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AN OLIGOCENE MUDMINNOW (FAMILY UMBRIDAE)
FROM OREGON WITH REMARKS ON RELATIONSHIPS
WITHIN THE ESOCOIDEI

BY TED CAVENDER

THE OLIGOCENE FISH *Novumbra oregonensis* described in this paper is the first reported fossil record of the family Umbridae in North America. Judging from the morphology of its skeleton this species is very close to the Olympic mudminnow, *Novumbra hubbsi* Schultz (1929), which lives today in the lowland streams from just north of the Quinault to the Chehalis River watersheds of western Washington (McPhail, 1967; Meldrim, 1968). Because of its restricted range, small size, and obscure habits, *Novumbra hubbsi* is rarely seen alive and is scarce in museum collections. Until recently (Meldrim, 1968) little or no information was available on the life history and behavior of this species although its osteology has been fairly well understood, thanks to a detailed study by Chapman (1934). The fossil material is of particular interest because it substantiates the statement (Schultz, 1929) that *Novumbra* is a survivor of a much older fish fauna in the northwestern United States and British Columbia (Amiidae, Catostomidae, Hiodontidae are families known to belong to this fauna, Cavender, 1966, 1968). During Middle Oligocene time *Novumbra* apparently had a wider distribution than at present since it lived further east in the John Day basin of northcentral Oregon (present day Columbia River drainage).

In addition to describing the fossil remains, I include a comparison with the European, Lower Tertiary, *Palaeoesox* and in the discussion section deal with the problem of relationships within the suborder Esocoidei using osteological data from the living forms. Finally, a brief report is given on a later Tertiary fish from Alaska which is referred to the genus *Dallia*.

MATERIALS AND METHODS

In dealing with the osteology of *Novumbra* and in reviewing the classification of the esocoid group, I have extended my observations to the three species of *Umbra*: *U. limi*, *U. pygmaea*, and *U. krameri*, to four species of *Esox*: *E. americanus*, *E. niger*, *E. lucius*, and *E. masquinongy*; and to *Dallia pectoralis*. Cleared and stained preparations were made with the enzyme method (Taylor, 1967) for each of the above including *Novumbra hubbsi* and dry skeletal preparations were examined for all except *Novumbra hubbsi*, *Umbra pygmaea* and *Umbra krameri*. The Recent specimens studied are from collections in The University of Michigan Museum of Zoology (UMMZ). All *Novumbra hubbsi* examined were collected from the type locality of Schultz (1929).

The fossil material (11 specimens including the holotype) is housed in The University of Michigan Museum of Paleontology (UMMP).

The type specimens of *Novumbra oregonensis* were collected in July, 1964, by two high school students from Portland, Oregon, Edward Frazer and William Prince, while participating in the summer science-camp program (Camp Hancock) of the Oregon Museum of Science and Industry (OMSI). Other specimens were collected in 1965 and 1966 by Lee Jenkins of Hood River, Oregon, and in 1966 by a field party consisting of Lee Jenkins, Michael Uhtoff, Michael Lappé, and the author.

The following fossil specimens comprise the total known material of *Novumbra oregonensis* (other specimens have probably been collected by young students from Portland, Oregon, staying at Camp Hancock but the whereabouts of these fossils is unknown): UMMP V57007—holotype, Knox Ranch loc., complete specimen except for caudal fin (part and counterpart), collected by Edward Frazer 1964; UMMP V57008—paratype, Knox Ranch loc., nearly complete specimen, part of axial skeleton disarticulated (part and counterpart), William Prince 1964; UMMP V57004, Knox Ranch loc., disarticulated skull, UMMP V57005, Knox Ranch loc., articulated skull, OMSI-Camp Hancock; UMMP V57014, Allen Ranch loc., disarticulated skull (part and counterpart), UMMP V57010, Allen Ranch loc., disarticulated skull (part and counterpart), Lee Jenkins, 1965; UMMP V57009, Allen Ranch loc., disarticulated skull, Lee Jenkins, 1966; UMMP V57006, Knox Ranch loc., right opercle, UMMP V57011, Allen Ranch loc., left frontal (part and counterpart), UMMP V57012, Allen Ranch

loc., right dentary (part and counterpart), UMMP V57013, Allen Ranch loc., ceratohyal, coll. T. Cavender and party 1966.

The fossil referred to *Dallia* sp. is the property of the University of Alaska. I do not have data on the exact discovery site. Troy Péwé, Department of Geology, University of Alaska, has communicated the following information concerning the locality. The fossil is from the Kenai Formation on the west end of the Kenai Peninsula near Homer, Alaska. The specimen was collected by Charles Rainwater in 1964. The fossil apparently was taken from a cliff on the north shore of Kachemak Bay and approximately 5 miles NE to E from Homer Spit.

Using this information the locality falls between Miller's Landing and Fritz Creek on the "Geologic map of the southern part of the Homer District, Kenai Peninsula, Alaska" (Barnes and Cobb, 1959). The sediments exposed in the bluffs between Homer and Fritz Creek are part of the type section of the Homerian stage of the Kenai Formation (Wolfe, Hopkins and Leopold, 1966), and are assigned a probable Late Miocene age based on a paleobotanical analysis of the Homerian flora by Wolfe (1966).

Fossil specimens from the John Day Formation were studied principally from latex casts stained black with India ink and highlighted with ammonium chloride. Photographs of the casts were taken on plus-x film with an SLR camera, 50 mm Miranda Soligor lens, and bellows extension.

LOCALITY AND AGE

The *Novumbra* fossils were found at two separate outcrops 20 miles apart within the lower member (Hay, 1962) of the John Day Formation. The first is the famous Bridge Creek flora (Allen Ranch) locality, Wheeler Co., Oregon which lies within the Painted Hills area, 9 miles northwest of Mitchell, Oregon (NE $\frac{1}{4}$, Sec. 10, T 11 S, R 20 E). Merriam (1901) gave a general geologic description of the area and Chaney (1924, 1927, 1948a) illustrated and discussed the locality in more detail.

The second fossil *Novumbra* locality, which yielded the type specimens, is known as the "Knox Ranch" leaf locality. It takes its name from the nearby old Knox Ranch (shown on the 1926 USGS Mitchell Quadrangle map). The fossil site is about 6.7 miles northeast of Clarno, 28 miles north of Mitchell, Wheeler Co., Oregon, NE $\frac{1}{4}$, S $\frac{1}{2}$, Sec. 20, T 7 S, R 20 E, on the south bank of the narrow dirt road leading to the Knox ranch house. Here buff-colored to whitish-gray, tuffaceous,

lacustrine shales outcrop in a small exposure. These beds are mapped by E. M. Taylor (unpublished thesis) as being John Day Formation (see Baldwin, 1964) for Taylor's geologic map of the Clarno basin, Mitchell Quadrangle, Oregon. Fossil leaves are abundant and probably belong to the Bridge Creek flora.

The fish at the Allen Ranch and Knox Ranch localities were found by splitting small blocks of the tuffaceous, lacustrine shale or mudstone. At both of these localities the fossils occur as imprints on the slabs together with impressions of leaves belonging to the Bridge Creek flora. The fossil-bearing rock is whitish-gray in appearance and turns to a buff color on weathering.

A potassium-argon date of 31.1 million years has been determined by Evernden et al. (1964) for the Bridge Creek flora horizon in the lower division of the John Day Formation. The locality from which the dated sample was taken was given as NW $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 1, T 11 S, R 20 E, Wheeler County, central Oregon. Since the fossil *Novumbra* was found in nearly equivalent strata to those which were radiometrically dated, its age at the Allen Ranch locality can be taken from the potassium-argon date. Evernden et al. (1964) assigned an Orellan (Middle Oligocene) age to the Bridge Creek flora. Chaney (1927) interpreted the Bridge Creek flora as being Upper Oligocene in age after a comparison with other Oligocene floras of America and Asia.

SYSTEMATIC DESCRIPTION

Taxonomic assignment of the new species is based on my interpretation and analysis of the fossil remains and thus involves only osteological evidence. I have used a numbering system below in order to compare the characters of the fossil with a revised list of osteological features of the suborder and family. The bone terminology conforms mainly to that of Weitzman (1962, 1967).

SUBORDER ESOCOIDEI (partly from Berg, 1936)

This Holarctic freshwater group possesses the following: 1) paired prothmoids, 2) maxilla toothless but bordering gape, 3) premaxilla bearing teeth but not protractile, 4) pelvic fins abdominal, closer to origin of anal fin than to insertion of pectorals, 5) at least part of dorsal fin opposed to anal, 6) upper and some lower intermuscular bones except in Recent *Dallia pectoralis*, 7) caudal skeleton with two ural centra, all hypurals and parhypural (last haemal spine and arch) auto-genous, first hypural much expanded distally, usually the largest of

four to six, one pair of uroneurals, 8) absence of an orbitosphenoid, 9) absence of a well ossified median endochondral ethmoid element (lateral ethmoids present), 10) absence of the mesocoracoid in the pectoral girdle, and 11) possession of cycloid scales. Two families: Esocidae and Umbridae.

The fossils show 1, 2, 3, 4, 5, 6, and 7. The remaining characters listed were not seen.

UMBRIDAE

Members of this family are small esocoid fishes characterized by the following: 1) torpedo-shaped body, 2) round to very slightly emarginate caudal fin, 3) 33 to 42 vertebrae, 4) a few to most of the vertebral centra elongate and constricted anteriorly, 5) snout and jaws not greatly elongate, 6) 4 to 9 branchiostegals, 7) cephalic sensory canals and pores relatively large in the frontals and preopercle, 8) no lateral line, 9) parietals diminutive, positioned on each side of the supraoccipital, 10) well-developed but sometimes shallow posttemporal fossae that are open above, 11) the infraorbital series is incomplete, 12) no supraorbital, 13) basibranchial dentition incomplete. Three genera: *Umbr*, *Novumbra*, *Dallia*.

The fossils show: 1, 3, 4, 5, 7, 10, 11.

Novumbra Schultz 1929

Umbrids possessing a supramaxilla, dentary carrying mandibular branch of preoperculomandibular sensory canal enclosed in bone with 2 or 3 pores, vertebrae 37-40, anal fin rays more than 8, small scales with basal radii but no more than 60 vertical scale rows on body. Two species, *Novumbra hubbsi* and the fossil form described below.

The fossil agrees in the above characters except that its squamation and tail fin are unknown.

Novumbra oregonensis, new species

HOLOTYPE.—UMMP V57007, a nearly complete individual, except for the caudal fin, is represented by impressions of the right and left sides; standard length 87 mm; collected at the Knox Ranch locality, Wheeler Co., Oregon, by Edward Frazer, July, 1964.

DIAGNOSIS.—An extinct species differing from *Novumbra hubbsi* in the structure of the cleithrum in the pectoral girdle and of the parasphenoid, frontal, opercle and dentary in the skull. Ossified lower limb of cleithrum expanded so that its deepest portion is at its anterior end. In *N. hubbsi* the ossified lower limb of the cleithrum is tapered

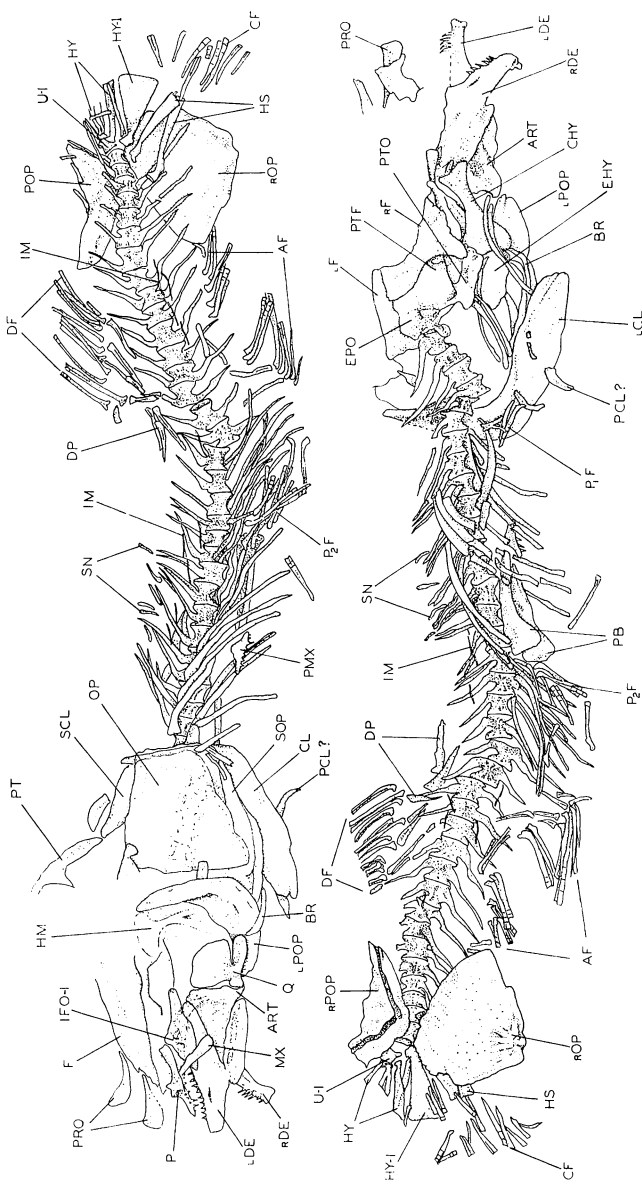


FIG. 1. *Naxumbra oregonensis* n. sp., holotype; UMMMP V57007, left side above, right side below, drawn from latex positives; AF, anal fin; ART, articular; BR, branchiostegal; CF, caudal fin; CHY, ceratohyal; CL, cleithrum; DE, dentary; DF, dorsal fin; DP, dorsal pterygiophore; EHY, epihyal; EPO, epiotic; F, frontal; HM, hyomandibula; HS, haemal spine; HY, hypural; IFO, infraorbital; IM, intermuscular bones; L, left; MX, maxilla; OP, opercle; P, palatine; PB, pelvic bone; PCL, postcleithrum; P₁F, pectoral fin; P₂F, pelvic fin; P₃F, pelvic fin; PMX, premaxilla; POP, preopercle; PRO, proethmoid; PT, posttemporal; PTF, posttemporal fossa; PTO, pterotic; Q, quadrate; R, right; SCL, supra-cleithrum; SN, supraneural; SOP, subopercle; U, ural vertebra. X2.

toward the anterior end. Parasphenoid broader anteriorly than in *N. hubbsi*, ossified ascending wings of parasphenoid tend to enclose the internal carotid foramina; posterior part of frontal barely showing transverse ridge marking anterior limit of posttemporal fossa. In *N. hubbsi* there is a very noticeable excavation on the posterior part of the frontal caused by the anterior extension of the posttemporal fossa; supraorbital sensory canal contained less conspicuously within the frontal bone whereas in *N. hubbsi* the bony tube of the canal is more elevated above the surface of the frontal; opercle with posterior border usually fimbriate, in *N. hubbsi* the opercle has a smooth, posterior border with rounded corners; dentary with a longer tooth row than in *N. hubbsi*, and, the mandibular sensory canal enclosed in the lower fork of the dentary is also not so elevated, superficially, in a bony tube, as in *N. hubbsi*.

DESCRIPTION OF HOLOTYPE.—The skeleton (Fig. 1, Pl. I) is mostly in an articulated condition although some of the fin rays and the skull roof are partly detached. The standard length measurement (given above), as some of the others, is only approximate because of a distorted vertebral column; an estimated undistorted standard length is slightly longer, about 90 mm; distance from snout to pelvic insertion 51 mm, to anal origin 63 mm, body depth at dorsal origin about 15 mm, head length 30 mm, length of lower jaw 14 mm.

The head appears proportionately very long, possibly due to a slight posterior displacement of the opercle. The head steps into the standard length about 3 times; in *N. hubbsi* the head goes into the standard length about 3.5.

The skull shows the presence of paired proethmoids, one of which is also visible in UMMP V57004 (Fig. 2, B). At the rear of the skull a large posttemporal fossa can be seen on the right side. The frontal borders the fossa anteriorly and has a concave posterior border. There is no sign of a parietal. The latter probably is very small and occupies a position lateral to the supraoccipital where it contacts anteriorly only the posterolateral corner of the frontal as in *N. hubbsi*.

The frontal appears to be a more heavily ossified bone (Pl. II, 3) than in *N. hubbsi* and the supraorbital canal although large is not so superficial.

Endochondral ossifications of the neurocranium are not visible in any detail. The parasphenoid although not preserved in the holotype is well shown in other specimens (UMMP V57014, Fig. 2, C; V57010, Fig. 3, C). It is a broader bone in its anterior part than in *N. hubbsi*

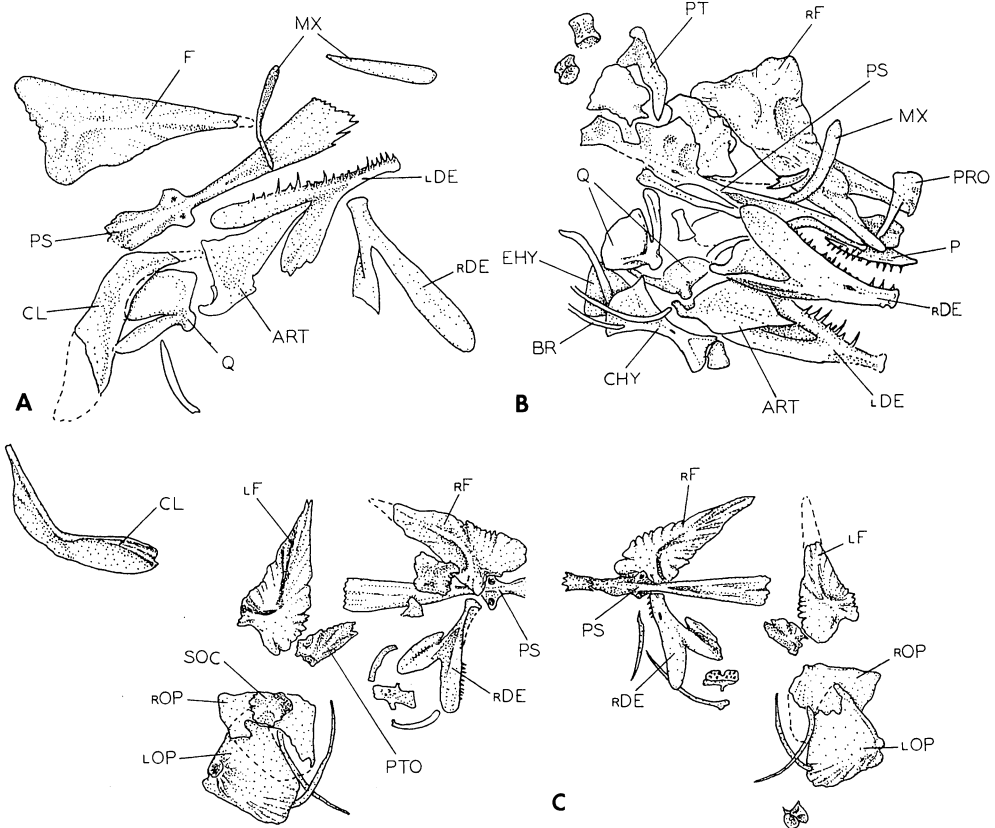


FIG. 2. Interpretations of specimens of *Novumbra oregonensis* drawn from latex positives. (A) disarticulated skull, UMMP V57009, X2.3, (B) right side of disarticulated skull, UMMP V57004, X1.8, (C) disarticulated skull, left and right sides, UMMP V57014, X1.5; PS, parasphenoid; SOC, supraoccipital; other abbreviations as in Fig. 1.

and the ascending wings have a greater anterior to posterior dimension and appear to enclose completely the internal carotid foramina.

In the bones of the opercular series, the preopercle is strongly bent with well-developed horizontal and vertical limbs. These meet at an angle slightly greater than 90° . The preopercular sensory canal is large; in the holotype it is collapsed. Other specimens (Fig. 3, A, C) indicate that 5 pores are present as in *Novumbra hubbsi*. There is a disarticulated right opercle that came to rest on the caudal peduncle.

It has a fimbriate posterior margin, a well-developed flange above the opercular socket, and a pronounced bulge along the middle of the anterior margin. Just enough of the subopercle is visible to show that it is elongate, with a large anterodorsal projection that is characteristic of esocoids. The branchiostegals are scattered and incomplete. About 8 (not all from one side) can be counted. Supporting them is a ceratohyal with the epihyal still articulated.

Of the palatoquadrate, the quadrate, mesopterygoid, ectopterygoid and palatine are visible. The latter is an elongate bone with strong teeth mainly in one row but apparently with a few small teeth placed mesially to the main row. The ectopterygoid is covered anteriorly by a triangular infraorbital-1 (lachrymal) little disturbed from its natural position and marking the anterior border of the orbit. There is a slight suggestion of a dorsal prominence above the bend in the ectopterygoid. In *Esox* there is a well-developed dorsal process of the ectopterygoid that articulates with the lateral ethmoid. *Novumbra hubbsi*, *Umbra*, and *Dallia* do not have such a structure. In *Dallia* the ectopterygoid and palatine are united into one bone.

One of the premaxillae of the upper jaw is disarticulated and lies in the abdominal region. It is a small, short bone with 7 or 8 relatively strong teeth in a single series. The maxilla is toothless. These last two bones are similar to those of *Novumbra hubbsi*. No supramaxilla is visible in the holotype but this bone is well shown in UMMP V57005 (Fig. 3, A).

The articulation of the lower jaw lies below the middle of the orbit. There is a single row of long sharp teeth on the dentary (Fig. 2, A). Each anterior tooth curves mesially and posteriorly. The teeth are approximately 1 mm long where the least depth of the dentary is 1.5 mm. The tooth row extends along 90% of the oral border of the dentary, a little farther up the coronoid process than in *N. hubbsi*. The lower forks of both dentaries bearing the sensory canals are nicely displayed in the holotype. The articular is a heavily ossified bone with a steeply rising posterior border.

Certain elements of the pectoral girdle (cleithrum, supracleithrum, posttemporal) show a fair amount of detail but there is no sign of the coracoid and scapula. A broken element is present that could be a postcleithrum.

The cleithrum has a distinctive expanded lower limb. A relatively large, strongly-forked posttemporal is partly visible.

Little is left of the paired fins. The pelvic bones and a few rays

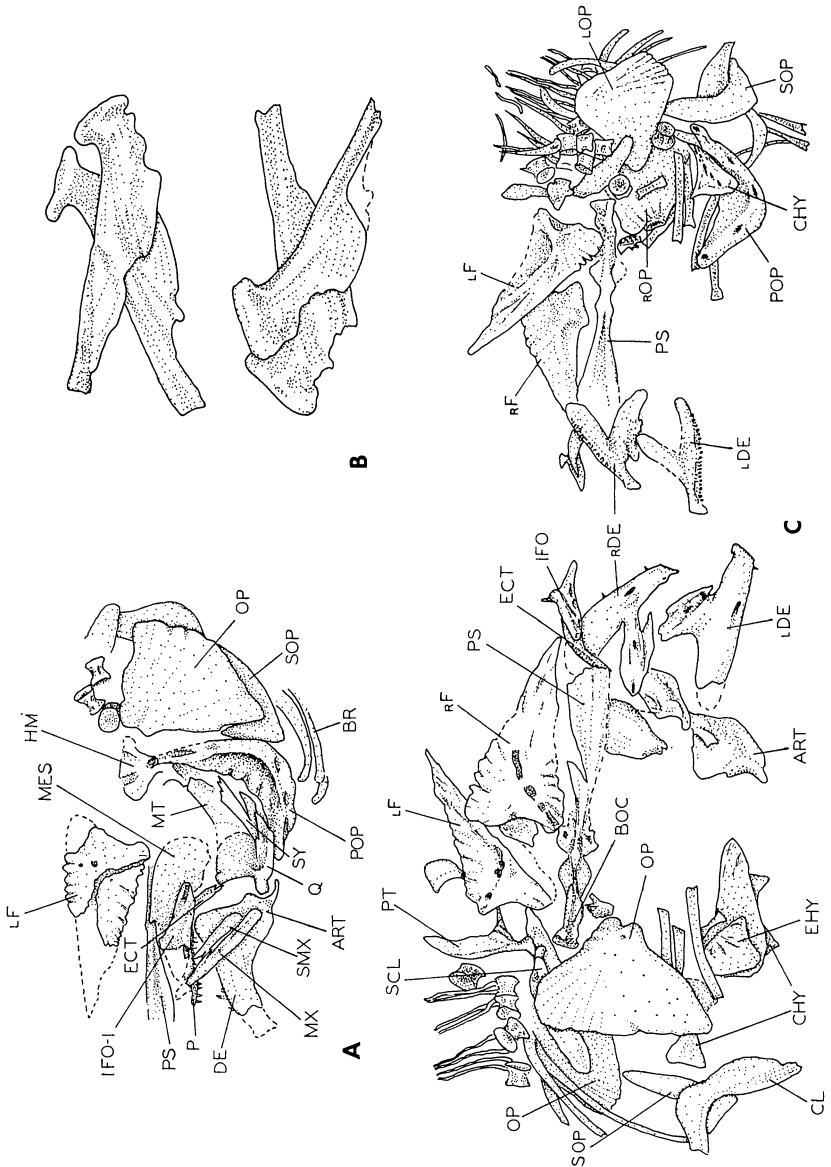


FIG. 3. Interpretations of specimens of *Novumbra oregonensis* drawn from latex positives. (A) left side of incomplete skull, UMMP V57005, X2.2; (B) pelvic bones, UMMP V57008, left side above, right below, X6; (C) disarticulated skull, UMMP V57010, right side on left, X2.3, left side to right, X1.5; ECT, ectopterygoid; MES, mesopterygoid; MT, metapterygoid; PS, parasphenoid; SMX, supramaxilla; SY, symplectic; other abbreviations as in Fig. 1.

indicate that the insertion of the pelvic fins was posterior to the mid-abdominal line.

There are 38 or 39 vertebrae in the axial skeleton; about 18 or 19 of these are caudal vertebrae. The last vertebral centrum (ural 2) is not visible but was included in the count since it is present in the paratype UMMP V57008. The caudal centra are constricted and mostly symmetrical in appearance (lateral view). There are fine ridges and reticulations on the sides of the centra but preservation is not good enough to determine if a uniform pattern exists. Small, very slender upper and lower intermuscular bones are present, the latter in the post-abdominal region only. Supraneurals are also present in front of the dorsal fin. The pleural ribs are strong and well ossified.

The caudal skeleton is slightly disarticulated and the upper hypurals are only partly visible. There is a large expanded hypural 1 that is separate from a slender hypural 2. Both articulate with ural centrum 1 which is well shown. These caudal parts are as they appear in *N. hubbsi* except that in the latter, hypurals 1 and 2 sometimes partially fuse.

Only a few proximal parts of the caudal fin rays are preserved. The dorsal and anal fins are approximately opposite one another well back on the body. It is difficult to establish their exact positions because of a distorted vertebral column. About 10 large rays and 10 pterygiophores can be counted in the dorsal fin and the anal shows a total of about 12 rays. These fins are partly disarticulated and are probably not complete.

The paratype UMMP V57008 (Fig. 4) is a slightly smaller individual than the holotype. It has the snout and caudal fin missing and the axial skeleton is disarticulated through the region of the dorsal and anal fins. There are 38 or 39 vertebrae. This specimen, represented in part and counterpart, confirms characters of the cleithrum, posttemporal, preopercle, subopercle, and pelvic bones described in the holotype.

DIAGNOSTIC BONES.—For comparative purposes I have illustrated the diagnostic skull bones of *Novumbra oregonensis* along with their equivalents of *N. hubbsi*.

Frontal (Fig. 5L, Pl. II, 3).—The sensory canals are raised above the dorsal surface of the frontal in *N. hubbsi* to a greater degree than in the fossil species. In both species the epaxial trunk muscles insert forward onto the top of the skull where there are depressions, here termed posttemporal fossae, to receive the muscles. In *N. hubbsi* these muscles reach forward onto the posterior parts of the frontals. The



FIG. 4. *Novumbra oregonensis* n. sp., paratype; UMMP V57008, right side above, left below; drawn from latex positives; BOC, basioccipital; PS, parasphenoid; UN, uroneural; other abbreviations as in Fig. 1. X2.3.

latter each shows a transverse ridge marking the anterior limit of muscle insertion. This feature is much smaller or non-existent in *N. oregonensis*, but *Dallia pectoralis* has a similar transverse ridge farther forward on the frontal although the posttemporal fossa itself is shallower. *Novumbra*, *Umbra*, and *Dallia* have in common a similar construction of the back part of the skull involving the posttemporal fossae which is considerably different from *Esox*, where the parietal sutures across the full width of the posterior margin of the frontal extending between the pterotic and supraoccipital and covering the anterior limit of the posttemporal fossa.

Parasphenoid (Fig. 5, A, C, Pl. II, 6).—The figure shows an obvious difference in relative width between the parasphenoid of the fossil and that of *N. hubbsi*. The more expanded anterior extension of the parasphenoid is also found in *Umbra* and *Dallia*. The parasphenoid of *Esox* is distinguished from the fossil by its more elongate proportions and its tapered anterior end. A pair of foramina are enclosed by the ascending wings of the fossil parasphenoid. These are interpreted as the internal carotid foramina, only evidenced as an emargination in the lower posterior border of the ascending wing in *N. hubbsi*. The difference lies in the extent of ossification of the ascending wings. In *hubbsi* only that portion of this structure in front of the internal carotid is ossified. The character appears to be a variable one within the suborder. In *Umbra limi* the foramina can be enclosed by the ascending wings (Fig. 5, D).

Opercle (Fig. 5, H, Pl. II, 1, 4).—The most distinctive characteristic of the fossil opercle is its fimbriate or crenulate posterior border, a feature found elsewhere among the esocoids in the genus *Esox*. *Novumbra hubbsi* possesses an opercle with a smooth posterior border. There are also distinctions in the anterior and dorsal borders of the fossil opercle of *oregonensis*.

Dentary (Fig. 5, J, Pl. II, 5).—A single row of teeth extends along almost the entire oral border (90%) of the dentary. This resembles the condition in *Esox*. In *Novumbra hubbsi* it extends about 65%. The fossil has the mandibular sensory canal contained in the well-ossified lower fork of the dentary and not so much in a superficial bony tube as in *N. hubbsi*. The so-called "inframandibular" bone of *Umbra* and *Novumbra* is either the divorced bony tube surrounding the sensory canal or the reduced part of the lower fork of the dentary supporting the sensory canal which is not enclosed in a bony tube.

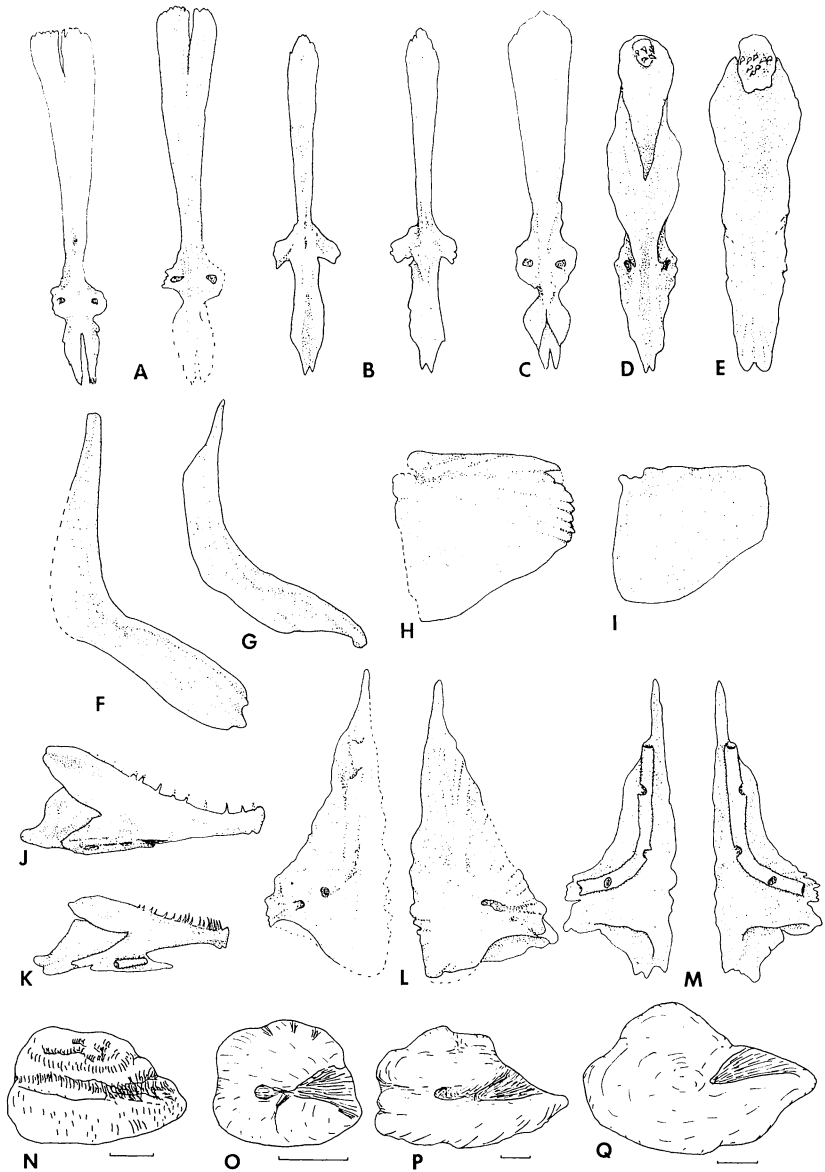


FIG. 5. Comparison of individual skeletal elements. (A) Parasphenoid of *Novumbra oregonensis* n. sp., UMMP V57014, X2.4, (B) same of *N. hubbsi*, UMMZ 179398, X5.4, ventral aspect to left, dorsal to right, (C) parasphenoid of *N. oregonensis* n. sp., UMMP V57010, X2.6, (D) parasphenoid of *Umbra limi*, ventral aspect, UMMZ 169053-S, Mich., S.L. 125 mm., X5.6, (E) parasphenoid of *Dallia pectoralis*, ventral aspect, UMMZ 171794-S, Alaska, S.L. 190 mm., X1.5, (F) cleithrum of *Novumbra*

Cleithrum (Fig. 5, F).—The difference between the cleithra of *N. hubbsi* and *N. oregonensis* lies in the degree of ossification of the lower limb. The anteroventral part of the lower limb is not ossified in *hubbsi* and is similar to the condition of the cleithrum found in *Umbra limi* and *Dallia pectoralis* (see Schultz, 1929, Plate I). The upper and lower limbs of the cleithra are about equal in length in *Novumbra* and *Umbra* whereas in *Esox* and *Dallia* the lower limb is much the longer.

COMPARISON WITH *PALAEOESOX*

In a detailed study Voigt (1934) described *Palaeoesox fritzschei* from the middle Eocene "Braunkohle of Geiseltal" near Halle, Germany (East). This species is of much importance in the history of the esocoid group from the standpoint of its age and also of its morphology, since it shares characters both with the esocids and the umbrids. Berg (1936) reviewed the problem of the classification of *Palaeoesox* and chose to erect a new family for it, the Palaeoesocidae.

My comments on *Palaeoesox* are based solely on Voigt's paper and illustrations. *Palaeoesox* bears a close or at least some resemblance to *Novumbra* in the following characters: (1) umbrid-type of body form; (2) shape of the caudal fin, truncated in *Palaeoesox*, slightly emarginate in *Novumbra*; (3) number of hypurals—2 lower, 4? upper; (4) posterior position of the dorsal and anal fins; (5) dorsal fin originating slightly ahead of the anal with the latter being the smaller of the two; (6) possession of supramaxillae; (7) presence of small tubular nasals; (8) shape of the opercle and preopercle. None of these characters indicates a decidedly close relationship because most are to be expected in an early member of the umbrid group and characters 3–7 are also found in the Esocidae. *Palaeoesox* resembles *Esox* in its complete infraorbital series, its numerous branchiostegal rays (14), and the relationship of the frontals and parietals. The latter are described by Voigt as being in full contact with the posterior margin of the frontals and extend between the pterotic and supraoccipital in the

oregonensis, UMMP V57014, X2.5, (G) same of *N. hubbsi*, UMMZ 179398, X5.6, (H) left opercle (lateral aspect) of *N. oregonensis*, UMMP V57010, X2.6, (I) same of *N. hubbsi*, UMMZ 179398, X5.4, (J) right mandible (lateral aspect) of *N. oregonensis*, articular displaced forward, UMMP V57004, X2.8, (K) same of *N. hubbsi*, UMMZ 179398, X5.6, (L) left and right frontals (dorsal aspect) of *N. oregonensis*, UMMP V57010, X2.8, (M) same of *N. hubbsi*, UMMZ 179398, X5.4. N–Q, otoliths (sagittae) mesial view, anterior end to right: (N) *Palaeoesox fritzschei* (after Voigt, 1934), (O) *Novumbra hubbsi*, (P) *Umbra limi*, (Q) *Dallia pectoralis*. Scale 0.5 mm.

same manner as in *Esox*, where they cover the anterior part of the posttemporal fossae. This character can be considered primitive since this is the condition more in common with other basal teleosts of Division III (Euteleostei) (Greenwood et al., 1966) and it was probably present in the earliest members of the esocoid group. The same can be said for the complete infraorbital series and more numerous branchiostegal rays.

Palaeoesox agrees with *Umbra* in body shape, number of vertebrae (33–34), vertebral centra constricted anteriorly, small anal fin with few rays (8–9), position of the pectoral fin and number of pectoral rays (15–17), in having the palatine broadened anteriorly (shared also with *Esox*), and in the dentition of the lower jaw and premaxilla. Voigt thought the scales resembled those of *Esox* but in his photograph the appearance of their circuli is closer to that of *Umbra*. However, the scales are small as in *Esox*, *Dallia*, and *Novumbra* and do not resemble the larger-scaled *Umbra* in this respect.

Palaeoesox has small undifferentiated teeth in several rows on the dentary and on the elliptical-shaped premaxilla. The latter character is distinctive for *Umbra* among the Recent esocoids. There are no specialized caniniform teeth on the lower jaw as in *Esox*. The premaxilla is very similar to that of *Umbra* especially in its relationship with the proethmoids and vomer. It is difficult to say whether this type of premaxilla is primitive or specialized. In other esocoids, in salmonoids, and in stomiatooids the premaxillae have a single row of teeth and are positioned lateral to the rostrum and except for *Esox* meet or nearly meet at the midline in front. In *Dallia* the premaxillae are elongated posteriorly but their anterior ends are positioned ventral to the proethmoids. The head of the vomer divides the premaxillae in *Esox* as pointed out and illustrated by Voigt. *Umbra* and *Palaeoesox* have depressed, plate-like premaxillae positioned underneath the anterior ends of the proethmoids. This condition with the premaxillae ventral to the anterior end of the ethmoid region is more reminiscent of that found in most siluriforms.

Another important character involves the functional jaw teeth (anterior part of dentary and premaxilla) of *Umbra* and *Palaeoesox*. The teeth are seated in small pits in two to several rows with only a few replacement teeth in nearby tissue in *Umbra*. This resembles villiform dentition. In *Esox*, *Novumbra*, and *Dallia*, the functional outer jaw teeth are in one row with a series of non-functioning replacement teeth situated in the tissue to their mesial side. *Esox* has developed a

series of large caniniform teeth on the lower jaw. Behind the single tooth row on each side of the mandibular symphysis in *Esox lucius* there is a small area where several little teeth are seated.

The subopercle of *Palaeoesox* is elongate as in all esocoids except *Umbra* and the ribs are weak as in *Dallia* and *Esox*.

In conclusion it appears that many osteological characters of *Palaeoesox* can be considered primitive for the whole esocoid group and others that are likely more specialized are shared with the umbrids. Two of these specialized characters (the structure of the vertebral centra, premaxilla and its dentition) extend particularly to the genus *Umbra*. Also the truncate caudal fin with apparently reduced number of principal caudal rays strongly suggests the mudminnow type. In a phyletic classification, *Palaeoesox* should therefore be shown to have a closer relationship to the Umbridae than to the Esocidae.

Voigt (1934) stated that there were 165 specimens (presumably still intact in the collections of the Geological-Palaeontological Institute, University of Halle) of *Palaeoesox fritzschei* three-fourths of which were more or less complete. This ample supply of study material should yield more information than is now known on the osteology of *Palaeoesox*. Although Voigt carefully gleaned a considerable amount of data from the specimens there are certain points concerning the cephalic sensory canals, especially the preoperculomandibular canal, presence or absence of a lateral line, presence or absence of a supra-orbital, the basibranchial dentition, the gill rakers, the neurocranium, and caudal skeleton, which need to be known.

RELATIONSHIPS OF *NOVUMBRA*

In several important characters the two species of *Novumbra* occupy a position somewhat intermediate between the species of *Umbra* and the Alaskan blackfish, *Dallia pectoralis*. Schultz (1929) reached this conclusion after assessing the external morphology, in particular the squamation and many-rayed, fan-like pectoral fins of *Novumbra* and *Dallia*. The external similarity is also apparent in the position of the dorsal and anal fins, the number of their fin rays, and the body form and pigmentation (especially that of the caudal peduncle) in the young.

After examination of vertebral characters I find *Novumbra* again intermediate if not closer to *Dallia* than to *Umbra*. In increasing number of vertebrae (two ural vertebrae included) the umbrid species fall in the following order, with the number of specimens given in parentheses:

<i>Palaeoesox fritzschei</i>	33-34	(Voigt, 1934)
<i>Umbra pygmaea</i> (10)	33-35	34.1 precaudal 18-20, caudal 14-16
<i>Umbra krameri</i> (5)	35-36	35.2 precaudal 20-21, caudal 15
<i>Umbra limi</i> (20)	36-37	36.5 precaudal 20-21, caudal 15-16
<i>Novumbra hubbsi</i> (32)	37-40	38.7 precaudal 19-21, caudal 18-20
<i>Dallia pectoralis</i> (14)	40-42	41.1 precaudal 20-21, caudal 20-21
Umbridae	33-42	
Esocidae (all species of <i>Esox</i>)	48-68	(Berg, 1962; Nikolskii, 1961) 44-68 (See below)

Crossman (1966) and Crossman and Buss (1965) counted a low of 43 vertebrae in *Esox americanus vermiculatus* to a high of 67 in *Esox masquinongy*. The "hypural" was not included in Crossman's counts so probably one more vertebra should be added.

It is interesting to note that among the first four genera there is an overlap in vertebral number at each species interval. Then a break occurs between *Dallia pectoralis* and *Esox*. Among the esocids, the lowest vertebral counts are found in *Esox americanus* (44-51) Crossman and Buss (1965) and the European Oligocene fossil *Esox papyraceus* Trosch which has 48 (Voigt, 1934). Also, the progressive increase of the vertebrae in the *Umbra-Novumbra-Dallia* group occurs primarily in the caudal series whereas in *Esox* the increase is in the precaudal series. This can be explained in that the longer body cavity of *Esox* is an adaptation to a piscivorous habit.

A distinctive feature of the vertebral column of *Umbra* is the pronounced anterior constriction of each centrum which gives it an asymmetrical appearance. Both *Novumbra* and the young of *Dallia* show this peculiarity but usually only in the midabdominal region. The other vertebral centra, especially in the caudal series, are symmetrical in lateral view. The larger species of *Esox* (*E. lucius* and *E. masquinongy*) have vertebral centra that do not show pronounced constriction even in the young. The pickerels, especially *E. americanus*, do have moderately constricted centra but they are perfectly symmetrical both in the abdominal and caudal series.

The ribs of *Dallia* are small and reminiscent of the condition in *Esox*, whereas in *Novumbra* and *Umbra* they are relatively larger. Chapman (1934) described the first ossified rib in *Dallia* as attached to the first vertebra (atlas) and extending outward and posteriorly to a junction with the pectoral girdle. *Novumbra* and *Umbra* possess a transverse process on the first vertebra (atlas) with a ligamentous con-

nection to the cleithrum. *Dallia* further differs from the mudminnows in the caudal part of its axial skeleton. There are usually five preural vertebrae that take part in the caudal fin support similar to the number in *Esox* and six elongated and thickened neural and haemal spines that support the procurrent caudal rays although there is no clear demarcation between the procurrent and principal caudal rays; one grades into the other as opposed to the caudal rays of the fork-tailed *Esox* which has a 1-9-8-1 count with a series of 12 to 16 procurrent rays in both the upper and lower caudal lobes. *Dallia pectoralis* typically has at least one fusion between preural vertebrae supporting the tail. Often preurals 1 and 2 fuse. This sometimes occurs in *Novumbra*, also. The latter possesses a caudal fin ray formula commonly 9 or 8 over 8 principal rays and 6 to 8 procurrent rays (above and below) and *Dallia pectoralis* has a total of 16 to 18 over 16 to 18. Although there is no clear break in size to distinguish between procurrent and principal rays, the gap above the uppermost hypural, which in the normal forked tail separates the bases of the epaxial and hypaxial rays (the procurrent and principal in the upper lobe) can be made out. Using this as a point of comparison in the upper lobe and the parhypural in the lower lobe, which usually supports the lowermost principal ray, the caudal fin of *Dallia pectoralis* can be interpreted as having six upper and six lower principal rays with about twelve procurrent rays in each division. *Umbra pygmaea* and *Umbra limi* also have a 6/6 split (*U. pygmaea* sometimes has 6/5) whereas *Umbra krameri* has 5/5. Placed in the same order, they tend to show a decrease in the number of procurrent rays in each lobe. *Palaeoesox* has 7 or 8 over 7 or 8 (15-17 total principal rays) and several short procurrent rays according to Voigt (1934).

Turning to the hypural elements *Novumbra* may have 2 lower and 4 upper hypurals although 1 and 2 sometimes partly fuse as do also 5 and 6. The first hypural is by far the most expanded and largest in the complex, resembling the condition in *Esox*. *Umbra* and *Dallia pectoralis* have 5 hypurals (2 lower and 3 upper). Sometimes 4 and 5 fuse. *Novumbra* may show a complete neural arch and possibly a spine on ural centrum 1 (see Chapman, 1934, Fig. 6) and also a ring-like ossification of the notochordal sheath behind ural centrum 2 (also seen in young *Esox*). In the former character *Novumbra* may be considered more primitive than *Esox* (Greenwood, 1966, considered neural arches on ural centra as primitive in osteoglossoids) although *Esox* has a more primitive caudal ray formula. *Umbra*, *Dallia* and *Esox* usually

have an unattached neural spine (epural) associated with ural centrum 1. In summing up the evidence from the caudal skeleton it seems likely that the trend to a rounded tail resulted in a loss of principal rays supported by the hypural series and the parhypural. *Novumbra*, with an emarginate tail, shows a caudal fin ray loss from the condition in *Esox* although in some other respects its caudal skeleton is the most conservative of the living esocoids. Also associated with the trend toward a round tail is a loss of the uppermost hypural in *Dallia pectoralis* and *Umbra* and the loss of some procurrent rays in *Umbra*. *Dallia* is exceptional in that it has either increased secondarily the number of procurrent rays or has retained the primitive number. *Dallia pectoralis* also exhibits a combination of fusions in the first few preural vertebrae which to a much lesser extent is also found in *Novumbra*.

Elsewhere in the skeleton there are few points in the osteology of *Novumbra* either not covered by Chapman (1934) or which I wish to emphasize. Small tubular nasals are present in *Novumbra hubbsi* although Chapman stated they were absent. Very minute, incomplete tubular nasal ossicles sometimes are present in *Umbra pygmaea*. Nasals are present at least in some *Dallia pectoralis*. *Novumbra* and *Umbra krameri* possess a mandibular sensory canal enclosed in a bony tube attached to the lower fork of the dentary. This is not a separate "infra-mandibular" bone since in the fossil *Novumbra*, the canal is more completely within the dentary itself, which is closer to the condition in *Esox*. *Umbra limi* and *U. pygmaea* do not have the canal enclosed in bone although it is partly supported by the dentary. *Dallia* lacks the bony tube and the canal is reduced with no pores. The taxonomic significance of the ossification related to the mandibular sensory canal was stressed by Berg (1958). It appears that within the umbrid group there is a tendency for a progressive loss of bone associated with the canal.

The dentary bears a single row of well-developed incurved teeth in *Novumbra* very similar to the dentary teeth of *Dallia*. *Umbra* bears two rows of small teeth which are reduced to one row posteriorly on the dentary. *Novumbra* has teeth on the lingual plate and third and fourth basibranchials (Chapman, 1934, found a few teeth on the second basibranchial) whereas *Dallia* lacks tongue teeth but possesses well-developed tooth patches on the second (occasionally), third, and fourth basibranchials. *Umbra* shows only a small patch of teeth on the fourth basibranchial. *Esox* has a full complement of tongue and basibranchial teeth.

In the morphology of its gill rakers *Novumbra* possesses a striking resemblance to *Esox*. Both of these genera have gill rakers in the form of small, finely toothed, rectangular plates arranged in two series on the arch—one along the anterior and the other along the posterior margin. The teeth on each raker are oriented toward the branchial cavity. The rakers are numerous in *Esox* from about 30 (anterior series of first arch counted) in *E. americanus* to over 50 in *E. lucius*. *Novumbra hubbsi* has about 12. *Umbra*, also with two series of rakers, has about the same number as *Novumbra* but the form is markedly different. In the former the rakers, especially those of the anterior series on the first arch, are produced into elongate, pointed structures that extend in an anterior direction from the arch and bear teeth. In *Dallia* the form of the gill rakers is somewhat intermediate between *Umbra* and *Novumbra* although possibly closer to the latter. *Dallia* has 12 to 16 stoutly triangular, finely toothed rakers that project very little from the supporting gill arch.

Umbra has 4 to 6 branchiostegal rays (personal observation, 4 to 5(6) in *U. pygmaea*), *Novumbra hubbsi*, 6 to 7, *Dallia pectoralis*, 7 to 9, usually 8 (personal observation) and *Esox*, 11 to 20 (Berg, 1936). Crossman (1960) counted as few as 9 on one side in *Esox americanus vermiculatus*. McAllister (1968) described the branchiostegal rays of *Esox*, *Dallia* and *Palaeoesox* as acinaciform in shape but this is also true of *Novumbra* (fossil and Recent). *Umbra* differs in having the upper two or three rays distinctly spathiform (see McAllister, 1968, for terminology). The subopercle in *Novumbra* is elongate as in *Dallia* and *Esox*. In *Umbra* the subopercle is shortened to a characteristic triangular shape (Chapman, 1934).

Novumbra, *Esox*, *Palaeoesox*, *Dallia*, and *Umbra* show considerable differences in the characters of their otoliths (sagittae, Fig. 5, N–Q). Otoliths of *Novumbra oregonensis* have not been found. Relative to head length, *Novumbra* and *Esox* (see Voigt, 1934, text fig. 18a, for sagitta of *Esox lucius*) have the smallest sagittae; that of *Palaeoesox* is slightly larger, then *Dallia*, and finally *Umbra*. The sagittae of *Umbra* (see Voigt, 1934, text fig. 19 for sagitta of *Umbra krameri*) are at least twice the size of *Novumbra* in the same size fish. Other than size, some of the obvious distinctions between sagittae of the different genera are found in the degree of development of the longitudinal sulcus and the rostrum, the length-height proportions and the relative thickness. *Umbra limi* (Fig. 5, P) compares with *Esox* in its very pronounced rostrum but it does not have the complete sulcus. *Novumbra* is unique

in the group with its nearly equal length-height dimensions, and the sagitta of *Dallia* is characterized by its thin, wafer-like appearance.

Novumbra, *Dallia*, and *Umbra* all have in common open posttemporal fossae between the pterotic and epiotic and extending forward at least to the posterior margin of the frontal. The parietals are reduced to small triangular bones overlying the anterior margin of the epiotic at each side of the supraoccipital. The parietals are vestigial or very minute in *Umbra limi* and *U. pygmaea* and somewhat larger in *Umbra krameri*, *Novumbra*, and *Dallia*. A crescentic ridge of bone on the posterior part of the frontal forms the anterior limit of the posttemporal fossa in *Dallia* and *Novumbra hubbsi* (Fig. 5, M). The preopercular canal of *Novumbra* has 5 sensory pores, one less than in *Esox* (*E. americanus* can have 5) and one more than in *Umbra* and *Dallia* although Chapman (1934) showed 5 for *Dallia*.

In the preceding paragraphs I have pointed out several osteological characters shared by *Dallia* and *Novumbra* and separating these two genera from *Umbra*. Chapman's detailed analysis of the skeletons of these three genera has shown the similarities between the umbrids and also the distinctions of each, especially *Dallia*. Several of the characters that *Dallia* and *Novumbra* share seem to be primitive for the mudminnow group. The comparisons made between *Novumbra hubbsi* and *Esox* have revealed a number of common features. Particularly close agreement is found in the type of gill rakers, caudal skeleton, pectoral fin placement, and the possession of supramaxillae and nasals. *Novumbra oregonensis* further resembles *Esox* in its fimbriate opercle, heavier frontal bones and large head.

The mosaic of characters present in the mudminnow group indicates that *Novumbra* is in a number of respects the most generalized and conservative of the living genera and that *Dallia* and *Umbra* are more specialized, each in its own way. For example, the paired fins of *Dallia* are specialized; in the pectoral fin which is positioned further up on the side of the body than in any other umbrid there is a high number of fin rays (33-37) and low number (3) in the pelvic fins. In contrast, *Novumbra* has the pectorals positioned close together more underneath the body as in *Esox*. The large peculiar scales and anteriorly constricted vertebrae are specialized structures of *Umbra*. *Dallia* and *Novumbra* have diverged less than *Umbra* in a number of characters but *Umbra* also shows possible ancestral characters of a different kind; for example, the less specialized lower jaw teeth. This may mean that the original mudminnow group was divided into two phyletic lines

represented by an ancestral *Umbra* type and by an ancestral *Novumbra* type from which *Dallia* split off. As far as a phylogenetic classification is concerned, *Novumbra* cannot be included with *Umbra* in the family Umbridae without also including *Dallia*. To combine the three under one higher taxon equivalent to the Esocidae interprets the esocoids as having split into two major adaptive groups. This scheme is supported by the structure of the neurocranium, snout and tail. One adaptive group is represented by the fork-tailed form with piscivorous habits, large elongated pike-like body, elongate snout, and with large mouth containing a full complement of teeth. The other adaptive group is represented by a truncated or rounded tail form with small torpedo-shaped body and smaller mouth and teeth. The Eocene *Palaeocox* lies in the umbrid group near the base of this split because it exhibits characters of both groups. It has a mudminnow body and tail combined with certain pike-like characters of the skull. Another possible interpretation that could be considered depending upon how the evidence is weighed, is to have three or four phyletic divisions: a stem line leading to *Novumbra* from which *Dallia* branched off, a piscivorous line leading to *Esox* and a third line giving rise to *Umbra*.

I have not attempted to construct a "phylogenetic tree" of the esocoid group since the fossil evidence is still too meager to decipher evolutionary lines and since the living members are mostly faunal relicts well separated from each other by time and probably also by unknown extinct forms. It is possible to show trends in specializations, e.g., increase in vertebral and branchiostegal number, rows of scales, increase in mandibular sensory pores, elongation of the snout (see Crossman and Buss, 1965) within the family Esocidae. I would like to emphasize the following points pertaining to interrelationships: *Dallia* appears to be closer to *Novumbra* than to any other living esocoid and could well have shared a common ancestry with *Novumbra*. Although *Dallia* itself has had a long independent history, I include *Novumbra* and *Dallia* in the Umbridae (also listed with the Umbridae by Greenwood et al., 1966). *Novumbra* is near to the stem line of the esocoids in many characters. Together with *Dallia* it can be viewed as showing intermediacy between *Esox* and *Umbra*.

FOSSIL *DALLIA*

The statement above that *Dallia* is a member of an ancient lineage is supported by a Miocene fossil from the Kenai Peninsula of Alaska.

The University of Alaska specimen consists of the posterior one-third of the body showing parts of the median fins, caudal peduncle and caudal fin. A *Dallia pectoralis* of the same proportions would have a standard length of about 240 mm. About 19 caudal vertebrae are visible. The centra do not appear to be elongated nor greatly constricted. Fin supports and a number of rays represent the dorsal and anal fins which oppose one another. At least 10 dorsal rays can be made out and parts of 5 anal rays. The most posterior dorsal fin ray is positioned over the 11th or 12th preural vertebra. The most posterior dorsal pterygiophore that can be made out lies between the haemal spines of the 13th and 14th preural vertebrae. Running obliquely backwards from the haemal arches of six or seven of the anteriormost vertebrae are slender bones that in every respect resemble lower intermuscular bones.

On the upper side of the caudal peduncle just posterior to the dorsal fin are a few imprints of small cycloid scales.

The caudal fin consists of at least 40 rays (total). Supporting the rays is an arrangement of haemal and neural spines, hypurals and single epural that I have illustrated in Figure 6, B. An upturned vertebral column is indicated in the position of the bases of hypurals but no distinct ural centra can be made out. There are about 6 neural and 6 haemal spines supporting caudal fin rays. The number of posterior haemal spines may possibly outnumber the preural centra supporting them indicating a fusion of preural vertebrae as commonly occurs in *Dallia*. In the hypural series there are 2 lower and most likely 4 upper hypurals.

The fossil resembles *Dallia pectoralis* (Fig. 6, A) in the following characters: many caudal rays (over 30) with no break between principal and accessory rays, indicating a round tail; in the number of neural (6) and haemal spines (6), arrangement of the hypurals, and single epural supporting those rays; in the shape of the caudal complex, the dorsal fin positioned far back on the body opposite the anal, anal pterygiophores simple strut-like bones that are weakly ossified, and scales small and cycloid.

The fossil differs from *Dallia pectoralis* in its larger size, in possessing posterior lower intermuscular bones found in esocoids except the above species, in slightly more numerous caudal rays (40), 14 of which are supported by the hypurals and parhypural versus an average of 34.5 (in 15 specimens), 12 of which are supported by the hypurals and parhypural, in possession of one or two more caudal vertebrae as in-

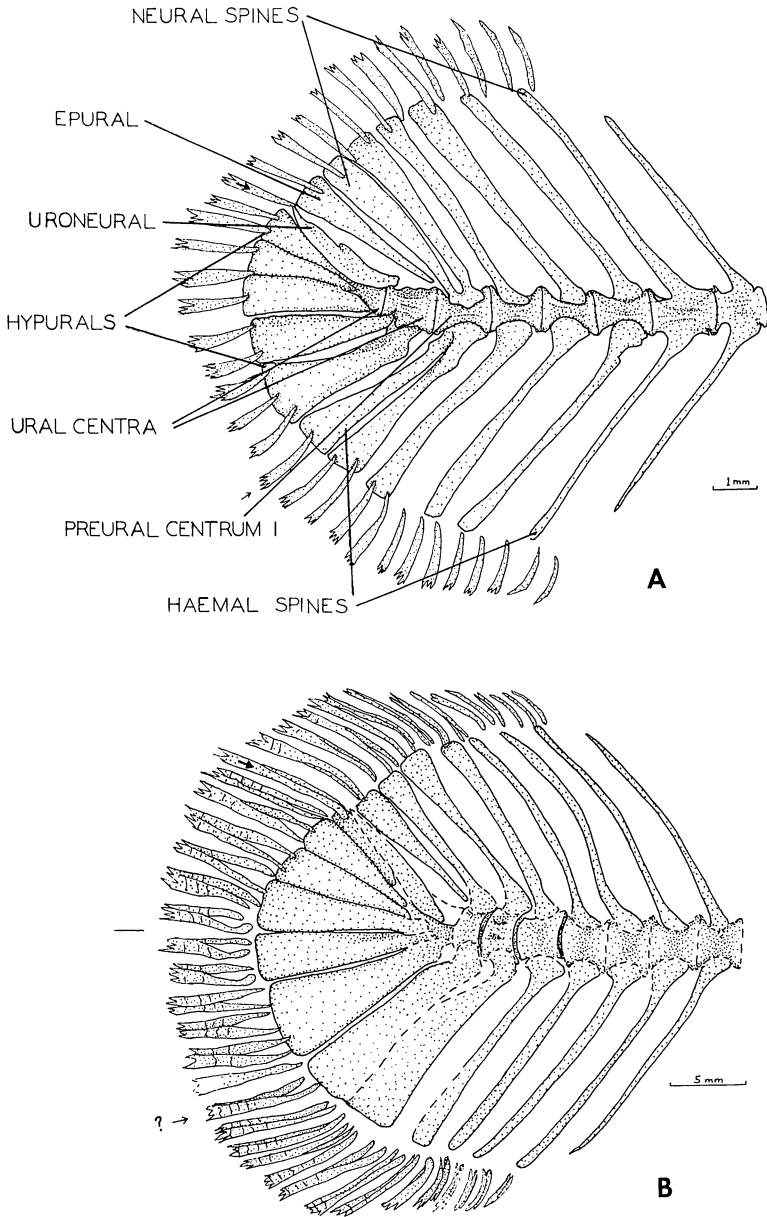


FIG. 6. Caudal skeletons of *Dallia pectoralis* (A), UMMZ 187272, Alaska, juvenile, S.L. 65 mm., and *Dallia* sp. (B) a fossil species from the Upper Miocene, Kenai Peninsula, Alaska, Univ. of Alaska specimen, est. S.L. 240 mm.

dicated by the number of preural vertebrae posterior to the dorsal fin, in the less elongated vertebral centra (more like those of *Esox*), and the possible possession of a 6th (4th upper) hypural.

Considering the osteological evidence, the location of the fossil, and preservation in a freshwater deposit of later Tertiary age (Late Miocene), I believe the fossil is best assigned to the genus *Dallia* although possibly belonging to a different species than that living today. Associated with the fish in the same piece of red sandstone are fragments of plants. A flora of 47 species has been recently described by Wolfe (1966) from the Homeric part of the Kenai Formation which also yielded the *Dallia*. Wolfe interpreted the flora as a "cool temperate," which seemingly receives support from the relationship of the fossil fish to *Dallia pectoralis*, a cold-loving vertebrate with a distribution today in western Alaska and eastern Siberia.

PHYSICAL ENVIRONMENT OF FOSSIL AND RECENT *NOVUMBRA*

The lower member of the John Day Formation that yielded the fossil is largely a deposit of air-laid volcanic ash which slowly accumulated on an eroded and highly weathered land surface. Hay (1962, 1963) has discussed the lithology and environment of sedimentation of this deposit and Fisher (1964, 1968) has reported on the mineralogy and the changes brought about by weathering of the surface soils in John Day time. Chaney (1927, 1948b, 1952) has given an environmental reconstruction of the associated Bridge Creek flora based on comparisons with Recent floras.

The following statements concerning the environment of *Novumbra oregonensis* are taken from the above investigations: the fossil mudminnows were buried in mud derived from volcanic ash and organic debris which accumulated in shallow, possibly stagnant water of a lake, swamp, or stream backwater. The topography during lower John Day time consisted of low forest covered hills separated by poorly drained depressions of limited areal extent in which thin lenses of water laid sediments were deposited; the climate was humid and warm temperate although Fisher (1968) suggested it was subtropical or tropical.

In a recent study on the ecology of *Novumbra hubbsi*, Meldrim (1968) has mapped the present known distribution of this species and summarized the habitat as follows: "an area of quiet water, having a mud substrate and dense aquatic vegetation." He also showed that

N. hubbsi has a wide range of tolerance for temperature and dissolved oxygen but relatively restricted tolerances to salinity and current strength when compared with associated fish species. The latter belong to the genera: *Cottus*, *Gasterosteus*, *Rhinichthys*, *Oncorhynchus*, and *Salmo*.

The sluggish stream and quiet backwater Oligocene environment where leaves collected and where *Novumbra oregonensis* probably lived does not seem to differ greatly from the habitat of *N. hubbsi* at least in its lowland to moderate relief setting with an equable (though warmer) temperate climate, and with the mud-bottomed sloughs rich in aquatic vegetation.

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LITERATURE CITED

- BALDWIN, E. M. 1964 *Geology of Oregon*. 2nd edition. Eugene, Oregon, 165 pp.
- BARNES, F. F., AND E. H. COBB 1959 *Geology and coal resources of the Homer district, Kenai coal field, Alaska*. Bull. U.S. geol. Surv. 1058-F:217-260.
- BERG, L. S. 1936 The suborder Esocoidci (Pisces). Bull. Perm. Biol. Inst., 10:385-391. In Russian and English.
- 1958 *System Der Rezenten und Fossilen Fischartigen und Fische*, Berlin, 310 pp. German translation of 1955 edition published in Russian.
- 1962 *Freshwater fishes of the U.S.S.R. and adjacent countries*. 4th edition, Vol. 1, 504 pp. English translation from original in Russian, 1948, Moscow.
- CAVENDER, T. 1966 Systematic position of the North American Eocene fish, "*Leuciscus*" *rosei* Hussakof. *Copeia*, 1966(2):311-320.
- 1968 Freshwater fish remains from the Clarno Formation Ochoco mountains of Northcentral Oregon. *The Ore Bin* (State of Oregon Department of Geology and Mineral Industries, Portland), 30(7):125-141.

- CHANEY, R. W. 1924 Quantitative studies of the Bridge Creek flora. *Am. J. Sci.*, 8:127-144.
- 1927 Geology and palaeontology of the Crooked River basin with special reference to the Bridge Creek flora. *Carnegie Inst. Wash. Contr. Palaeont. Publ. No.* 346:45-138.
- 1948a The ancient forests of Oregon. *Condon Lectures. Oregon State System of Higher Education, Eugene, Oregon*, 56 pp.
- 1948b The bearing of the living *Metasequoia* on problems of Tertiary palaeobotany. *Proc. natn. Acad. Sci. U.S.A.*, 34(11):503-515.
- 1952 Conifer dominants in the Middle Tertiary of the John Day basin, Oregon. *Palaeobotanist* 1:105-113.
- CHAPMAN, W. M. 1934 Osteology of the haplous fish, *Novumbra hubbsi* Schultz, with comparative notes on related species. *J. Morphol.*, 56(2):371-405.
- CROSSMAN, E. J. 1960 Variation in number and symmetry in branchiostegal rays in the family Esocidae. *Can. J. Zool.*, 38:363-375.
- 1966 A taxonomic study of *Esox americanus* and its subspecies in eastern North America. *Copeia*, 1966(1):1-20.
- CROSSMAN, E. J., AND K. BUSS 1965 Hybridization in the family Esocidae. *J. Fish. Res. Bd. Canada*, 22(5):1261-1292.
- EVERNDEN, J. F. D., D. E. SAVAGE, G. H. CURTIS, AND G. T. JAMES 1964 Potassium-argon dates and the Cenozoic mammalian chronology of North America. *Am. J. Sci.*, 262:145-198.
- FISHER, R. V. 1964 Resurrected Oligocene hills, eastern Oregon. *Am. J. Sci.* 262:713-725.
- 1968 Pyrogenic mineral stability, lower member of the John Day Formation, eastern Oregon. *Univ. Calif. Publs. geol. Sci.* 75:1-36.
- GREENWOOD, P. H. 1966 The caudal fin skeleton in osteoglossoid fishes. *Ann. Mag. nat. Hist., Ser. 13*, 9:581-597.
- GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS 1966 Phyletic classification of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* 131(4):345-455.
- HAY, R. L. 1962 Origin and diagenetic alteration of the lower part of the John Day Formation near Mitchell, Oregon. *In Geol. Soc. Am. Buddington Vol.*, p. 191-216.
- 1963 Stratigraphy and zeolitic diagenesis of the John Day Formation of Oregon. *Univ. Calif. Publs. geol. Sci.*, 42:199-262.
- MCALLISTER, D. E. 1968 Evolution of branchiostegals and classification of teleostome fishes. *Bull. natn. Mus. Can.*, 221:1-239.
- McPHAIL, J. D. 1967 Distribution of freshwater fishes in western Washington. *Northwest Sci.* 41(1):1-11.
- MELDRIM, J. W. 1968 The ecological zoogeography of the Olympic mudminnow. Ph.D. Dissertation, University of Washington, 157 pp.
- MERRIAM, J. C. 1901 A contribution to the geology of the John Day basin. *Univ. Calif. Publs. Bull. Dep. Geol.*, 2(9):269-314.
- NIKOLSKII, G. V. 1961 Special Ichthyology. 2nd edition. English translation of 1954 Russian edition, Moscow. 538 pp.

- SCHULTZ, L. P. 1929 Description of a new type of mudminnow from western Washington with notes on related species. Univ. Wash. Publs. Fish. 1(6): 73-82.
- TAYLOR, W. R. 1967 An enzyme method of clearing and staining small vertebrates. Proc. U.S. natn. Mus., 122(3596):1-17.
- VOIGT, E. 1934 Die Fische aus der mittelcozänen Braunkohle des Geiseltales. Nova Acta Leopoldina. New Ser. 2(1 and 2):21-146.
- WEITZMAN, S. H. 1962 The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford ichthyol. Bull., 8(1):3-77.
- 1967 The origin of the stomioid fishes with comments on the classification of salmoniform fishes. Copeia, 1967(3):507-540.
- WOLFE, J. A. 1966 Tertiary plants from the Cook Inlet Region-Alaska. Prof. Pap. U.S. geol. Surv. 398-B:1-32.
- WOLFE, J. A., D. M. HOPKINS, AND E. B. LEOPOLD 1966 Tertiary stratigraphy and palcobotany of the Cook Inlet Region, Alaska. Prof. Pap. U.S. geol. Surv. 398-A:1-29.

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PLATE I

Photograph of latex positives of *Novumbra oregonensis* n. sp., holotype, UMMP V57007, left side above, right below. X2.

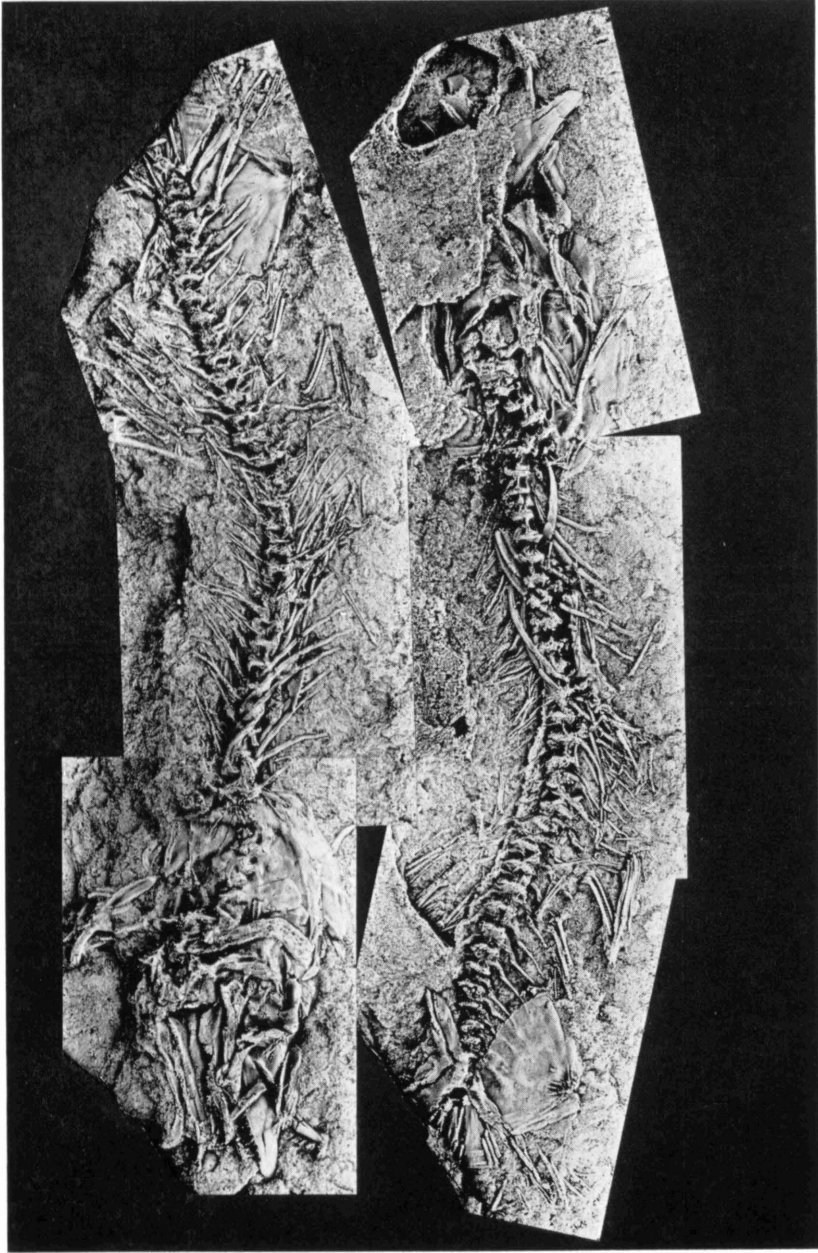


PLATE I

PLATE II

Photographs of individual skull elements of *Novumbra oregonensis* n. sp. (1) Left opercle, lateral aspect, UMMP V57010, (2) right subopercle, UMMP V57010, (3) right and left frontals, dorsal aspects, UMMP V57014, (4) left opercle, mesial aspect on left, lateral on right, UMMP V57014, (5) right dentary, lateral aspect on left, mesial on right, UMMP V57014, (6) parasphenoid, ventral aspect, UMMP V57014. X4.

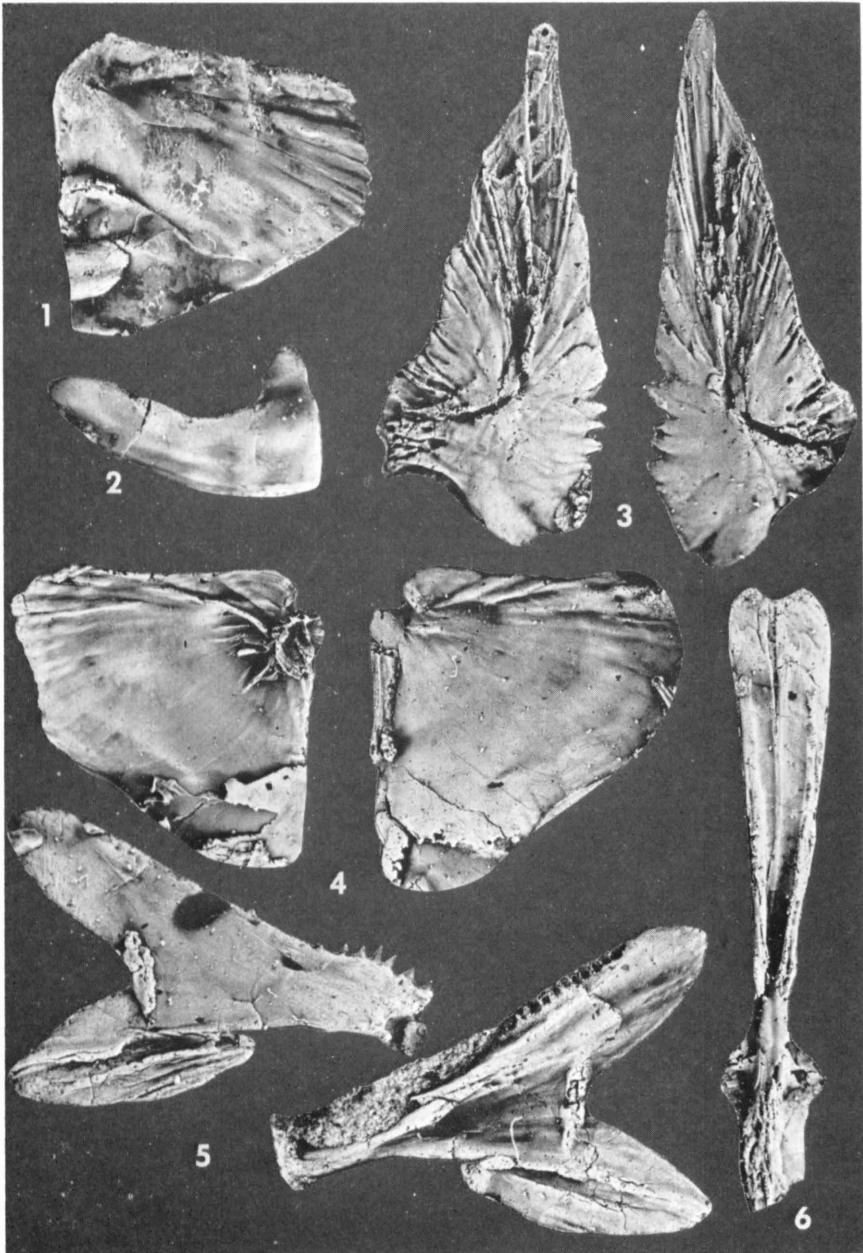


PLATE II

