoid is somewhat keel-shaped, with large lateral surfaces. However, this part is not much compressed and the myodome has a wide posterior opening.

At the anterior end of the ossified braincase, the ascending wings of the parasphenoid extend high up on the anterior margins of the prootics and may have reached as far as the sphenotics. Each ascending wing has a long free anterior edge that curves to a junction with the main longitudinal part of the parasphenoid. At this point of junction, the parasphenoid is quite narrow but very thick. The thickened area and the ascending wings present an exceptionally long and sturdy place of origin for the adductor arcus palatini muscles already mentioned in *Oncorhynchus*. Just posterior and mesial to the ascending wings, a pair of foramina are visible that penetrate the parasphenoid directly below the anteroventral corner of the prootic. They are the openings for the internal carotid arteries that are positioned as in Recent *Oncorhynchus*. Unlike the latter, however, there appear to be no openings for passage of the efferent pseudobranchial arteries within the parasphenoid itself.

Anterior to the ascending wings, the thickening of the parasphenoid extends forward along its lateral edges as the bone gradually widens. The parasphenoid reaches its greatest width just ahead of the lateral ethmoids. The broad anterior portion of the parasphenoid is matched by a broad posterior half of the vomer which overlaps it. The latter possesses a distinctive shape when compared with other salmonines. It looks like an elongated diamond. At the tapered anterior end, the lateral edges parallel those of the supraethmoid above. Also, at the anterior end, the vomer is thickened, but there is no evidence of a pronounced constriction that sets it off from the posterior part. It is possible that the edges may have extended farther laterally forming a "head," since there is some evidence of breakage. One striking feature of the vomer is the absence of teeth or of any kind of tooth-bearing platform.

There are no other ossifications visible in the ethmoid region than those described. It is concluded that the area between the supraethmoid and vomer must have been occupied by a large ethmoid cartilage, as in *Oncorhynchus* and other salmonines.

The bones of the otic region are similar to those of *Oncorhynchus* in their shape and relationships to each other. One apparent difference concerns the lateral process of the sphenotic which projects directly outward instead of curving backward to form a well defined fossa. Also, the anterior border of the prootic is in contact for most of its length with the ascending wing of the parasphenoid.

Both posterior processes of the pterotics are broken off in the holotype. These are well developed in *Oncorhynchus* and other salmonines but less pronounced in coregonines. There is a long, well-defined groove on the ventral surface of each pterotic which extends obliquely forward along the zone of contact between the prootic and sphenotic. This groove seats the head of the hyomandibular. The intercalars are present at the posterior corners of the braincase. They possess long projections that extend anteriorly to unite with, and partly extend onto, the prootics. At the posterior end of the basiocranium the basioccipital condyle is formed by the fusion of the first vertebral centrum (proatlas) with the basioccipital in both the holotype and paratype. This structure forms the entire circular facet for articulation with the vertebral column, excluding the exoccipitals. The lines of contact between the exoccipitals and the proatlas are visible in these two specimens.

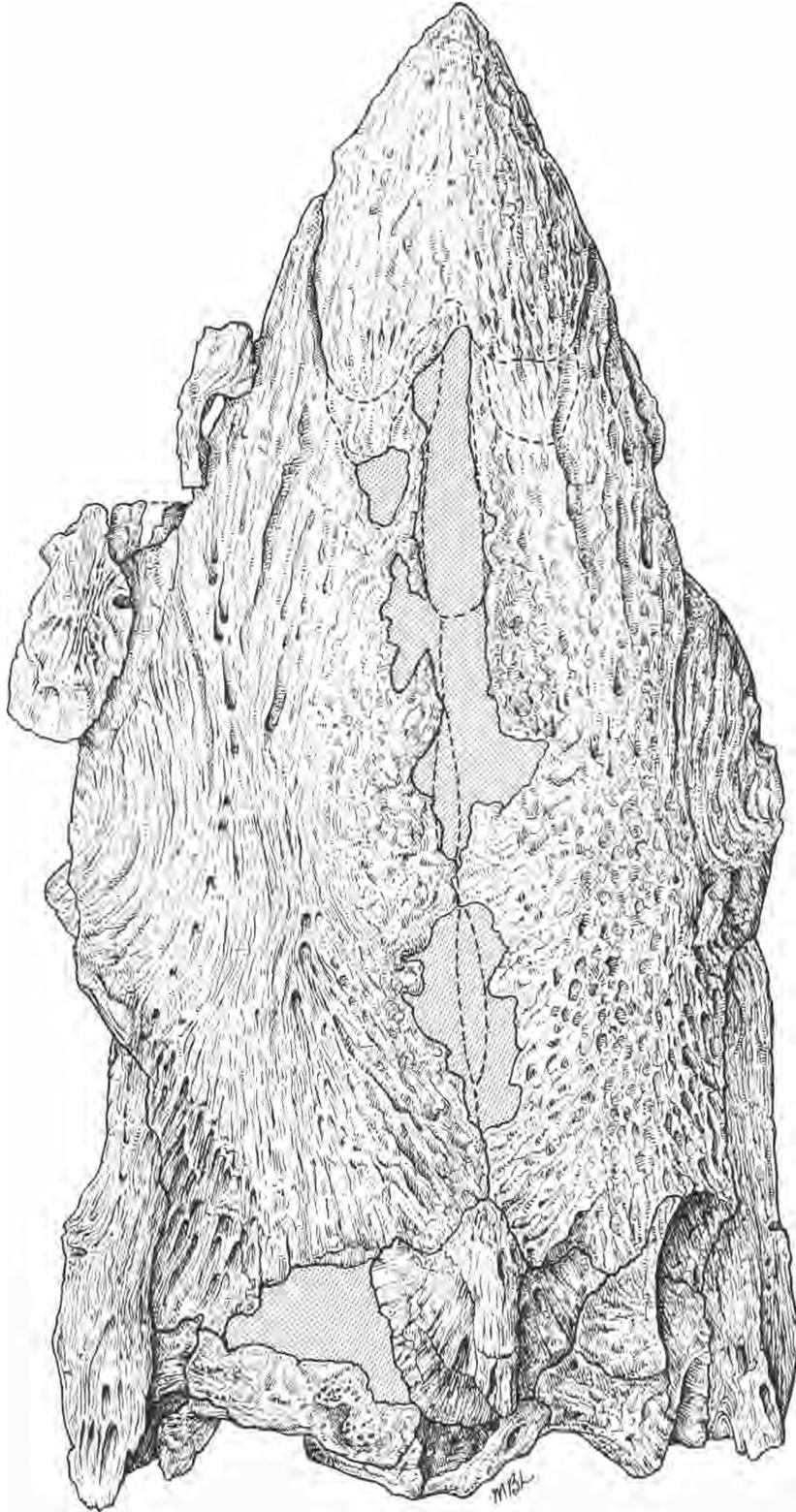
At the anterior end of the braincase a pair of badly crushed, highly cavernous ossifications are present that represent the pterosphenoids. Neither the orbitosphenoid nor basisphenoid was preserved.

**BRANCHIOCRANIUM:** Except for the absence of the gill covers, the external bones of the branchiocranium (Figs. 5-6) are nicely displayed on the holotype and needed very little preparation. Internally, however, the orobranchial cavity was completely filled with coarse sand and gravel which had to be removed to expose the gill arches and associated elements.

The branchiocranium possesses a complex of distinctive, yet interrelated, characters that nearly all appear to be associated with the

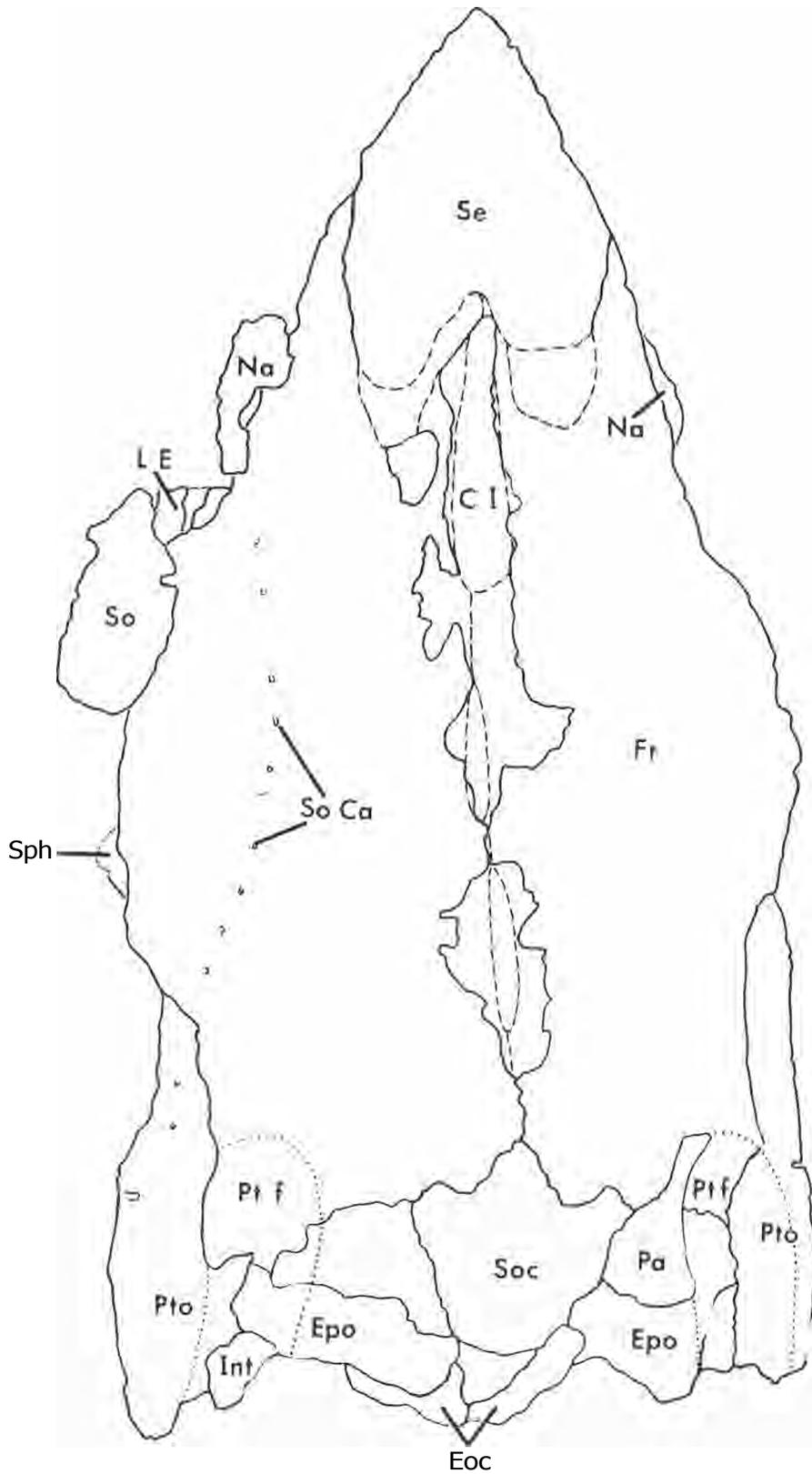
#### ABBREVIATIONS USED ON THE ILLUSTRATIONS

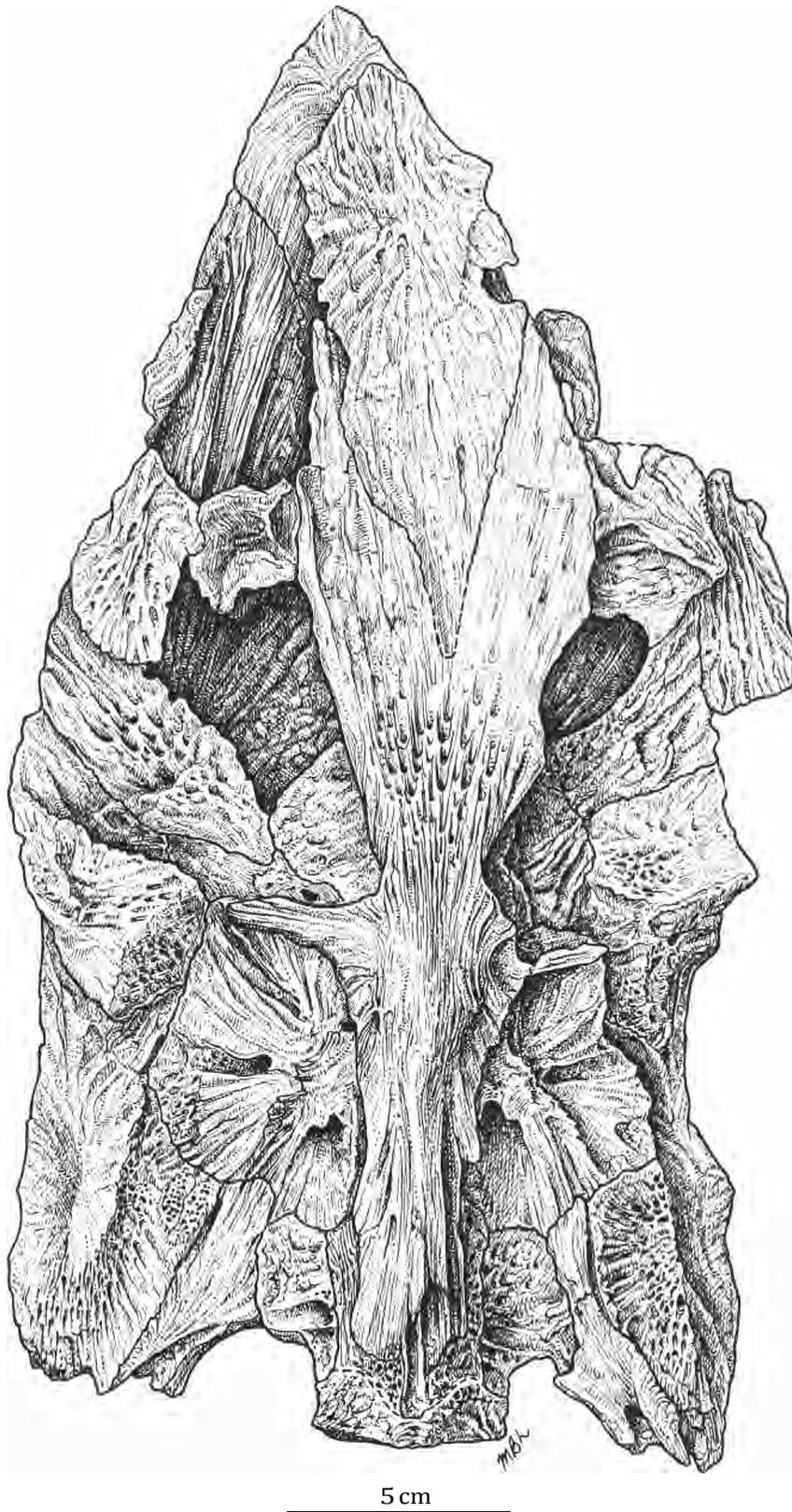
|  |   |
|--|---|
| Ao = antorbital                                      | <b>L Iop</b> = left interopercle                      |
| A <b>R</b> = adductor ridge of hyomandibular         | <b>R Iop</b> = right interopercle                     |
| Art = articular                                      | La = lacrimal   |
| <b>Bh</b> = basihyal                                 | <b>LE</b> = lateral ethmoid                           |
| Boc = basioccipital                                  | <b>M Ca</b> = mandibular canal                        |
| Br = branchiostegals                                 | Met = metapterygoid                                   |
| <b>L Br</b> = left branchiostegals                   | Mx = maxilla  |
| <b>R Br</b> = right branchiostegals                  | <b>LMx</b> = left maxilla                             |
| C I = cartilage interspace                           | <b>RMx</b> = right maxilla                            |
| <b>L DA 1, 2, 3</b> = left dorsal limb of gill arch  | <b>Na</b> = nasal                                     |
| <b>R DA 1, 2, 3</b> = right dorsal limb of gill arch | <b>OBT</b> = osseous base of tooth                    |
| De = dentary   | Op = opercle  |
| <b>L De</b> = left dentary                           | Pa = parietal   |
| <b>R De</b> = right dentary                          | Pal = palatine  |
| De <b>T</b> = dentary teeth                          | <b>Pmx</b> = premaxilla                               |
| <b>Dsph</b> = dermosphenotic                         | <b>Pmx T</b> = premaxillary tooth                     |
| <b>Ect</b> = ectopterygoid                           | Pop = preopercle                                      |
| End = endopterygoid                                  | <b>Pra</b> = proatlas (fused first centrum)           |
| <b>Eoc</b> = exoccipital                             | Pro = prootic   |
| <b>Epo</b> = epiotic                                 | Ps = parasphenoid                                     |
| Fr = frontal   | <b>Pt f</b> = posttemporal fossa                      |
| <b>f ic</b> = foramen for internal carotid artery    | <b>Pto</b> = pterotic                                 |
| <b>f j</b> = jugular foramen                         | <b>Pts</b> = pterosphenoid                            |
| <b>f VII</b> = foramen for 7th cranial nerve         | Qu = quadrate   |
| <b>f X</b> = foramen for 10th cranial nerve          | Se = supraethmoid                                     |
| <b>D Hh</b> = dorsal hypohyal                        | <b>Smx</b> = supramaxilla                             |
| <b>V Hh</b> = ventral hypohyal                       | So = supraorbital                                     |
| Hm = hyomandibular                                   | Soc = supraoccipital                                  |
| <b>L Hm</b> = left hyomandibular                     | So Ca = supraorbital canal                            |
| <b>R Hm</b> = right hyomandibular                    | <b>Sph</b> = sphenotic                                |
| <b>Int</b> = intercalar                              | Sop = subopercle                                      |
| <b>Io 2-6</b> = infraorbitals 2-6                    | <b>Spop</b> = suprapreopercle                         |
|  | Sy = symplectic                                       |
|  | <b>Uh</b> = urohyal                                   |
|  | <b>L VA 1, 2, 3</b> = left ventral limb of gill arch  |
|  | <b>R VA 1, 2, 3</b> = right ventral limb of gill arch |
|  | Vo = vomer  |



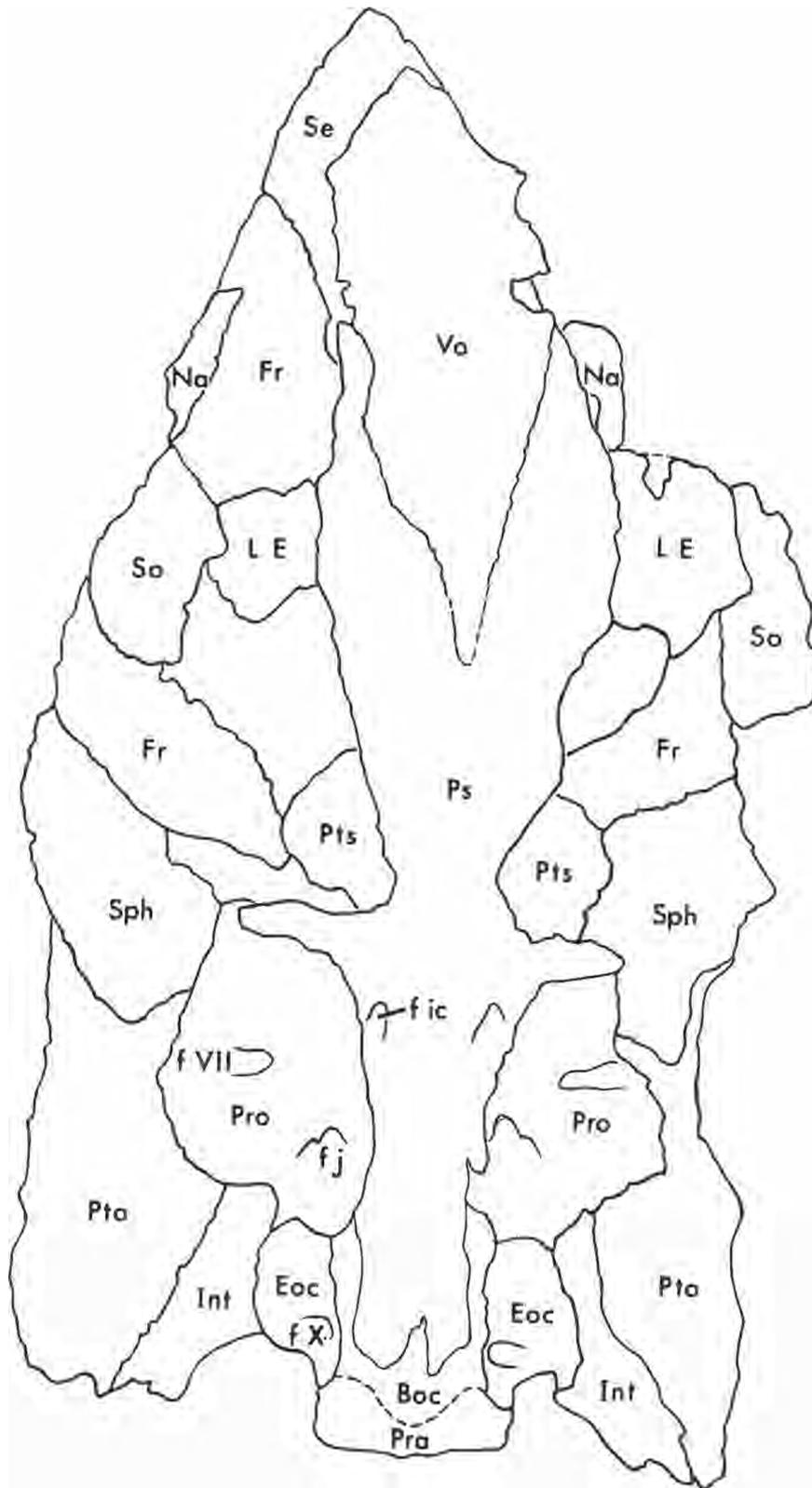
5 cm

**Figure 3.** Cranial roof of holotype of *Smilodonichthys rastrosus*. Abbreviations are given on the preceding page.





**Figure 4.** Ventral view of neurocranium of holotype. Abbreviations are given on the page preceding Figure 3.



usual feeding mechanism. The most important of these are the very high gill-raker number on the branchial arches, the enlarged endopterygoid, the shape of the quadrate, the massive interopercle with its elevated posterior end, the shape and relationships of the upper and lower jaw bones, and the absence of teeth on any of the bones except a pair of breeding teeth on the lower and upper jaws, the upper premaxillary pair being enormous in size.

*Hyoid Region.*—Almost nothing is known of the opercle and subopercle of *Smilodonichthys*. A small portion of the right opercle showing the opercular fossa is present on the paratype. It is similar to that part of the opercle in *Oncorhynchus*. Both the vertical and horizontal limbs of the preopercle are well developed. The anterior margin of the vertical limb is particularly thick and heavy. It fits firmly together with the hyomanidbular where it contacts the adductor ridge to form a large, strong area of attachment for the adductor mandibulae muscles. The proportions of the preopercle are unusual for salmonines. The ventral and horizontal limbs have very broad laminate expansions that coalesce into a curved sheet of bone covering much of the cheek region.

A small tube-shaped bone, the suprapreopercle, is present on the left side of the holotype just above the preopercle. It transfers the preoperculo-mandibular canal from the pterotic to the preopercle.

The interopercle is developed to a similar degree as the preopercle. It is a large bone, quite thick through its central and posterior regions. An important feature of this bone involves the posterior portion which is projected dorsally, much as the upper limb of the preopercle, and occupies a position taken by the anterior end of the subopercle in *Oncorhynchus* (Fig. 7).

The branchiostegal series appears to be complete in the holotype. There are 14 branchiostegal rays on the left side and 15 on the right. The individual rays are long, wide, and broadly overlapping.

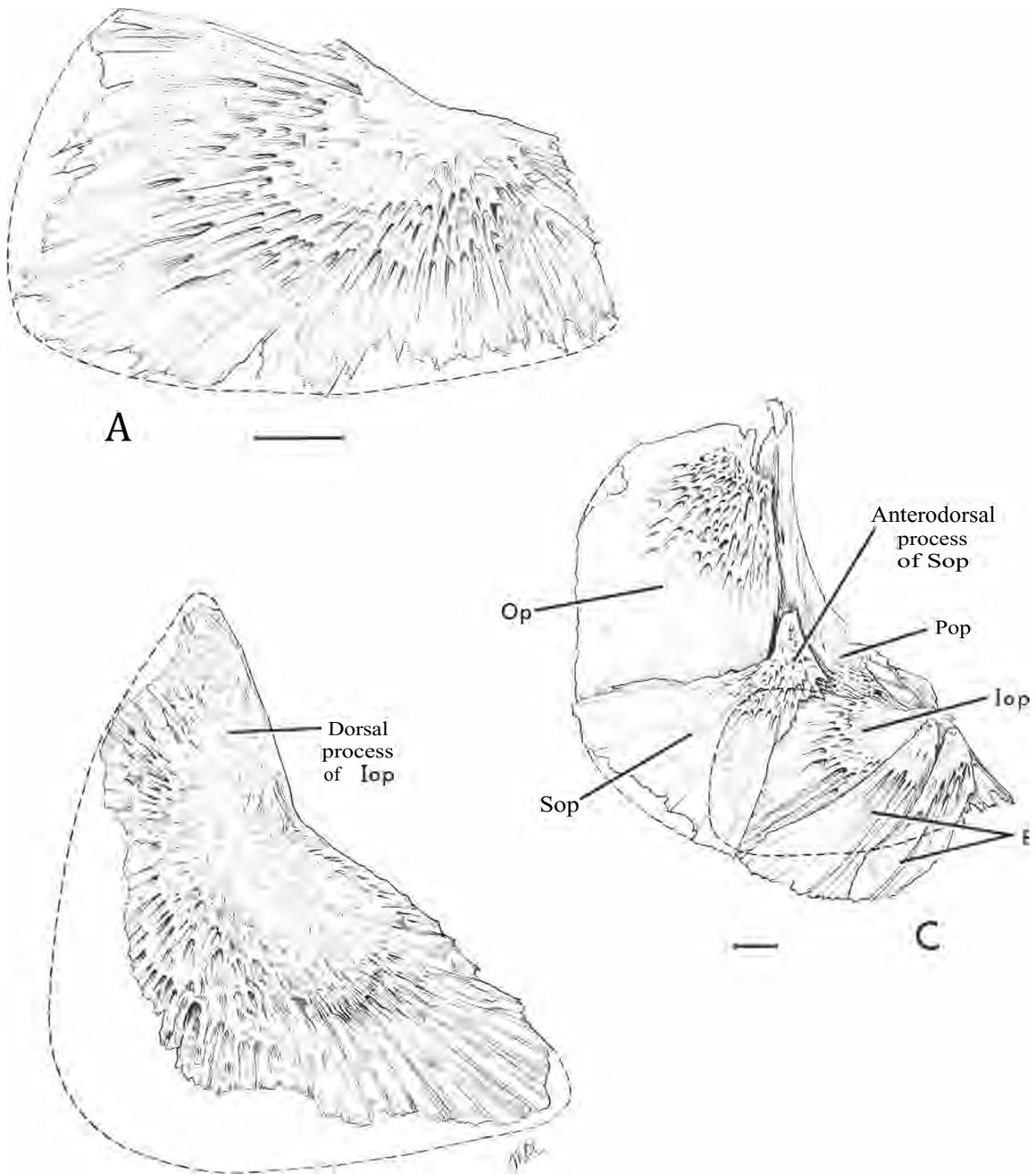
In the suspensorium, the hyo mandibular is

the largest component. Dorsally, it has a single broad head for articulation with the neurocranium. The bone tapers ventrally into a strong vertical limb that meets the symplectic. Posteriorly, the opercular condyle is barely represented by a rounded protuberance and must have consisted almost entirely of cartilage.

One of the important characters of the hyomandibular is the adductor ridge protruding from its lateral surface. This ridge meets the upper arm of the preopercle to form the place of origin of the major portion (A2) of the adductor mandibulae muscle. It also forms a notch posteriorly for passage of the hyomandibular trunk of the facial nerve.

The remaining bones in the hyoid arch are too obscured by the branchial arches or other bones to allow satisfactory study. A portion of the symplectic is visible below the hyomandibular and the epihyal can barely be seen pressed against the mesial surface of each interopercle. Anteriorly, the hypohyals are situated in their normal position but are in a poor state of preservation. The basihyal plate (sometimes termed supralingual or glossohyal) is missing from the holotype. This bone may be present in the paratype as a disarticulated element; however, its identification is too uncertain to warrant description as such. Belonging to the paratype are several bones of the hyoid arch, among them a left epihyal and a right ceratohyal. These elements are large and strong. A distinct groove for the hyoidean artery crosses the entire length of the ceratohyal and part way across the epihyal to a large foramen, as in *Oncorhynchus keta* (Hikita, 1962: Fig. 48).

The urohyal is one of the longest bones in the branchiocranium. The holotype possesses a complete urohyal measuring 215 mm from the anterior end at the hypohyals to the posterior border situated almost beyond the termination of the epihyals. In the same individual, the complete right mandible measures 265 mm long. The shape of the urohyal resembles that in *Oncorhynchus* where it is proportionately longer than in other salmonines. Nevertheless, the urohyal in *Oncorhynchus* barely reaches



**Figure 7.** Comparison of right interopercles in *Oncorhynchus tshawytscha* (A), UMMZ 178987-S, and the holotype (B). Position of the anterodorsal process of the subopercle in relation to the interopercle (with dashed margin) shown at (C), drawn from same specimen as (A) but mesial view of left side. Note the similarities between the dorsal process of the interopercle in the holotype and that of the subopercle in *Oncorhynchus*. Scale bars, 1 cm.

75% of the proportionate length of the fossil urohyal. The increased size of this element can be correlated with similar development of jaw bones, branchial apparatus, and opercular series. It probably reflects the size of the sternohyoideus muscle and the important role this muscle plays in opening the mouth and branchial apparatus.

**Palatoquadrate.**—The bones of the palatoquadrate, although similar to those in other salmonines, show some pronounced modifications associated with the feeding mechanism. The endopterygoid and quadrate are the most altered from their typical condition in predatory salmonines.

Posteriorly, the endopterygoid is extended mesial to the metapterygoid and across the top of the quadrate (possibly reaching to the hyomandibular). It is in direct contact with the quadrate over this entire extension. In most other salmonines, the endopterygoid joins only the anterior dorsal corner of the quadrate while the metapterygoid is fastened by cartilage along most of the quadrate's dorsal border. The endopterygoid of *Salvelinus namaycush* parallels that of the fossil in its contact with the quadrate. The metapterygoid in the fossil has been displaced somewhat by the endopterygoid but it still may have had a cartilaginous connection with part of the dorsal edge of the quadrate. A pronounced ridge transversely crosses the dorsolateral surface of the endopterygoid at a point just in front of the junction with the metapterygoid and can be seen through the orbital opening. The metapterygoid is firmly seated on the curved posterodorsal portion of the endopterygoid and also is securely fastened to the hyomandibular. The construction and arrangement of these two pterygoid bones provide an extensive but strong area of insertion for divisions of the levator and adductor arcus palatini muscles which function in lifting the palatoquadrate arches and pulling them toward the midline, thus assisting in the closure of the mouth.

The ectopterygoid is present as in other salmonines. The palatine is rigidly united with

both the ectopterygoid and endopterygoid posteriorly. Anteriorly, it combines with the maxilla to form a large fossa for articulation with the ethmoid cartilage. Such a large fossa reflects the importance of a strong hinge between the palatoquadrate and ethmoid region facilitating the swinging out of the upper jaw on the rostrum. There appears to be no anterior palatine extension beyond this point of junction with the maxilla, as sometimes occurs in salmonines that have a continuous row of vomerine and palatine teeth. No teeth are present on the palatines of the holotype. However, there is a shelf on each bone that could have supported several strong teeth. A peculiarity of the palatine exists at its junction with the endopterygoid. In *Oncorhynchus*, the endopterygoid extends forward along the mesial side of the palatine for a considerable distance and is usually only joined to it by cartilage and soft tissue. There is no interdigitation of the two bones. As observed in the holotype of *Smilodonichthys*, the posterior end of the palatine overlaps, and fits tightly with, the anterior lateral face of the endopterygoid in the same area where it joins the ectopterygoid. The overlap involves only the posterior  $\frac{1}{3}$  of the palatine. It should be noted that the palatine is immovably joined to both pterygoids in coregonines.

Besides the broad junction with the endopterygoid, the quadrate differs from that of other salmonines in its posterior proportions. Behind the deep notch (on the mesial side) for the symplectic, the quadrate is extended downward and backward, forming a broad lateral surface to seat the anterior end of the preopercle.

**Circumorbital Series.**—In a number of its characteristics, including the proportions of the posterior infraorbitals, the circumorbital series is similar to that of *Oncorhynchus*. Except for a small missing piece below the eye at the lower orbital margin, the circumorbitals are intact on the left side of the holotype. There are a total of nine, one more than is usually found in *Salmo* and *Oncorhynchus*. Five infraorbital bones are situated behind the eye, the uppermost one, in this case infraorbital 7 (dermosphenotic, Nel-

son, 1969), receives the infraorbital canal from the pterotic. The next two posterior infraorbitals situated below the dermosphenotic have broken posterior ends; the fourth (infraorbital 4) extends at least  $\frac{3}{8}$  of the distance from the orbital rim to the anterior edge of the preopercle.

The slender bone carrying the infraorbital canal under the eye (infraorbital 2) is not complete as stated above. It joins the lacrimal, a heavy, elongate bone shaped something like a common milkweed pod. It has a blunt anterior projection and tapered posterior end. The lacrimal articulates directly, over an extended area, with another large element, the antorbital. Dorsal and posterior to the antorbital is a tear-shaped supraorbital. The form and relationships of the individual elements in the circumorbital series indicate that the eye and nares of the fossil were similar to those of other salmonines. The major difference noted is the enlargement of the three bones (lacrimal, antorbital, supraorbital) associated with the pumping mechanism of the olfactory organ (see Gosline, 1961) and the extended contact between the lacrimal and antorbital.

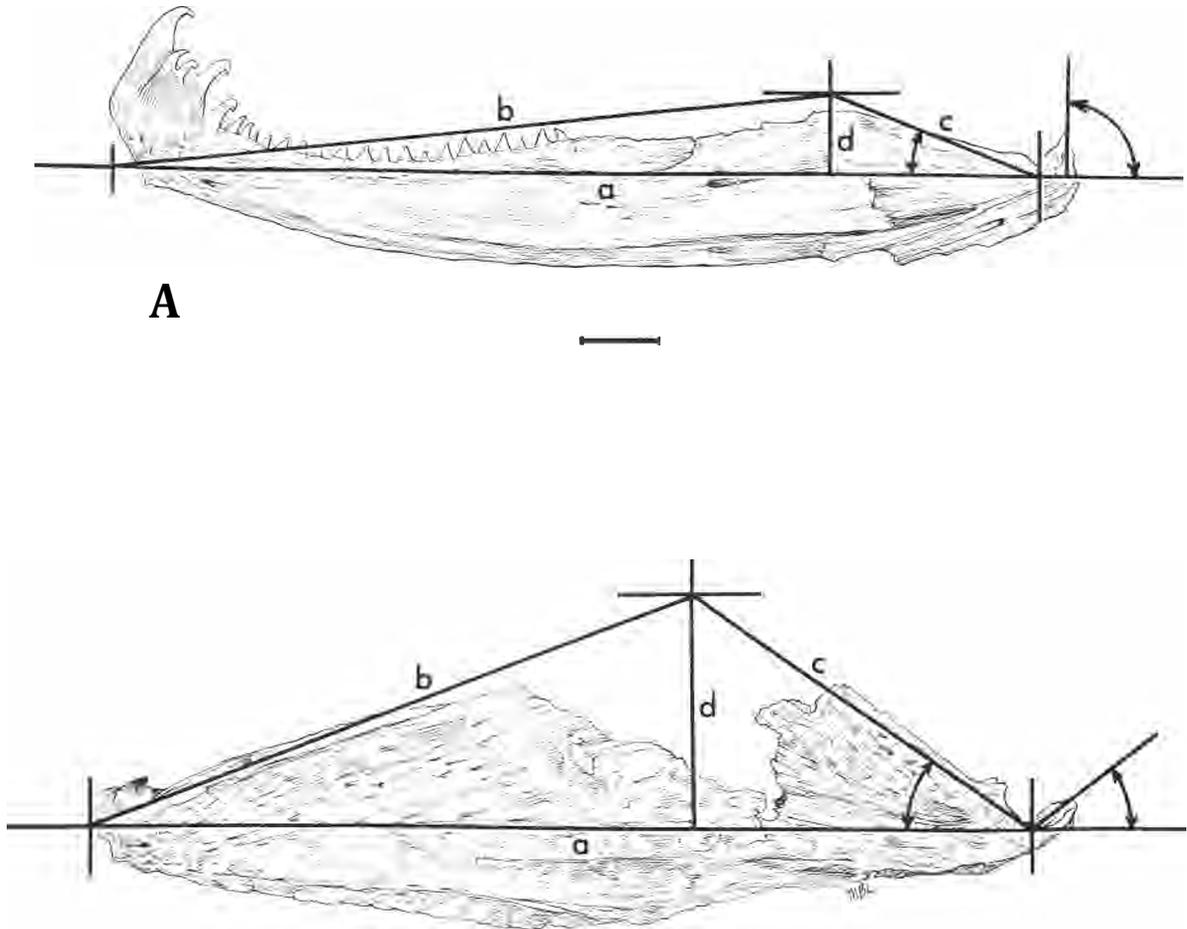
**Mandibular Region.**—The upper and lower jaw bones of the fossil are so distinctive that the species can be identified from their isolated occurrence such as at the Oregon Worden Locality (Fig. 13). In lateral view, the lower jaw has a massive appearance, being long, very deep, especially at the coronoid process, and heavy through the anterior part of the dentary. The shape is much different from the long slim jaw of *Oncorhynchus* (Fig. 8) which has a depth at the coronoid process of 20-25% of its length. Reconstructed, the depth of the fossil lower jaw is about 34% of its length. Other proportional differences are apparent in the shorter oral border of the dentary and in the longer elevated border of the articular. A linear analysis of the lower jaw is given in Figure 8.

The short oral border of the dentary can be correlated with the reduction of its dentition. One or two small teeth are seated on a

brief shelf at the anterior end of each lower jaw near the symphysis. One tooth is present on UCMP 93170; a main cusp and an accessory cusp are present on each side in the holotype. A single-cusped tooth is present on the dentaries of the paratype; in addition, on the right side, there is a smaller replacement tooth seated in a reclined position behind the first. These teeth have large osseous bases fused to the dentary and resemble in certain aspects the breeding teeth in male Pacific salmon such as *Oncorhynchus keta*. Excepting the short tooth-bearing shelf, the oral border of the dentary is a sharp ridge which shows no evidence of bearing teeth. In contrast, the tooth-bearing shelf on the dentary in *Oncorhynchus* extends nearly the entire length of the oral border. The thick anterior portions of the fossil dentaries indicate that this area was subject to considerable stress. The anterior ends of the dentaries curve toward the symphysis. When the two bones are united at their symphyseal joint, a wide interspace results. The lower jaw is quite straight, without an upturned anterior end (Fig. 8).

Another easily identifiable character of the lower jaw is the dorsal process of the articular which projects from behind the articular fossa and carries the mandibular canal. This process forms an angle of 30 degrees with a line drawn through the symphysis to the floor of the fossa (Fig. 8). In other salmonines, this angle is close to 90 degrees. The angle reflects the width of the articular fossa.

**Upper Jaw.**—When viewed from their mesial side (Fig. 9 A), the premaxillae show, anteriorly, flat triangular surfaces that were seated against a bluntly shaped azygous rostrum. In lateral and dorsal views (Fig. 9 B, C), the premaxilla has the appearance of a curved, wing-like bone, proportioned longer than wide and tapered anteriorly. The lateral surface is convex and faces slightly upwards. The curve of the dorsal border in the holotype inscribes a 65 degree arc of a circle 140 mm in diameter. Since the lateral surfaces of the premaxillae help mold the contour of the snout in salmonines, it is possible to obtain some idea of the



**Figure 8.** Linear analysis of left mandibles in *Oncorhynchus keta* (A), UMMZ 175915-S male, and the paratype (B). a, length of mandible; b, length of oral margin of dentary; c, length of ascending margin of articular; d, height of coronoid process (determined from complete mandible of holotype); anterior angle measuring slope of ascending margin of articular; posterior angle measuring orientation of dorsal process. Scale bar, 1 cm.



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TABLE 3  
COMPARISON OF OSTEOLOGICAL CHARACTERS BETWEEN *Smilodonichthys* AND  
SOME OTHER SALMONID GENERA

| Character   | <i>Smilodon-<br/>ichthys</i> | <i>Oncorhynchus</i>             | <i>Salmo</i>                  | <i>Salvelinus</i>               | <i>Corygonines</i>             |
|---|------------------------------|---------------------------------|-------------------------------|---------------------------------|--------------------------------|
| Rostral cartilage azygous (not forked)                                  |                              |                                 |                               |                                 |                                |
| Supramaxilla greatly enlarged   |                              |                                 |                               |                                 |                                |
| Premaxillary breeding teeth much enlarged                               |                              | ( <i>O. keta</i> )              |                               |                                 |                                |
| Mandible with high coronoid process                                     |                              |                                 |                               |                                 | X                              |
| Dorsal process of articular obliquely oriented                          |                              |                                 |                               |                                 | (except <i>Stenodus</i> )      |
| Cephalic sensory canal with many small pores                            |                              |                                 |                               |                                 |                                |
| Preopercle with well developed horizontal limb                          |                              |                                 |                               |                                 |                                |
| Anterior process of intercalar reaching pterotic                        | X                            | X                               | (except <i>S. gairdneri</i> ) | (except <i>S. alpinus</i> )     |                                |
| Anterior part of parasphenoid exceptionally broad (spatulate)           |                              | X                               |                               |                                 |                                |
| Posterior myodome strongly compressed                                   |                              |                                 |                               |                                 |                                |
| Supraethmoid triangular, usually notched posteriorly                    |                              | X                               | (subgenus <i>Parasalmo</i> )  |                                 |                                |
| Posttemporal fossa small  |                              |                                 |                               |                                 |                                |
| Interopercle with strong dorsal process                                 |                              |                                 |                               |                                 |                                |
| Branchiostegal rays over 15   |                              | X                               |                               |                                 |                                |
| Gill rakers over 100  |                              |                                 |                               |                                 |                                |
| Gill rakers long and compressed   |                              |                                 |                               |                                 | (subgenus <i>Leucichthys</i> ) |
| Gill rakers without teeth   | X                            | (teeth reduced in some species) |                               | (teeth reduced in some species) |                                |
| Adductor ridge of hyomandibular well developed                          | X                            | (some species)                  |                               |                                 |                                |
| Most cranial bones highly cavernous                                     | X                            | X                               |                               |                                 |                                |
| Laminar parts of dermal skull bones expanded and with fimbriate margins | X                            | X                               |                               |                                 |                                |
| Lower jaw hooked in spawning male                                       |                              | X                               | X                             | (some species)                  |                                |

stands apart among the Salmoninae by possession of the toothless maxilla and enormous premaxillary breeding teeth.

The premaxilla is an elongate, wing-shaped bone that is slightly curved (convex side faces dorsally), most likely to conform to the shape of the snout. There is no anterior ascending process. The mesial side of the bone is flat, without any articular fossa. This side was intimately

bound to the cartilaginous rostrum, a conclusion that can be reached after comparing the fossil premaxilla with that of other salmonines. Only *Oncorhynchus* among Recent salmonids possesses a premaxilla similar to the above type. Its characteristics, along with those of the snout, clearly separate *Oncorhynchus* from other salmonines. The latter all possess a premaxilla with an anterior articular fossa on its

mesial side which receives a cartilaginous knob protruding from each side of the rostrum (labial cartilage of Tchernavin, 1938, 1943). The rostrum in *Oncorhynchus* is azygous, without protruding cartilages. In addition this genus has an extended area of attachment for the posterior wing of the premaxilla.

A toothless condition of the maxilla has occurred a number of times in the evolution of the Salmoniformes, both in conjunction with microphagous and piscivorous adaptations of the jaws and teeth. When piscivorous, the maxilla tends to be excluded from the gape by an enlarged premaxilla and the palatines tend to form a powerful dentition that becomes a major part of the bite. Examples can be found in the esocids, galaxioids, and the extinct *Apatodus*, *Cimolichthys*, *Enchodus* and *Eurypholis pulchellus* (Goody, 1969). Among the Salmonidae, the predaceous types possess strong maxillary teeth but these teeth have been lost in the microphagous feeders, such as the Coregoninae. *Smilodonichthys* has no trace of the maxillary teeth, although the bone itself enters a large part of the gape. The oral border is slightly convex (suggestive of the condition in the coregonines) which appears to be a primitive teleostean feature.

Besides the toothless oral border of the maxilla, a further distinctive feature of the upper jaw of *Smilodonichthys* is the exceptionally large supramaxilla. This bone is usually an elongate structure positioned along the dorso-lateral part of the maxilla in salmonines. In *Salvelinus* it is very slender but in *Salmo* and *Oncorhynchus* a deep laminal portion extends down over the outer side of the maxilla. The supramaxilla is deepest in *Oncorhynchus*, where it is similar in form to that of *Smilodonichthys*. None of the living salmonines possess a supramaxilla of the size found in this extinct genus. Nor do we know of any teleost possessing a supramaxilla of comparable size.

The possession of modified anterior jaw teeth in anadromous breeding male individuals of some salmonine species, such as *Salmo salar*, *Salmo trutta*, *Salvelinus fontinalis* and all

members of the genus *Oncorhynchus*, is a highly specialized feature for teleostean fishes. These breeding teeth are a secondary sex character best developed in the largest mature spawning males of those forms that migrate upstream to spawning areas. Their function appears to be in display and fighting behavior between male individuals for possession of females and territory as well as display in mating with the female. Among living Salmoninae, the breeding teeth reach their largest size in members of the genus *Oncorhynchus*. In *Smilodonichthys* the premaxillary breeding teeth have reached an extreme size, so large that there is room for only one tooth on each side of the snout.

The black pigmentation of the tips of these breeding teeth appears to be a further specialization, perhaps accentuating the display behavior of the breeding male. Large black teeth are found in *Smilodonichthys* (both those of the premaxilla and dentary) and in certain species of *Salmo* (Tchernavin, 1943).

A stout mandible with a high coronoid region is found in *Smilodonichthys* and the Coregoninae among the Salmonidae. This type of mandible is characteristic of umbrids, clupeoids, some elopoids, ichthyodectids and leptolepids. It may be primitive for at least some of the lower teleosts. A similar lower jaw also occurs in the pholidophorids. Dimensions of the *Smilodonichthys* lower jaw are indicated in Figure 8. There is a large area on its mesial side for insertion of the adductor mandibulae muscle. There was little encapsulation of the muscle anteriorly by the dentary. An unusual feature of the lower jaw is its open articular fossa. Typically in salmonines a dorsal process of the articular forms the posterior enclosure of the articular fossa. This process is bound to a ridge on the posteroventral margin of the quadrate by a strong ligament. The articular fossa is deep and narrow and closely bound to the articulating condyle on the quadrate.

In *Smilodonichthys* the dorsal process of the articular is well developed but unlike the condition in other salmonines it is directed ob-

fossa is formed by the parietal, a part of which still covers a small anterior area of the fossa. The epaxial body muscles that insert in the posttemporal fossa bury most of the dorsal portion of the pterotic in salmonines, including *Oncorhynchus*. Only a narrow ridge of the pterotic bone forming the lateral wall of the fossa and carrying the supratemporal sensory canal extends above the muscle mass. In *Smilodonichthys* the fossa is a very shallow cavity of limited extent but entirely open above. The floor appears to be formed completely of bone without intervening cartilage. The small size of this fossa is explained by the fact that it has not extended as far forward as in other salmonines nor has it eroded into most of the dorsal part of the pterotic. A considerable area of this bone was exposed to the surface and not covered by the inserting muscle mass. The small and shallow depth of the posttemporal fossa in *Smilodonichthys* appears to be a primitive feature, since an evolutionary trend in the subfamily often has been toward an enlargement of the fossa in forms with large jaws and teeth. The small size of the fossa may also be correlated with the simple type of basicranial-vertebral joint.

A bone associated with the articular of the lower jaw is the interopercle. A strong ligament joins the posterior margin of the articular with the anterior end of the interopercle. All salmonids possess an interopercle—in which the height is typically less than its length (except possibly in some *Oncorhynchus*)—as appears to be true of most lower teleosts. A deep interopercle is found in the myctophoid *Aulopus filamentosus* (Goody, 1969). Among the extinct suborders Cimolichthyoidei and Enchondontoidei, discussed by Goody (1969), the interopercle is absent. These are large-jawed predators with strong teeth. In *Smilodonichthys* the shape of the interopercle with its strong dorsal process is unique among salmonids and apparently exceptional among most other lower teleosts. We suggest that the peculiar interopercle of *Smilodonichthys* is associated with the

operation of the lower jaw and the expansion of the branchial cavity.

There is a total of 29 branchiostegal rays in the holotype of *Smilodonichthys* (14 on the left and 15 on the right side). Salmonid species with this many branchiostegals are found only in the Salmoninae. Coregoninae have up to 12 on one side (*Stenodus*). *Salvelinus* usually has 10 to 12 on each side but may have an extreme of 31 rays (15 right, 16 left) in the interior western North American form of *S. "malma."* Norden (1961), Rounsefell (1962), and McAllister (1968) have summarized branchiostegal ray counts in salmonids. Of all the salmonid genera, *Oncorhynchus* possesses the highest counts, up to 19 or 20 on one side. *Hucho* has up to 14 and *Salmo* 13. *Smilodonichthys* appears to be closest to *Oncorhynchus* and *Salvelinus* in this character. McAllister (1968) concluded that the higher branchiostegal-ray counts were most likely primitive for the Salmonoidei. A similar conclusion was reached by Nelson (1970) for clupeoids. In *Smilodonichthys* the branchiostegal formula is 9-1-5, with 5 supported by the epihyal, 9 by the ceratohyal, and 1 articulating with the cartilage between these two bones.

*Smilodonichthys* has upwards of 110 gill rakers on the first arch. The number is probably not complete for there are more than this on the second arch, which is better exposed than the first and easier to count. This is an exceptionally high number for a salmonid as it exceeds the highest known number by more than 30. *Coregonus muksun*, a species of the subgenus *Coregonus* living in northern and western Siberia, has been reported by Himberg (1970) to range as high as 78 gill rakers. *Prosopium* may have up to 45 in *P. gemmiferum* (Norden, 1970), *Stenodus* has a maximum of about 30, 32 in *Salmo* (*S. obtusirostris*, Behnke, 1968), *Brachymystax* 31 (Shaposhnikova, 1968), *Hucho* 19 (Shaposhnikova, 1968), *Salvelinus* 33 (Berg, 1948) and a maximum of 42 in *Oncorhynchus* (Hikita, 1962). The upper limit for the number of gill rakers on the first arch in the

Salmoninae is close to 40 and almost twice that number in the Coregoninae. *Thymallus* has a maximum of 33 gill rakers ( Berg, 1948). *Smilodonichthys* has a greater resemblance to the Coregoninae in its numerous gill rakers.

Those teleosts that possess a great number of closely spaced, long and attenuated gill rakers are in most cases adapted for feeding on planktonic organisms. Examples can be found in the Clupeoidei, Scombroidei, Chanoidei, Cyprinoidae, Characoidei, Elopoidei, Atherinomorpha, and Carangidae.

The length and spacing of individual gill rakers may indicate as much about the diet as does the number (Kliewer, 1970) . Among the species of *Prosopium*, *P. gemmiferum* is a planktonic feeder with the longest and greatest number of gill rakers of any species in that genus. Unlike *Smilodonichthys*, however, the gill rakers of *P. gemmiferum* are well equipped with many small teeth ( Norden, 1970) . Those coregonines in the subgenus *Leucichthys* that are characteristically planktonic feeders, such as *Coregonus artedii*, have long, tapered gill rakers equipped with many small teeth. These teeth form an interlocking mesh as illustrated by Vladykov (1970, Fig. 13) . The same is true of *Allothunnus fallai* (Tominaga, 1966, Fig. 2 B) of the Scombroidei.

In *Smilodonichthys* the large number of long, attenuated rakers, their toothless condition and closely spaced and overlapped arrangement, plus the elongation of the rows, suggest a feeding method adaptable to small pelagic organisms such as are now present in the North Pacific Ocean. The special features of this feeding mechanism and the geographic location of the fossil leave little doubt that this species fed in the ocean during its life history.

Among the Salmonidae a well developed (laterally projecting) adductor ridge of the hyomandibular is found in the Coregoninae, Thymallinae and sporadically through the Salmoninae where it occurs in *Brachymystax* and in some species of *Oncorhynchus* and *Salmo*. Elsewhere among lower teleosts it is variously developed but particularly noticeable in *Elops*,

*Tarpon*, and *Esox*. The ridge appears in the Myctophiformes, Percopsiformes, Beryciformes and widely through the Perciformes. The adductor ridge is assumed to be a primitive character where it occurs in the Salmonidae including *Smilodonichthys*.

The dermal bone structure in *Smilodonichthys* combines a highly cavernous internal organization throughout the thicker portions of the bone with very thin laminate-like marginal areas. The latter are expanded in the bones of the cheek region such as the posterior infraorbitals, preopercle, and interopercle, and probably also in the opercle and subopercle. Due to the delicate nature of the peripheral parts of these expanded areas, preservation was poor. What sections remain, as on infraorbital 3, indicate that the margins were not entire but fimbriate as in *Oncorhynchus*.

The cavernous internal structure is nicely displayed in bones that have been fractured transversely to the longitudinal course of the trabeculae such as the right interopercle of the holotype. Here the cross section of the bone has the appearance of a honeycomb with numerous partitions enclosing interstices. The total effect is probably one of lightness plus strength. Other salmonines exhibit this type of dermal bone structure but to a lesser degree. Transverse sections were made through the anterior dentaries of *Smilodonichthys*, *Oncorhynchus*, and *Salmo* for the purpose of comparison (Fig. 12). It is readily apparent that the cavernulous condition of *Oncorhynchus* exceeds that of *Salmo* and approaches the condition in *Smilodonichthys*. Various authors have remarked about the fat storage ability of muscle and bone in anadromous *Oncorhynchus*. The unusual structure of the fossil bone described here might be correlated with anadromous behavior.

The lower jaw of large male salmonines in spawning condition is often curved upward or hooked at the tip ( Morton, 1965 ) . This hook or kype is both the result of growth of the dentary bone at the symphyseal region and addition of soft tissues dorsal to the symphysis. Tchernavin (1943, in reference to *Salmo*

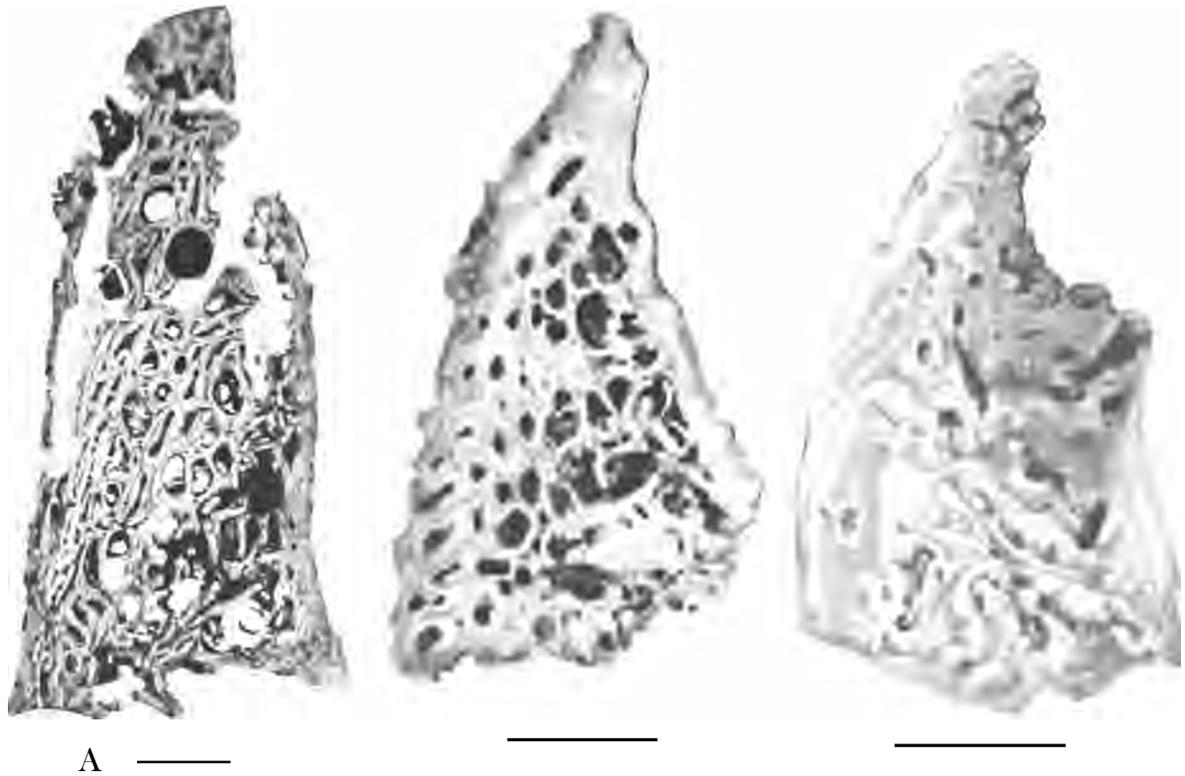


Figure 12. Transverse sections of dentaries showing bone structure. A, *Smilodonichthys rastrosus*, UCMP 93170; B, *Oncorhynchus tshawytscha*, UMMZ 178987-S male; C, *Salmo trutta*, UMMZ 175169-S male. Scale bar, 0.2 cm.

salar) stated that the extent of the kype is mainly dependent on the size of the individual but it is also better developed in anadromous than in resident populations of the same species. UMMZ collections include examples of male fish with hooked lower jaws among the following species: all North American species of *Oncorhynchus*, *Salmo trutta*, *S. gairdneri*, *S. aguabonita*, *Salvelinus fontinalis*, *S. alpinus* and *S. malma*.

The absence of any apparent modifications in the symphyseal area of the lower jaw of individuals believed to be males in spawning condition, indicates that no kype was developed in *Smilodonichthys*.

Comparison with *Stenodus*.—A fruitful comparison can be made between the fossil and *Stenodus* because of certain important cranial characters shared by both genera. *Stenodus* is

a fairly large-mouthed predaceous genus that is believed to have evolved from a smaller-mouthed microphagous feeder like *Coregonus* (Norden, 1961). The primary evidence for believing this is that *Stenodus* has lost its maxillary teeth and that it possesses an enlarged branchial apparatus with long, finely toothed gill rakers. The toothless maxilla unites all the Coregoninae but can no longer be regarded as diagnostic for this subfamily if the toothless character of the fossil maxilla proves to be constant. In *Stenodus*, the oral margin of the maxilla is convex, the supramaxilla is large, and the mouth opening is slightly superior. The anterior ends of the maxillae bend sharply inward and have rounded articular surfaces for efficient rotation on the palatine and rostral cartilages. The lower jaw is particularly interesting because it shares with the fossil: a nearly

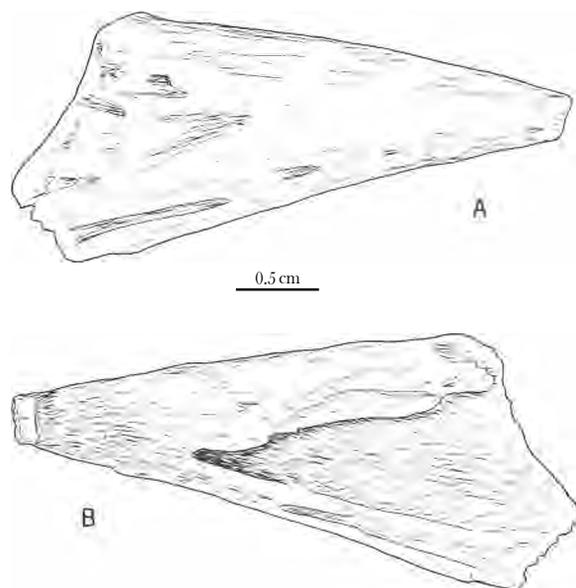


Figure 13. Right dentary referred to *Smilodonichthys*, from *Worden* Locality, UMMP V58064. A, lateral view; B, mesial view.

straight ventral border, a high coronoid process, a large area for Meckel's cartilage and the insertion of the mandibular portion of the adductor mandibulae muscle, a similarly placed coronomeckelian ossification, a heavy construction of the dentary, teeth present only near the symphysis, a pronounced inward curve of the anterior end of the dentary, and an open articular fossa. The articular has a tube-like posterior projection that receives the preoperculo-mandibular canal. Other characters of *Stenodus* of interest in reference to the fossil are its large *preopercle* with well developed horizontal arm, and the long, tapered gill rakers, mostly with denticulations.

The agreement in features of the mouth and gill rakers between *Stenodus* and the fossil indicates similarities in the method of feeding. However, this may not be the only explanation. Some of the osteological characters which in the past have been used to divide the salmonines and coregonines break down in this comparison. This is further evident in the branchiostegal count of *Stenodus*, highest among the Coregoninae, the large, heavy orbitosphenoid,

and the parietals partly divided by the supra-occipital. Boulenger (1895) recognized some of these intermediate characters in *Stenodus*. The complete circumorbital ring in *Stenodus* appears to be a very primitive character in teleost fishes (Gosline, 1965), as well as its completely toothed tongue and basibranchials (Nelson, 1969; Vladykov, 1970). It is suggested here, in light of evidence brought forth, that *Stenodus* possesses many primitive features shared by both the Coregoninae and Salmoninae.

**Comparison with Other Fossil Salmonids.**—There is practically no published fossil record for *Oncorhynchus* in North America. Jordan (1907) referred to a few toothed bones from Pleistocene Fossil Lake, Oregon, but these specimens are very doubtfully those of an *Oncorhynchus* (see Uyeno and Miller, 1963). An otolith of *O. tshawytscha* was recently reported and illustrated from Pleistocene sands in northern California (Fitch, 1970: 27). Although Neave (1958) expressed the view that *Oncorhynchus* arose from *Salmo* during Pleistocene time, evidence presented below shows that *Oncorhynchus* is at least as old as Middle Pliocene.

Fragmentary remains of what appears to be an extinct species of *Oncorhynchus* have been recovered from the Glens Ferry Formation of southern Idaho. Identification is based on the anterior part of a dentary with three enlarged breeding teeth attached (Fig. 14 A) of the type characteristic of the spawning male *Oncorhynchus*. An incomplete left dentary and posterior half of a parasphenoid closely resemble those of *Oncorhynchus*. A median ridge located at the point of flexion on the fossil parasphenoid (Fig. 14 B) matches that of *Oncorhynchus*, particularly *O. kisutch*.

Abundant remains of at least one extinct *Oncorhynchus*-like species have recently been found at the Worden Locality near Klamath Falls, southwestern Oregon (Fig. 14 E-I). They occur there in association with *Smilodonichthys*. The Worden specimens are distinguished from Recent species by the high coronoid re-

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