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

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. kramerii*, 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 kramerii*. 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.

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 (Wolle, 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 ¼, 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 ¼, S ½, 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 1/4, NE 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 proethmoids, 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) autogenous, 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 mesocoracoil 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 posttemporal fossae that are open above, 11) the infraorbital series is incomplete, 12) no supraorbital, 13) basibranchial dentition incomplete. Three genera: *Umbra, Novumbra, Dalia*.

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. *Novumbra oregonensis* n. sp., holotype; UMMP V57007, left side above, right 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, epiphyal; 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; PF, pectoral fin; P₃F, pelvic fin; PMX, premaxilla; POP, preopercle; PRO, proethmoid; PT, posttemporal; PTF, posttemporal fossa; PTO, pterygoid; Q, quadrato; R, right; SCL, supracleithrum; 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*.
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 *Novumbræ 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 epiphysial still articulated.

Of the palatoquadrate, the quadrate, mesopterygoid, eopterygoid 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 eopterygoid is covered anteriorly by a triangular infradorbital-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 eopterygoid. In Esox there is a well-developed dorsal process of the eopterygoid that articulates with the lateral ethmoid. Novumbra hubbsi, Umbra, and Dallia do not have such a structure. In Dallia the eopterygoid 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. *Novumbrapropterygii, 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 esocooids in the genus *Esox*. *Novumbrapropterygii, 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 *Novumbrapropterygii, 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 *Novumbrapropterygii* 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) Paraphenoid 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) paraphenoid of *N. oregonensis* n. sp., UMMP V57010, X2.6, (D) paraphenoid of *Umbra limi*, ventral aspect, UMMZ 169053–S, Mich., S.L. 125 mm., X5.6, (E) paraphenoid 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

*Oregon*, UMMP 179308, X5.6, (L) left and right frontals (dorsal aspect) of *N. hubbsi*, UMMP 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 stomiatoids 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 Palaeoe-
sox 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 num-
ber 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 Insti-
tute, 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 num-
ber of vertebrae (two ural vertebrae included) the umbrid species fall
in the following order, with the number of specimens given in paren-
theses:
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<th>Genus</th>
<th>Species</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palaeoesox fritzschei</td>
<td></td>
<td>33–34</td>
</tr>
<tr>
<td>Umbra pygmaea (10)</td>
<td></td>
<td>33–35</td>
</tr>
<tr>
<td>Umbra krameri (5)</td>
<td></td>
<td>35–36</td>
</tr>
<tr>
<td>Umbra limi (20)</td>
<td></td>
<td>36–37</td>
</tr>
<tr>
<td>Novumbra hubbsi (32)</td>
<td></td>
<td>37–40</td>
</tr>
<tr>
<td>Dallia pectoralis (14)</td>
<td></td>
<td>40–42</td>
</tr>
<tr>
<td>Umbridae</td>
<td></td>
<td>33–42</td>
</tr>
<tr>
<td>Esocidae (all species of Esox)</td>
<td></td>
<td>48–68</td>
</tr>
</tbody>
</table>

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 precurrent caudal rays although there is no clear demarcation between the precurrent 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 precurrent 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 precurrent 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 precurrent 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 precurrent 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 precurrent 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 precurrent rays in each lobe. *Palaeoesox* has 7 or 8 over 7 or 8 (15–17 total principal rays) and several short precurrent 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 procurent rays in Umbra. Dallia is exceptional in that it has either increased secondarily the number of procurent 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 kramerii 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 kramerii_ 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 *Umbara* 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 *Umbara limi* and *U. pygmaea* and somewhat larger in *Umbara 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 *Umbara* 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 *Umbara*. 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 *Umbara* 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 *Umbara*. *Dallia* and *Novumbra* have diverged less than *Umbara* in a number of characters but *Umbara* 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 *Umbr* 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 *Umbr* 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 *Palaeoesox* 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 *Umbr*.

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 *Umbr*.

**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 15th 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.
dictated 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 Homerian 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 mud-minnows 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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PLATE I

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