HARRIS DORSAL SPINE OF CLADOSELACHE 1938

THE DORSAL SPINE OF *CLADOSELACHE*

• • •

THE NEUROCRANIUM AND JAWS OF *CLADOSELACHE*

By
John Edward Harris, Ph. D.

SCIENTIFIC PUBLICATIONS
OF THE
CLEVELAND MUSEUM OF NATURAL HISTORY
Vol. VIII, No. 1, pp. 1-12; plates I-II
Issued, March 18, 1938
CLEVELAND, OHIO

SCIENTIFIC PUBLICATIONS
OF THE
CLEVELAND MUSEUM OF NATURAL HISTORY

VOL. VIII ISSUED, MARCH 18, 1938 No. 1

1. THE DORSAL SPINE OF CLADOSELACHE

BY

JOHN EDWARD HARRIS, PH. D.

DEPARTMENT OF ZOOLOGY

UNIVERSITY OF CAMBRIDGE

Cladoselache has always been considered to be a form which possesses no fin spines or armouring of any kind. Eastman (1907), it is true, makes an obscure reference to the fact that Dean had discovered traces of such armour, but as Dean himself in his later memoir (1909) does not mention the topic, it becomes difficult to explain Eastman's remark. The absence of spines has been regarded by many authors as indications that *Cladoselache* is a primitive form; recently, however, Gregory (1936) has suggested that the possession of such spines is a primitive feature in shark organization, and that the absence of them in *Cladoselache* indicates that this form is to be regarded as more advanced than *Ctenacanthus*.

It was with some interest that the present writer, in examining a large collection of *Cladoselache* specimens in the Cleveland Museum of Natural History, noted the presence of an undoubted spine in the region of the first dorsal fin of this genus. The existence of this spine is well established by the specimens in the collection, since in two cases the spine has been found in its natural position on the body of the shark, while in seven or eight other specimens the detached spine is found associated with portions of neurocranium, jaws or pectoral fin.

The best spine in the collection (C.M.N.H. 5678) is illustrated in figures 1 and 2, and in the photographs of Plate I. It was found in its natural position, almost perpendicular to the body surface of a large *Cladoselache* (*sp. ? fyleri*). The species is given with some hesitation, since from the size of the pectoral fins the shark must have been over two meters in length, far larger than any previously known specimen of *C. fyleri*. Only the head and anterior part of the body are at present available for study, and the shape and structure of the pectoral fins agree more closely with *C.fyleri* than with *C.kepleri*. The only other possibility (apart from that of a new species) is that the

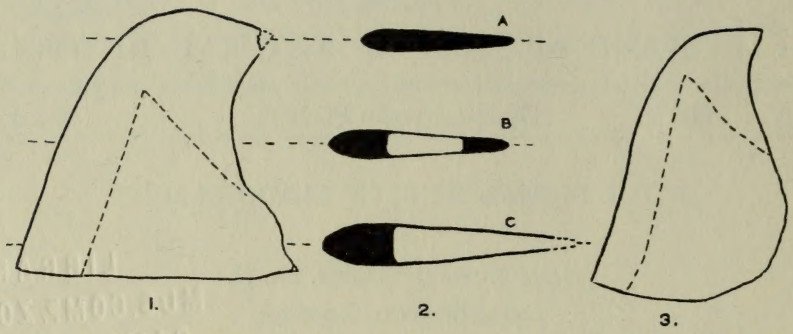

FIG. 1. DIAGRAM OF THE DORSAL SPINE OF *Cladoselache (?fyleri)* SEEN FROM THE LEFT SIDE. The dotted line marks the boundary of the hollow part of the spine. A small portion at the extreme tip is missing.

FIG. 2. CROSS SECTIONS THROUGH THE (RESTORED) SPINE OF *C. fyleri*. The levels are indicated by the dotted lines which cross Figure 1 at the corresponding heights.

FIG. 3. THE DORSAL SPINE OF *Cladoselache kepleri*.

fish is *C.clarki*, and this seems to be ruled out by the pectoral fin ray formula, as there are 20 primaries, 10 secondaries and 4 tertiaries. It must be admitted, however, that the taxonomy of this genus is in an extremely unsatisfactory state. Dean's (1909) species characteristics, whether taken singly or in combination, have been found absolutely unreliable when applied to some of the best specimens in the Cleveland collection. A complete revision of the genus is needed.

The height of the spine is only about 8 centimeters, and as the figures show, its length along the body axis is almost as great. At its broadest point, near the base, it is about 8 millimeters in thickness, so that in shape and size it differs very markedly from the anterior dorsal fin spine of *Ctenacanthus*. Horizontal sections of the spine at three different heights above the base are shown in figure 2. The anterior border, and the whole of the upper portion are solid, but in the lower part, the posterior region is a hollow structure. Pressure has caused the surface over this hollow region to collapse on one side of the spine, as is clearly shown by the photographs.

The surface of the spine is traversed by numerous grooves, but though the texture of the material is similar to that of the *Ctenacanthus* spine, the grooves are not arranged in a regular and parallel manner, and there is no evidence of ornamentation. It is important to note that in this and in all the other spines found, there is no trace of a basal portion sunk below the skin surface. The absence of this characteristic suggests that, unlike the spine of *Ctenacanthus*, this spine must have been rather loosely anchored to the body, which may explain its absence from all previously described specimens.

PLATE I. THE DORSAL SPINE OF *Cladoselache (?fyleri)* PHOTOGRAPHED FROM THE LEFT AND RIGHT SIDES.
On one side the surface above the hollow portion of the spine has been crushed in, showing clearly the boundary of the cavity. There is no basal (internal) portion to the spine; the projection seen at the lower part of the right hand photograph is matrix, and lies more or less perpendicular to the plane of the spines.

Specimen C.M.N.H. 5047 also possesses a dorsal spine in the natural position, but only the basal portion of the spine is preserved. Though the length of this shark (which is almost complete, and in an excellent state of preservation) is 145 centimeters to the base of the tail, its general characteristics agree with those of *C. fyleri* rather than with those of *C. kepleri*.

In both C.M.N.H. 5047 and C.M.N.H. 5678 the anterior border of the spine is situated just in front of the anterior border of the pectoral fins.

In about seven or eight other specimens of *Cladoselache* in the Cleveland collection, a similar spine is found, frequently associated with fragments of the pectoral fin, occasionally with jaws and neurocranium. In one such specimen, the pectoral fin is very similar to that of *C. kepleri*, and the spine is distinctly different in shape from those described above. Such a spine, from C.M.N.H. 5420, is illustrated in figure 3. It is significantly higher relative to its basal length than that of C.M.N.H.5678, and the solid portion occupies a smaller area of the spine. The general structure of the spines, and the appearance of the striations, are in other respects similar in all the specimens.

Many other specimens of *Cladoselache* are seen to have a slight protruberance near the mid-dorsal line between the insertion of the pectoral fins. This is almost certainly the indication of the existence of the spine in the matrix beneath the body; it was from such a specimen that the spine of C.M.N.H. 5047 was excavated.

In *Ctenacanthus* and in the Hybodont sharks the dorsal spines form part of the fins, the anterior border of the fin membrane being closely applied to the grooved posterior surface of the spine. It might therefore be expected that the dorsal spine of *Cladoselache* was similarly related to the first dorsal fin. Nevertheless, a careful consideration of the structure and position of the spine would suggest that this is not the case, but that the anterior fin border was separated from the spine by some little distance. The reasons for this suggestion may be summarized as follows:

(a) The posterior surface of the fin spine in *Cladoselache* has no definite groove to receive the anterior border of the dorsal fin, as it has in *Ctenacanthus* and *Hybodus*.

(b) The shape of the posterior border of the spine, with its strongly curved outline, is such that it is difficult to imagine the shape and structure of a dorsal fin which could be applied to it.

(c) None of the previously known specimens which show the first dorsal fin appears to have had the spine in position. And in the two specimens from the Cleveland collection described above, the spine is present, but there is no trace of a dorsal fin associated with it.

(d) The spine is situated somewhat anterior to the position of the first dorsal fin, according to Dean's restoration.

(e) There is little or no basal portion to the spine. The fin spines of *Ctenacanthus*, *Hybodus*, &c. all possess a well marked unornamented portion which lies below the body surface, and which is frequently associated with a triangular basal plate on which rest the radials of the fin.

These considerations would lead one to suggest that the spine is merely an enlarged scale (or possibly a mass of fused scales) situated almost entirely on and external to the body surface. It is perhaps tempting to suggest that the central hollow portion is the pulp cavity of a single greatly enlarged scale.

Though the position and shape of the spine in *Cladoselache* is so different from that in *Ctenacanthus*, the structure of the spine in the former does not differ fundamentally from that of the spine in the latter. It may be recalled that *Ctenacanthus* possesses a spine which is hollowed out on the posterior surface by a deep groove. Along the lower portion of the spine this groove is open, and encloses the fin, but the upper part of the groove is covered over by a posterior ridge, more or less semicircular in cross section, which runs down from the tip of the spine for about half of its length. This ridge very probably represents the posterior solid region of the *Cladoselache* spine. The groove in *Ctenacanthus* would then correspond exactly to the hollow portion of the spine in *Cladoselache*; the difference between the two could be explained by the presence of the fin in *Ctenacanthus* preventing the closure of the groove in the lower part, at the same time not permitting any great extension of the spine base along the length of the body.* One might conceivably go a step farther. If the approximation of the spine to the dorsal fin is still closer, the antero-rosterior thickness of the spine would be still further reduced, and the spine would probably become shorter (in height). Passing through a Hybodont type of spine, a stage might thus be reached similar to that found in *Goodrichia* (Moy-Thomas, 1936), followed by the ultimate disappearance of the whole structure. This series is perhaps too highly speculative to be taken very seriously. At all events, the presence of the dorsal spine in *Cladoselache* and its definite homology with that of *Ctenacanthus* gives additional weight to Moy-Thomas' argument (*loc. cit.*) that the fishes *Cladoselache*, *Ctenacanthus* and *Hybodus* form a series showing increasing specialization. Gregory's hypothesis (1935) that *Cladoselache* is an advanced form becomes extremely unlikely.

* It is quite possible that the first dorsal fin of Cladoselache was inserted into the hollow of the spine for a very short distance above its base. The fossil spines are so compressed laterally that it is impossible to know whether the posterior border was totally closed in the lower portion. It has therefore been represented in the cross section in Fig. 2C by a dotted line.

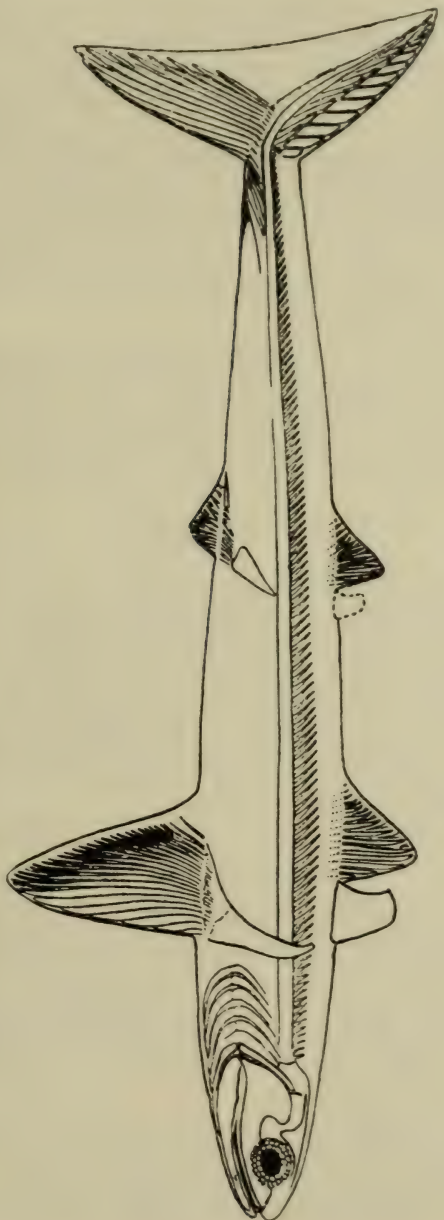

FIG. 4. A RESTORATION OF *Cladoselache fyleri*, MODIFIED FROM THAT OF DEAN (1909).

It would be interesting to know if a similar structure exists in front of the second dorsal fin of *Cladoselache*. Up to the present no such spine has been discovered, but it is hoped that the opportunity may arise for a more careful search through the material.

Though this is the first record of the dorsal spine known to the writer, it is perhaps interesting to note that in Dean's memoir (1909), in the photograph of a crushed skull of *Cladoselache kepleri* in Plate XXVII, there is a very obvious dorsal spine to be seen on the right hand side of the photograph. The original specimen confirms this interpretation, and also shows that the general form of the spine is the same as that in figure 3, which the writer had already ascribed to *C. kepleri*.

A restoration of *Cladoselache*, modified after that of Dean (1909), is shown in figure 4. In addition to the presence of the spines, changes have also been made in the shape of the dorsal fins, and the cranial region has also been slightly modified in accordance with the specimens described in the later communication.

SUMMARY

Two species of *Cladoselache* have been shown to possess a large spine, situated immediately in front of the first dorsal fin. The shape of the posterior border of the spine suggests that it could not have been so closely approximated to the fin as is the case in *Ctenacanthus*. It seems probable, however, that the spines in the two genera are homologous structures, that of *Cladoselache* showing a number of more primitive features. Such a hypothesis agrees with the generally accepted view that *Cladoselache* is the most primitive of all the known Cladodont sharks.

BIBLIOGRAPHY

Dean, B. 1909. The Cladoselachian Sharks. *Mem. Am. Mus. Nat. Hist.*, *vol.* 9, 211.

Eastman, C. R. 1907. Devonic Fishes of New York Formations. *N. Y. State Mus. Mem.* X., 57.

Gregory, W. K. 1936. The Transformation of Organic Designs. *Biol. Rev. vol.* 11, 311.

Moy-Thomas, J. A. 1936. The Structure and Affinities of Fossil Elasmobranch Fishes. *Proc. Zool. Soc. London*, 1936, 761.

2. THE NEUROCRANIUM AND JAWS OF CLADOSELACHE

BY

JOHN EDWARD HARRIS, PH. D.
DEPARTMENT OF ZOOLOGY
UNIVERSITY OF CAMBRIDGE

In the palaeontological collection of the Cleveland Museum of Natural History there are a number of specimens of *Cladoselache* showing portions of the neurocranium, jaws, dorsal spine (see previous note) and pectoral fin. Two of these specimens appear to be of sufficient interest to be described in a special note, as they increase considerably our knowledge of the morphology of the genus.

Specimen C.M.N.H. 6233 is undoubtedly the finest in the collection. It is illustrated in the drawing of fig. 1., and the portion of the block containing the neurocranium is shown in the photograph of Plate II. The neurocranium is seen in ventral view, and the specimen shows also the upper and lower jaws of both sides, traces of hyomandibular and ceratohyal on one side, and a well preserved dorsal spine. From the shape of the spine, the species represented is almost certainly *Cladoselache kepleri*. (see previous note.)

The ventral neurocranial surface of the specimen closely resembles that of *Cladodus wildungensis*, described and figured by Stensio (1937), and the general resemblance to the neurocrania of *Chlamydoselachus*, *Heptanchus* and other primitive modern sharks is equally striking. The ethmoidal region is lacking, as it is in Stensio's specimen, and the general appearance suggests that this region was relatively thin and delicate, in contrast to the heavier posterior portion of the skull. The occipital region is preserved complete, but is largely covered by the left palatoquadrate cartilage, which is seen from its inner side.

The post orbital process is long, as in *Cladodus;* but instead of turning sharply forwards at its distal end, it seems to be much straighter, and more or less perpendicular to the long axis of the cranium. The wall of the orbit has been crushed down almost to a

level with the ventral surface, so that the detailed outline of the shape of the post orbital process is not well shown. There is, however, no suggestion of an articular surface for the reception of an otic (quadrate) process of the palatoquadrate, in which respect the skull resembles that of *Cladodus* (Stensio, *loc. cit.*) and that of the modern *Chlamydoselachus* (see Allis, 1923).

The otic capsule is well preserved on the right side, showing a very strongly marked bulla acoustica. The occipital region posterior to the otic capsule differs somewhat from the restoration of Stensio in that the central portion, traversed by the foramen magnum, projects much farther posteriorly.

Several foramina are clearly visible on the neurocranial surface. The paired common carotid foramina (*c.c.*) are clearly shown, as are the openings (*p*) for the canals of the posterior branch of the r.palatinus VII. Anterior to these last, and slightly more mesially placed, are the paired foramina for the passage of the orbital (external carotid) arteries (*o.*). Unlike the neurocranium of *Cladodus*, the internal carotids apparently entered the brain through a single median foramen (*i.c.*), which may indicate that the neurocranium of *Cladoselache* had thinner walls than that of *Cladodus*. This is also suggested by the complete absence of any trace of superficial grooves traversed by the internal carotid and orbital arteries. Though both these differences (the thinness of the neurocranial wall and the single internal carotid foramen) might suggest that *Cladoselache* is slightly more advanced than *Cladodus*, they are probably too insignificant to carry much weight. Anterior to the internal carotid foramen in the mid-line is seen the fenestra hypophyseos (*f.hy.*).

The large foramen (*o.p.*) is visible on one side only of the specimen, though there is a small slit like depression at the corresponding position on the opposite side which may represent the same passage. From its position and its direction of penetration of the neurocranium, it may represent the common opening through which the orbital artery and the anterior r. palatinus VII enter the orbit. Since this foramen would lie on the lateral boundary of the ventral surface of the neurocranium, it might be well preserved on one side and closed on the other, due to a slight pressure asymmetry in preservation.

A large part of the orbital wall is preserved in this specimen, flattened down to a level with the ventral surface of the skull. Assuming that the flattening has not badly distorted the general proportions, the large area of this wall suggests that the eye of *Cladoselache* was protected by a large overhanging orbital roof.

An interesting feature of the specimen is the pair of pits which can be clearly seen in the photograph, just anterior to the post orbital process. The groove leading into them passes outwards and dorsally, so that it does not lead towards the cranial cavity. It might conceivably correspond to the numerous openings in *Chlamydoselachus* by which the r. buccalis VII communicates with the post-orbital latero-sensory canal. No other passages for the nerves to the sensory canals can be seen in the specimen, which would therefore differ very greatly from that of *Chlamydoselachus*.

The jaws of the specimen are similar to those of *Cladodus wildungensis*, described and figured by Jaekel (1925). The quadrate (otic) process of the palatoquadrate, though greatly expanded, shows no trace of an articulation with the post orbital process of the neurocranium, and presumably served only for the origin of a large adductor mandibularis muscle. The orbital process (*pr.*) is not strongly developed, as in recent forms.

The presence of the tooth grooves on the outer surface of the right palatoquadrate indicate that there were relatively few teeth —not more than eight or nine on each side. This would be expected from the large size of the teeth in Cladoselache.

The hyomandibula is not clearly seen in this specimen — it is probably represented by the small rudiment shown at *hm.* The right ceratohyal is visible as the fragment *r.ch.* It is very imperfectly seen in this specimen, but is well shown in the next specimen to be described. The dorsal spine, (*d.s.*) has already been dealt with in the preceding note.

C.M.N.H. 5769 is also a specimen of *Cladoselache kepleri*, showing a similar ventral view of the neurocranium, which, however, is not so well preserved in this specimen. The foramina on the ventral surface are identical with those of C.M.N.H. 6233. The distal parts of the two palatoquadrate cartilages are absent, but on the left side, the hyomandibular has been preserved in two pieces, as a thin rod like cartilage. The right ceratohyal is well shown, its lower border agreeing well with the contour of the right mandible.

Figure 3 represents a restoration of the skull of Cladoselache, seen in side view. The jaws etc., have been fitted to the position of the skull by cutting out tracings from the actual photographs of the specimen. The restoration has been completed with a relatively short rostrum, making the mouth sub-terminal rather than ventral. This would seem to agree best with the extremely long mandible. The general resemblance to the head of Chlamydoselachus is seen to be extremely close.

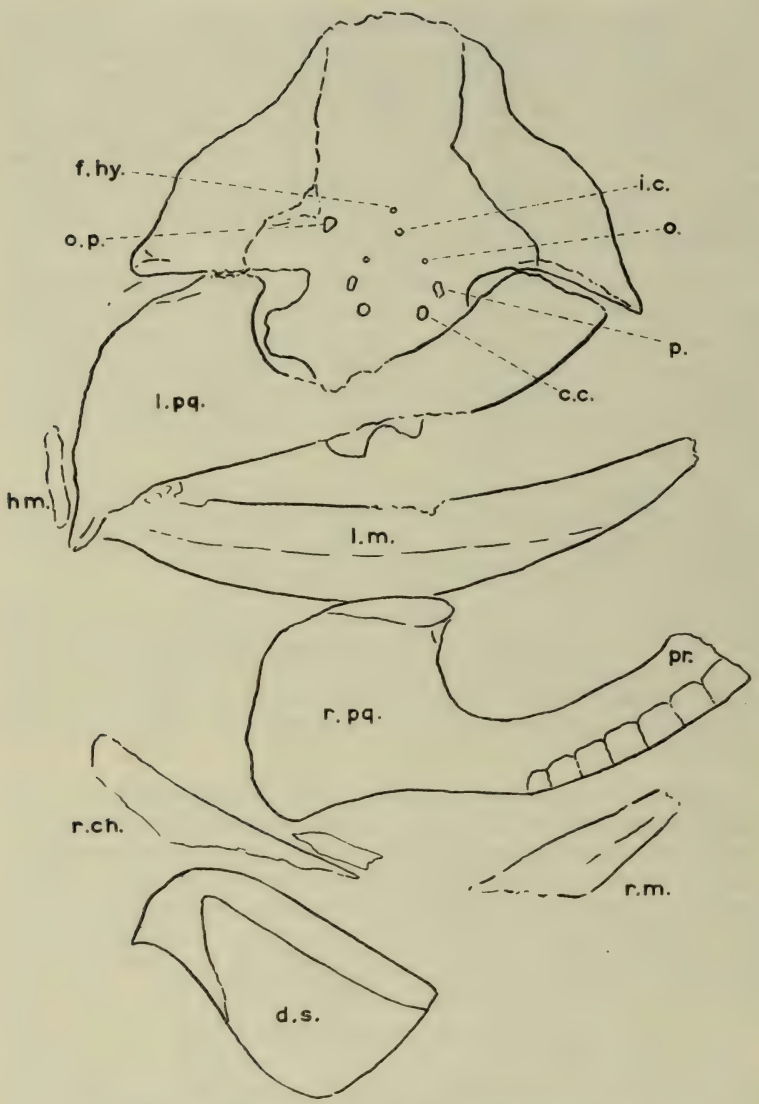

FIG. 1. DIAGRAM OF C.M.N.H. 6233. *Cladoselache kepleri*.

c.c.: common carotid foramen; *d.s.*, dorsal spine; *f.hy.*, fenestra hypophyseos; *hm.*, ?hyomandibular; *i.c.*, internal carotid foramen; *l.m.*, left mandible; *l.pq.*, left palatoquadrate; *o.*, orbital (external carotid) foramen; *o.p.*, foramen for exit of orbital artery and of the anterior ramus of pal. VII.; *p.*, foramen for posterior r. pal. VII.; *pr.*, orbital process of palatoquadrate; *r.ch.*, right ceratohyal (?); *r.m.*, right mandible; *r.pq.*, right palatoquadrate, showing tooth grooves in distal portion.

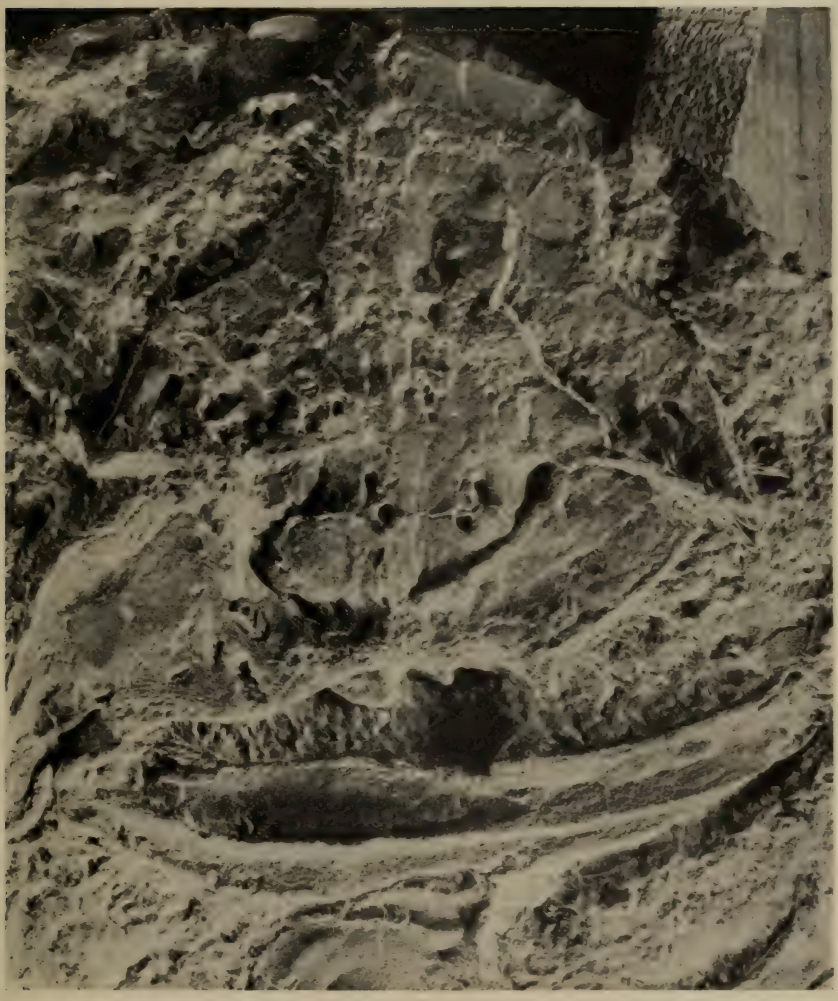

Plate II. Photograph of Part of Specimen C.M.N.H. 6233, Showing the Neurocranium and the Upper and Lower Jaws of One Side. The relationship between the post orbital process and the palatoquadrate is accidental, as the jaws are those of the left side.

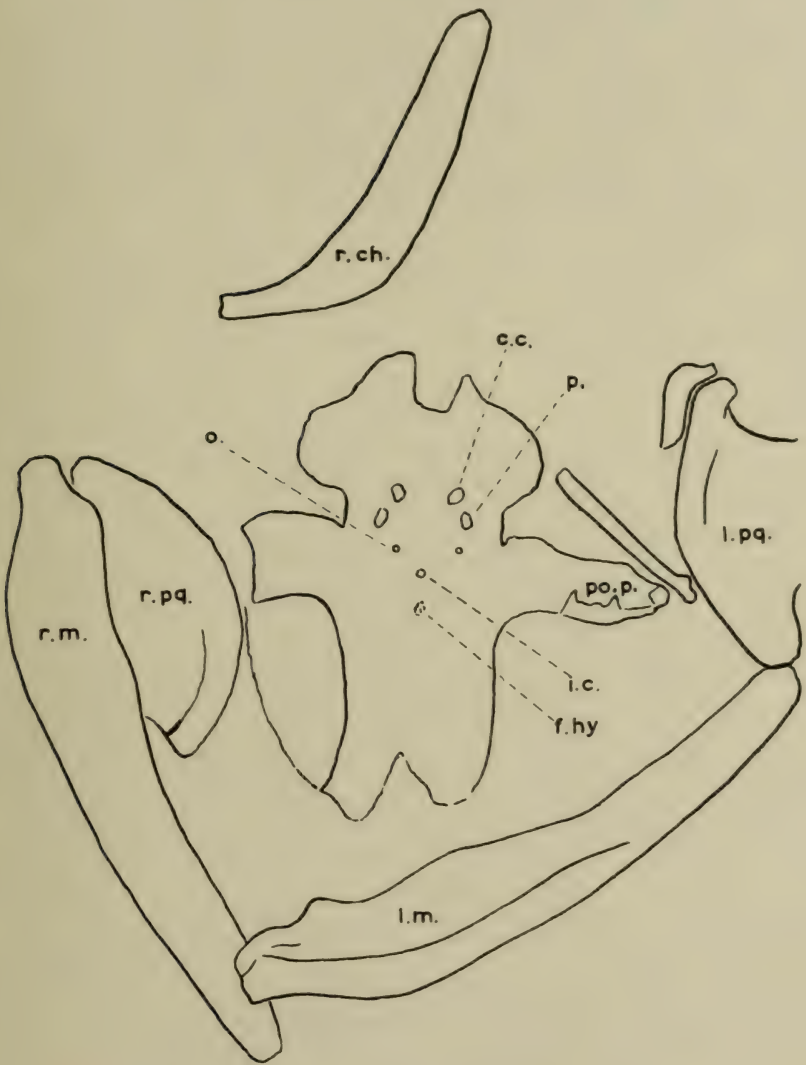

FIG. 2. DIAGRAM OF C.M.N.H. 5769. *Cladoselache kepleri*. *po.p.*, post orbital process. Other lettering as in FIG. 1.

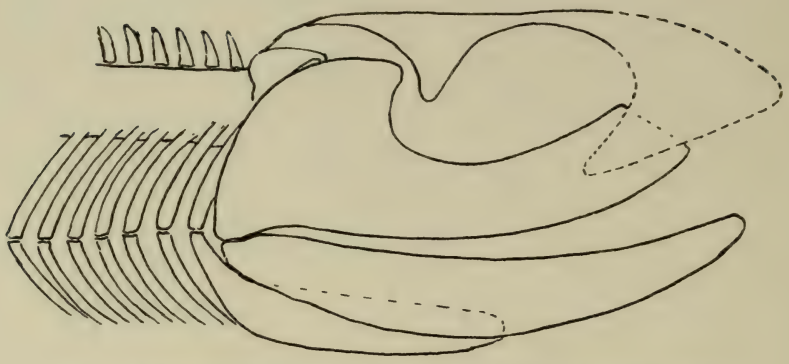

FIG. 3. RESTORATION OF THE HEAD OF *Cladoselache kepleri* IN LATERAL VIEW.

SUMMARY

A description is given of two neurocrania, with their associated mandibular and hyoid arches, of *Cladoselache kepleri*. Apart from slight differences in shape, and the possession of a single internal carotid foramen, the neurocrania agree very closely with that of *Cladodus wildungensis*, as dercribed by Stensio. A reconstruction of the skull suggests that the mouth was sub-terminal, and that the general appearance of *Cladoselache*, as well as its anatomy, would strikingly resemble that of *Chlamydoselachus*.

I am greatly indebted to Mr. H. L. Madison, the Director of the Cleveland Museum of Natural History, for his kindness in allowing me to work on the collection, and for the facilities he provided during my stay in Cleveland. It is a pleasure also to acknowledge the unfailing courtesy and assistance of Mr. P. A. Bungart, who was originally responsible for the collection and preparation of the specimens described.

BIBLIOGRAPHY

ALLIS, E. P. 1923. The cranial anatomy of *Chlamydoselachus anguineus*. *Acta Zoologica*, *vol.* 4, 123.

JAEKEL, O. 1925. Das Mundskelett der Wirbeltiere. *Morph. Jahrb. vol.* 55.

STENSIO, E. A. SON, 1937. Notes on the endocranium of a Devonian *Cladodus*. *Bull. Geol. Inst. Upsala. vol.* 27, 128.