

OSTEOLOGY OF THE PALAEOCENE TELEOST *ESOX TIEMANI*

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ABSTRACT. The Palaeocene pike *Esox tiemani* combines many typically esocid features such as an elongate body, depressible and canine teeth, elongate snout and jaws, almost straight preopercle, small second and third hypurals separated by a gap, large ethmoid process on the ectopterygoid, and anteriorly lobed scales with other features in which it is intermediate between Recent umbrids and esocids. Branchiostegal rays are almost equally divided between the ceratohyal and epihyal, while in Recent umbrids they are more numerous on the ceratohyal and in Recent esocids they are more numerous on the epihyal. The opercle of *E. tiemani* has a prominent dorsolateral flange that probably covered part of the insertion of the levator operculi muscle. The flange is larger in umbrids and virtually absent in Recent esocids, in which much of the insertion for the levator operculi is on the dorsolateral surface of the opercle.

WE now know that the pikes (genus *Esox*, family Esocidae) have lived in North America apparently continuously since the Palaeocene, sixty million years ago. Fossils of *Esox* have been reported from the Pleistocene of the Yukon and Ontario (Crossman and Harington 1970) and of Florida (Cavender *et al.* 1970), the Miocene of Oregon (Cavender *et al.* 1970), the Oligocene of Montana (Cavender 1977), the Eocene of Ellesmere Island (Estes and Hutchinson 1980) and Colorado (Wilson 1981), and the Palaeocene of Alberta and Saskatchewan (Wilson 1980).

The Palaeocene esocid *E. tiemani* Wilson (1980), from the Paskapoo Formation of Alberta, is known from several articulated specimens including the holotype, a complete fish, and from numerous disarticulated bony elements at several sites within the same formation.

The osteology of *E. tiemani* is of special interest because it is the oldest-known esocid, and yet clearly possesses many of the unique specializations of the living pikes. The oldest Eurasian esocoids, which are also of Palaeocene age, belong to the Palaeoesocidae (Sytchevskaya 1976, 1982) and represent rather different skeletal adaptations.

The purpose of this paper is to present a detailed account of the osteology of *E. tiemani*, based on additional preparations of the holotype specimen, in addition to information obtained from the numerous disarticulated bones collected from the type locality and other sites in the Paskapoo Formation. In addition, a skeletal reconstruction and comments on the phylogenetic relationships of the species are presented.

MATERIALS AND METHODS

The holotype specimen (UAVP 15002) was briefly described by Wilson (1980). The specimen is complete except for the distal portions of the dorsal fin and the dorsal lobe of the caudal fin. The skull was preserved in part and counterpart and, since the original description, has been prepared by transfer methods. The right side of the skull in the counterpart (text-fig. 1) was embedded in bioplastic and the opposite (left) side prepared (text-fig. 2). This face is referred to in the present paper as UAVP 15002B.

The other material which was part of the original collection (UAVP 15005, a skull, and 15006, 15070, 15071, and 15072, four small partial fish) has been supplemented by additional disarticulated bones collected at the type locality in 1979 and prepared more recently. These consist of two dentaries (UAVP 17685 and 17686), an angular (UAVP 17670), a parasphenoid (UAVP 17678), an opercle

(UAVP 17676), and a group of scales possibly representing a coprolite (UAVP 17677). In addition to these, a great many *Esox* fossils continue to be recovered from other sites in the Paskapoo Formation. The most notable of these is a series of partial fish, primarily skulls, from the Lovettville Creek site (Wilson 1980, fig. 1, site 4), with catalogue numbers UAVP 15024, 15027-15031, and 17259.

Description of the skeleton of *E. tiemani* involved a detailed comparison of the skeletal elements of the fossil species with skeletons of Recent esocoids, primarily *E. lucius*, *E. masquinongy*, *Novumbra hubbsi*, *Dallia pectoralis*, *Umbra krameri*, *U. pygmaea*, and *U. limi*. Osteological features of the Umbridae were summarized by Wilson and Veilleux (1982). Those of esocids have not recently been described in detail, but the descriptions of Sytchevskaya (1976) were supplemented by observations on Recent skeletal material in the University of Alberta Museum of Zoology. For catalogue numbers of the Recent osteological material available for comparative purposes in this study, see Wilson and Veilleux (1982).

In almost all features the fossil species was found to be much more similar to the Recent esocids than to the Recent umbrids. Where information on particular parts of the skeleton was lacking in the fossils from the type locality, the reconstruction was prepared by using additional data, first from other fossil specimens from the Paskapoo Formation, and secondly from Recent esocids.

The following is a list of the abbreviations used in the figures:

AA	angulo-articular	HS	haemal spine	PP	pelvic plate
BH	basihyal (glossohyal)	HU	hypural	PR	pteroic
BR	branchiostegal	IO	infraorbital	PS	parasphenoid
CH	ceratohyal	LA	lachrymal	PT	post-temporal
CL	cleithrum	LE	lateral ethmoid	PU	preural centrum
CT	canine or fixed teeth	MS	mesopterygoid	QU	quadrate
DE	dentary	MT	metapterygoid	SC	supracleithrum
DT	depressible teeth	MX	maxilla	SM	supramaxilla
EC	ectopterygoid	OP	opercle	SN	supraneural
EH	epihyal	PA	palatine	SO	subopercle
ES	extrascapular	PC	postcleithrum	UC	ural centrum
EU	epural	PE	proethmoid	UH	urohyal
FR	frontal	PH	parhypural	UN	uroneural
HH	hypohyal	PM	premaxilla	VO	vomer
HM	hyomandibula	PO	preopercle		

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The skull roof of *E. tiemani* closely resembles that of the Recent species *E. lucius* and *E. masquinongy*. Frontals are elongate and narrow anteriorly, rounded posteriorly, and have a prominent supraorbital sensory canal, enclosed in bone, as in the Recent species (text-fig. 1). Nasals are not preserved in any specimen. UAVP 15005 has a pair of small supraorbitals. Parietals are separated by the supraoccipital and extend laterally to the pterotics. A canal-bearing extrascapular is present in the holotype (text-fig. 1).

Proethmoids are elongate and tapered posteriorly, broader and diverging anteriorly. Lateral ethmoids are seen in UAVP 15002B where they have a conical shape, convex anterolaterally (text-fig. 2A). Pterotics, also visible in this specimen, are elongate anteroposteriorly as in *E. lucius*. Infraorbitals and lachrymal are only poorly preserved in UAVP 15002B, where they appear to be similar to those in Recent *Esox* (text-fig. 2).

The parasphenoid is preserved in UAVP 15002B and 17678. It is narrow and elongate, as in Recent *Esox*. The vomer is broad and truncate anteriorly (text-fig. 1), narrower and tapered posteriorly, and possesses depressible teeth along its ventral surface. There are no fixed or canine teeth on the vomer such as are found at the anterior end of the vomer in *E. masquinongy* (Cavender *et al.* 1970).

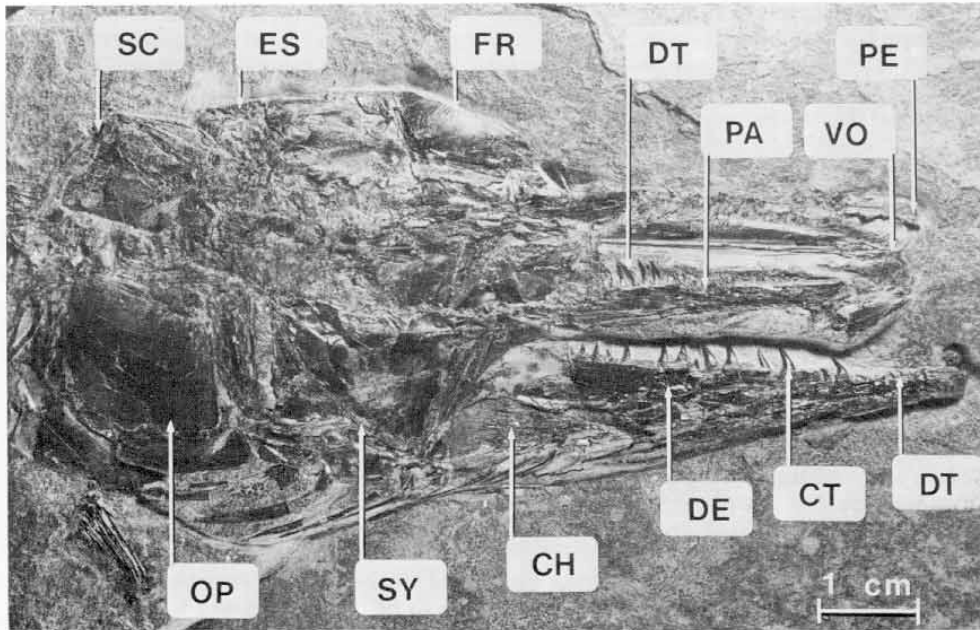
Premaxilla, maxilla, and supramaxilla are preserved best in UAVP 15002B (text-fig. 2). The premaxilla bears a series of small depressible teeth along its oral margin. Anteriorly the bone is

triangular and posteriorly a narrow extension underlies the anterior portion of the maxilla. The maxilla is markedly curved medially at its anterior end, where it articulates with the palatine. Posteriorly it is narrow and gently curved. A single elongate supramaxilla extends just beyond the posterior end of the maxilla, as in Recent *Esox*.

The dentary and angulo-articular are preserved in UAVP 15002, 15002B, 15005, 17670, 17685, and 17686. Dentaries are among the most common *Esox* fossils at other localities. The mandible is more elongate than in other early Tertiary *Esox* described by Sytchevskaya (1976), having an 'articular angle' of about 50 degrees (text-figs. 1, 2). The dentary is slender anteriorly and bears the mandibular sensory canal in a bone-enclosed tube near its ventral margin. Fixed or canine teeth are borne anteriorly and depressible teeth anteriorly. About ten canine teeth are present per ramus, from a point ventral to the anterior end of the maxilla, to a point just anterior to the coronoid process. The largest canine teeth are at the mid-point of the series. For a fish of comparable size, the canine row appears to have slightly more teeth and to extend slightly further anteriorly than in *E. lucius*.

Palatines are like those of *E. lucius*: elongate bones with numerous depressible teeth which grade in size from largest anteromedially to smallest posteriorly and along the posterolateral margin (text-figs. 1, 2). The largest anterior teeth (text-fig. 2) have the characteristic truncated bases of depressible teeth (Wilson, 1980, fig. 2h, i), unlike anterior palatine teeth of *E. masquinongy* which are of the canine type (Cavender *et al.* 1970).

The ectopterygoid is robust and angled, with a prominent ethmoid process as in Recent *Esox* (text-fig. 2). The mesopterygoid is small, the metapterygoid is large, and the quadrate robust with a prominent anterodorsal strut that supports the ectopterygoid, as in Recent *Esox*. The symplectic is nearly straight, as in *Esox*, *Novumbra*, and *Dallia*, but not *Umbra* (Wilson and Veilleux 1982).



TEXT-FIG. 1. Skull of *Esox tiemani* holotype, UAVP 15002, in dorsolateral view.

The shapes of the hyoid arch bones can be seen in UAVP 15002B (text-fig. 2) and 15005, where they are very similar to the corresponding bones in *E. lucius*. The hyomandibula has a long, posteroventrally directed opercular arm, a prominent laterally directed preopercular strut, a thin anteroventral flange lying against the metapterygoid, and a shaft directed slightly anteroventrally, forming a right angle with the opercular arm and about one and a half times as long as the latter. The epihyal is elongate, tapered posteriorly, and with a gently curved ventral margin as in Recent esocids but not umbrids. The ceratohyal is also elongate and hourglass shaped, very similar to that of Recent *Esox*. Ventral hypohyals are small conical bones with slightly projecting ventral tips (text-fig. 2). Branchiostegals are acinaciform and in the holotype number eleven on the right side and twelve on the left, where six attach to the medial and posteroventral surfaces of the ceratohyal, and six to the ventrolateral surface of the epihyal (text-fig. 2). The total number of branchiostegals is low for known Esocidae (Crossman 1960, Sytchevskaya 1976), agreeing only with some specimens of *E. americanus*, but differing in the distribution of branchiostegals between the epihyal and ceratohyal. Also in the holotype (text-fig. 2), the urohyal is seen to be a long, slender bone, tapered anteriorly, somewhat expanded dorsoventrally at its posterior end, and slightly wider than deep at its anterior end. Branchial-arch bones are not preserved, except for the dermal tooth-plate of the basihyal (glossohyal). In UAVP 15002B and in 15005 it is seen to be thin and broad, tapering gradually from its truncated anterior end, as in Recent esocids.

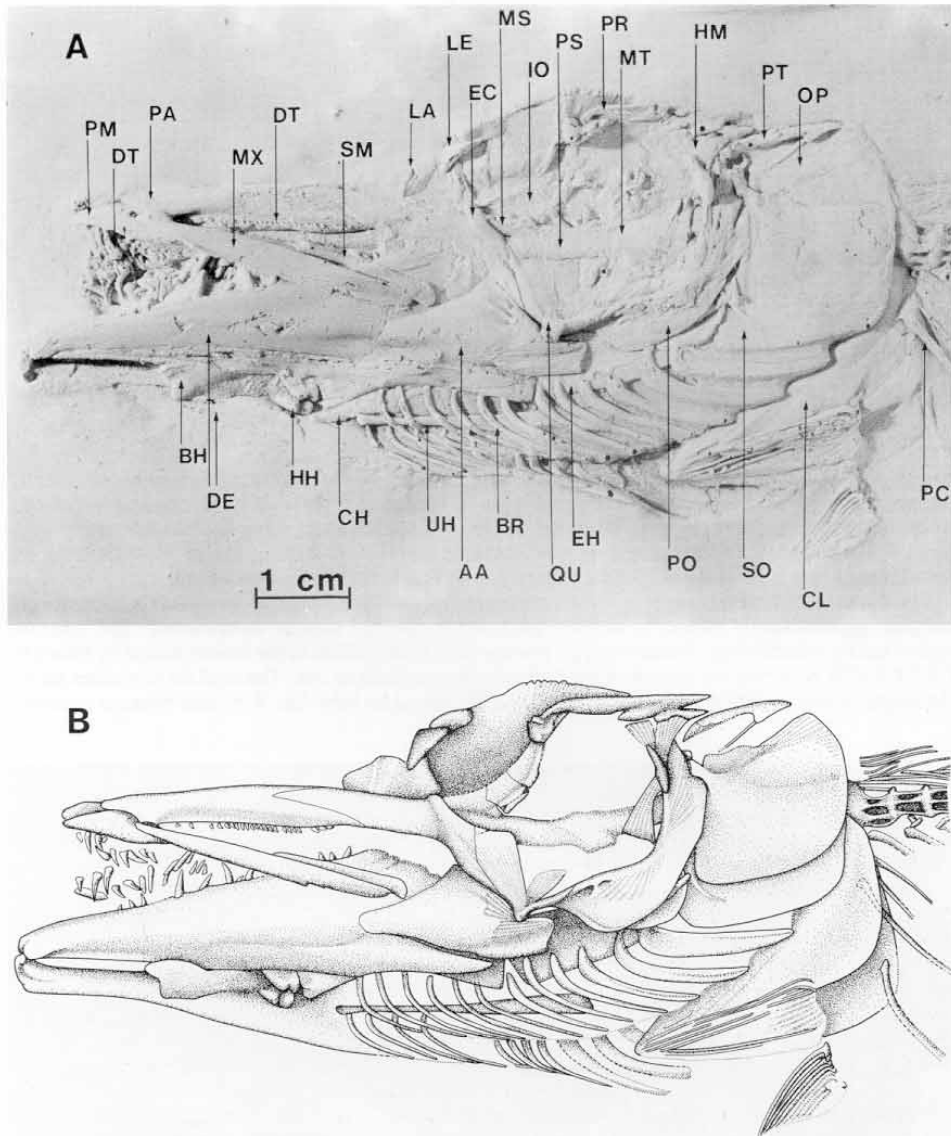
The preopercular is like that of Recent *Esox* but appears stouter. It is slightly bent at the angle (text-fig. 2), with a bone-enclosed sensory canal running the entire length of the bone and an anteromedial flange somewhat larger than the one in Recent *Esox* and reminiscent of that in *Novumbra*. Details of the interopercle are not visible but the subopercle (text-fig. 2) is only slightly curved, has roughly parallel dorsal and ventral margins, and has a prominent vertically directed articular process at its anterodorsal corner, as in Recent *Esox*. It differs from subopercles of the latter in being somewhat less elongate for its depth.

One of the most striking differences between *E. tiemani* and all other esocids, including Eurasian fossil forms (Sytchevskaya 1976), is the shape of the opercle (text-figs. 1, 2). Like those of Recent *Esox* the opercle has vertical anterior and posterior margins, but the ventral and posteroventral margins are more rounded, the articular process at the anterodorsal corner is more slender, and in overall proportions the bone is deeper relative to its length than in the modern species. In addition, the dorsal margin near the articular process bears a thin, plate-like dorsal extension which is continuous with the lateral surface of the body of the opercle, except for a shallow groove. On the medial surface a ridge, corresponding to the dorsal margin of the bone in other esocids, extends from the articular process to the posterolateral corner of the bone, and is separated from the dorsal extension by a narrow fossa, seen best in UAVP 15029 where it is filled with sediment. The fossa extends about two-thirds the distance from the articular process to the posterodorsal corner.

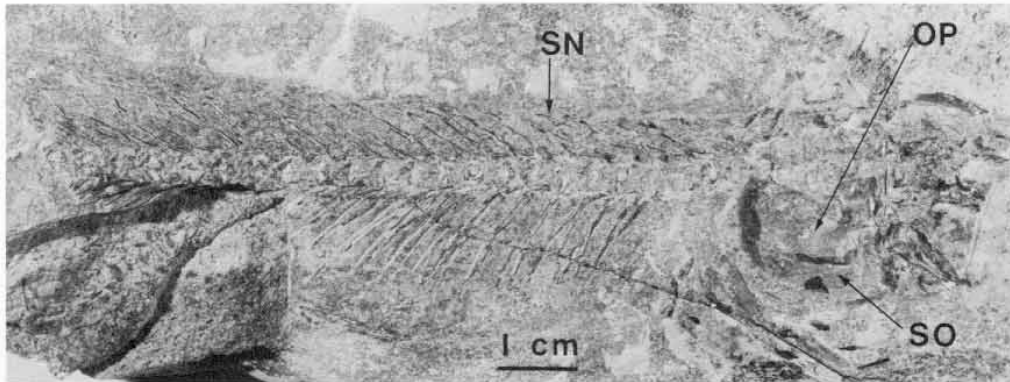
Few significant differences are seen between the pectoral girdle of *E. tiemani* and modern esocids. The cleithrum has a greatly elongated ventral arm, seen in UAVP 15071, and a slender postcleithrum extends posteroventrally from the angle, which is located just behind the posterior end of the subopercle. The supracleithrum, visible in the holotype (text-fig. 1) and in UAVP 15006 (text-fig. 3), bears a canal along its posterodorsal border. The post-temporal is forked, but whereas in modern esocids this bone is thin and plate-like, it appears in the holotype to be more strut-like (text-fig. 2). Pectoral rays number fourteen on the right side of the holotype.

Pelvic plates are virtually the same as those of modern esocids and umbrids other than *Dallia* (Wilson and Veilleux 1982): elongate pubic processes anteriorly, flanked medially by thin pubic plates, with rounded iliac plates posteriorly upon which the fin rays are borne in an anterolateral to posteromedial oblique row. Pelvic rays consist of a splint and approximately eleven rays, as counted in UAVP 15070 (text-fig. 4).

The vertebral column consists of nineteen caudal and approximately forty precaudal vertebrae, including ural centra. The first caudal vertebra, taken to be the first vertebra with an expanded haemal arch, is above the middle of the anal pterygiophore series, and below the middle of the dorsal pterygiophore series. Precaudal vertebrae bear slender ribs which do not appear to have autogenous



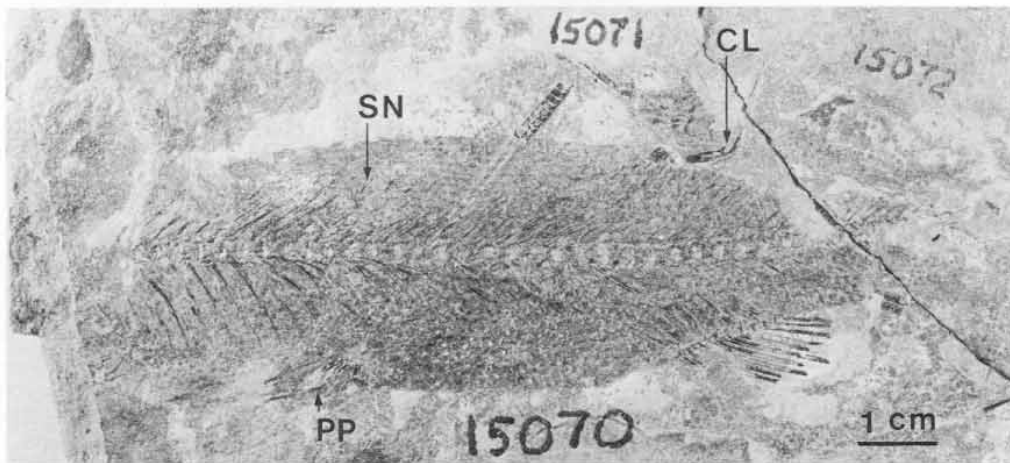
TEXT-FIG. 2. Skull of *Esox tiemani* holotype, UAVP 15002B, in ventrolateral view. a, ammonium-chloride-coated cast of the specimen. b, Drawing of the same specimen.



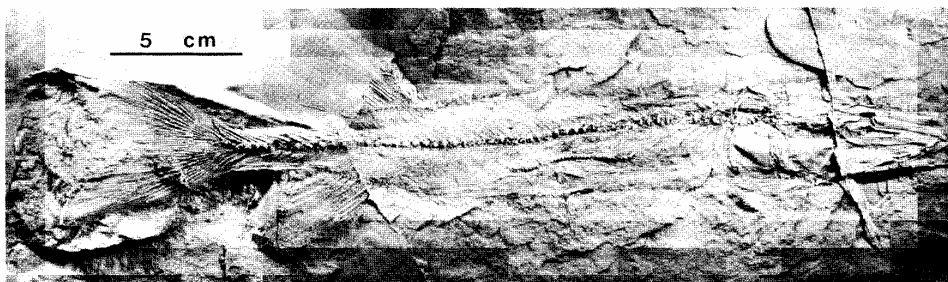
TEXT-FIG. 3. Trunk and posterior portion of skull of *Esox tiemani*, UAVP 15006, a specimen with estimated standard length of 215 mm.

parapophyses. Neural spines are also slender, but neural arches are expanded somewhat, especially on anterior vertebrae. Epineurals are present on all precaudal and the first few caudal vertebrae. Epipleurals or epihaemals are present on the last few precaudal and the first few caudal vertebrae. A series of slender, S-shaped supraneurals, seen best in UAVP 15006 (text-fig. 3) and 15070 (text-fig. 4), extends from just behind the pectoral girdle to just in front of the dorsal fin origin.

The dorsal and anal fins are situated far posteriorly (text-fig. 5) as in other esocoids. Dorsal rays number approximately fifteen or sixteen, preceded by several shorter unbranched rays, and are supported by sixteen long, slender pterygiophores (proximal radials) in the holotype and by fifteen in UAVP 15070, counting the anteriormost-forked pterygiophore as one. The anal fin originates about the length of two vertebrae more posteriorly than the dorsal fin (text-figs. 4, 5), and consists of twelve



TEXT-FIG. 4. Trunk and anterior caudal region of UAVP 15070, estimated standard length 150 mm; ventrolateral portion of skull and portions of trunk of UAVP 15071, estimated standard length 70 mm; and portions of the trunk and caudal region of UAVP 15072, estimated standard length 70 mm.



TEXT-FIG. 5. Complete specimen of *Esox tiemani*, holotype, UAVP 15002, ammonium-chloride-dusted cast of original specimen.

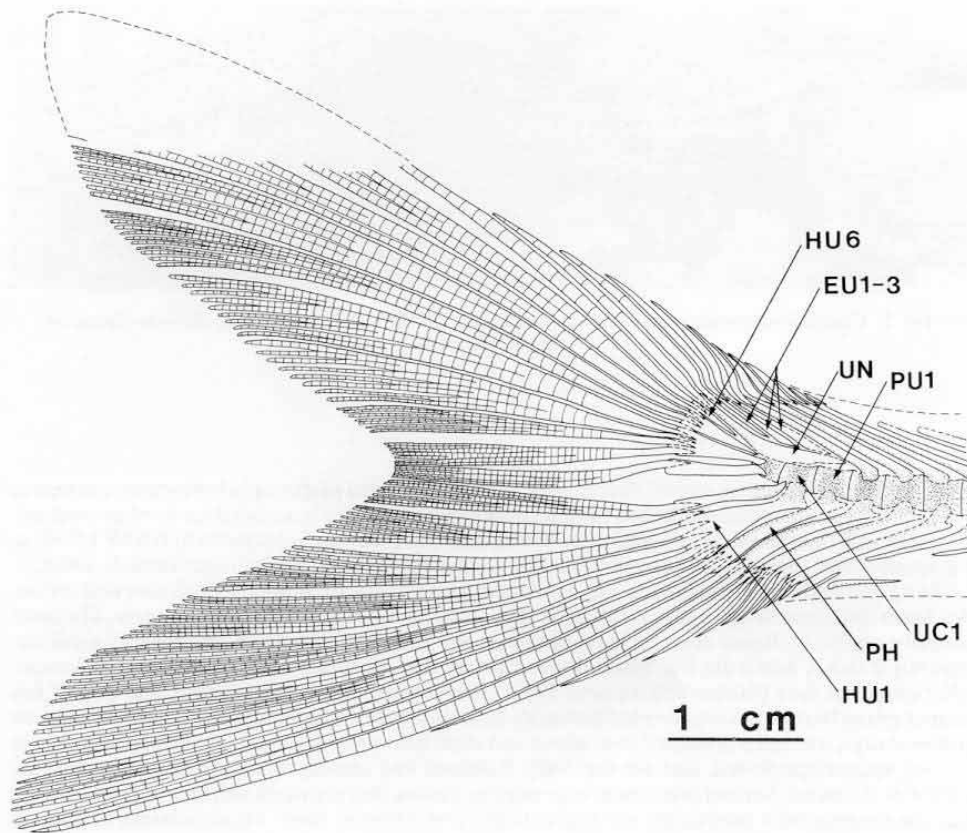
principal rays, preceded by several shorter unbranched rays. Anal pterygiophores number thirteen in UAVP 15070 and fifteen in the holotype. The margin of the anal fin is rounded, as in other esocoids. Ossified middle and distal radials cannot be distinguished in either the holotype or in UAVP 15070, so it is possible that they remain unossified as they do in some umbrids (Wilson and Veilleux 1982).

The caudal skeleton is preserved well in the holotype (text-fig. 6), in which it has two ural centra, two lower and four upper hypurals, a single uroneural, and three very slender epurals. The most posterior neural arch and spine is that on the second preural centrum. A distinct gap separates hypurals 2 and 3, which are less broad dorsoventrally than hypurals 1 and 4, as in *Novumbra* and other species of *Esox* (Wilson and Veilleux 1982). The first hypural, the parhypural, and the last few haemal spines bear anteriorly directed processes near their bases. The caudal fin consists of nineteen principal rays, with nine branched rays above and eight below the mid-line. Dorsal procurrent rays number approximately ten, and are decidedly S-shaped and anteroposteriorly expanded near the middle of the series. Ventral procurrent rays number eleven, and are more uniform in shape, except that the anteriormost procurrent ray seems larger and oriented more anteroposteriorly than its neighbours.

The articulated specimens display only the exposed portions of their scales. These are circular to slightly elongate, with fine, closely spaced, concentric circuli. No trace of cardioid scales (Scott and Crossman 1973) was seen on any specimen. Extrapolating from the presence of eight scale lengths within the length of three vertebrae on UAVP 15070, the species has a total of approximately 144 lateral-line scales, making it comparable to *E. masquinongy* in this respect. Entire scales are preserved in UAVP 17677, in which they can be seen to have the typical features of modern species of *Esox*: focus about two-thirds the length of the scale from the anterior margin, scale broadly oval to almost rectangular, anterior field deeply cleft by one to three (usually two) radii which produce a lobed anterior edge to the scale. Scales like these have also been reported from the Eocene of Colorado (Wilson 1981).

RECONSTRUCTION AND COMPARISONS

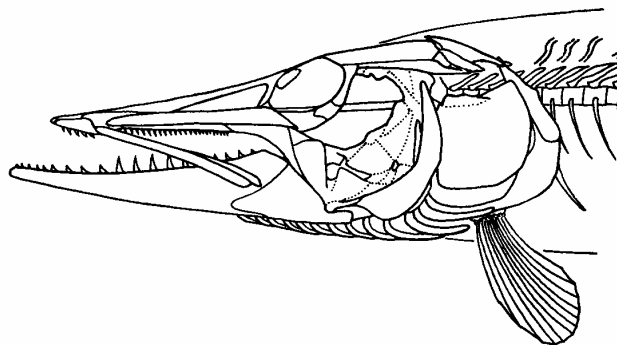
E. tiemani is reconstructed in lateral view in text-figs. 7 and 8. The skull is restored with an elongate lower jaw projecting anterior to the snout, and with the quadrate lower jaw articulation ventral to the posterior margin of the orbit. These features are essentially as preserved in the holotype. The lachrymal, although not well preserved in any specimen, is reconstructed as extending anteriorly



TEXT-FIG. 6. Drawing of caudal region of *Esox tiemani*, holotype, UAVP 15002.

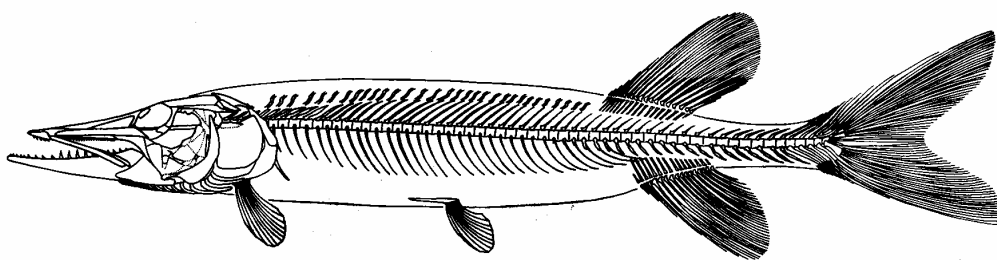
on to the snout as in Recent *Esox* (text-fig. 7). Sytchevskaya (1976) has used the ratio of snout length to postorbital head length to distinguish certain species of *Esox*. The ratio for *E. tiemani* is approximately 1.1, somewhat lower than values for *E. masquinongy*, higher than values for *E. americanus*, *E. borealis*, and *E. lepidotus*, and about the same as values for *E. lucius*, *E. reicherti*, and *E. niger*.

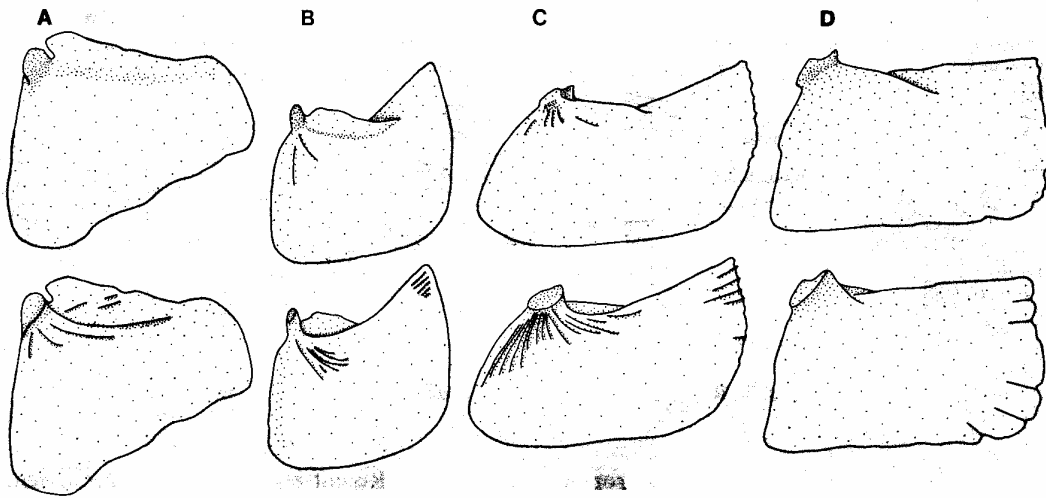
The number of branchiostegals is lower than for Recent esocids. Some specimens of *E. americanus* and rarely *E. lucius* have a similar total number. However, in the great majority of specimens of all Recent esocids (Crossman 1960) the number of branchiostegals on the epihyal exceeds that on the ceratohyal by two or three, whereas in *E. tiemani* the branchiostegals are distributed almost equally between the two bones. The situation is reversed in Recent umbrids (Wilson and Veilleux 1982), where more branchiostegals are found on the ceratohyal. The presence, in the fossil, of more branchiostegals on the left ceratohyal than on the right is the usual situation for modern esocids (Crossman 1960), in which the left branchiostegal membrane usually overlaps the right.

TEXT-FIG. 7. Reconstruction of skull of *Esox tiemani* in lateral view.

The opercular region is shorter anteroposteriorly than in Recent esocids, and the prominent anterodorsal flange (text-fig. 9B) on the opercle distinguishes the species from all other esocids. In young specimens of *E. lucius* the dorsal opercular margin is in two sections, a lateral ridge extending posteriorly and slightly ventrally from the articular process across about two-thirds of the width of the bone, and the posterodorsal margin, which runs from the posterodorsal corner of the bone, anteriorly and slightly ventrally along the dorsomedial edge to a point about one-third the width of the bone from the articular process. Where the two ridges overlap, in the middle third of the bone, there is a shallow groove (text-fig. 9D). The levator operculi muscle (Winterbottom 1974) inserts along the lateral ridge and on the lateral face of the opercle posterodorsal to it, as well as on the dorsal edge and dorsomedial surface of the bone. The situation in young specimens of *E. masquinongy* is similar (text-fig. 9C), except that the lateral ridge forms a flange, like that in *E. tiemani* but much smaller in extent. As well the overlap between the ridges and the groove between them is scarcely present.

The opercle of the Palaeocene to Eocene palaeoesocid *Boltyschia* has what might be interpreted as an incipient or remnant anterodorsal flange, and a ridge on the medial surface of the bone running posteriorly from the articular process (Sytchevskaya 1976, pl. i, figs. 3-4). In most umbrids, the opercle is not as rectangular as it is in esocids or even *Boltyschia*, and all three extant genera have a plate-like extension dorsal to a line joining the articular process with the posterodorsal corner of the bone. Opercles of *Novumbra* are most similar to those of *Boltyschia*. In *Novumbra* (text-fig. 9A) there is a medial ridge running posteriorly from the articular process, and the dorsal flange is broadest anteriorly. The levator operculi inserts entirely on the medial surface of the opercle, dorsal to the ridge.

TEXT-FIG. 8. Reconstruction of *Esox tiemani* in lateral view, intermuscular bones and scales omitted.



TEXT-FIG. 9. Comparison of opercles in lateral view (upper drawings) and medial view (lower drawings). A, *Novumbra hubbsi*, UAMZ 3713. B, *Esox tiemani*, UAVP 15029. C, *E. masquinongy*, UAMZ 3744. D, *E. lucius*, UAMZ 4876.

The articular process of the opercle is also longer in *E. tiemani* than in Recent species. In overall shape the opercle of *E. tiemani* is somewhat intermediate between those of *Boltyschia* and *Novumbra* on the one hand, and extant species of *Esox* on the other, because it is more rectangular than the former but less rectangular and less elongated than the latter. One can visualize a transformation series from a *Novumbra*-like opercle, through *Boltyschia*, *E. tiemani*, and *E. masquinongy*, to the condition in *E. lucius* (text-fig. 9). The majority of the dorsal margin of the opercle of Recent esocids is thus probably homologous with the medial ridge of umbrids. The dorsal opercular flange of umbrids is the homologue of the anterodorsal and lateral ridge in esocids. The opercle of the Oligocene species *E. dispar* differs further from these in having an elongate yet rounded opercle (Sytchevskaya 1976).

In overall body form (text-fig. 8) *E. tiemani* is a long, slender fish. Postcranially the skeleton is comparable to that of Recent North American esocids with the exception of meristic differences. A meristic comparison of relevant features of *E. tiemani* with other fossil and Recent species is given in Table 1.

DISCUSSION

Esox tiemani is anatomically the best-known fossil esocid, thanks mostly to the excellent preservation of the holotype. There is no doubt that it represents a distinct species because of the mosaic of meristic differences between the fossil and other known esocids (Table 1). In one of these, the branchiostegal ray distribution, the fossil is intermediate between Recent umbrids and esocids. In addition to the meristic characters, there is a unique combination of proportional and shape features of the skull which serve to distinguish this species from others. The most striking of these is the shape of the opercle, as described above. Others include the somewhat stouter, slightly bent preopercle with well-developed anteromedial flange, and the elongate lower jaw with perhaps a greater ratio of fixed or canine teeth to depressible teeth along the oral margin of the dentary.

TABLE 1. Comparison of meristic features of *Esox tiemani* with other Recent and fossil species of *Esox*. Data for other esocids from Sytchevskaya (1976). BR—branchiostegal rays, P—pectoral fin rays, V—pelvic fin rays, D—total dorsal fin rays, A—total anal fin rays, CS—supplementary caudal rays, TV—total vertebrae, CV—caudal vertebrae.

	BR	P	V	D	A	CS	TV	CV
<i>E. lucius</i>	11-20	11-18	8-13	17-26	14-21	20	56-65	21-22
<i>E. masquinongy</i>	16-19	14	11	21-24	20-22	27	63-67	21-22
<i>E. reicherti</i>	13-14	12	9-12	17-22	15-18	27	64-65	21-22
<i>E. americanus americanus</i>	11-16	13-17	8-10	15-19	14-17	?	44-51	19
<i>E. a. vermiculatus</i>	9-14	14-15	9-10	17-21	15-19	26	42-49	18
<i>E. niger</i>	12-16	15	10-11	20-21	16-19	22-28	49-54	20-21
<i>E. borealis</i>	13-15	12-13	9-11	18-19	?	?	56-58	21-23
<i>E. papyraceus</i>	?	13?	10?	17	15	13	48	20
<i>E. lepidotus</i>	14	15	13	19-21	19	17-18	52-60	18
<i>E. dispar</i>	?	13	11	19	?	?	61	18
<i>E. tiemani</i>	11-12	14	11	19	15	21	59	19

The question of the phylogenetic relationships of the Palaeocene species is more difficult to answer, because the position of the esocids within the fossil and Recent esocoid families is poorly understood, as are the relationships among esocid species.

Nelson (1972) proposed a division of Recent *Esox* species between two subgenera: *Esox*, including *E. lucius*, *E. reicherti*, and *E. masquinongy*; *Kenoza*, including *E. americanus* and *E. niger*. Unfortunately, the features of the cephalic sensory canals used by Nelson to separate the subgenera are not clearly visible on the available specimens of *E. tiemani*. Nelson did, however, suggest that the number of total vertebrae seen in *Kenoza* (42-54) was primitive for the genus as a whole, and that the greater number seen in the subgenus *Esox* (56-67) was a derived condition. Nelson's hypothesis would suggest that the vertebral number in *E. tiemani* (59) is indicative of a closer relationship to the subgenus *Esox*.

On the other hand, the low branchiostegal number and the distribution of branchiostegals between ceratohyal and epihyal, as discussed above, together with the opercular structure, are all features in which *E. tiemani* is intermediate between Recent umbrids and esocids. These features therefore indicate that the Recent subgenera of *Esox* are more closely related to each other than either is to *E. tiemani*. The evidence bearing on this question is admittedly slim, and a more reliable estimate of relationships must await further study.

With respect to the question of the position of the esocids within the Esocoidei, *E. tiemani* demonstrates that a large number of fundamental esocoid features (including posteriorly situated dorsal and anal fin, S-shaped supraneurals, and toothless maxillae) and esocid features (depressible and canine teeth, elongate snout, jaws, and trunk, elongate vomer and palatines, ethmoid process on ectopterygoid, nearly straight preopercle, squared opercle, small second and third hypurals separated by a gap, and anteriorly lobed scales) are geologically much older than was previously known.

The significance of this is that in the absence of *E. tiemani*, the fossil record of esocoids appeared to show a tendency for the older esocoids (*Boltychia*, *Palaeoesox*) to be anatomically more like umbrids than like modern esocids (Sytchevskaya 1976). Eurasian fossil esocids, similarly, tended to have such features as less elongate jaws and fewer vertebrae compared with some modern esocids. Whether these features are indeed primitive for esocids remains to be seen. But the apparent correlation with greater geologic age must be rejected in view of the structure of *E. tiemani*, which suggests that such esocid features as elongate bodies and jaws and depressible teeth were completely evolved before features such as branchiostegal ray numbers and opercular structure, in which *E. tiemani* is still intermediate between Recent umbrids and esocids.

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