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V. — STUDIES ON FOSSIL FISHES (SHARKS, CHIMÆROIDS, AND ARTHRODIRES).

By BASHFORD DEAN.

February, 1909.

Vol. XI. Anthropology (not yet completed).

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PART I.— The Chukchee: Material Culture. By W. Bogoras. Pp. 1–276, pll. i–xxxi, 1 map, and 199 text figures. 1904.

PART II.—The Chuckchee: Religion. By W. Bogoras. Pp. 277–536, pll. xxxii–xxxiv, and 301 text figures. 1907.

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# ETHNOGRAPHICAL ALBUM.

*Jesup North Pacific Expedition.*

Ethnographical Album of the North Pacific Coasts of America and Asia. Part 1, pp. 1–5, pll. 1–28. August, 1900. Sold by subscription, price, $6.00.

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VOLUME IX, PART V.


STUDIES ON FOSSIL FISHES (SHARKS, CHIMÆROIDS, AND ARTHRODIRES).

# MEMOIRS

OF THE

# AMERICAN MUSEUM OF NATURAL HISTORY.

PART V.— STUDIES ON FOSSIL FISHES (SHARKS, CHIMÆROIDS AND ARTHRODIRES).

By Bashford Dean.

Plates XXVI–XLI.

## CONTENTS.

## I. The Cladoselachian Sharks.

The Devonian Sharks known generally as "Cladodonts" and technically as Cladoselachians, *i. e.*, a particular group of Cladodontid sharks, have, during the past decade, figured prominently in studies on the morphology of fishes. For there is weighty evidence that these early sharks not only furnish a key to the puzzling structures of contemporary and earlier fishes (*e. g.*, acanthodians), but picture in the most interesting way many of the conditions believed to have been present in the ancestral vertebrate.

The morphology of these early sharks has, it is true, been dealt with, but only in the broadest lines. (*Cf.* bibliography on p. 248.) And it is accordingly desirable that all of the documents extant which deal with the group should be gathered together in a more or less monographic form. Particularly important, in this connection, are the beautifully preserved specimens of *Cladoselache* from the concretions of the Upper Devonian (Black Cleveland shales) of Ohio which have been brought to light from time to time by the veteran collectors, Dr. William Clark of Berea, and the Rev. Dr. William Kepler, now of Oberlin, Ohio. In fact, with conspicuous exceptions, all specimens of these forms have passed through their hands. Such material is at present preserved in the American Museum of Natural History and in the British Museum, the latter possessing all of Professor Claypole's types: a few specimens only remain in Ohio.

In the present paper especial reference is made to the cladoselachians preserved in the American Museum,— which represent in all, more than forty individuals. These have been examined in the light of previous studies and in comparison with the material now in London, and an attempt has been made to summarize both their taxonomy and their structural features.

### 1. CLADOSELACHIANS IN GENERAL.

Cladoselachians, originally described by Professor Newberry, are palæozoic sharks having a notochordal axis and paired fins of a peculiarly archaic form, *i. e.*, resembling the unpaired fins, and of the "dermal fold" pattern, about which so much has been written in recent discussion of the origin of the limbs of the vertebrata. Their caudal fin was upturned abruptly, appearing at first sight almost teleostean in its truncated "homocercy" and provided on either side with a horizontal flange, a structure which—judging at least from numerous analogies among rapidly swimming fishes — kept the stroke of the fin constant in a vertical plane. In the matter of teeth, *e. g.*, in shape, succession, arrangement in banks, and in their relation to scales, they were essentially like living sharks (notidanids). The scales protecting the body were small in size,

inconspicuous,— only around the eyes did they attain large size, forming sclerotic shields. It is clear they bred in a fashion widely different from modern sharks since their pelvic fins are not provided with intromittent appendages: and it is a reasonable inference, therefore, that they spawned in the primitive piscine way, fertilizing the eggs externally. Especially interesting, finally, is the evidence that in these ancient sharks the digestive tube was continued behind the ventral fins nearly to the base of the caudal fin,— a condition pictured in recent forms only in the postanal gut of embryos.

Cladoselachians are known at present from the Upper Devonian of Ohio and New York and from the Lower Carboniferous of Kentucky. But their range possibly extended, judging from the occurrence of detached teeth, into the Middle Devonian on the one hand and the Coal Measures on the other. Thus far we are able to distinguish with reasonable accuracy about ten species, five of which are here described for the first time. As a rule they are sharks of moderate size, the smallest having a length of about 50 cm., the largest 150 — or even perhaps 300, if *"Cladoselache" magnificus*, which was described from jaws only, proves to have really belonged to this genus.

## 2. OCCURRENCE.

With but few exceptions the associated remains of cladoselachids have been obtained in but a single region, the banks of Rocky River, near Berea, Ohio, and nearby in the immediate neighborhood of Cleveland. The specimens are found in concretions, some of which are of large size, six feet or more in length, which are brought to light in the weathering of soft shale along the steep sides or in the beds of waterways. The concretions contain sometimes a fragment, sometimes an entire fish. The preservation of the fossil is apt to be excellent, in some cases marvellous. The fish usually — in nine cases out of ten — appears in exact ventral or dorsal aspect (Plate XXVI A), just as it was enclosed in sediment, the ventral side having probably shifted uppermost as the gases of decomposition distended the digestive tube. Only in exceedingly rare cases is the fish shown in lateral aspect, disclosing caudal fin, dorsal, or gill region (Plate XXVI B). In general the fish is little altered in form: its fins are often admirably displayed, and show the delicate membrane which extended from the hinder border along the side of the body. Occasionally specimens are found which have been crushed and completely macerated. In the material of the American Museum there is a specimen of this type in which the fins have softened and are spread about in all possible positions: in another case the head is flattened out and is twice the usual width (Pl. XXVII). In general the fossil is preserved in a single plane in the concretion: sometimes, however, the paired fins pass into the overlying matrix in inclined planes, and now and then a caudal fin can be traced above and below into the stone. Dorsal fins are rare: in two or three instances they are shown (Figs. 18 and 24)

flattened into nearly the same plane as the remainder of the fish: and in a few cases they are fossilized in a vertical plane, (*i. e.*, at right angles to the general plane of the fossil) and are discovered when the concretion happens to be thus fractured. Such cases occur in specimens P. 9280 and 9282 in the British Museum. A marvellous feature in these fossil sharks is the preservation of soft structures. In numerous cases muscle bands (Fig. 23, 34, 35, 36) are preserved at various points, and sections demonstrate that the preservation extends to histological details, *e. g.*, transverse striation of the fibers. Gill lamellæ are frequently fossilized, and in a unique case, the kidneys (Figs. 31, A and B). On the other hand the firmer structures within the walls of the body did not lend themselves favorably to fossilization: the vertebral arches are rarely and rather poorly preserved: the cranium is imperfectly known and the pelvic and pectoral arches are uncommon.

The conditions under which these ancient sharks lived can be inferred, with reasonable probability, from the foregoing conditions — as well also from our general knowledge of the mode of deposition of the Cleveland shales. That they were salt-water fishes is undisputed: but we may reasonably query whether they were truly marine. They were, we believe, estuarine, passing up into the mouths of rivers, and it is to the estuarine sediments, which were soft, deep and rich in phosphates, that we are indebted for their preservation. We know that these ancient sharks preyed upon small ganoids, for the remains of palæoniscids are frequently found in their fossils. After death they sank speedily to the bottom, predicating an absence of swimbladder, for otherwise their soft structures would hardly have been preserved. And because of the conditions and character of the sediment into which they sank they probably fossilized quickly. In any event they must have attained a position in a kind of sediment in which they were relatively free from the attacks of bacterial or other disintegrating agents. It is also evident that they lay in a deep and unstable sediment since the body of the fish could in many cases orient itself (as gases developed in the digestive tube) so that the visceral side came to be upmost.

### 3. MORPHOLOGY.

a. *Scales, eye-defenses, teeth.*—The scales of cladoselachians are minute and tubercular. They are somewhat cuspid, quadrangular in section, the exposed portion more or less indented or subdivided, as indicated in Figs. 1 and 2. In the latter case the shape of the denticle is depressed and "triconodont." In other cases the scales become indented to such a degree that their surface bristles with cusp-like points or ridges, appearing altogether like the "teeth" of *Stemmatodus* (St. John and Worthen). Fig. 3. As a rule scales are not preserved uniformly, and one is often given the impression that they were absent over a large extent of the fish's body. They certainly vary in size, shape and ornament in different regions, very much indeed as in modern sharks: they are

most conspicuous on the exposed rims of the fins, around the eyes, and along the sides of the jaws; and in the latter region they are obviously tooth-like. On the fin margins they are enlarged and arranged in close order suggesting the origin of the spine ornaments in the kindred acanthodians. (*Cf.* the white line along the anterior rim of the pectoral fin in *C. kepleri*, Pl. XXVIII).

The scales surrounding the eyes, Pl. XXVII, XXVIII and Fig. 4, are arranged in several rows, and form together a strong compact cup encircling the cornea and protecting the outer wall of the eye. It has accordingly been suggested by the writer that the perfection of this orbital defense preceded the evolution of the sclera in the vertebrate eye, for it is difficult to conclude that so elaborate a defense as this armored cup would have been evolved if the



Fig. 1. Fig. 2.

Fig. 1. Placoid scales of *Cladoselache fyleri*. × 25.

Fig. 2. Placoid scales of *Cladoselache fyleri*. Trifid type from near margin of mouth. Am. Mus. 1711. × 20.

underlying capsule had already been strengthened in the modern way: — moreover, judging *à priori*, it is less difficult to 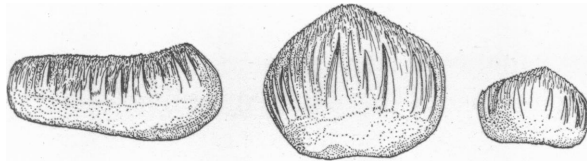picture the cerebral optic outgrowth of the primitive gnathostome protected by clustering scales than by a hardening of the outer wall of the brain vesicle itself. For we have every reason to believe that in this vesicle the transformation of the outer wall, which was early a nervous and sensory structure,



Fig. 3. Scales of *Cladoselache*, sp. (probably *C. clarki*). After specimen P 9266, British Museum. × 10.

into a protecting capsule would have involved the more complicated readjustment of tissues.

The teeth are of the familiar "cladodont" form, having a large central cusp, and on each side two minor cusps, of which the outer, or marginal, is the longer. This type of tooth undergoes modification in different parts of the mouth (Fig. 5): in general the central cusp becomes more prominent in the symphyseal region, and the lateral cusps in the region of the hinge of the jaw. The smallest cusps, the pair more nearly median, are apt to be reduced and are often indistinguishable: and the marginal pair become proportionately small and inconspicuous. In cases, indeed, where the teeth are poorly preserved (the rule rather than the exception among these
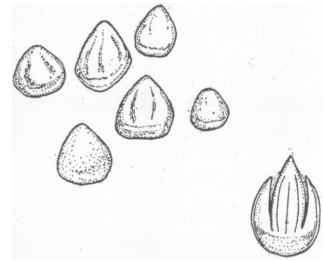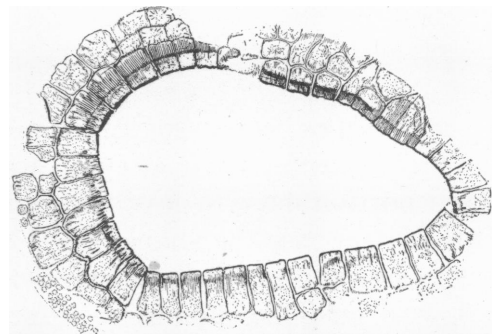


Fig. 4. Circumorbital ring of enlarged placoid scales. (*C. kepleri.*) From specimen 250, Am. Mus.

sharks), one can readily believe that lateral cusps are absent. Thus Professor Claypole, unable to find lateral denticles in a specimen in the Clark collection, has described it as "*Monocladodus*," a genus which I have been led to abandon since I found that in the type specimen one of the teeth, when better exposed, showed the lateral denticles. Characteristic of the early cladodont tooth is the broad base on which the cusps are set, which is a means of distinguishing it from similar forms (*e. g.*, hybodont), for it is of course known that "cladodont" teeth are found in several genera, families, even in two orders of sharks.

The dentition of a cladoselachian is best known from Claypole's description [1] of a specimen of *C. clarki*, now preserved (P 9273) in the British Museum. From this specimen and from several others, the latter in the American Museum, we now know that on each palatine ramus were about a dozen banks of teeth, each including seven or eight close-set elements (*cf.* reconstruction, Fig. 6). The banks were separated from one another by intervals, whose width was that of the banks themselves, somewhat, for example, as in the recent *Chlamydose-*
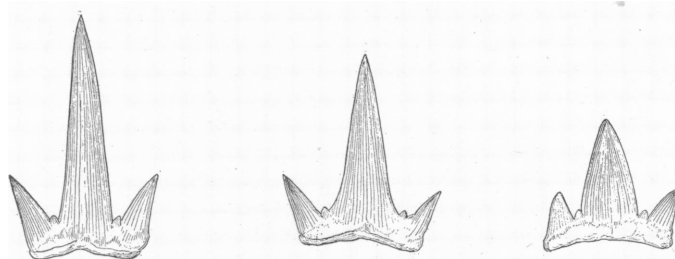


Fig. 5. Teeth of *Cladoselache fyleri*. From different parts of the mouth. Am. Mus. 1711. × 5.

*lachus*. The teeth of the mandibular rami are known only imperfectly: their arrangement was probably the same as in the palatine; and the apposing banks of teeth probably interlocked, for this follows apparently from the fact that the mandible bore a symphyseal bank of teeth, (Claypole, *op. cit.*), a condition paralleled in the interlocking dentition of *Chlamydoselachus.*

In further detail: the teeth are flattened on their outer faces, and are here unornamented: their cusps are convex on their inner faces and are sometimes sculptured in a series of close-set grooves. Their bases are broad, rendering possible a firm attachment to the jaws. The teeth fit together closely in their bank, and in this compression the lower rim of the outer face of each tooth is indented, and there is a slight sigmoid flexure of the cusps.

In the finer structure of the tooth the vaso-dentine is extraordinarily thick (*cf.* the cross section of a tooth, Fig. 8) and there is no enamel present, as Claypole earlier noted (1894, Pro. Am. Micr. Soc., pp. 194–195). The latter character, however, is of less significance in selachian morphology than one might assume, since Röse has demonstrated (1897, Anat. Anz., XIV, pp. 34, *et seq.*) that enamel (in a strict sense) is not present in sharks in general. Claypole's suggestion, therefore, that "in Devonian Cladodonts.... the highest form of

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[1] Am. Geol., Jan. 1895, pp. 1–7, pl. i.

tooth tissue had not at that date been reached" can hardly be taken literally: it can, however, I think be taken in this sense that in *Cladoselache* there was no vitrodentine, and that there was no "enamel" layer of the dentine, which Röse admits is present in modern sharks.

b. *Vertebral Column.*— *Cladoselache* was notochordal: for while vertebral arches are found there are no traces of centra. Moreover in the tail the space
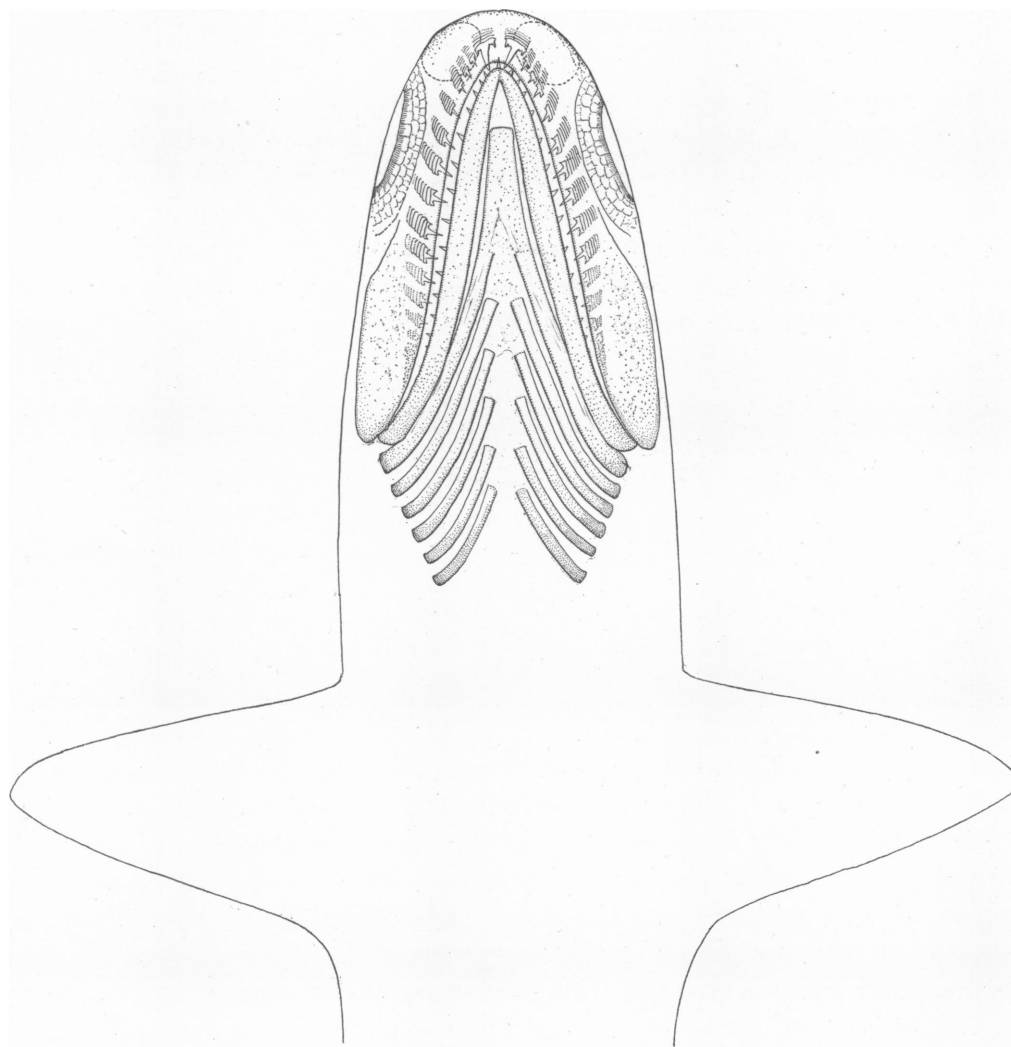


Fig. 6. *Cladoselache fyleri.* Head and pectoral region in ventral aspect. Reconstruction, especially after three specimens in Am. Mus. Anterior rim of mouth after 7331, remainder of mouth, eyes, etc. after 1711,— gill basket after 1670.

occupied by the notochord is shown with great distinctness (Figs. 15, 16) and in this region the notochord was evidently unconstricted. A careful revision of the material showing vertebral structures has now convinced the writer that only neural arches can be determined in the trunk region: and that the arches were metameric in arrangement, for they correspond in number quite accurately

with the fossilized remains of the muscle plates.    Each arch is a stout tapering rod of cartilage, enlarged at its base (Fig. 9), where it bridges the neural axis. It is not of great length, shorter for example than in *Pleuracanthus*, and extends apparently but half way from the notochord to the integument (Figs. 9, 10, and 18).    There are no interneurals.    In the tail both hæmal and neural arches can be distinguished (Figs. 15, 16, 17).    In the region of the tip of the tail the



Fig. 7.   *Cladoselache* sp.   Outline of palato-quadrate and meckelian cartilages.   After specimen P 9285 in British Museum.   × ⅔.

hæmal arches are continued in a band of cartilaginous tissue which the writer early referred to as a sub-notochordal rod, *i. e.*, a tract of hæmal elements.   (*Cf.* p. 220.)
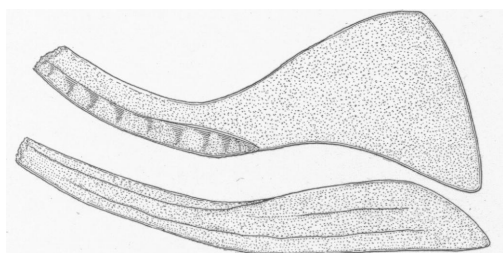
c.   *Skull and Branchial Arches.*— The cranium is very imperfectly known. From the side view of the head shown in Fig. 9, it was apparently similar to that of a notidanid shark; but there is no evidence as to the condition of its dorsal roof, fontanelles, etc.   In a single specimen, already referred to (Brit. Mus. P. 9273) the anterior region of the cranium is shown, indicating large nasal capsules in a terminal position.   (*Cf.* also Pl. XXVIII, from specimen 7317, Am. Mus.)   The jaws, seen in lateral aspect in Figs. 7 and 9, and in ventral in Fig. 6, are proportioned as in the recent *Chlamydoselachus*, long and slender, closely drawn together on the ventral side of the head.   In several specimens they are well preserved: they show nowhere the subdivisions described in the mandibular arch of *Acanthodes bronni* as elements homologous with those of gill-arches.   The gill-arches themselves while shown in several specimens have never been satisfactorily defined: they certainly number five on each side, and there may be a sixth and even a seventh.   It is clear however that the gill-arches were delicate rather than stout, and that they were long, extending far backward (*cf.* Fig. 9).   In this regard they resemble closely the acanthodians.   (*Cf.* Am. Jour. Anat., 1907, Vol. VII, p. 222, figs. 28, 29: also Kner, in SB. Wien. Akad. Cl. LVII, B. 1, 1868, pl. v.)   The suspension of the jaw is not



Fig. 8.   Section of tooth of *Cladoselache kepleri*, showing absence of an enamel layer.   × 50.

definitely known: in a single specimen there is an element which may be interpreted as an elongate hyomandibular.   The palatine element has no superior process by which it may be attached to the cranium in the orbital region. The ceratohyal element, as in *Chlamydoselachus*, is long and narrow, and similarly disposed with respect to the meckelian cartilage.   In none of the specimens have cartilaginous extra-branchial supports been determined.

d.   *Fins and Girdles.*— The fins of cladoselachians are distinctly of the
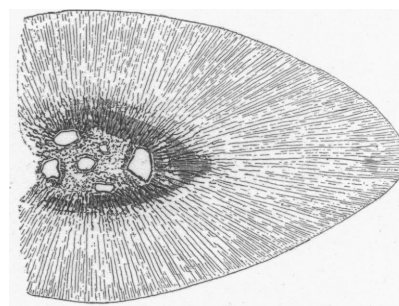
type of dermal folds: for the paired fins are, in outward structure at least, quite similar to the unpaired fins, *i. e.*, their hindmost web continues in the plane of the fin and fades away on the side of the body, (Plate XXXII and Figs. 20, 21,
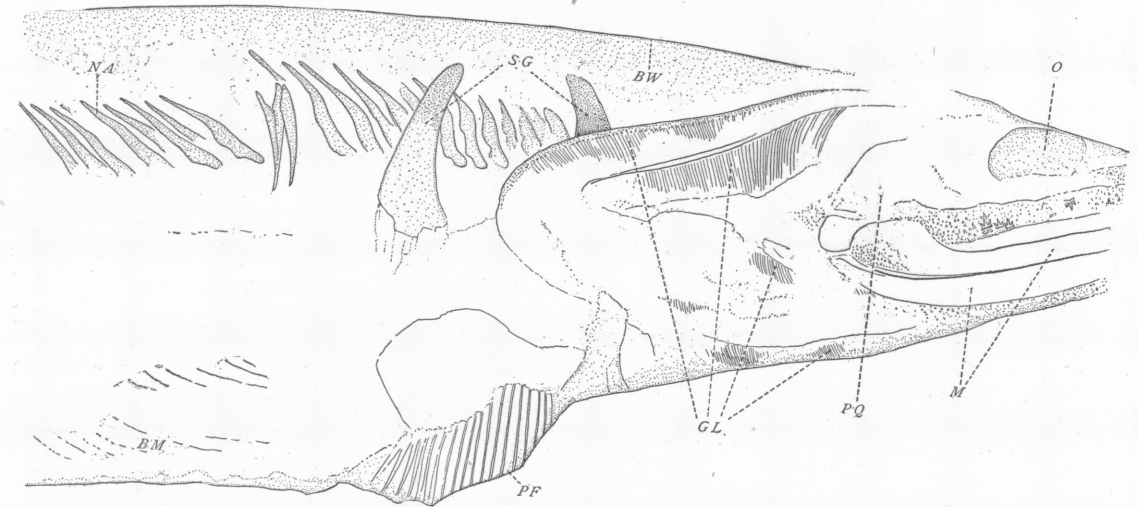
Fig. 9.  *Cladoselache fyleri*.  Lateral view of head of specimen.  Am. Mus. 7333.  *B M*. Body muscles, *B W*. Body wall, *G L*. Gill lamellæ, *M*. Mandible, *N A*. Neural arches, *P F*. Pectoral fin, *P Q*. Palatoquadrate, *S G*. Shoulder girdle, *O*. Orbit.

22, 23) and the entire fin must therefore have functioned, like the unpaired fins, as a balancing organ rather than a paddle.

As to the typical structure of a cladoselachian fin: It is supported by radial cartilages which begin at the wall of the body and proceed outward to or near to the curved rim of the fin.  There are no dermal supports, save in the form of actinotrichia, which are, however, so delicat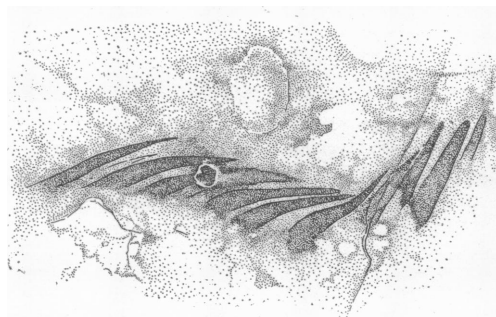e that they can be distinguished clearly only in the stout membrane of the caudal fin.  The radials form a graded series, increasing in length as they pass from the anteriormost point of the fin to its middle region, and thence decrease till they vanish in the hindmost web. The radials, moreover, are always concentrated in the direction of the front margin of the fin, and here they are stout even to their tips: they become progressively delicate and more widely separate in the hinder web of the fin.

Fig. 10.  *Cladoselache fyleri*.  Neural arches. From specimen 7326, Am. Mus.

The dorsal fins have the foregoing arrangement in its simplest form.  (Figs. 11, 12, 13, 14, 18 A, 24.)  The radials are about 12–15 in number in the first dorsal and about 9–15 in the second.  The fins themselves are disposed as follows: The first dorsal is situated above the pectorals and is continued for a short dis-

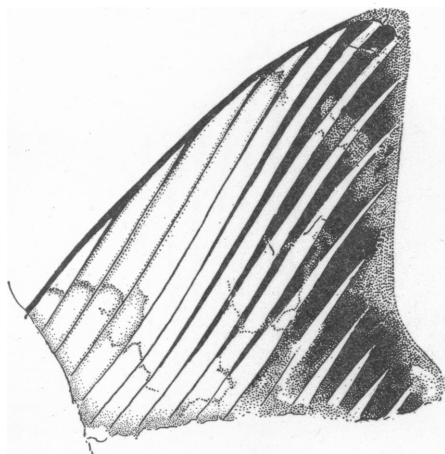tance behind them: the second dorsal arises in front of the ventrals and termi-nates above them (Fig. 41). It may be added that the determination of these fins has hitherto been by no means satisfactory: at first it was believed that but a single dorsal was present, and it was so indicated in the earliest restoration of Cladoselache (1894, Trans. N. Y. Acad. Sci., Vol. XIII, pl. i): thereafter the writer observed two dorsals in a specimen preserved in the cabinet of the Ohio Wesleyan College at Delaware, Ohio.[1] And later dorsals were noted in specimens in the Clark Collection (now in the British Mu-seum).[2] Finally, in the American Museum are two specimens showing these rare fins in situ: specimen 7006 showing first dorsal, and 7892 showing second dorsal. In no instance, save in the Delaware specimen are both fins preserved in the same fossil. In



Fig. 11. (First) Dorsal fin of Cladose-lache fyleri. Am. Mus. 1672. Natural size.

several cases detached dor-sals are preserved, as in Figs. 11 and 12, but they cannot now be associated definitely with the speci-mens from whose matrix they were taken.

An unpaired anal fin is lacking, and for the reason which will be given below.
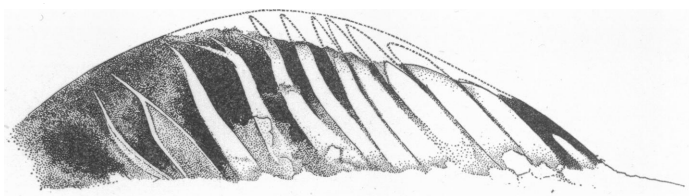


Fig. 12. (Second) Dorsal fin of Cladoselache kepleri (?): from detached specimen in Am. Mus. 271.  × ½.

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[1] A sketch of the fossil was made in 1896: subsequently, thanks to the courtesy of Professor E. L. Rice, the counterpart of the specimen was sent to the American Museum for reëxamination. In this, unfortunately, the second dorsal is not evident. For the present the actual specimen cannot be found.

[2] These specimens I reëxamined during the present summer (1908) in company with Dr. Arthur Smith Woodward, to whom I acknowledge many courtesies shown during a stay in the British Museum. Especially appreciated was the loan of Dr. Woodward's notes on the cladoselachians and his plate-proofs. I was disap-pointed in the specimen of C. clarkii showing the first dorsal fin. I had not recalled that the fin was so defective. It was exposed in its natural position (i. e. vertical) in developing the fossil — the shark having been preserved in the usual dorso-ventral position. And all that can be seen I have attempted to outline in Fig. 13: the tips of the radials are defective, and there is a rift through the middle of the fin. There are about 13 radials and there is no trace of intercalated rays. The fin, in short, corresponds fairly well with the detached dorsal fin shown in Fig. 11, in which also no intercalated rays are shown. So also no rays of this kind appear in the dorsals pictured in Figs. 12 (detached fin), 18 A and 24 (these two fins but faintly indicated, appearing in the same plane as the pectorals), and it seemed fair to conclude that in the dorsals the radials had not yet attained such a condition of concentration as to cause them to interdigitate. This inference, however, is not a just one. For in the clado-selachian P 9282 in the British Museum intercalated rays occur to the number of half a dozen (Fig. 14, but not shown in Woodward's unpublished plate). It is probable accordingly that in some species at least intercalation may occur in both dorsal fins. It is of interest finally that the specimen just referred to indicates that the dorsal had an extended hinder border free from radial supports.

The caudal fin is of a form unique among sharks: for it is truncated, like
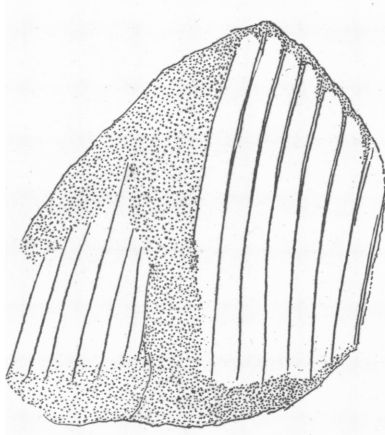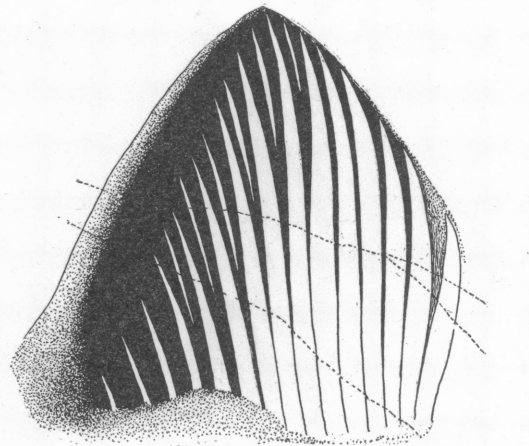


Fig. 13.

Fig. 14.

Fig. 13.   First dorsal fin of *Cladoselache clarki*.   After specimen in British Museum P. 9280.
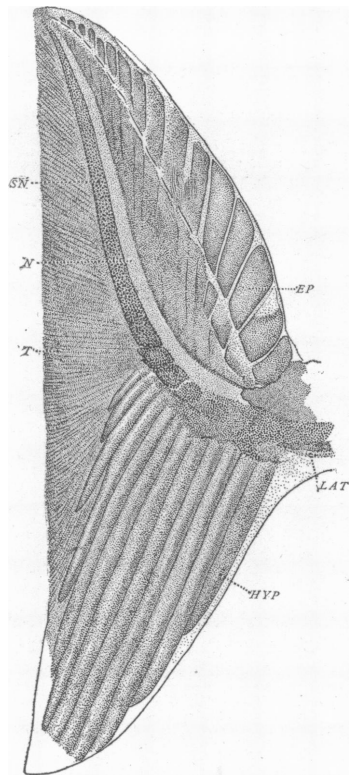Fig. 14.   Second dorsal fin of *Cladoselache fyleri*.   After specimen in British Museum P. 9282.



Fig. 15.   Caudal fin of *Cladoselache fyleri*.   After specimen Am. Mus. 7527.   × ⅔.

*EP*, Epurals, *HYP*, hypurals, *LAT*, lateral caudal fold, *N*, notochord T, actinotrichia.

the tail of a teleost. (Figs. 15, 16, 17, also Pl. XXVI.) But here its resemblance to the "homocercal" tail ends: its supporting rays are cartilaginous, not dermal; the notochord is retained quite to the tip of the upper lobe of the tail; and a large part (over half) of the upper lobe is epural, for strange to say, this lobe has practically no hypural supports, a fin web extending in this region from the tip of the tail to the stout mass of supports of the lower lobe of the fin. In further detail: the lower lobe is somewhat the longer and narrower: it is supported by a row of stout radial elements, about a dozen, which pass in a graded series to and from the middle member (sixth) of the row: they are close set, and there are no intercalated rays. At the base of each of these radial elements is a discrete basal. (*Cf.* Fig. 16.) It may, however, be queried whether the basalia are due to artifact rather than to an original jointing, but the latter condition is probably the normal one, in view of the condition of the fossil itself and from the fact that in the paired fins such separate basals occur. In addition to these supporting elements we note a band of cartilage which continues from the line of the basals along

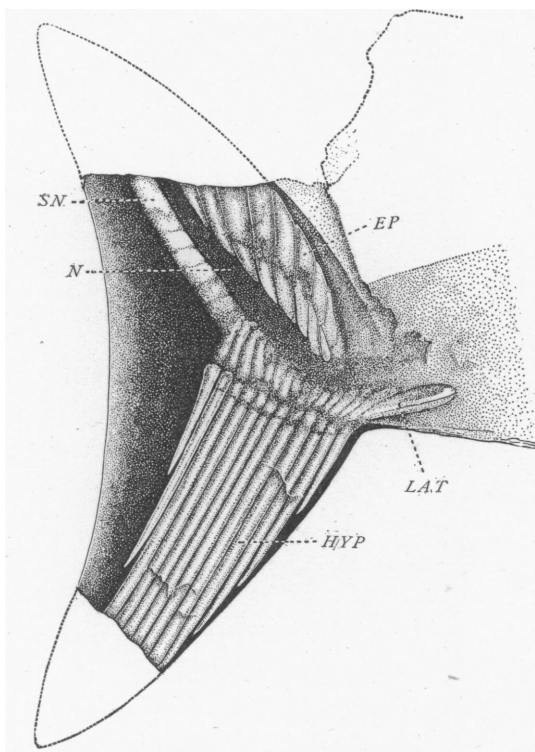the under side of the notochord as far indeed as the tip of the tail. In two of the specimens this cartilaginous band shows a kind of segmentation (Figs. 15, 16) which suggests a continuation of the line of basalia; in any event it is closely apposed to the notochord, and may reasonably be regarded as a subnotochordal rod, which is morphologically the continuation of the hæmal cavity in the region of the tail tip. The web of the fin, already observed to extend from the tail tip to the row of radials of the lower caudal lobe, is without radials: at the most its supporting elements are delicate actinotrichia. The epural supports of the dorsal lobe are arranged in a short plate which forms a stout cut-water in this region of the fin. It consists of three rows of elements. The distal, a series of fifteen or more elements, may be identified as radials; for, although short, these elements form a graded series, passing to and from the median member: the middle row of supporting elements represents apparently the basals: and the proximal row the neural arches. In this regard compare especially Fig. 16, from a specimen lately collected in the Lower Carboniferous of Kentucky. This is characterized by exceedingly stout supporting elements and may be referred to as *Cladoselache pachypterygius*.



Fig. 16. Caudal fin of *Cladoselache fyleri*. After specimen 7325 Am. Mus. × ¾. (Letters as in Fig. 15.)

It is worthy of note that upon the anterior rims of the unpaired fins the shagreen denticles are enlarged and closely clustered, often giving the fossil fin a white anterior rim (Pl. XXVIII). Such a condition, it may be remarked, reinforces the concentrated radialia of this fin-margin, and such a fin, with a compact cut-water, gives a reasonable picture of the ancestral fin of the acanthodian.

Of the paired fins the ventrals agree structurally more nearly with the dorsals, as indeed Wiedersheim's results (Das Gliedmassenskelet der Wirbelthiere, 1892, Jena.) would have led us to predict. And we observe with interest that in these, the oldest specimens of paired fins extant (acantho-
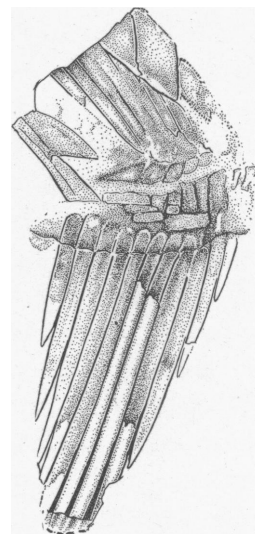


Fig. 17. Caudal of *Cladoselache pachypterygius*, n. sp. After type specimen, Am. Mus. 7583. Natural size.

dians' alone excepted), the fins exist in the condition of a lateral fold, giving palæontological evidence to the Thacher-Balfour theory of the origin of the paired limbs of vertebrates. The ventral of *Cladoselache*, in a word, fulfils with almost diagrammatic clearness the requirements of the fin-fold theory: the fin is low and extends backward, falling away along the side of the body, as in the embryo of a recent shark (*cf.* Pl. XXVI, B, text figs. 18, 19). In actual measurement (in the specimen in which the hinder web is preserved) it is three times as long as high (*C. fyleri*): it extends accordingly along the side of the body across many metameres, the number of which is not less than fifteen nor more than twenty, estimated from the antero-postero thickness of well-preserved muscle layers. This condition, it will be seen, is of no little significance when we note that the radial supports of the fin are approximately of the same number,— say from 15 to 21, or, in other words, there is little disparity between the number of the supports of the fin and the number of somatic segments which the fin traverses.[1] It is true, however, that the supports are not spaced accurately from the anteriormost to the posteriormost margins of the fin: they are drawn together into the anterior two-thirds of the web, with the result that in the widest part of the fin the supports are concentrated and their tips intercalate. The radials, it may be remarked, are supported in the body-wall by basals in approximately corresponding number: we note only that there is probably a fusion in the two most anterior basals, a condition interesting since it indicates that the origin of the fewer proximal supports is due to a concentration of distal elements.
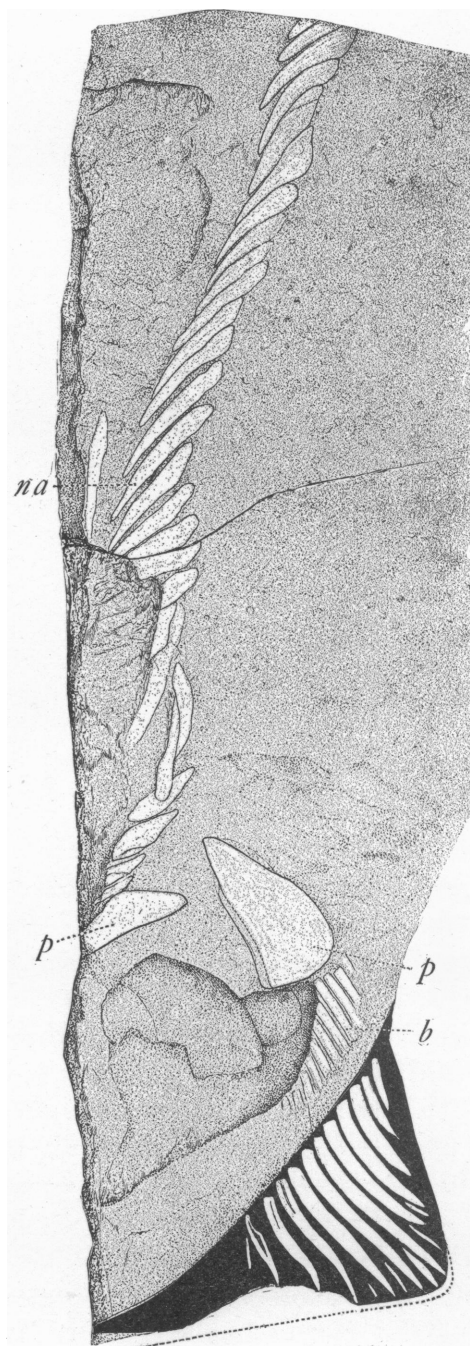


Fig. 18. *Cladoselache kepleri*. Pelvic fin and girdle, and vertebral arches. *b*, basals; *na*, neural arches; *p*, pelvic arch. Am. Mus. 7590. × ⅓.

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[1] It is apparent, therefore, that the formula, number of muscle-segments $= \frac{\text{Radials}}{2}$, which is more or less constant in the paired fins of recent sharks, had not yet been acquired.

The pectoral fin is structurally like the ventral fin, but with a greater width (*i.e.*, height from the body wall) and with rays more numerous, more sharply differentiated, and more closely concentrated in the anterior reach of the fin (figs. 19 A–28). The extent of this larger fin along the side of the trunk is scarcely greater (a few per cent only of the fish's entire length) than the ventral. The radials however are far more numerous, for they number in all from thirty odd
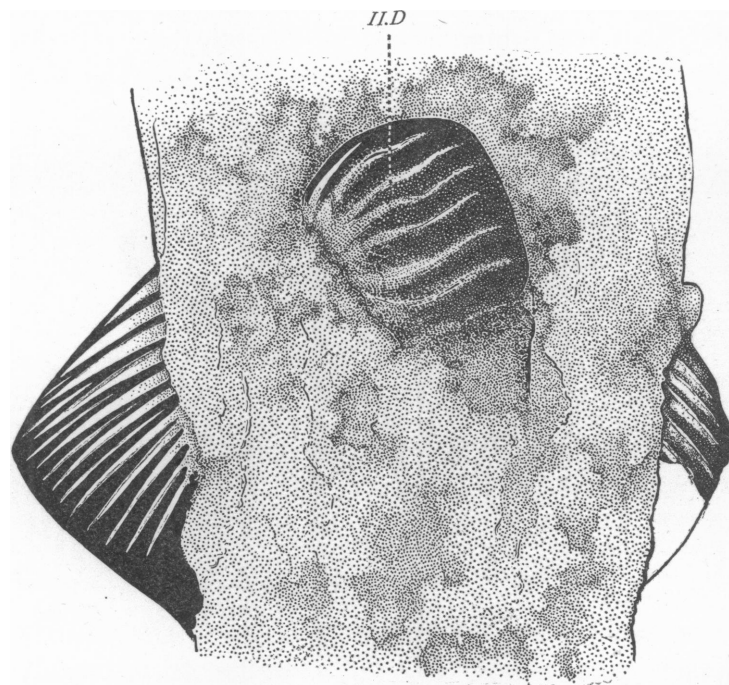


Fig. 18A. *Cladoselache clarki.* Ventral fins and second dorsal. (II*D*). Am. Mus. 7892.

to nearly eighty in the different species. The radials, also, have altered in shape, as well as in length in the various parts of the fin: the anteriormost becoming heavy, broad, almost blunted, sometimes bent into a slight sigmoidal curve; and the posteriormost delicate and narrow — changed conditions which are obviously correlated with the fin's growth outward from the side of the body. And accompanying this growth there has been a concentration of the radial elements in an anterior direction: the fin has become a stout plate, firm in its anterior, delicate in its posterior margin: and in this process the radials have intercalated their tips, as they did indeed in the case of the ventral fins. In fact, this process of intercalation has become a complicated one: for in the first place the tips of adjacent radials become pressed into the fin web between one another ("secondary" radials) then they appear in the intervening next spaces which thereafter are left ("tertiary" radials): even "quaternary" radials are known. And in certain cases a branch-like
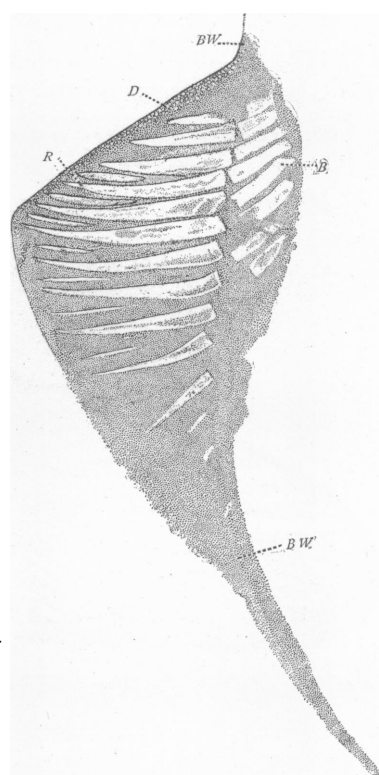


Fig. 19. *Cladoselache fyleri.* Ventral fin. Am. Mus. 229. × ⅔. *B*, basal; *B W*, body wall; *D*, dermal denticles; *R*, radials.

condition of the tips of rays in the most crowded portion of the fin (as in *C. kepleri*, Fig. 20) is evidently an expression of a supreme concentration. In this connection it is possible, indeed, that the intercalated radials may lose attachment to their basals and be carried out as apparent "free radials" into the web
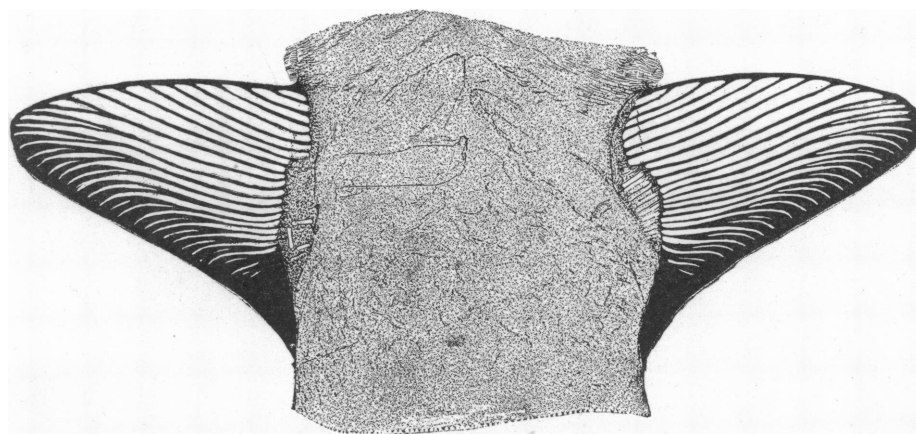


Fig. 19A. *Cladoselache fyleri.* Pectoral fins. Am. Mus. 7527. × ¾.

of the fin (Fig. 21). That this however is not a primitive process follows clearly from the conditions of the radials in other fins (*cf.* Fig. 20) as well as from a study of the sections of the bases of pectorals, for some of these intercalating radials which are apparently "free" can be traced proximalward behind the other radials.

From the foregoing features it is evident that the pectoral fins in *Cladose-*
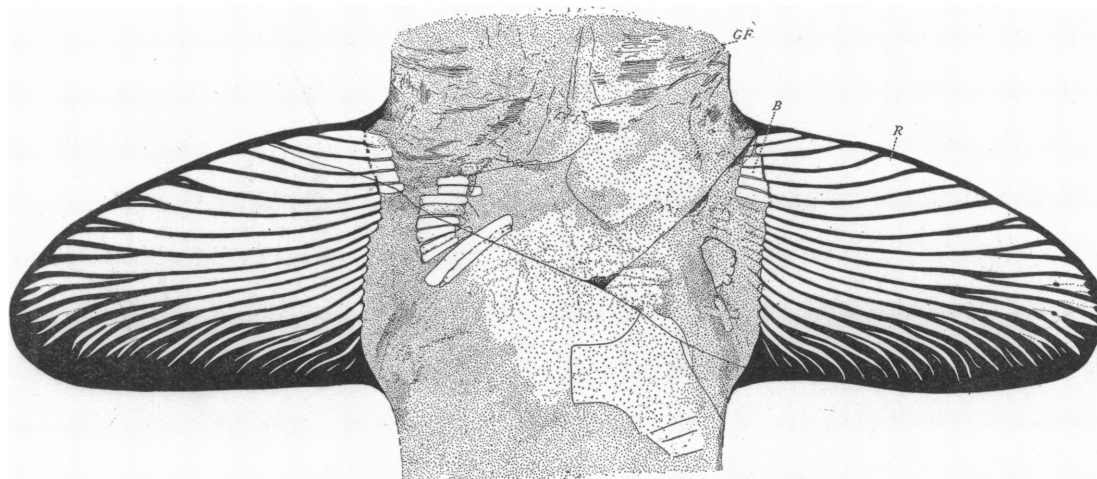


Fig. 20. *Cladoselache kepleri.* Pectoral fins. Am. Mus. 7317. *GF*, gill lamellæ; *B*, basalia; *R*, radialia. × ²⁄₇.

*lache* were more complicated in function than the ventrals. The heavier and strongly braced anterior fin-margin served as an efficient cut-water, rounding outward and backward. The great spread of the fin from the side of the body enabled it to "balance" the fish accurately, and its frail posterior web, with its

slender and more nearly separate radials could, by numerous analogies, serve as
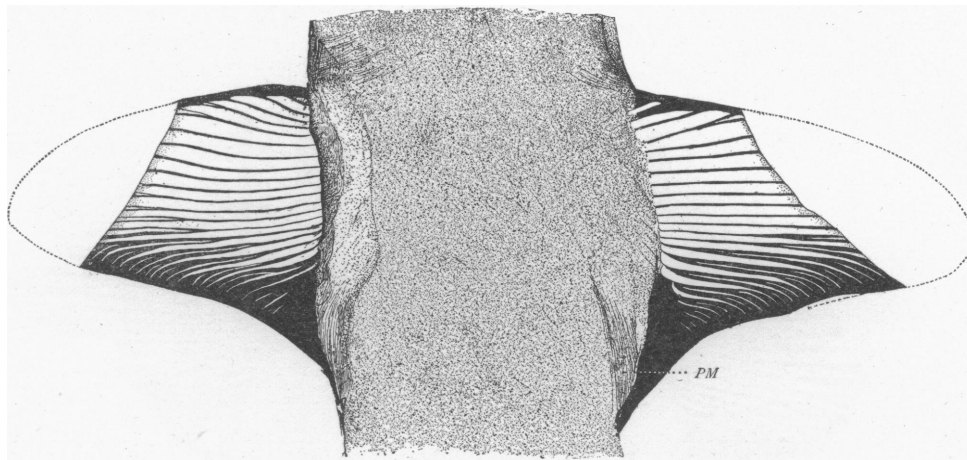


Fig. 21. *Cladoselache clarki.* Pectoral fins. Am. Mus. × ⅓. *PM*, pectoral musculature.

a vibratile membrane, causing the fish to change its direction or even to advance.

We note in this connection the continuation of the fin membrane backward along the side of the body (Figs. 20–23), for this, one suggests, is a beginning of an evolutionary stage in which the posterior border of the pectoral was continued backward from the tip of the fin in a straight line (as suggested in Fig. 40) — not directly inward toward the body and then backward as we see it in these Upper Devonian species (Fig. 41). In the pectorals here described the posterior region of the fin web was evidently mobile,[1] foreshadowing the stage in the evolution of the vertebrate paired limbs when the hinder border of the fin lost its primitive membraneous attachment to the body wall and developed freely, the axis of basalia growing into it, and the radials, no longer concentrating anteriorward, came to cluster around the free posterior end of the fin, as we see them in "monoserial" and "biserial" archipterygia.
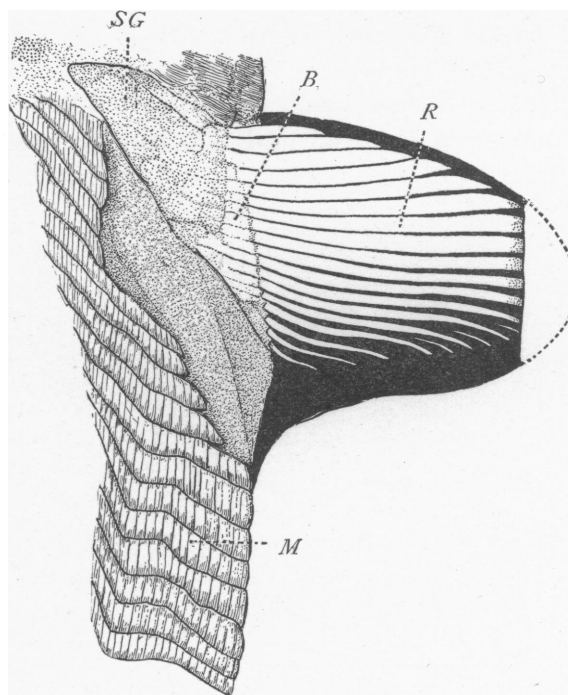


Fig. 22. *Cladoselache brachypterygius* n. sp. Pectoral fin. Type. Am. Mus. 1731. × ⅓. *B*, basalia; *M*, muscle segments; *R*, radialia; *SG*, shoulder girdle.

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[1] Note in this connection the preservation of muscles supplying this region of the fin preserved in several specimens in the Newberry collection. (Figs. 22 and 23.)

In this connection we may compare the three diagrams given in Fig. 28.
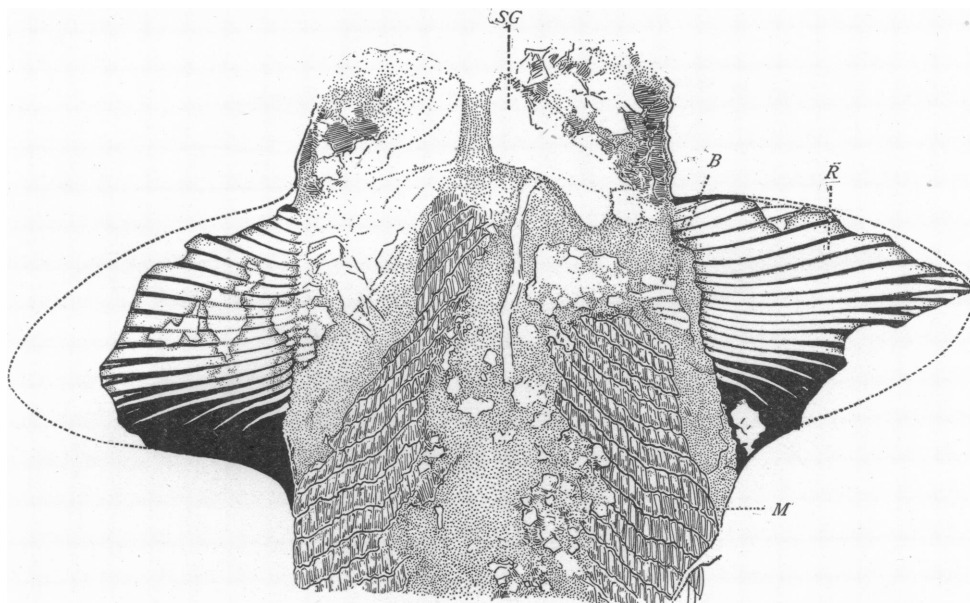


Fig. 23.  *Cladoselache brachypterygius* n. sp.  Pectoral fins.  Am. Mus. 1739.  $\times \frac{2}{3}$.  Lettering as in Fig. 22.

In *A* (*Cladoselache*), the radials are concentrating in the region of the anterior border of the fin, and the hinder basalia are reduced.  In *B* (*Ctenacanthus*),
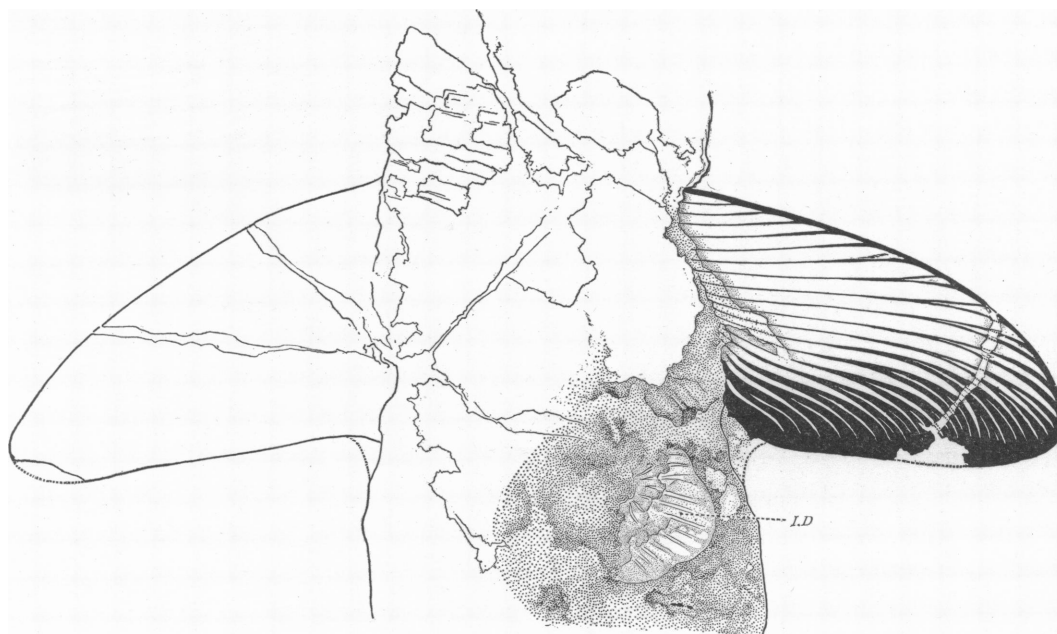


Fig. 24.  *Cladoselache desmopterygius* n. sp.  Pectoral fins and first dorsal (I. *D*).  Am. Mus. 7006.  $\times \frac{3}{5}$.

the radials have not suffered marked concentration and the basalia, admirably

preserved in the fossil, form together a stout fin-supporting axis, wide in front,



Fig. 25. *Cladoselache eastmani* n. sp. Pectoral fin. Type. × ½.

narrow behind, giving in the latter region an excellent picture of a primitive metapterygial axis. In *C* ("*Cladodus*" *neilsoni*), the condition of a definite metapterygium has been attained, although it is doubtful whether the "lobe" of the fin protruded from the body wall. It will be observed that in *A* the hinder radials are more numerous than basals (metamerism at this point having become disturbed), in *B* the basals are the more numerous in the region of dysmetamery (in the proportion of 5 to 3), and in *C* the basals are far more numerous (in the proportion of 8 to 3) — granting always that the fossil is complete. In these diagrams the imprint of the muscles belonging to the region of the hinder finweb is indicated at *M*.

Before passing from the theme of the paired fins we note the concentration of shagreen, strengthening and protecting the fins' anterior margin, and the presence of actinotrichia. The last, however, occur obscurely and only in the posterior web.

*Girdles.* —In the earlier material of *Cladoselache* no traces of a pelvic girdle were found. Later specimens, however, demonstrated that a pelvic girdle was present, and took the form of two separate



Fig. 26. *Cladoselache brachypterygius* n. sp. *SG*, half of shoulder girdle. Am. Mus. 1686. Natural size.

cartilages.[1] These (Fig. 18, *p*. from an imperfect specimen probably of *C. kepleri*) are of moderate size, appear at the proximal ends of the concentrated basals and terminate each in a pointed process. From their shape and from their position in the fossil, there is no evidence



Fig. 27. *Cladoselache acanthopterygius* n. sp. Pectoral fin. After specimen in British Museum. × ⅗.

that they were joined together in the median line. In a word they are of such

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[1] These conditions in the girdles are also indicated in material in the British Museum (Clark collection).

a character that they may be morphologically the segmented-off areas of basalia which have pressed proximalward, coalesced and established new functional adjustments. And it is worthy of note that in these, the earliest pelvic elements known (the Acanthodians' excepted), the girdle is by no means like a gill-arch, a structure which it should resemble if Gegenbaur's theory of the origin of the paired limbs were true.

The pectoral girdle is known in lateral aspect, thanks to a specimen in the Kepler collection lately acquired.[1] (Fig. 9.) It had clearly a "scapular" process which continued from the region of the basalia as far dorsalward as the region of the notochord, very much as it does in modern sharks (*Chlamydoselachus* for example), in fact the general shape of this element reminds one of a notidanid shark. *Cf.*, in a second specimen, Fig. 26, *SG*, half of the shoulder girdle shown in somewhat different position. In ventral view the girdle has
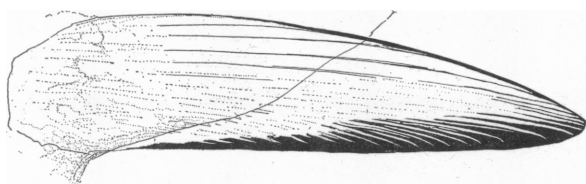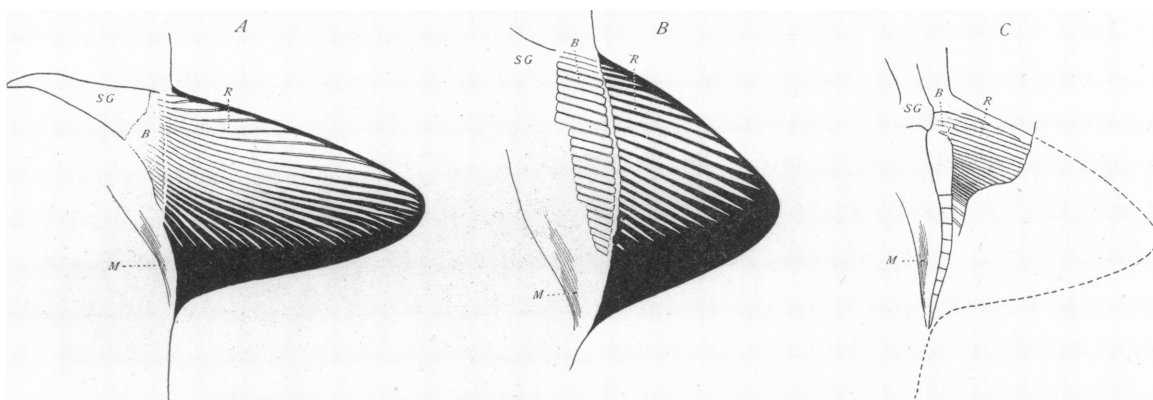


Fig. 28. Pectoral fins of *Cladoselache* (A), *Ctenacanthus* (B), and "*Cladodus*" *neilsoni* (C), indicating the mode of origin of the metapterygial axis. In (C) the outline of the pectoral fin is of the same size in relation to the head and neck as in *Cladoselache*.

*B*, basalia; *M*, muscle of hindmost region of fin; *R*, radials; *SG*, shoulder girdle.

already been described (*Cf.* Jour. Morph., 1894, Vol. IX, pl. vii, fig. 1, *bas.* 1, and the present text fig. 22). From a specimen more favorably preserved it is pictured in Fig. 23, indicating that the "coracoid" elements approached each other in the median line but were conjoined, unlike the condition in modern sharks. There are also known the basal supports in the hinder portion of the fin. (Figs. 19A, 20, 22, 23.) As shown in Fig. 22, the radials are drawn together proximalward and the basalia within the body-wall show apparent fusions. Whether, however, the basalia are actually segmented off from the outer radials, or whether the segmentation is artifact is not altogether clear. And even more doubtfully defined are the elements lying in front of this. On the other hand we can conclude definitely that cladoselachians did not possess a posterior fin axis, such as Traquair has figured in *Cladodus neilsoni* (Fig. 28). Many specimens are admirably preserved in the region of the hindmost part of

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[1] The conditions in this girdle are also indicated in material in the British Museum (Clark collection).

the pectoral fin, and the relations are always as we have indicated them, *e. g.*, in Fig. 22.
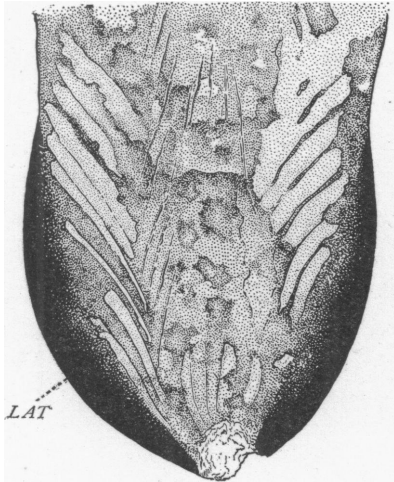


Fig. 29. *Cladoselache fyleri.* Base of tail, showing horizontal flaps (*LAT*), serving as cut-waters. Am. Mus. 7593. × ⅗.

The question of a third pair of fins, post ventral, in *Cladoselache* has now to be seriously considered. It has long been known that a pair of elements similar in general appearance to radials, are preserved, and in a number of specimens (British Museum, *cf.* No. 8765, 9270) along the side of the tail. In this region, moreover, on either side of the tail occurred the broad lateral dermal flap whose evident function (for analogies are numerous in swift-swimming fishes, whether sharks or teleosts) was to keep the stroke of the

caudal fin in the vertical plane. (*Cf.* Pl. XXVI, and Figs. 29, 29A and 30.) In addition to the pair of radial-like elements above noted, it is now known that there were other elements, similarly placed, paired, and arranged in a graduated series. For they are shown in a specimen in the American Museum's collection, pictured in Fig. 29 A, as well also, but less perfectly preserved, in a specimen (P. 5815) in the British Museum. From this evidence it is quite clear that there existed in *Cladoselache* at the base of the caudal fin a series of paired radial elements, a half dozen on either side, of which the anteriormost were the largest and most widely separate; and that the posteriormost drew together into the region of the base of the ventral lobe of the caudal fin. (*Cf.* Fig. 16.) Doubtful is only the



Fig. 29 A. *Cladoselache fyleri.* Base of tail, showing lateral ridges (*LAT*), hypural (*HYP*), and epural (*EP*) supports of caudal fin,— supposed position of anus (*A*), and the supporting elements (*P*) of postpelvic paired fins. Am. Mus. 7595. × ⅗.

manner in which these radial elements were

continuous with the radials of the great hypural tail-lobe. It is certain that they are not to be confused with the caudal radials themselves, for these are present in the same specimen, both epural and hypural.

The query, therefore, remains whether these paired radial-like supports are a vestige of a third, or post-pelvic pair of fins? Claypole has declared in favor of a third pair of limbs in Cladoselache [1] on the strength of the peculiar pair of folds which are seen so conspicuously at the sides of the caudal, and for one I am willing to subscribe to this great heresy, — not, however, merely from the presence of the lateral caudal folds (which might have had another origin) but on the following grounds: (1) The presence and arrangement of the paired supporting elements which are now described.[2] (2) The evidence that the cloaca (or anus) was situated not between the ventral fins but at the base of the caudal fin! And it is the latter evidence which has been especially convincing to me. In one of the specimens of Cladoselache, Fig. 30, the posterior portion of the fish is preserved with remarkable completeness. The ventral fin is indicated at $V$, the caudal at $C$, and two masses of tissue are fossilized at $K$. Microscopic examination demonstrates that these masses of tissue which extend from behind the region of the ventrals to nearly the region of the caudal, are visceral structures, that they contain elements readily identified as tubules and that
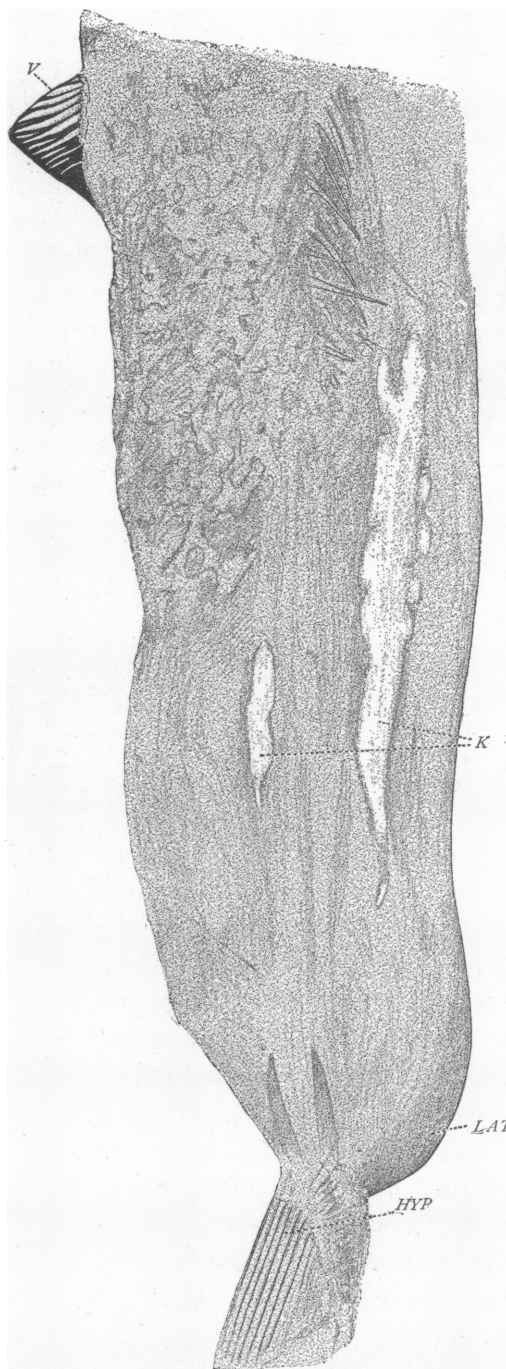


Fig. 30. *Cladoselache fyleri.* Hinder region, showing a ventral fin, $V$, kidneys, $K$, lateral dermal folds, *LAT*, and paired post-pelvic supports, $P$. Am. Mus. 1671. × ⅓.

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[1] Am. Geologist, June, 1895, p. 367.

[2] In his material Claypole was able to detect "no trace of fin rays," but the texture of these lateral folds was that of "the membranous margin of the pectoral fins."
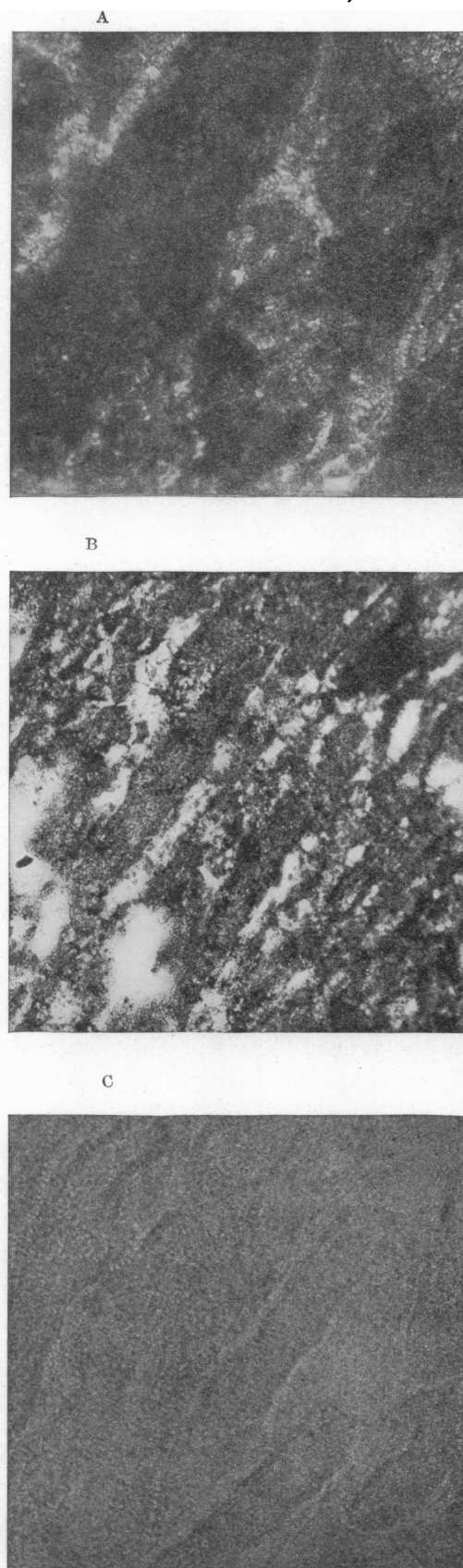
they therefore represent the kidneys.[1] *Cf.* p. 231. And this being the case, *i. e.*, accepting the data that the visceral cavity extended thus far hindward, *the cloaca was in all probability located near the base of the tail -- where these paired*

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[1] The most caudal portion of the kidney of various recent fishes is, of course, known to extend beyond the cloacal (or anal) region. This condition, however, is not to be confused with the present one, in which the kidney extends behind the ventral fin to a distance equal to 20–30% of the post-pectoral length of the fish.
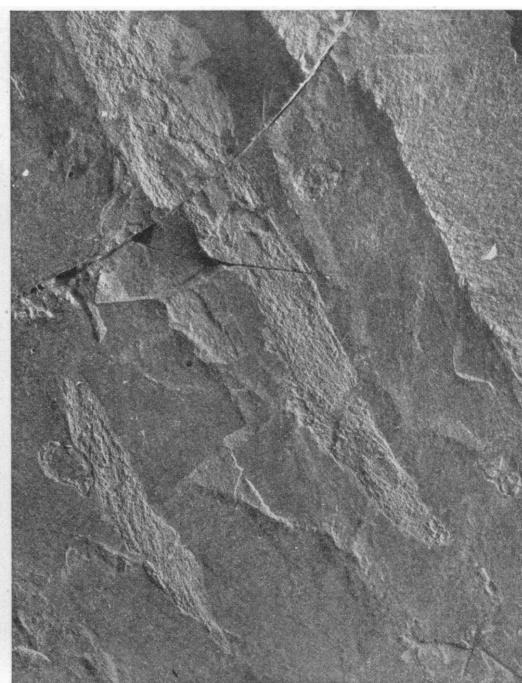


Fig. 31. *Cladoselache fyleri.* Photograph of the kidneys (pair) shown in the fossil of Fig. 30. About natural size. The tailward end of these organs appears in the lower part of the figure, and from this region striæ may be traced forward and medianward.

A. Microsection of fossil kidney. × 500. Tubules (two of them) appear as long dark masses (nearly an inch in width) in the mid-region of the photograph, the one on the left straight, the one on the right apparently bent.

B. Microsection of fossil kidney. × 200. In the figure the tubules may be traced from the lower left hand, upward and diagonally to the right: note especially two of the tubules in the mid-region of the figure.

C. Microsection of recent kidney (Centrophorus) × 200. Photograph of unstained section cut by hand without embedding. The tubules agree closely in size with the fossil tubules shown in the foregoing figure.

*radial-like structures are not only present but where they converge.* The testimony, in short, which leads us to believe that the anus was subcaudal, supports us also in our conclusion that the anal fin was a paired structure. In this connection we recall observations in the ontogeny of fishes as to the paired character of the anal fin, and as to the postanal gut.

e. *Viscera, Muscles.*— Notes on visceral features of a Devonian shark cannot in the nature of things be profuse. But they are interesting none the less. The mouth of *Cladoselache* was long and narrow, ending subterminal. The gill filaments were about of the length of those in a modern shark, and they are frequently preserved. *Cf.* Fig. 9 and Pls. XXVIII, XXIX. Notably in a specimen, No. 239, in the American Museum, the natural overlap of the lamellæ is shown, Pl. XXXI. In the visceral cavity the stomach contents are occasionally preserved *in situ*: and in a specimen in the Clark collection (Brit. Mus. P. 9271, type of *clarki*) there is a great flattened mass of ingesta, Fig. 32, which yields a cast of the wall of a portion of the digestive tract, showing three wide turns of the spiral valve and probably a series of smaller ones, indicating that the intestine had many absorptive ridges. Unfortunately we cannot determine to what part of the tract the above mentioned cast belongs: it is altogether too large, we believe, for the terminal portion: and from its position (granting always that this has not notably shifted during the process of fossilization) it may have been contained in the stomach: but the fact that it bears imprint of a spiral valve is very strong evidence that it does not represent a cast of this region. Against its having been moulded in the terminal portion of the alimentary canal is, again, its position, for we have reason to conclude that the intestine ended near the tail. Furthermore, in another specimen, Fig. 30, a small spirally indented mass is preserved in the region of the ventral fins, which in spite of its small size, is probably a coprolite:[1] it has a number of spiral lines about it indicating that the folds of the spiral valve were both low and numerous.

The preservation of visceral organs in the region between the ventral fins and the tail has already been noted. These take the form of two elongated bodies which were clearly a pair. When photographed they show a distinct texture, Fig. 31, indicating a series of tubules closely compacted, which pass backward on each side, somewhat as do the uriniferous ducts in recent sharks. When sectioned the tissue of these petrified organs shows in all regions elongated bodies. These are usually parallel to one another, Fig. 31 *A* and *B*, sometimes bent, and sometimes contorted. That they resemble the nephric tubules of modern sharks is seen by comparison with the photomicrograph in Fig. 31 *C*.

The identification of the elongated organs in *Cladoselache* as kidneys becomes, therefore, little less than certain. They are (1) paired, of the requisite (2) size and (3) shape, wider in front, tapering behind: they show (4) a texture whose elements pass backward on either side as in the collecting ducts of the

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[1] *Cf.* Dean, Trans. N. Y. Acad. Sci., Vol. XIII, pp. 115–119; also, Hollick, *ibid.*, p. 119.

modern kidneys; and they show (5) in different regions elongated histological elements which are similar in size and shape to nephric tubules of recent sharks. On the other hand from such characters they could be confused with no other organ in the vertebrate series.

Accepting this determination, it is exceedingly interesting from the point of view of vertebrate morphology that these visceral organs occur in the post-pelvic region.[1] For this demonstrates that the visceral cavity of the cladoselachid extended into the hindmost trunk region, since if the kidney occurred in this position, tapering backward as well, it is clear that the intestine also must have extended into the same region. The concentration of paired radial supports in the direction of the base of the lower lobe of the tail in *Cladoselache* is further evidence of the presence here of a cloacal opening. In short, we are led to believe that in *Cladoselache* a condition is functional in the adult which in modern forms appears only in the embryo, *i. e.* in the postanal gut.



Fig. 32. Food-mass preserved in visceral region of a specimen of *Cladoselache* "*clarki*" in the British Museum (P. 927). × ⅝.



Fig. 33. Food-mass preserved in visceral region of the type specimen of *Cladoselache newberryi.* × 2.
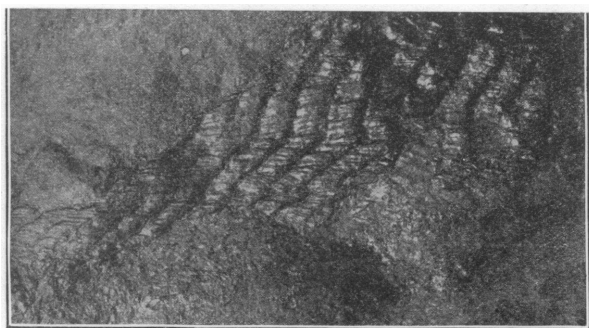


Fig. 34. *Cladoselache fyleri* showing fossilized muscle bands. About natural size. (Cut kindly loaned by *American Geologist*).

*Muscles.*—The preservation of muscle bands in these sharks has already been commented on by the present writer (Am. Geol., 1902, Vol. XXX, No. 5): in some instances their preservation is so perfect that they appear like the mummified tissue of a recent fish. (Fig. 34.) Microsectioned and viewed under a low power, this tissue is readily resolved into muscle "cells," whose distinct margins can well be seen in Fig. 35: indeed in this regard it differs notably from muscular tissue in living sharks, a difference which

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[1] It cannot reasonably be maintained that the position of these organs in the fossil is artifact. They are too accurately disposed and their histological characters are too clear to warrant such a belief. The kidney in its retro-peritoneal position could only be displaced when the entire wall of the visceral cavity had broken down, and when this change had taken place the softer tissue of the kidney would certainly have been in a condition poorly suited for fossilization,— to say nothing of a fossilization which retains histological details.

can be interpreted either as due to artifact in fossilization or to an originally greater discreteness of the muscle "cells" in this primitive form. In favor of the latter interpretation is the extraordinary preservation of histological detail in this fossil. Viewed under a high power the striation of fiber is sometimes shown (Fig. 36), with great clearness, indicating, one concludes, that the tissue must have been in fairly fresh condition when subjected to mineralization, for the striæ are undistorted and even fragments of the muscle sheath can be detected, as at the points * and *. These ancient fibers, in fact, preserve their contours more accu-
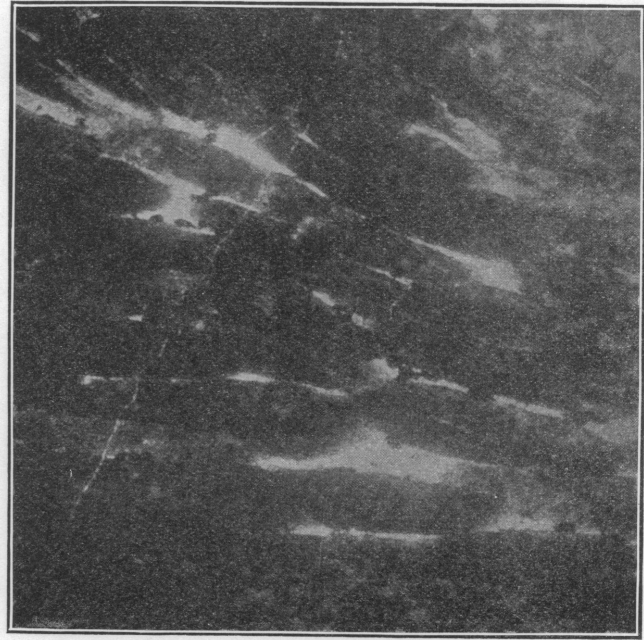


Fig. 35. *Cladoselache fyleri*. Section of fossilized muscle bands. Low power, showing muscle fibers. (Cut kindly loaned by *American Geologist*).
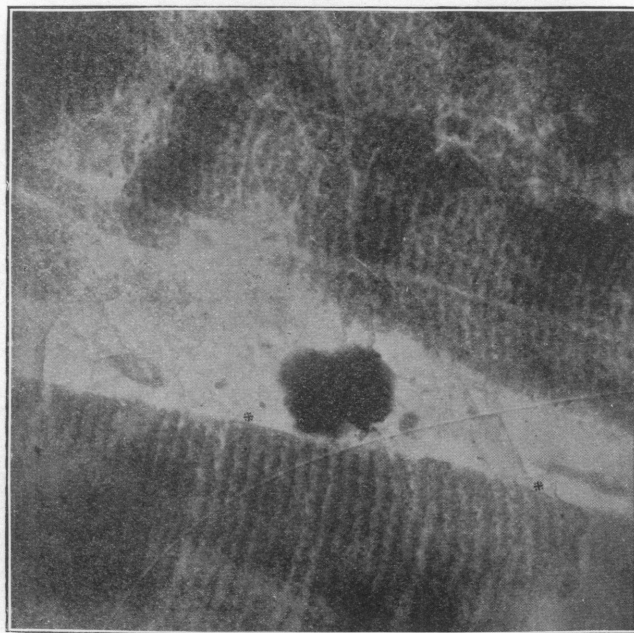


Fig. 36. *Cladoselache fyleri*. Section of fossilized muscle fibers, showing transverse striation. Magnified 1000. (Cut kindly loaned by 'American Geologist.')

rately, as it happens, than do the fibers of recent tissue shown in the photograph, Fig. 37, taken from a well-preserved specimen of *Heterodontus*.

Comparing the preparations (equally magnified) of the Devonian and of the recent shark we cannot fail to note the greater coarseness of the transverse striæ in the ancient form. For here the striæ are one third or thereabouts less numerous. I am accordingly inclined to believe, even taking into account the changes due to fossilization, that the ancient shark had not yet attained in its muscles the high degree of specialization of modern forms,— a belief which is not weakened by our knowledge of other primitive characters in cladodonts.

f.  *Sense Organs.*— The nasal capsules are indicated faintly in several speci-mens (*e. g.* that of Pl. XXVIII): in size and shape they show minor differences from modern sharks: in position they appear to have been more nearly terminal in position.

The eyes, judged from the circumorbital rings of shagreen, were not remarkable in point of size or position. It is probable that the sclera was either unde-veloped or imperfectly devel-oped, for otherwise so perfect a dermal defense for the eye would
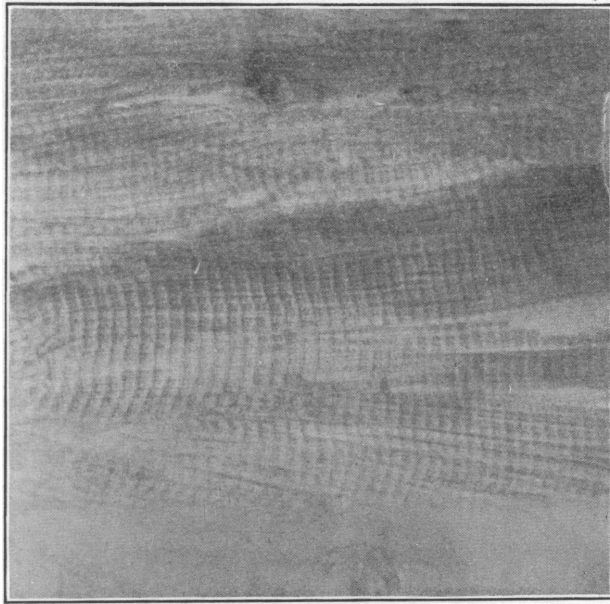


Fig. 37.  *Heterodontus  (Cestracion) japonicus* (Macleay). Muscle fibers showing transverse striation.  Magnified 1000. (Cut kindly loaned by ' American Geologist '.)
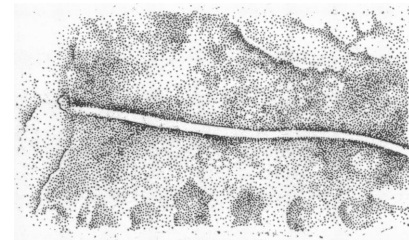


Fig. 38.  *Cladoselache newberryi.* Lateral line.  × 8.

hardly have been evolved.  One infers, also, on this account, that a nictitating eyelid was not present.

The lateral line is rarely preserved.  In the type specimen of *Cladoselache newberryi* a small portion of it is shown, and is here pictured, Fig. 38.  · It was margined by enlarged denticles, somewhat as in *Chlamydoselachus.*  The present drawing was made from a portion of the canal in the region between pectoral and pelvic fins.

## 4.  TAXONOMY OF CLADOSELACHIAN SHARKS.

The taxonomy of the Cladoselachians has always been a difficult problem. The teeth are in most instances imperfectly preserved and they vary so widely in shape, size and degree of ornamentation in various parts of the mouth that they give little practical aid in distinguishing species.  And such characters as the shape of the head or the relative thickness of the body are of little taxonomic value owing to different conditions in preservation.  I am convinced that the structures of the fin are the most reliable of our present tests of specific differences.  Useful also is the distance apart of pectoral and ventral fins, for

the relation of these, as measured on the long axis of the fish's body, is little apt to become altered during the process of fossilization. Thus, by analogy of modern forms, we assume that the number of the fin-rays will not vary greatly within the limits of a species. And although the outline of the fin may vary to a limited degree depending upon whether the fin is fossilized in a transverse or more or less inclined position (as we note for example, in fins of opposite sides of the body in a specimen in the British Museum collection P. 9281), conspicuous differences of this type are not known. Thus a fin whose hinder margin is altogether transverse to the axis of the fish's body and whose hinder border is membranous, the supporting rays extending not to its margin, belonged clearly to a different species from one in which the hinder border of the fin extends obtusely forward (we assume that the fins are inclined in the same position with respect to the axis of the fish's body, remembering, of course, that the hinder web of the fin is attached to the wall of the body) and is supported by more numerous rays extending to its very rim. By comparison of the material in the American Museum and in the British Museum, I am convinced that eight and probably eleven species can be distinguished (the latter if we include the forms known only from detached elements [fins and jaws]). The species which is open to question, is the one having long and very narrow fins, which is now named *C. acanthopterygius.* This may possibly be a *C. kepleri,* or a *C. clarki,* which became fossilized in such a way that the rays of the fin were compressed into a spine-shape fin. On the other hand I am led to subscribe to this species since in one specimen the extreme web of the fin is delicately preserved,— a condition which would hardly be retained if a fin had softened to such a degree that it could be compressed before fossilization. In the accompanying table are summarized the writer's notes upon the available material.

| | NAME. | Length (Approximate). | Pectoral begins: % of body length from head. | Extent of pectoral along side of body. | Pectorals, proportion of breadth to height. | Pectoral rays, number of. | | | Ventral begins: % of body length from head. | Extent of ventral along side of body (% of total length). | Ventrals: proportion of breadth to height. | Ventral rays, number of. | | | REMARKS. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | I | II | III | | | | I | II | III | |
| 1. | *Cladoselache fyleri* (Newb.) | cm. 50–75 | 25 | 10–12 | 3:4 | 19–20 | 10–13 | 1–2? | 58 | 7+ | 3:1 | 13 | 8 | .. | Average of about 12 almost complete specimens and numerous fragments. Type specimen, No. 240, Amer. Mus. Also Nos. 7527, 7325, 7036, British Museum, P. 9274, 8765, 9288, 9275, 9283, 9282, 9286. |
| | (=Cladodus sinuatus Claypole) | (60)+ | 25 | 13 | 3:4 | 20 | 14 | 3? | 62 | .... | .. | ..... | ... | .. | Br. Mus. P. 9270. |
| | (=rivi-petrosi Claypole) | (60) | (21) | 8+ | (3:4) | 18–19 | 10 | tip broken 6 (branched) | (58) | (7) | .. | 13 | 7 | .. | Br. Mus. P. 8764. |
| 2. | *kepleri* (Newb.) | (150) | ? | ? | 4:5 | 19–20 | 12 | | ..... | .... | .. | ..... | ... | .. | Type in Amer. Mus. No. 7316, 7317. |
| | (=pinnatus Claypole) | 200 | (16) | 8 | 4:5 | 19–20 | 13 | 5 | (52) | (10) | 5:3 | 12–13 | 3–5 | .. | Based on type specimen (Br. Mus. P. 9269): to this species are referable several fragmentary specimens. Also, British Museum, "Monocladodus clarkii," P. 9268, also 9280 and the fragment 9281, teeth 9 (+3) on each ramus. Intercalation begins between 3 and 4 rays: double intercalation in 3 subterminal intervals. |
| | (=Monocladodus clarkii). | (150) | ..... | ..... | 4:5 | 19 | 11–13 | 3 | ..... | .... | .. | ..... | ... | .. | Br. Mus. P. 9268. |
| 3. | *clarki*, (Claypole) | (130) | ..... | ..... | 3:5 | 22–25 | 16–24 | 20–23 | ..... | .... | .. | ..... | ... | .. | Radials more intercalated than in other species. (Coprolite.) Br. Mus. P. 9271, 9276. (Teeth with more conspicuous lateral cusps, with more marked striæ. Scales of "Stemmatodus" type. |
| 4. | *newberryi*, Dean. | (50) | (22) | (7–8) | 6:7 | 20 | 11 | .......... | (50) | .... | .. | ..... | ... | .. | Fins like *fyleri*, but ⅔ size. Type in Amer. Mus. No. 7019. |
| 5. | *brachypterygius*, n. sp. | (50) | ..... | (14) | 1:1 | 18–19 | 17 | 2 | ..... | .... | .. | ..... | ... | .. | Type in Amer. Mus. No. 1731. |
| 6. | *desmopterygius*, n. sp. | 70+ | 31 | 14.5 | 7:10 | 18–19 | 11–12 | 8–10 | ..... | .... | .. | ..... | ... | .. | Type in Amer. Mus. No. 7006. |
| 7. | *acanthopterygius*, n. sp. | 70 | ..... | ..... | 1:3 | (18) | (7) | ? | ..... | .... | .. | ..... | ... | .. | Specimen in Brit. Mus. P. 9277. |
| 8. | *eastmani*, n. sp. | (115) | ..... | ..... | 2:3 | 77 | ..... | .......... | ..... | .... | .. | ..... | ... | .. | Type in Buffalo Soc. of Nat. Hist. Figured by Eastman as *Sp. indet.*, N. Y. State Mus. Mem. 10, 1907, pl. 8. |
| 9. | *?magnificus*, Claypole. | (300?) | ..... | ..... | ..... | ..... | ..... | .......... | ..... | .... | .. | ..... | ... | .. | Type in Brit. Mus.— Jaw only. |
| 10. | *pachypterygius*, n. sp. | (40) | ..... | ..... | ..... | ..... | ..... | .......... | ..... | .... | .. | ..... | ... | .. | Caudal only: characterized by heavy rays. Type in American Museum, No. 7583. |

## Cladoselache *Dean*, 1894.

Synon. CLADODUS (pars) . . . .

### 1. Cladoselache fyleri (*Newberry*).

PLATES XXVI AND XXVI A, figs. 19, 19 A.

1889. *Cladodus fyleri* NEWBERRY, Paleoz. Fishes N. Amer., p. 322, pl. xlvi (no description).
1893. " *sinuatus* CLAYPOLE, Am. Geol., Vol. XI, p. 327, pl. vii.
1893. " *rivi-petrosi* CLAYPOLE, Am. Geol., Vol. XI, p. 328, pl. viii.
1894. *Cladoselache fyleri* (Newb.), DEAN, Journ. Morph, Vol. IX, p. 88.

Small, 20–30 inches in length. Pectorals begin at one quarter the length of the body, and extend along the side of the body a distance equal to about ten percent of the total length. The fin is somewhat pointed, and extends outward from the side of the body a distance which is to the base-line of the fin as 4 is to 3: it bears about 20 primary rays, about half as many secondary, and very few tertiary. The ventral fin begins at about sixty percent of, and has an extent of about seven percent of, the entire length of the body: it is low and long, its length measured from the body-wall being proportioned to its base as one to three. It has about a dozen primary and about half as many secondary rays.

### 2. Cladoselache kepleri (*Newberry*).

PLATE XXVIII, fig. 20.

1888. *Cladodus kepleri* NEWBERRY, Trans. N. Y. Acad. Sci., Vol. VII, p. 178.
1889. " " " Paleoz. Fishes N. Amer., p. 103, pl. xliv, xlv.
1893. *Monocladodus pinnatus* CLAYPOLE, Am. Geol., Vol. XI, p. 330, pl. viii.
1893. " *clarki* CLAYPOLE, Am. Geol., Vol. XI, p. 327, pl. vii.
1894. *Cladoselache kepleri* (Newb.), DEAN, Journ. Morph., Vol. IX, p. 103.

Large, fifty inches or more in length. Pectorals are well rounded at their ends: they extend outward from the body a distance somewhat greater than their base line (5: 4). In number the rays are as follows, primary about 20, secondary 12, tertiary 6. The tertiary and secondary rays are sometimes conjoined in the region of the tip of the fin, giving these rays a branched appearance. The ventral begins at about 50 percent and has an extent of about 10 percent of the entire length of the body: its length measured from the body wall is proportioned and its base as one is to three: there are about a dozen primary and about four secondary rays.

### 3. Cladoselache clarki (*Claypole*).

FIG. 21.

1893. *Cladodus clarki* CLAYPOLE, Am. Geol., Vol. XI, p. 327, pl. vii.

Large, about fifty inches in length. Pectorals longer, narrower and terminating more acutely than in *C. kepleri* (height to base as 5 is to 3). Characterized especially by numerous radials, in all upward of sixty, of which two thirds are secondary and tertiary.

## 4. Cladoselache newberryi *Dean*.

PLATE XXX.

1893. *Cladoselache newberryi* DEAN, Trans. N. Y. Acad. Sci., Vol. XIII, p. 115, pl. i.

Small, about 20 inches in length. Pectorals small, the distinguishing character of the species, for they are proportionately a third smaller than in *C. fyleri*. And at their base they are slightly broader than in that species.

## 5. Cladoselache brachyptergyius, n. sp.

PLATE XXXII.

Small, about 20 inches in length. The pectorals are wide in their base line (measuring about 14 per cent of the length of the body), and they are of equal measurements in height and base: Their rays correspond with *C. fyleri* but with a greater number of secondary rays. Characteristic in this fin is a broad hinder web lacking in rays: the anterior rim of the fin is rounded, and the radials which support it are more sharply differentiated from the remaining radials than in *C. fyleri*. Contrast Plate XXXII with Plate XXVI.

## 6. Cladoselache desmopterygius, n. sp.

PLATE XXIX.

Moderate in size, about 26 inches in length. A short bodied form, with pectoral placed further tailward, and of relatively large size, its base measuring nearly 15 percent of the fish's total length,— its height proportioned to its base as 10 is to 7. The rays are similar to those of *C. fyleri* but are more abundantly represented in tertiary elements, having four or five times as many as in *C. fyleri*. The general fin pattern, however, corresponds more closely to *C. clarki*, and on this account this specimen was at first regarded by the writer as an immature *C. clarki*.

## 7. Cladoselache acanthopterygius, n. sp.

FIG. 27.

Larger, about 30–50 inches in length. Diagnosed by long and spine-shaped fins. Trunk greatly shortened, the span of the pectoral fins measuring eighty percent of the body length (without head).

## 8. Cladoselache eastmani, n. sp.

FIG. 25.

Fairly large in size, about 45 inches in length. A narrow-finned species, having a great number of pectoral rays (nearly eighty): secondary and tertiary rays absent (?). Known from a pectoral fin only. From Naples shale of Eighteen Mile Creek (Portage), N. Y. Figured by Dr. C. R. Eastman and now named in his honor.

## 9. Cladoselache magnificus (*Claypole*).

1894. *Cladodus magnificus* CLAYPOLE, Am. Geol., Vol. XIV, p. 137, pl. v.

A huge species, known from jaws only.

## 10. Cladoselache pachypterygius, n. sp.

FIG. 17.

Of small size — probably 30 inches in length. Known from caudal fin only, but this is provided with such definite and stout radial and basal elements that we refer it to a new species. It occurs also in a later horizon,— Waverly (Lower Carboniferous) of Kentucky.

The following arrangement is suggested as to the taxonomic relationships of the cladoselachids:—

### Superorder I. PLEUROPTERYGII (Dean, 1894, as "order").

Proselachians having paired fins arranged along the body as lateral dermal folds (*i. e.*, with no extruded skeletal fin-axis), functioning as balancers rather than as paddles. Caudal with deep and strongly supported hypural lobe. Column notochordal. No claspers. Anus probably sub-terminal. Eyes protected with enlarged dermal plates. Teeth cladodont.

### Order 1. CLADOSELACHIA (Dean, 1894, as "sub-order" Cladoselachii).

Pleuropterygians in which the fin-supporting elements are concentrating in the anterior region of the fins. No "archipterygial" fin-axis (emerging from the body-wall as a continuation hindward of the row of basalia). Pectoral with anterior radials large, stout, compressed, and with broad basals and a well marked shoulder girdle. Ventrals with radials little differentiated, with separate and radial-shaped basalia, and with a single more proximal support, the last separate from the similar element on the opposite side. Caudal widely heterocercal, in proportions not unlike those of swift swimming teleosts, but in structure different, its supports cartilaginous. It is margined laterally (in a horizontal plane) by wide dermal keels, supported in part by radial elements. Eyes protected by numerous dermal plates. Sensory canals as open grooves. Teeth arranged in numerous rows each of several (about half a dozen) successional elements. Interneurals absent (unlike Ichthyotomi and other sharks).

### Family 1. *Cladoselachidæ* (Dean, 1894).

Cladoselachians having two dorsal fins, spineless, corresponding closely in structure with the paired fins. Eyes protected by three or more concentric

rows of dermal plates. Pectoral fins with basal supports produced proximal-ward; with radials concentrating in the anterior margin of the fin, and becoming intercalated. In this condition of intercalation we may distinguish the radials as *primary*, *secondary* and *tertiary*: the primary radials extend from body wall to fin margin: the secondary arise near the fin-margin and extend inward between the primaries; the tertiary, still smaller, extend inward between the secondaries and the primaries. (Middle and) Upper Devonian — Lower Carboniferous.

### Family 2.   *Ctenacanthidœ* (n. fam.).

Cladoselachians having two dorsal fins, spine-bearing. Pectorals show less concentration in an anterior direction, and lack secondary and tertiary radials. Upper Devonian and Carboniferous.

### Family 3.   *Symmoriidœ* (n. fam.).

Cladoselachians in which the pectorals have well developed basalia, which coalesce in the hindmost region, thus indicating the beginnings of a metapterygial fin-axis. Coal Measures.

### Family 4.   *Cladodontidœ*.   (Incl. *Cladodus neilsoni* Traq.)

Cladodonts having in the pectoral fin a delicate segmented "metapterygial axis." The arrangement of the radials in this early archipterygial type of fin are imperfectly known. Thus it is not known whether the posterior fin-axis bore radials and was still retained within the body wall or whether it protruded and functioned as in ichthyotomes. In the latter event this family may come to be transferred to the order Ichthyotomi. Lower Carboniferous.

### Order 2.   ACANTHODIA.   (A. S. Woodward, 1891.)

Pleuropterygians in which the radial elements in paired and unpaired fins are represented largely, if not entirely by coalesced elements encased in calcified dermal defenses, forming fin-spines. The tail, however, still retains the discrete radialia. Eyes protected by a few dermal plates. Sensory canals as open structures. Upper Silurian — Permian.

### Superorder II.   ICHTHYOTOMI (Cope, 1884, Pal. Bulletin, No. 38, pp. 572-590).

Early sharks (Xenacanthids) having a body-form resembling the recent Ceratodus (*Neoceratodus*), with diphycercal tail and archipterygial pectorals. (Cope's original definition inadequate,— he describes it as including elasmo-branchs having "a basioccipital bone and condyle. Occipital, pterotic, and

frontal bones distinct. Supraorbital (or nasal) bones present.") Were it not that name Ichthyotomi has come into general use a new term would be preferable.

## Superorder III.  EUSELACHII (Parker and Haswell, 1897).

Here may be placed all living sharks, together with hybodonts, and, for the present at least, petalodonts, psammodonts, and probably *Chondrenchelys*, having short metapterygia extending from the side of the body, and with radials clustered in the hinder rather than in the anterior region of the fin. Mixipterygia present. Eyes unprotected by dermal plates. Cloaca opening immediately behind ventral fins.

## Superorder IV.  HOLOCEPHALA (Bonaparte, 1832).

Holocephalic sharks, having several pairs of dental plates furnished with tritoral areas. Caudal opisthural. Notochord strengthened with heavy sheath and numerous small calcified rings.

## 5.  Conclusions.

The foregoing data strengthen materially, we believe, our conception of cladoselachians as primitive sharks. In many structural characters they were generalized, and as evidence of this, one need only recall the notochordal axis, the absence of interneurals, the close structural relations of paired and unpaired fins, the presence of a third pair of limbs, the absence of mixipterygia, the open or groove-like condition of the lateral line, the probable absence of a well-developed sclera and, most remarkable of all, the strong evidence that in these forms the visceral cavity extended backward nearly to the base of the caudal fin. On the other hand it is clear that the group of cladoselachians had already (Upper Devonian) evolved many specialized characters. Thus in their movements in swimming they had become darters, the tail truncated, in shape almost like the homocercal caudal of the swift-swimming mackerels, and furnished with lateral-caudal keels which function in swift swimmers to keep the stroke of the fin in a vertical plane. Their pectorals are elongated and strong, with supports sometimes elaborately specialized in form, interwedged to attain strength, and the margins of the fin differentiated into an anterior immobile and a posterior mobile region, in which the web was wide and the radials reduced and slender. In dermal structures similar specialization is present: teeth are highly evolved in matters of form and arrangement, and the shagreen denticles surrounding the eyes are elaborately developed to form a special shield for these sensory organs. We may justly conclude, therefore, that cladoselachians as we know them had already branched off distinctly from the stock of the "pro-

selachia" (Silurian). None the less, however, we may rely upon them to give us some of the essential features of their ancestral forms. For it is clear that if we soften down the sharp edges of cladoselachian specializations we may portray with reasonable accuracy the earlier conditions both in the organs themselves and in the creature in which they appear. It may be of interest therefore
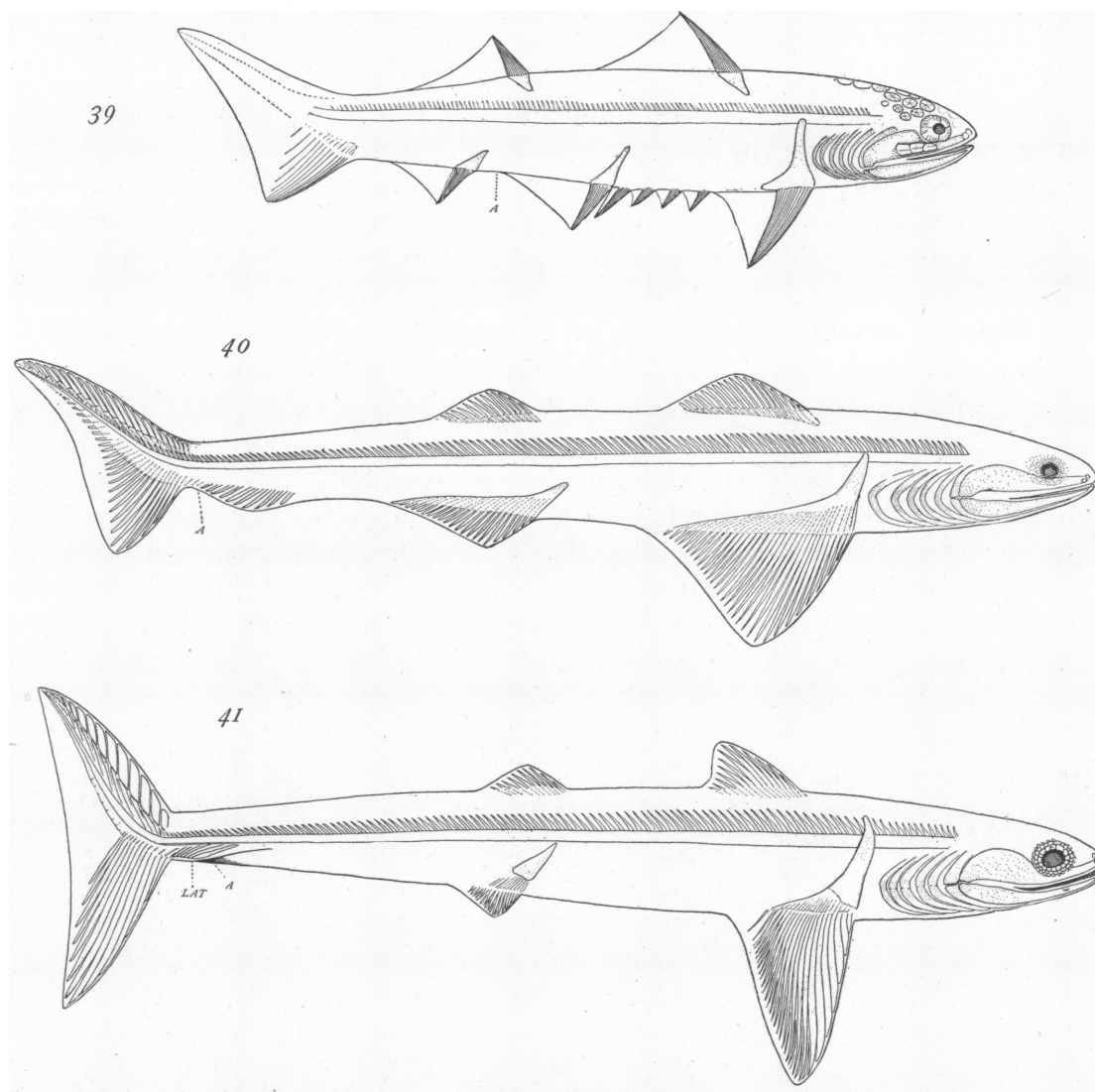


Fig. 39.　Restoration of a primitive acanthodian (essentially *Climatius*).
Fig. 40.　Restoration of a primitive cladoselachian.
Fig. 41.　Restoration of *Cladoselache*.

to compare Figs. 40 and 41: in the second of these is pictured the typical structures of a cladoselachid: in the first the hypothetical form, in which the circumorbital plates are reduced, caudal less homocercal, the margins of the fins slightly extended, their rays arranged somewhat more regularly, thus reducing the con-

trast between the pectoral and the remaining fins. The result gives us the picture of what we would naturally expect in the ancestral cladoselachian, say of Lower Devonian or of Upper Silurian times.

The question of the relationships of cladoselachians and acanthodians might be profitably discussed at this point. The view has been maintained by the writer that both of these groups of Palæozoic sharks are to be brought together into a superorder (Pleuropterygii) and thus distinguished from such groups of coördinate rank as ichthyotomes, euselachians and chimæroids.

For it is certain that there are numerous points which on the one hand indicate affinity between cladoselachians and acanthodians; and which sharply separate them from the other major groups of elasmobranchs. They are thus alike in the relations of their paired and unpaired fins, in the absence of mixipterygia, in their lack of interneurals, and in their extraordinary circumorbital dermal shields,— resemblances all in all which could not have arisen by parallelism. Especial stress has been laid on the similarities in fin structures (1907, Am. Jour. Anatomy, pp. 215–222) since these are so detailed that we can hardly convince ourselves that the peculiar conditions in acanthodians could have arisen in any way other than by modification of cladoselachian beginnings.[1] For in both groups the paired and unpaired fins are obviously pleuropterygial, the paired fins evidently serving as balancers. Indeed the only distinguishing mark in the fins of the two groups is this, that in one the anterior margin of the fin is strengthened by radial supports which are closely concentrating anteriorward, and that in the other the anterior fin support is a spine, which represents but a further stage in the anterior concentration of the radials. This homology, it may be remarked, is supported on the following evidence: in the acanthodian the caudal shows the typical cladoselachian conditions, *i. e.*, a clustering of radials in the anterior border of the fin: the anal also shows this condition but in a more marked degree, the anterior margin of the fin, with its heavy encrusting shagreen becoming a veritable spine, and a similar condition is known in the posterior dorsal. The spine, then, of the unpaired fin in acanthodian is homologous with the radial elements of the anterior margin of the fin: and this being the case the spines of the paired fins have obviously the same morphological value. For otherwise the similar structures in paired and unpaired fins must be non-homologous structures, a conclusion which the studies on the paired fins in general and on the paired fins of *Cladoselache* in particular will not permit us to accept. That the spines of acanthodians are dermal, as Smith Woodward

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[1] It might be queried whether an acanthodian type of fin, a dermal web supported by a purely dermal structure, might not *à priori* be a more ancient condition than a fin having cartilaginoid basal supports? This, however, could not be answered affirmatively for the following reasons. We find: (I) that such radial supports are already present in caudal and other unpaired fins of acanthodians, and from our knowledge of fin-morphology we can hardly conclude that these supports had had an independent origin. (II) That there are good reasons, even in Acanthodii, for believing that the fin-spine is genetically related to the radialia. (III) That, by numerous analogies, sharks, dipnoans, ganoids, the fin surface grows in its dermal margin at the expense of the cartilaginous supports, rather than in the opposite sense, *i. e.* losing its dermal margin on account of the peripheral extension of its radials.

has objected, is met, by the answer that they have come to be largely formed of dermal elements (shagreen denticles) which have encased the radials and led to their reduction in the core of the spine,[1] — a condition which is clearly fore-shadowed in cladoselachian where the anterior rim of the fin is conspicuously strengthened by a crust of enlarged and closely crowded dermal denticles.

Admitting then the general kinship of acanthodians to cladoselachians, we have next to contrast the morphological characters which are more or less specialized in the two groups. In this regard we can only conclude that the acanthodians, in spite of their earlier appearance, exhibit the greater number of specialized features. Thus in their fins the radial supports have largely dis-appeared as discrete structures, and the fins themselves have become reduced to a condition of web and spine. Indeed we would even have grounds for believing that the acanthodian fins were never supported by segmentally arranged radials, cladoselachian in fashion, were it not that such supports occur in their caudal, anal and hinder dorsal fins. But notably specialized in the acanthodians were dermal elements: their placoid scales are of huge relative size, in some cases even mistakable for ganoid plates (compound). This is true of the scales not only of the side of the body, but of those bordering the sensory canals, on the roof of the head, in the throat region, and especially around the eyes, where the numer-ous scales of cladoselachid are represented by but a few, usually four or five, but these of great relative size. In view of this tendency in acanthodians to specialize dermal structures it is in no way remarkable that the anterior margins of the fins should be strengthened by spines, which still, however, indicate in surface ornament the part played in their formation by shagreen elements. Der-mal structures, in short, have in these ancient sharks run riotous careers. They have even invaded the bases of the fins (op. cit., 216–217), encrusting in part at least the girdles and causing these endoskeletal structures to appear outwardly as dermal elements.[2]

But we should not conclude from this evidence that acanthodians were in all respects more specialized than cladoselachians. In certain regards we must give them the credit of the primitiveness which their earlier appearance leads us to expect. Thus if we assume that the ancestral gnathostome was of small size the acanthodian might claim primitiveness, since its members include some of the smallest known fishes, for in certain species (Traquairia) they meas-ure hardly more than an inch in length. Then, too, the segmentation of the mandibular arch, if admitted, would give the acanthodian a conspicuous place in the early pages of vertebral morphology. So, too, the dentition would be archaic if we concede that these forms had not yet evolved a complete succes-sional series of teeth. And finally we recall the evidence that in the earliest genera the paired fins existed in greater number than two.

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[1] Witness numerous analogies of this kind in vertebrate morphology, e. g., reduction of chondrocranium or meckelian cartilage by dermal elements.

[2] In this regard the girdle of an acanthodian would be related to the cartilaginous girdle of its pleuropterygian ancestor, somewhat as the dermal mandible of a specialized teleost would be related to the cartilaginous mandible of its elasmobranchian ancestor.

The upshot of such a general comparison, however, is this:— That the acanthodian of the Upper Silurian could not have been the ancestor of the cladoselachian of the Upper Devonian. It was, on the evidence we have cited above, far too specialized a creature. On the other hand, with equal reason, one cannot claim that the Upper Devonian cladoselachian with its varied specializations pictured the parental form of the earlier acanthodians. For even the time-honored appeal to the defective nature of the palæontological record cannot make such a pedigree a valid one. But we can, I believe, by the following explanation reconcile the apparent discrepancies between the morphological characters and the occurrence in time of these two groups.

If we admit that the acanthodians as we know them at present were preserved *by reason of their specializations* —spines, heavy shagreen —we can easily convince ourselves that there existed then, or shortly before, primitive members of the group which were less suited to fossilization. Similarly we cannot deny that there must have been cladoselachians in the Lower Devonian or the Upper Silurian, which lacked the specializations of the Upper Devonian forms. In short, primitive acanthodians and primitive cladoselachians would be traced back gradually to a common ancestor, which was rather acanthodian than cladoselachian in some characters and *vice versa*, in others.

In fact, on purely morphological grounds, the evidence is exceedingly strong that the cladoselachian of the Upper Devonian in the majority of its characters pictured this "proselachian" ancestor more nearly than did the acanthodian. It is the difference in time of occurrence only which makes such a conclusion the less obvious: but this difference is after all not a very pronounced one. We have reason to believe, *i. e.*, in the evidence of detached teeth, that cladoselachids existed as early as the Middle Devonian, and in view of the fact that these sharks were frail in their structures (teeth, excepted), little suited to fossilization, it is not remarkable that they have not yet been found in the earlier horizons, even if in these horizons their kindred forms are preserved, thanks to their elaborately developed dermal defenses.

Certain it is, in conclusion, that the extension of our knowledge of these earliest sharks strengthens our faith in the "elasmobranch theory." For we can maintain more emphatically than before that "if the earliest true fish could be found, it would almost certainly fall within the subclass"[1] to which belong our modern sharks. And the fundamental characters of the cladoselachian have given us a less ghostly picture of a direct vertebrate ancestor.

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[1] A. Smith Woodward, Natural Science, Vol. VI, p. 38.

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## II.  A Ctenacanth Shark from the Devonian of Ohio.

Among the undescribed specimens in the American Museum (Newberry Collection) is a ctenacanth shark from the same horizon in the Cleveland shale which has furnished the remains of cladoselachids and numerous "placoderms." It was found at Linndale, Ohio, by the veteran collector, Rev. Dr. William Kepler, about 1893, and shortly thereafter it was sent by him to Professor Newberry. The concretion in which it had been found was a large one, measuring 1 meter by 2 meters, but it contained only the anterior portion of the fish. The region from the ventral fins backward existed doubtless in a separate concretion, and the hope was entertained by the discoverer that this would later, perhaps in a few years, be forthcoming, after a longer weathering of the hillside. This hope, however, was never realized, and the specimen must be described in its present imperfect state, for it is, nevertheless, a valuable document in shark morphology.

Ctenacanth sharks have long been a puzzle to palæontologists. Until the discovery of a fairly well-outlined specimen in the Lower Carbon of Eskdale, described by Traquair in 1884 (Geol. Mag., Dec. iii, Vol. I, p. 3), these forms were known only from numerous and well preserved spines which occurred from the Devonian to the Mesozoic. And the earlier efforts to associate their spines with well-known types of teeth have given the morphology of fossil sharks many a false path. Thus Agassiz was confident that *Ctenacanthus* was the spine of *Psammodus*, in spite of the fact, as Egerton showed, that *Psammodus* and *Ctenacanthus* never occurred associated. Newberry, on the other hand, was equally confident that *Ctenacanthus* was the spine of *Orodus* (Pal. Ohio, Vol. II, p. 54). Hancock and Atthey, like Romanowsky (Bull. Soc. Nat. Moscow, 1864, Vol. LXXXVII, pp. 157–170) associated it with *Cladodus* (Ann. Mag. Nat. Hist., [4], 1872, IX, p. 260): and earlier than this, James Thomson, with *Hybodus* (Trans. Geol. Soc. Glasgow, Vol. IV, 1861, p. 59–62). In fact J. W. Barkas, (1874, Feb., Dental Surgery, and Geol. Mag., April) even suggested the propriety of merging *Ctenacanthus* and *Cladodus* in the genus *Hybodus*.

With the discovery of *Ctenacanthus costellatus* in the Lower Carbon of Dumfrieshire (East Eskdale), however, the puzzle neared its solution. It enabled Traquair to give in outline the characters of this ancient shark, and demonstrated that *Ctenacanthus* was cladodont, and "may be *hybodont*," and the later discovery of *Cladodus neilsoni* (1888) gave him the opportunity to declare that the early cladodonts were probably of "different types possibly very different from each other," and whether with or without spines they were undoubtedly of a different family from the hybodonts, and a "more primitive group," while the hybodonts, on the other hand, were "closely allied to the Cestraciontidæ."

Traquair guided by the Eskdale fossil, pictured *Ctenacanthus* as a shark having a well rounded, bluntish head and a stout heterocercal tail: its vertebral axis was notochordal; it had two dorsal fins, each bearing its spine: its ventrals were opposite the second dorsal and it had probably an anal fin: its dentition was cladodont although the teeth were poorly shown in the fossil: and the shagreen denticles were minute, "delicately ridged and pectinated, though sometimes they appear smooth."

The specimen from the Newberry Collection is of value in the present discussion since it presents several characters in a ctenacanth which have not been recorded. We note especially structures of the pectoral fins, general form of body, character of dentition, and details of the lateral line. And these data are found of value when we consider the morphological position of this early type of shark.

The general shape of the head and anterior half of the trunk is seen in the photograph on Pl. XXXIII. From this it appears that the body-form was somewhat depressed,[1] *e. g.*, as in *Rhina*. The head region is fairly well preserved. The jaws attained a subterminal position and were well arched forward, *i. e.*, unlike the condition in modern depressed elasmobranchs. The teeth were large, cladodont, set in close files, of which there were about twelve on each mandibular or palato-pterygoid ramus. Each file, or bank of teeth consisted of about seven elements which were closely apposed, each element fitted conformably in its bank. The teeth are of the broad-based type typical of *Cladodus* (*mirabilis*): they are boldly striated, Fig. 42, and vary in size perceptibly from in front marginalward, but the cladodont pattern of the individual teeth does not change notably. And the specimen has preserved no small marginal teeth which present forms transitional to dermal denticles.
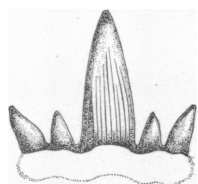


Fig. 42. *Ctenacanthus clarki*. Tooth. × 3/2.

There is no evidence as to the character of the shagreen denticles margining the eyes.

The number of gill arches cannot be determined. Nor are there traces of gill filaments which appear so prominently in large cladoselachian sharks from the same locality.

The first dorsal fin was situated above the pectoral fins beginning at a point opposite their tips. The spine has lost its apex, but it may be identified as *Ctenacanthus clarki* (Newberry), of the same horizon and locality. Its cartilaginous support is unknown, unless it be identified as *SG*, Fig. 43. This element, however, bears stronger evidence of representing a displaced half of a shoulder girdle, to which is still attached a proximal row of basalia.

The pectoral fins are of no little interest from the standpoint of the origin of the paired limbs in the vertebrata. For they are almost diagrammatic ex-

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[1] That this is not due in any great degree to artifact is evident from the excellent preservation of the paired fins, the jaws and lateral line. It is known that sharks from the same locality and formation when well preserved in fin structures show no extreme distortion in body width.

amples of fin folds. They continue backward along the sides of the body and are attached continuously, *i. e.*, the posterior portion of the fin was not separated from the body-wall by a nick: and the basalia did not pass out into the fin as a skeletal axis, but remained within the body wall. From this we conclude that the fin must have functioned less as a paddle than as a balancer, resembling in this regard the cladoselachians. Noteworthy, also, are the facts, that the radial cartilages, as in the latter sharks, extend from the body-wall outward to, or near to, the fin margin, that they increase in length and stoutness as they pass from the hinder to the median portion of the fin and then, further forward,
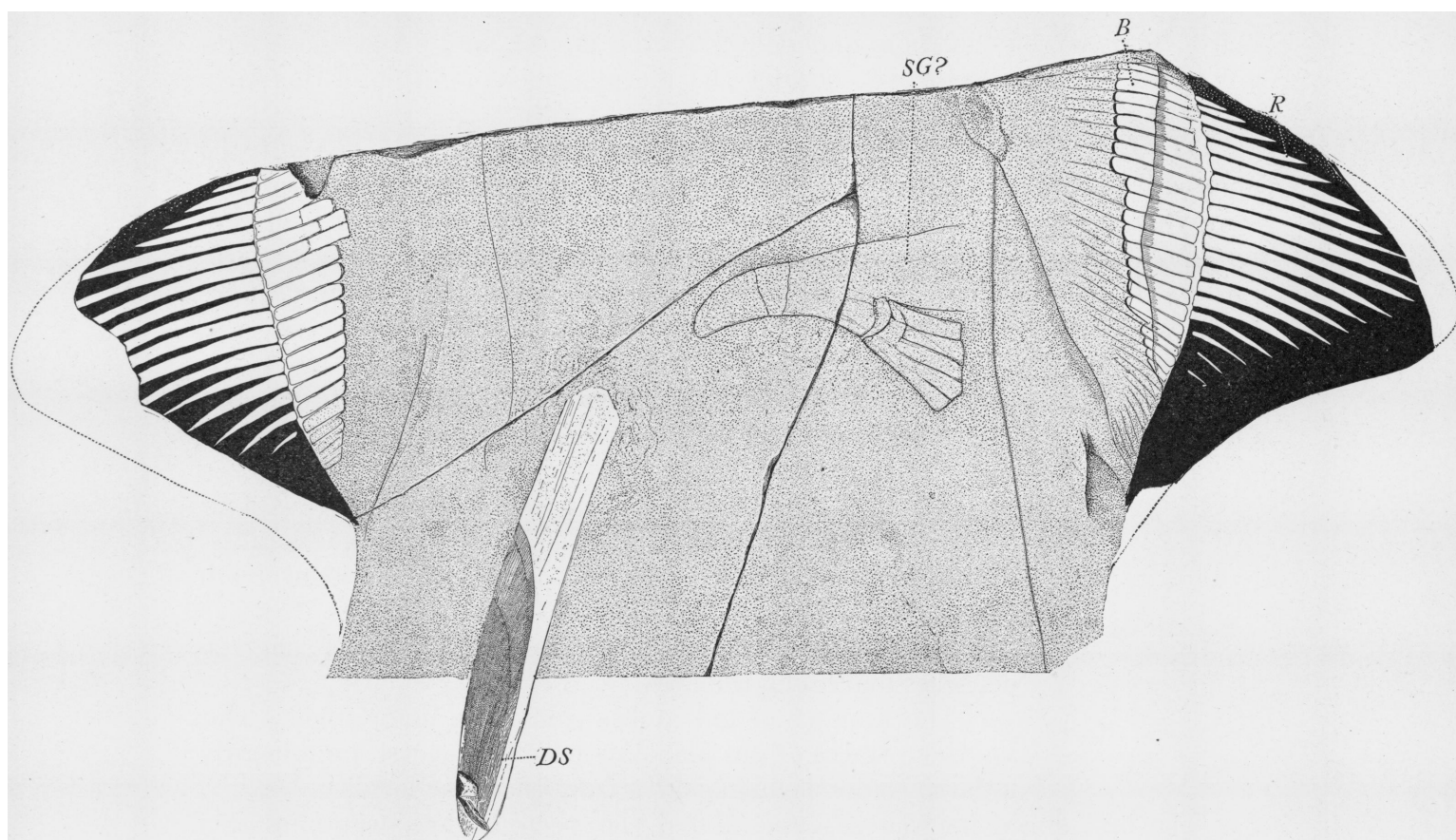


Fig. 43. *Ctenacanthus clarki.* × ¼. Region of pectoral fins. *B*, Basalia, *R*, Radialia, *DS*, dorsal spine; *SG*, shoulder girdle?

decrease in length but increase, more or less, in stoutness; that they are concentrated in the anterior part of the fin; that they are each provided with a separate basal element, which begins at the junction of the fin and the body-wall; and that actinotrichia are not perceptibly developed. Aside from the basalia there is little evidence as to the deeper skeletal supports of the pectoral fins: there were doubtless already evolved large proximal cartilages, "coracoids," which had conspicuous dorsal and mesial moieties (*cf.* Fig. 43, *SG* ?) for these elements have already been developed in cladoselachians in their closely related

type of fin. And by a similar comparison the belief is warranted that the pelvics possessed a hip-girdle arising from the proximal basalia. It is clear that the pectoral fins and the supporting radials and basals were of large size but less compressed (concentrated) than in *Cladoselache*. We note also that the anterior margin of the paired fins was encrusted with large and closely studded shagreen denticles. And this fact is important since it indicates, as the writer has previously pointed out, that the continued concentration of radial supports in the anterior margin of the fins, combined with a calcified outer crust, which was derived from the fusion of dermal denticles, may well have been the ancestral condition of the fin-spines of acanthodians.



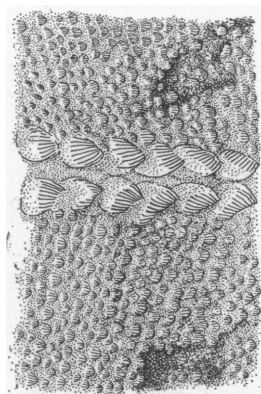Fig. 44.  *Ctenacanthus clarki.*
Lateral line.  × 6.

The proportions of the paired fins in *Ctenacanthus* are by no means unlike those of the fin-fold type of fin which was assigned on theoretical grounds to the earliest sharks (*cf.* Anat. Anz. 1896, p. 675, figs. 1, 2). As shown in Fig. 43 they are low and long; and their radials are not so closely set that their tips interlock. In arrangement, therefore, these elements were the more nearly metameral.[1] Above all things there can be absolutely no question, judging from the perfect way in which the basalia are preserved, that no longitudinal skeletal fin axis was present, unlike the condition in the later "*Cladodus*" *neilsoni* (Traquair).

The lateral line existed in the form of an open groove, Fig. 44, as in various acanthodians; this can be plainly made out in the fossil, for the dermal denticles terminate abruptly on either margin. The marginal denticles, moreover, are exaggerated in size, as in many acanthodians.

In general, the dermal denticles of *Ctenacanthus* are not of conspicuous size. In certain regions of the fish they are seen to be rather richly sculptured, as in Fig. 45 ("*Stemmatodus*"): in other regions the sculpturing is obscure, in others still it is wanting.



Fig. 45.  *Ctenacanthus clarki.*
Stemmatodus-like dermal tubercles.  × 8.

In summary, then, the present fossil demonstrates that in a shark bearing a ctenacanth spine the paired fins are typically of the fin-fold type. There was no archipterygial axis, and the fins functioned rather as balancers, than as paddles. It cannot, on the other hand, be maintained that the fins in this form were specifically adapted to a bottom life, in spite of the general depressed shape of the body. This view is untenable for the following reasons: the large mouth with jaws well arched forward is unknown in any depressed form highly specialized for bottom living: and a dorsal spine situated between the
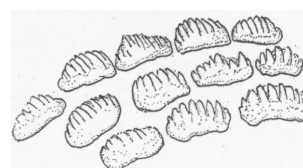
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[1] They were less numerous, however, than in several species of *Cladoselache*. In the pectoral there were about 21 radial elements, as opposed to about 30 in *Cladoselache fyleri* and 77 in *Cladoselache eastmani*.

pectorals is never associated with flattened elasmobranchs, rays, rhinas, pristio-phorids, pristids or rhinobatids.   If this late Devonian shark were depressed and suited for living on or near the bottom, its conditions were probably paralleled in numerous modern sharks, cestracionts, for example, but in such an event the structures of the fins would not have undergone noteworthy structural changes.

It is of interest, finally, that the present shark associates so clearly the clado-dont dentition with the ctenacanth spine.   For it yields another instance of the fallacy of comparing entire animals upon the basis of a single character, *e. g.*, dentition.   When teeth of the type of *Cladodus* were discovered in different horizons from the Devonian well into the Mesozoic, it was naturally concluded that the sharks themselves would be found to correspond closely,— to belong if not to the same genus at least to the same family.   When, however, associated remains of the earlier forms were discovered, it became clear that these sharks were by no means closely allied.   Instead of being proven to be cestracionts, one type of "*Cladodus*" (*Cladoselache kepleri*, *C. fyleri*), (Upper Devonian), was found to be spineless, and quite different in essential structures from the modern cestraciont:  another type of "*Cladodus*," *Symmorium* Cope (Coal Measures), was then shown to be unlike both *Cestracion* and *Cladoselache;* and still another, "*Cladodus*" *neilsoni*, was demonstrated by Traquair to be quite different in fin characters from all the rest.   And now a fourth cladodont, *Ctenacanthus*, is found notably discrepant.   It is, then, only the mesozoic group of "cladodonts" typified by *Hybodus* which remains faithful to our preconceived notions as to what kind of a shark a cladodont tooth should predicate.   The fact of the matter is that the cladodont type of tooth is as ancient as it has been useful in the subclass Elasmobranchii, and that it has appeared in many different lines, either as an heirloom from primitive sharks, or, less probably, as an independent acquisition.   Certain it is that it appears with little variation in as many as seven families of sharks, and in at least three distinct orders.

### III. A Well-preserved Specimen of the Liassic Shark, Palæospinax priscus.

There are reasons for believing that the ancient cestraciont sharks underwent a remarkable evolution, and during a long period, at least from the middle palæozoic to the middle mesozoic. But the lines of this evolution are still to be understood, for the data upon which our conclusions rest give little knowledge as to the soft structures of the fish. There is, however, the indication
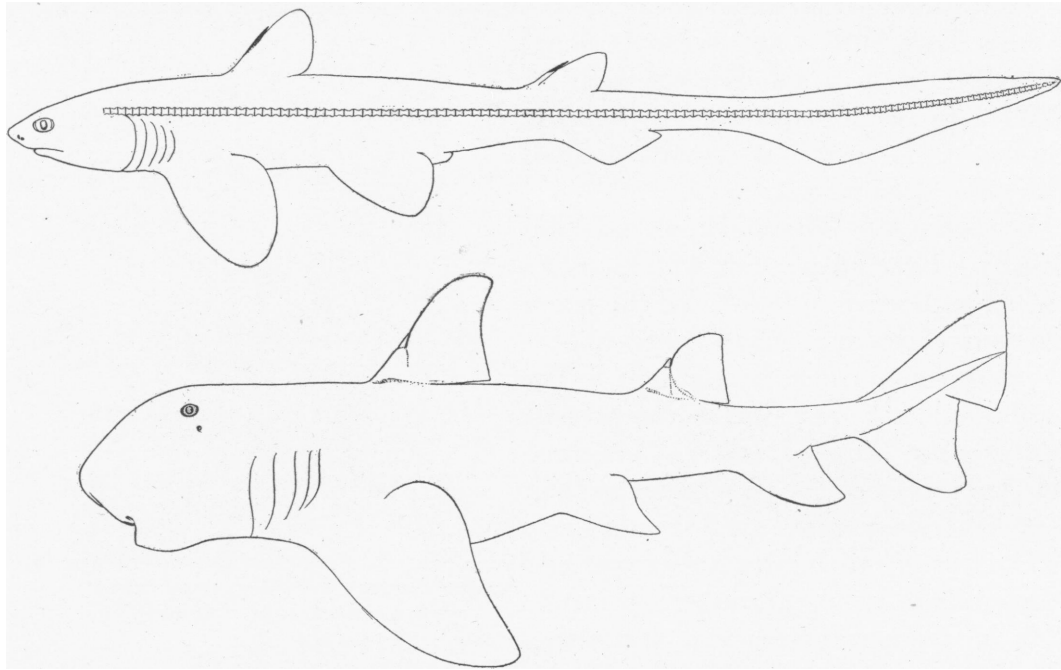


Fig. 46. *Palæospinax priscus* Agassiz. Reconstruction. × $\frac{2}{5}$.
Fig. 47. *Heterodontus japonicus* (Macleay). × $\frac{1}{9}$.

that already in the early Mezozoic the subfamily to which the recent *Heterodontus* belongs had already appeared. And that by Jurassic time, cestracionts had been evolved which were quite similar to several more recent sharks. This resemblance, indeed, is sometimes so close as to suggest that certain families of recent sharks may trace their pedigree directly back to the cestracionts. And it is in this connection that we may refer to the small shark *Palæospinax priscus* Agassiz, known from well-preserved specimens from the lower Lias of Lyme Regis (Dorset): for this is a cestraciont which is modern in a number of essential features.

The accompanying restoration, Fig. 46, has been drawn to scale after measurements of a number of specimens, notably those in the British Museum, and

it gives a reasonably accurate picture of this Jurassic shark, save, perhaps, in the matter of the thickness of the trunk. And one cannot fail to be impressed with its resemblance less to a surviving cestraciont, Fig. 47, than to typically modern sharks, such as spinacids or squalids, e. g., in shape, proportions, fin-characters, etc. Indeed we would be inclined to include it with the latter were it not for the fact that its lateral teeth are blunted, a typical cestraciont character, and that it bears enamelled spines.

Further details of structure strengthen our conception as to the modern cast of this early shark: and in this regard we refer particularly to a specimen in the American Museum, No. 7085, lately collected near Lyme Regis (Plate XXXIV). Among structural features we note:—

SHAGREEN.—Its elements are close-studded, and of about the same relative size and show about the same regional differentiation as a modern spinacid or scylliid. In some regions, as Egerton early noted, the denticles are ornamented with rather definite markings.

DENTITION.—The teeth, already described by Egerton, are not widely unlike those of a modern squalid: in the more nearly symphyseal position they are proportioned somewhat as in a lamnid. The lateral teeth (not preserved in the present specimen) are blunted, but not enlarged after the fashion of the pavement teeth in the typical cestraciont. (Cf. Fig. 48.)

COLUMN.—Its centra are strong and cyclospondylic, unlike the asterospondylic centra of modern Cestracion, a discrepancy early commented upon by Hasse: from such conditions were possibly derived the centra of such modern sharks as scymnids or squalids. The column contains in all, about 130 vertebræ, from estimates based upon various specimens and descriptions: of these 15 (Davis), 16 (Egerton), or 18 (present specimen) lie between the cranium and first dorsal, 50 (Egerton) or 56 (Davis) in front of second dorsal,— in these regards comparing with Cestracion (15 and 48, Egerton), or more closely with Acanthias (24 and 58). Its entire column contains fewer centra than Notidanus (about 150), but a greater number than Cestracion (about 115) or Scyllium (about 108).

HEAD.— Contour not unlike that of a modern shark (e. g., Scyllium). No evidence of the head spines, which occur, however, in the kindred hybodonts. Shape of mandible suggests Notidanus. (Fig. 48.) Mouth sub-terminal. Nasal capsules not remarkable in size or position.
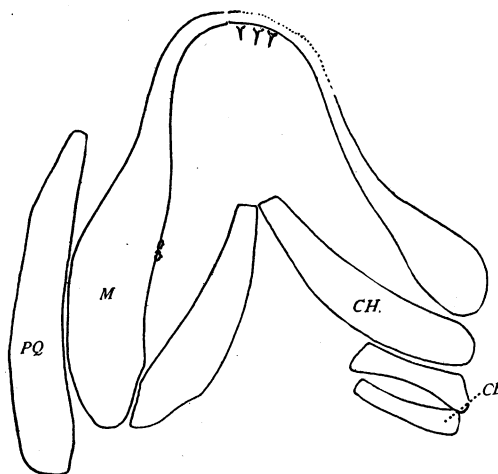


Fig. 48. Palæospinax priscus. Region of jaws. After specimen P 3190. British Museum.

CB, ceratobranchial; CH, ceratohyal; M, mandible; P Q, palatoquadrate.

GILL REGION.—Strikingly modern in character. Five gill-openings can be counted (Pl. XXXIV), with interspaces of marginal flaps as *e.g.*, in *Scyllium*, not compressed and overspread with larger anterior flap as in *Chlamydoselachus*, or to a less degree in *Heterodontus*. (This condition is shown, but obscurely, in specimen P 7788, British Museum, described by Davis ('81).) From the complete encasement of the marginal flaps in shagreen we conclude that external gill filaments were absent. We are also able to conclude that the elements of the branchial basket were not unlike those of such a form as *Scyllium*,—in this regard witness the size and sequence of the pharyngo- and epibranchials (Pl. XXXIV). Note also the ceratohyals shown in Fig. 48 (after specimen P 3190, British Museum), as well as the ceratohyal elements, meckelian and palato-quadrate.

FINS AND GIRDLES.— The present specimen shows that the first dorsal was provided with a cartilaginous (apparently unsegmented) plate supporting the dorsal spine and the hinder fin. Of the latter we note with Egerton that the rays (Fig. 49), in the dermal web of the fin were dense and hornlike. In this regard the fin is clearly cestraciont, but its proportions were smaller, and the
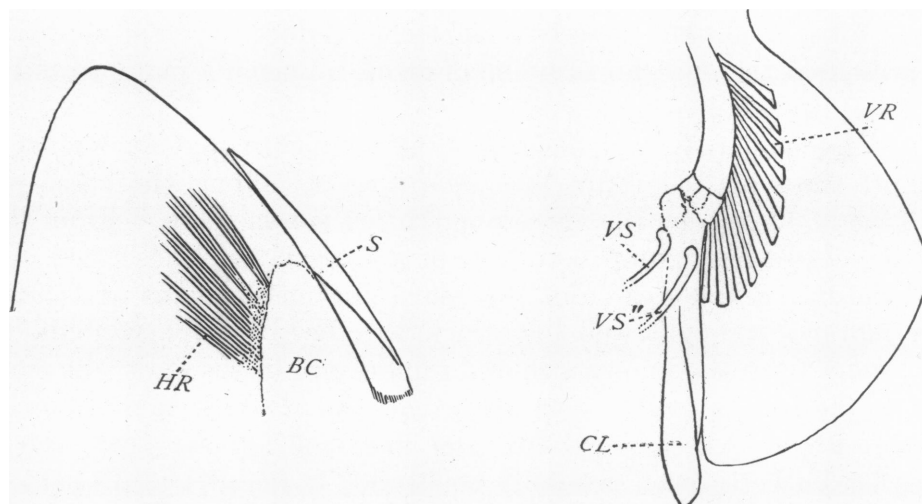


Fig. 49.                                    Fig. 50.

Fig. 49. *Palæospinax*. Dorsal fin. *B C*, basal cartilage; *H R*, horn-like fin rays; *S*, spine.
Fig. 50. *Palæospinax*. Ventral fin. *C L*, clasper, *V S'*, *V S''*, spines of clasper *V R*, radialia.

fin was probably more generalized than in the recent members of this family. The pectorals are moderately large, proportioned about as in *Scyllium*: but they are notably smaller than in a recent cestraciont. The proportion of the dermal margin to the cartilaginous base of the fin is of modern type, as is also the row of radialia: of these, 14 are clearly present, with a possibility of several additional (posterior) elements. The shoulder girdle is slender, lighter in proportion even than in *Scyllium*: and the writer is unable to agree with the diag-

nosis of Egerton (1837) that "the framework of the fins is more solid than in more recent placoids." The ventral fin (Fig. 50) has at least 11 radials (probably not more than 13). The mixipterygium shows two conspicuous elements. According to Smith Woodward (Cat. Br. Mus., Pt. I, 323), "each clasper appears to be provided with two bifurcating spines in contact at their base, which is expanded and flattened upon the apposed side; and the exserted portion of each of these consists of two compressed divergent branches, gently curved, and unequal in size." These extraordinary structures are not shown in detail in the present specimen: the position of one of them, however, is indicated at the extreme base of the (right) mixipterygium: accordingly they cannot be homologized with the elements of the antero-lateral clasping organs of *Chimœra*, elements which probably occurred in early cestracionts.

The present note emphasizes, in summary, the modernness of this early Jurassic shark: in many regards it might well have stood in the line of the other Euselachii, but in other regards it is evidently too specialized to have occupied this position. For it is exceedingly doubtful whether a form which has already become so specialized in its dorsal fins (with spines and single basal cartilages) could have given rise to such forms as notidanids, scylliids, etc., which lack fin spines and retain segmented bases to the dorsal fins. It may also be questioned whether a form which has already a somewhat reduced type of dentition could have represented the ancestor of a line of forms in which a more primitive number of dental rows is present.

In any event it may be looked upon as significant that among the ancient cestracionts there existed forms like *Palœospinax*, among the most primitive of which might have been the ancestors of other euselachians. From this point of view the cestraciont group becomes not a narrowly circumscribed one; and, as its structural differences from the remaining euselachians are thus not so strongly marked, it might well have included the primitive scylliids, lamnids, etc. In short from the known size and importance of the early cestracionts, as opposed to the lack of evidence as to the early euselachids, it may some day be demonstrated that cestracionts are the ancestral, rather than the derived forms, as has hitherto been generally believed. It makes less probable the opposing view that the resemblance of *Palœospinax* to the modern *Spinax*, for example, is a case of pure parallelism, developed out of the many forms of early sharks.

## IV. Note on *Archæobatis gigas* Newberry.

From the Lower Carboniferous of Greencastle, Indiana, Professor Newberry received (1886?) a number of dental plates of a large elasmobranch which he regarded (1889, Paleozoic Fishes of North America, p. 184) as "closely allied to *Psammodus*." And to this form he gave the name of *Archæobatis gigas*. Regarding it he notes briefly (*op. cit.*, p. 184): — "The dentition of this genus formed a pavement of many teeth, of which the largest were six inches long by four inches wide, and one and a half inches thick. To prevent the slipping of the objects operated by this powerful crusher the enameled surface was rough-ened by transverse, parallel ridges, precisely as in the living *Rhynchobatus*." It is clear from Dr. Newberry's remarks that he regarded *Archæobatis* as an early form of ray. And the plates obviously suggest those of a myliobatid, or better, an aëtobatid. And this Dr. Newberry has further indicated, *op. cit.*, pl. xxii, fig. 3, in his conception of the relations of the various plates. Thus he pictures the dentition built up of a series of four plates arranged in an alternating series with four adjacent plates, and he leaves open the possibility that there existed a greater number of plates on either side.

In a renewed examination of the dental plates of *Archæobatis* the present writer has been led to associate them as indicated in Pl. XXXV. Four of the plates, those on the right in the figure, evidently belonged together: their contacts are perfect. But there has been found no trace of a fifth element which might be placed next to the smallest plate (at the top of the figure): in fact a rounding margin of the latter renders it very doubtful if an additional element could have here been present. Moreover, the neatly rounded lateral margins of the plates when conjoined make it even improbable that marginal plates occurred in this type of dentition. The opposite margin of the four com-ponent plates is a perfectly straight one, and this feature, together with the general half-symmetry of the associated plates has lead to the restoration of the missing ones as indicated in the figure. For in this general type of dentition in elasmobranchs, in cases where dental plates are present in a greater number of rows in each ramus, there is usually, if not always present an oblique curvature of the crushing surfaces. (*Cf.* A. S. Woodward, Nat. Sci., Vol. I, p. 672). In connection with the ray-like character of *Archæobatis* we recall the interesting fact that *Tamiobatis vetustus* Eastman (Am. Jour. Sci., Vol. IV, pp. 84 *et seq.*) occurs in the neighboring region (Kentucky), although at a somewhat earlier horizon, indicating therefore that we may expect a ray-like type of dentition, even highly specialized, among early elasmobranchs. For the rest it does not follow that on such evidence, plausible though it be, we are to conclude that the true rays had their origin at so early a period. Until complete specimens are forthcoming we can best assume that a number of ray-like characters had been acquired among the cestracionts, for we recall that these sharks were then at their apogee in evolution.

## V. The Jurassic Chimæroid, *Ischyodus*.

Fossil chimæroids are among the rare objects of museums: and associated remains of these fishes, that is, fossils which exhibit more than dental plates and fin-spines, are supremely rare,— a fact the more to be deplored since it is precisely specimens of this kind which are needed to give the key to the nearly solved puzzle of the relationships of these primitive vertebrates. From this point of view, accordingly, we may now welcome a splendid "document," in the shape of a well-preserved and almost complete Jurassic chimæroid, *Ischyodus avitus*, which has recently come into the possession of the American Museum.

This specimen (secured through the generosity of a trustee of the museum, Cleveland H. Dodge, Esq.) was discovered about 1905 in a tile-quarry in Eichstätt, in the classic region of the Bavarian lithographic-stone. It is of large size, measuring about a meter in length,[1] and in point of preservation is unquestionably the best hitherto recorded. As shown in Plate XXXVI it presents for examination the entire fish and lacks only the ends of the fins. In the head such structures are preserved as the fleshy portion of the snout, the outline of the interorbital septum, *OS*, the hinder region of the palatoquadrate, *PQ*, and traces of the pharyngobranchials, *PB*. In the trunk, both girdles, *SG* and *PQ* can be distinguished, as well as the outline of the visceral cavity, *VC*. Mucous canals *MC*, can be traced here as well as in the snout. The fin bases retain both radial and basal cartilages, *R* and *B*, and the outline of the ventral fin can be followed. Altogether the specimen gives an excellent idea of the ensemble of this ancient form, impressing the observer at once with its likeness to the long-nosed genera (*Harriotta* and *Rhinochimœra*) on the one hand and to *Callorhynchus* on the other.

Of more or less complete fossil chimæroids there are previous records of only five specimens,— in spite of the richness of the collecting field and decades of earnest collecting. They are:—

I. *Ischyodus quenstedti*. Quenstedt's specimen — from Solnhofen (?), now in the Munich Museum. Described in 1857 by A. Wagner in Gelehr. Anz. k. bay. Akad., Vol. XLIV, p. 228; again described by A. Wagner in 1862 in Abh. Math.-phys. Cl. k. bay. Akad. Wiss., Vol. IX, p. 286, pl. 1.; and in 1887 by J. Reiss in Palæontographica, Vol. XXXIV, p. 6, pl. 1, figs. 1–5. This specimen shows the jaw parts *in situ*, and parts of dorsal fins and vertebral region. It lacks the skull (in large part), paired fins and girdles. The sex was probably female. There are no traces of claspers.

II. *I. avitus*. Von Meyer's specimen from Solnhofen, now in the Munich

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[1] If the tapering tail region were complete the total length would probably attain from 120 to 135 cm.

Museum. Described in 1862 by M. von Meyer in Palæontographica, Vol. VII, pp. 14–18. A miniature specimen, about a foot in length, better preserved than the preceding. A cast of this specimen is now exhibited in the American Museum's hall of fossil fishes.

III. *I. avitus.* Reiss's specimen from Eichstätt, now in the Munich Museum. Described in 1887 by J. Reiss in Palæontographica, Vol. XXXIV, p. 15, pl. 1, fig. 6. Unfigured *in toto*, but not remarkable: according to Philippi "is probably as fragmentary as the specimen from the Häberlein collection" (No. I. above).

IV. *Ischyodus ?* A. S. Woodward's specimen, and the only one not Bavarian, — this from the Oxfordian of Christian Malford (Wiltshire), and preserved in the Northampton Museum. Described in 1892 by A. S. Woodward, Ann. and Mag. Nat. Hist., Jan. pp. 94–96. May be *Ganodus?* Dentition imperfectly exposed, head crushed. Measures in all about 32 cm. in length. Shows frontal clasper and traces of ventral claspers. Paired fins "too imperfectly preserved for description."

V. *I. avitus.* Von Ammon's specimen, from Eichstätt, now preserved in the Museum of the Natural History Society in Regensburg. Described in 1896 in Berichte d. Naturwiss. Ver. z. Regensburg, V. Heft. f. d. Jahre 1894–95; and in 1899 in Geognos. Jahresheften, 3 pp., 1 pl. A male head (admirably preserved) and trunk as far at least as the region of the tip of the ventral clasper: pectoral fin and girdle poor, base of ventral good.

The present specimen is accordingly the sixth in which the body has been preserved. It lacks indeed only the tail tip, and it is particularly perfect in regions poorly shown in earlier specimens,—paired fins, girdles, posterior dorsal fin and the basal portion of the caudal fin. From such a specimen, we may therefore add a number of details to our knowledge of this Jurassic chimæroid.

*Ischyodus,* Plate XXXVI, differed little from modern chimæroids in general proportions. Interesting, however, from the point of view of the relationships of the group, is the fact that the differences from the modern forms lie more closely in the direction of the sharks. Thus we observe that the snout, well indicated in nearly all specimens, is distinctly shark-like (*e. g.,* like *Oxyrhina,* or *Carcharias*): it has neither the rostrum of *Harriotta,* nor of *Rhinochimæra,* nor the trunk-like proboscis of *Callorhynchus,* nor yet the blunt fleshy snout of *Chimæra.* The proportion of face to cranium is, as Philippi has already observed ('97, Palæongraphica, Vol. XLIV, p. 2), greater in the case of *Ischyodus* than in modern chimæroids: or more precisely the portion of the cranium which lies in front of the mandibular articulation is in *Ischyodus* relatively longer than the posterior portion of the cranium. Thus in *Ischyodus* the anterior region of the cranium is to the remainder as 3 is to 2, while in *Chimæra* it is only as 3 is to 5,— a character in *Ischyodus* again distinctly shark-like. So also the neck is longer, and therefore more shark-like, in *Ischyodus* than in any modern

chimæroid. The orbit, however, appears to have been of about the same proportions as in a modern form, *Rhinochimæra*, for example.

It has long been known that the dorsal fin-spines of these mesozoic chimæroids were more shark-like than in modern forms. In the latter the spines have been reduced, have a more superficial attachment and have lost their surface shagreen ornament and to a large degree even the characteristic serrate denticles of the hinder margin. In *Ischyodus* the spine is a very conspicuous structure, and the frontal "clasper" of the male indicates clearly its origin, not as mere frontal dermal fold, as Garman for example pictures it, but as a spinelike structure, even bearing a tuberculate ornament along its sides, interestingly intermediate in form between the still longer and conical spine in the more ancient *Squaloraja* and *Myriacanthus* and the greatly reduced frontal organ of recent forms. In this regard it is to be presupposed that in the most ancient chimæroids the *female* as well as the male bore frontal spines, and it is probable that the condition in the latest specimen of *Ischyodus* offers some evidence in this direction. In front of the cranium there appears a curiously shaped depression in the matrix which at once suggested the outline of some fleshy structure (a soft and obsolescent spine?).[1]

Further details in head structures: — The jaw cartilage outlined in the latest specimen indicates a longer meckelian cartilage (*i. e.*, more shark-like) than in any modern form, not excepting *Rhinochimæra*. The dental incrustation, moreover, laps more widely over the cartilaginous supports than in modern genera. On the other hand, more as in modern chimæroids, *cf. Rhinochimæra*, was the series of enlarged branchiostegal elements of the hyoid arch. Few details of the branchial basket have been made out: in one of the fragmentary specimens of *Ischyodus* preserved in Tübingen (*cf.* Philippi, *op. cit.*), however, some of the elements (dissociated) have been made out, but too meagerly to warrant comparisons.

The paired fins differ little from those of modern forms. The shoulder girdle is, however, stouter. The pectoral basalia have not been determined: the radialia numbered about 27 plus an anterior compound element, while in *Callorhynchus* and *Rhinochimæra* about 29, and 25, plus in each case an anterior compound element,— unimportant differences. The pelvic girdle has not been satisfactorily outlined: it appears, however, to have borne "iliac processes" of extraordinary length and delicacy, whose position was a nearly vertical one. The pelvic basalia are poorly preserved; the radialia were probably 20 in number as compared with about 18 in *Callorhynchus*, and about 13 in *Rhinochimæra*. The condition of greatest number in *Ischyodus* may reasonably be interpreted

[1] A note on the probable evolution of this organ: — The spine may have attained its present condition by the intervention of processes which altered its tempo of development. In the ontogeny of primitive chimæroids it probably arose at the same time as the neighboring dorsal spine: it then appeared at a later and later period in ontogeny in the chimæroid series until its full development came to coincide more or less accurately with sexual maturity. In the female, on the other hand, its tempo of development may have been further reduced: in very old specimens ( ♀ ) a trace of this structure may some day be discovered in living species.

as primitive, although the differences from the modern condition are not impressive.

The structures of the unpaired fins, which are now fairly well known, resemble closely those of modern forms. The posterior dorsal with its long row of small basal cartilages is almost the same as in *Rhinochimæra* (and probably *Harriotta*). The anal fin is represented only in a fleshy pad, in the present specimen about 11 cm. long, reminding one of the condition in recent chimæroids. The anterior dorsal has the same triangular basal plate and supporting saddle (formed of enlarged and fused neural arches), but the latter structure is hardly preserved in sufficient detail to warrant comparisons. We note only that the anterior limit of the spined dorsal fin was further forward than in modern genera: and that the frontal clasper is not merely more spine-like, but that its place of origin is nearer the fin spine, thus suggesting a closer serial relationship of these structures, judging at least from numerous analogies in teleosts.

The visceral cavity is well outlined in the present specimen: it is of large size but presents no features of especial interest. On its wall are numerous inscriptions of tendons.

The sensory canals, on the other hand, deserve detailed notice. They can be followed clearly in the fossils (especially in specimens V and VI) owing to the fossilization of the rouleaux of ring-like "cartilages" which support the canals. In nearly every case, moreover, it is possible to distinguish the canals of right and left sides so that one is not apt to confuse an opposite canal with a serial structure.

In Fig. 51 is a reconstruction of the side of the head and shoulder regions of *Ischyodus avitus*. It is taken from a tracing of von Ammon's specimen (V) with details controlled from specimens I and VI. And the distribution of the sensory canals here shown may be compared profitably with modern genera (*cf. Callorhynchus*, Fig. 52, *Rhinochimæra*, Fig. 53, *Harriotta*, Fig. 54, *Chimæra*, Fig. 55).

The canals, rostral, cranial, ocular, orbital and suborbital — and here we may follow conveniently Garman's nomenclature — are quite similar to those in modern genera. The aural is longer and is deflected in the region of the base of the frontal spine. Does this indicate a newly established readjustment? For in the chimæroid ancestor in which the frontal "clasper" was in the position of a more normal dorsal fin-spine this canal traversed the occiput *in front* of this organ. In the Jurassic form, accordingly, the swing of the aural canal in an anterior direction may well represent the ancient trend of this canal: unique, certainly, in known chimæroids are its sudden sweep hindward, at more than at right angles indeed, to its former direction, and then another right angled turn to traverse the head. This evidence would be of greater interest were it not that erratic undulations in sensory canals are not uncommon in chimæroids,— although, as far as I am aware, never as pronounced as in the foregoing case.
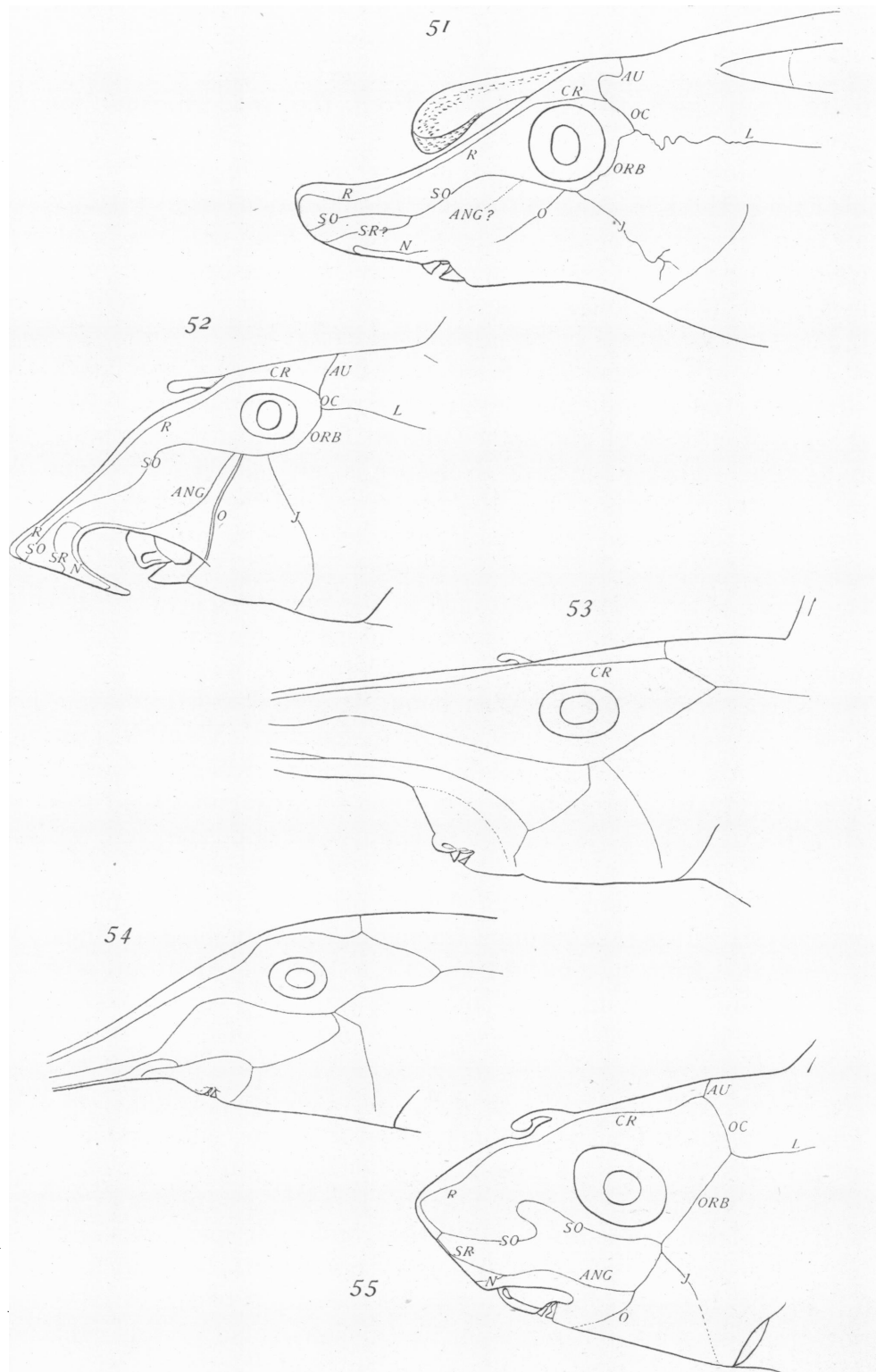
Figs. 51–55.   Heads of Chimæroids showing the arrangement of sensory canals.

Fig. 51.   *Ischyodus avitus.*

Fig. 52.   *Callorhynchus antarcticus.*

Fig. 53.   *Rhinochimæra pacifica.*

Fig. 54.   *Harriotta raleighana.*

Fig. 55.   *Chimæra monstrosa.*   Canals: *ANG*, angular; *AU*, aural; *CR*, cranial; *J*, jugular; *L*, lateral; *N*, nasal; *O*, oral; *ORB*, orbital; *R*, rostral; *SO*, suborbital; *SR*, subrostral.

The jugular (opercular) canal is interesting for two reasons. In the first place it passes backward more directly, than in any other known chimæroid, thus indicating that the gill-slits were at a higher level on the side of the neck (a distinctly shark-like condition). In the second place this canal breaks up in clustered branches which denotes a wider anteriormost gill-flap, conditioned somewhat perhaps as in the recent frilled shark *Chlamydoselachus*.

The oral canal passes more directly forward than in other known forms, and possibly indicates that the mouth in ancient chimæroids was further in advance of the eye. The angular canal cannot be positively identified, and may perhaps be represented only as a branch of the oral as it occurs in the majority of recent forms.

The really perplexing feature, however, in *Ischyodus* is the sensory canal designated doubtfully as subrostral (*SR* ?) for this arises from the suborbital, and not from the angular (or nasal) element. There is, I think, no doubt that this branching actually occurred, for this portion of the fossil is well preserved in two of the specimens. But what does this condition mean? It is unknown in other chimæroids and the only suggestion that one can offer is that it is a survival of a shark-like structure. But unhappily we have for comparison no satisfactory data as to the head canals of early sharks. And these structures in recent sharks, *Cestracion*, for example, do not throw any light on the puzzle. For the rest, the whole plan of the canals in chimæroids cannot be reduced satisfactorily to the one pictured in modern types of sharks.

## VI. A Chimæroid Egg-capsule from the North American Cretaceous.

The relations of palæontology to embryology are in these days so strained that from the standpoint of either study an object is worthy of especial notice which claims a place within the borderlines of both subjects, i. e., in "palæ-embryology." One of the latest discoveries in this direction is the egg-case of a cretaceous chimæroid, which enables rather definite comparison to be made with the capsules of recent forms. This specimen, as recorded by Dr. Gill,[1] was collected in the Upper Cretaceous near Laramie, Wyoming, by a collecting party of the United States Geological Survey, under the leadership of N. H. Darton. And through the courtesy of the survey and at the kind suggestion of Dr. Gill it was loaned to the present writer for more detailed examination. Since this time a cast of the fossil has been made, and is exhibited in the American Museum in the alcove devoted to fossil chimæroids.

The capsules of chimæroids, as the writer has shown (Biol. Bulletin, 1904, Vol. VII, pp. 105–112), are peculiarly adapted to the structures of the young fish which they are later to contain. Indeed the form and size of even an adult chimæroid can be predicted from its egg-capsule with considerable accuracy. Thus the size of the capsule stands in direct ratio to the size of the fish; the narrowness of the "tail sheath" of the capsule predicates the narrowness of the fish's tail, and the length of the opisthure; while the shape of the trunk sheath foretells the slimness or stoutness of the fish's trunk. This can be induced so clearly from a study of the known recent genera and species that the same kind of evidence can, in all probability, be employed in our examination of fossil forms.

The present fossil, Plate XXXVII, presents features which recall the capsules of what have generally been regarded as the older forms of chimæroids,—callorhynchids, harriottids and rhinochimærids.[2] It suggests the capsule of *Callorhynchus* in the proportions of its body- and tail-sheaths and in the structures of the lateral webs; that of *Harriotta* in the great width of the lateral webs and in number and direction of its costæ; that of *Rhinochimæra* in the character of the lateral web and in the proportions of the trunk-sheath. On the other hand in the character of its web it is widely unlike the capsules of the more modern families of chimæroids.

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[1] Science, N. S., Vol. XXII, p. 601, 1905. Dr. Gill states that "three figures have been published of Jurassic egg-cases, two by Emil Bessels and one by Otto Jaekel." This should, however, not be read in the sense that three distinct capsules were figured. There are known (to be painfully accurate) only a capsule and a half, and these were originally figured by Bessels (JH. d. Verein f. vaterl. Naturkunde in Württ., 1869). Jaekel repictured these in 1901 (Neues JB. Min. Geol. Pal. Berlin., Vol. XIV, pp. 540–564).

[2] Cf. Dean, Bashford, 1906, Carnegie Memoir on Chimæroid Fishes and their Development, pp. 28 et seq.

More detailed comparison may be given in tabular form:—

| Length (cm.) | Genus and Species | Percentage of breadth to length. | | Percentage of length of tail-sheath to entire length. | Proportional length of opening of valve, from hinge to anterior end of capsule (in percentage of total length of capsule. | Character of respiratory openings appearing on either side of opercular valve. | Character of respiratory openings appearing on either side of tail-sheath. | Rugæ, number of. | Rugulæ (=costæ), number of. |
|---|---|---|---|---|---|---|---|---|---|
| | | Breadth of trunk-sheath only | Entire breadth. | | | | | | |
| 18 | *Ischyodus* ( = Aletodus, Jaekel). | 17% | 40% | 37% | 36% | ?single slit on each side | ?single slit | 12 | 28 |
| 17 | *Callorhynchus* Jaekel's. | 16 | 45 | 30 | 36 | single slit on each side | slit on each side | 20 | 58 |
| 15+ | American Cretaceous capsule | 17 | 50 | 50 | ? | ? | ? | ? | 50 |
| 15 | (?) *Harriotta* (?) *raleighana* | 18 | 37 | 39 | 31 | serrated margin, with over 70 apertures. | Many (110) couples of minute perforations. | | 50 |
| 16 | (?) *Harriotta* *indica* | 15 | 32 | 38 | 18 | ? | " (185) | | 70 |
| 26 | *Rhinochimæra* *pacifica* | 13 | 33[1] | 32 | 35 | serrated margin, with about 50 apertures. | " (45) | | 56 |

From this examination it appears, even if allowance is made for its slightly defective proportions, that the present capsule is peculiar in its great breadth, wide tail sheath, the alternating thickness and thinness of rugulæ (or costæ), the thicker ones suggesting rugæ; in the prominent subdivision of the trunk-sheath, showing a large depression for the head; finally in its felty and ragged margin,— this shown at a point in the upper left hand portion of the capsule. It differs essentially from both "*Ischyodus*" (Jaekel's) and *Callorhynchus* in showing no conspicuous rugulæ or costæ marking the hinder limit of the opercular valve. It clearly, therefore, belonged to a form which was distinct from these genera, and possibly belonged to a different family. Unfortunately, however, no details can be made out regarding the respiratory structures of the opercular valve or of the margin of the tail-sheath. For these would have given the safest clue to the closeness of kinship of the present form with harriottids and rhinochimærids.

Judging this fossil capsule in the light of our knowledge of recent forms, I think we may safely assume certain characters in respect to the parent fish. It was a fish of moderate size, less than a meter in length; it was heavy bodied, with a head of conspicuous size, probably terminating in a long snout (in this

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[1] Into the table given in the Carnegie Memoir (Dean, 1906) there are several unfortunate errors, the proof having been corrected during the writer's absence. Here 3 is given for 33.

we judge from the way in which, in the capsule, the head region is set inward,— *i. e.,* far back from the anterior rim as in *Harriotta, Rhinochimœra,* and to a lesser degree in *Callorhynchus).* The trunk was long and broad, with a larger caudal fin and a smaller opisthure than in chimæroids. Indeed, if we balance all the evidence yielded by a study of the capsule, especially in its likeness to *Harriotta* and *Rhinochimœra,* we might even hazard a guess as to the cretaceous chimæroid which deposited it.[1] I fancy that *Elasmodus* (possibly the closely related *Elasmodectes*) might well have been the parental form in question, since, judging at least from dental plates, this chimæroid might reasonably have been the ancestor of the modern genera. (*Cf.* Carnegie Memoir above cited, pp. 147–148.)

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[1] I fear that my friend Professor Otto Jaekel will not sympathize with me in this conclusion. . He has expressed the belief (1901, Neues Jahrbuch für Mineralogie, Geologie und Palæontologie, Vol. XIV, pp. 554–555) that the Jurassic capsule above noted corresponds in the most striking way with the capsule of the modern *Callorhynchus,* yet the latter genus had not at that time appeared. Hence he concludes that "a very specialized egg-capsule has remained unchanged during long geological periods, while the form of the parent fish has proceeded to evolve a generic difference." I think, however, that one need only point out that the capsule of "*Aletodus*" referred to differs in certain regards from those (about six known) of the various species of recent *Callorhynchus,* *e. g.,* in the recurved rugulæ demarking the hinge of the opercular valve, and in the curiously indented rugulæ of the anterior portion of the web. These features alone might well stand for generic differences occurring within a family from which the modern form is derived. In short, if we now add the testimony of another and different type of fossil chimæroid, I think we may safely conclude that the evolution of the capsules in chimæroids kept pace with the evolution of the parental forms,— and not that the type of development became fixed while the characters of the adult continued to transform, as Jaekel maintains. But even if it were admitted that Jaekel's capsule was exceedingly similar to that of *Callorhynchus* the fact now established that the modern genus is known from the cretaceous would tend to nullify his conception of such an evolutional disparity.

## VII.  A MOUNTED SPECIMEN OF *DINICHTHYS TERRELLI*.

*Dinichthys*, the most powerful and predatory animal of the Devonian, or of any earlier age, is an attractive subject for restoration.  And the museum has selected a specimen of *Dinichthys terrelli*, which is a large species of this genus, as the central object in its gallery of fossil fishes.  A brief notice may be given of this exhibit:

The Newberry collection, which is deposited in the Museum by Columbia University, is especially rich in dinichthyids, and of the species *Dinichthys terrelli* enough material was present to make possible a restoration built up in large part of the original "fish."  Indeed many of the parts appear to have belonged to a single individual which was secured by Dr. Newberry with the Terrell collection (in the seventies).  Unfortunately, however, this identification cannot be given beyond question since the plates were separated from the matrix by the collector and his notes are not preserved.  With great probability, however, the following parts belonged to the same individual: cranial shield, dentition, dorsomedian and antero-dorsolaterals.  The suborbitals belonged to another specimen, as did also three plates of the abdominal armor.  The parts which have been copied are postero-dorsolaterals, "claviculars," a postero-ventrolateral and the ventromedian.

The present composition pictures an impressive monster (the length of its head and shoulders, by the way, measures a meter and a half),— and an effect is given which is extraordinary even to one who has long been familiar with the detached or partly arranged elements.  And it is only a wonder that a complete restoration was not earlier attempted.  Professor Newberry himself never reconstructed his material; and in addition to the present exhibit the writer is aware of only two somewhat similar compositions, one in the museum in Harvard, the other in the natural history museum in South Kensington.

The present *Dinichthys* is shown in four positions in Plates XXXVIII and XXXIX.  There is nothing particularly novel in the associations of the component plates: it is merely that they are here for the first time photographed in these positions and to a large degree from actual material.  It is probable, even, that a number of changes will have to be made in the specimen in the light of advancing discoveries.  Thus the question of the greater flatness or roundness of the creature's body will have to be further considered.  So also a number of details in the position of the various plates.  The space between the "clavicular" and the suborbital, which has so often puzzled the student, may ultimately have to be reduced by the extension of the lower margin of the suborbital.  And the "hinge" of the "mandible" may have to be drawn closer to, and even under the rim of the suborbital.  In the former re-

gard, it may be mentioned that the latest contribution to dinichthyid anatomy (E. B. Branson, 1908, 'Notes on *Dinichthys terrelli* Newberry, with a restoration,' Ohio Naturalist, Vol. VIII, pp. 363–389) is not convincing, for the "clavicular" elements, on which much depends in demonstrating the closure of the "opercular space," are not complete (one "has several parts broken away," the other is lacking "the lower part"). Moreover, in another detail, we are not quite assured that the marginal plate did not extend further lateralward (as it appears in the present restoration) since in the newly described material Dr. Branson indicates that the outlines of the antero-dorsolateral and of the marginal are imperfect.

## VIII.  Notes on a Newly Mounted *Titanichthys*.

The Devonian vertebrate fauna of Ohio, well represented in the collections now in the museum, included forms adapted to various conditions of living and specialized in a variety of ways.  Among them the Arthrognathi were fish-like in form but so curiously organized that students of this special group entertain very different views as to their real relationships,— whether they were kin to our modern sharks or sturgeons or lung-fishes,— or whether they were even fishes at all, in the modern sense of the term.

A member of this curious group has recently been mounted in the hall of fossil fishes, and is figured herewith, Plate XL.  It is *Titanichthys clarki* and has the distinction of having been the largest vertebrate that had been evolved up to its time, that is, to the end of the Devonian period.  The mounted head (cranial roof) measures 140 cm. in breadth, and was over 90 cm. long,— dimensions which indicate that the entire "fish" had a total length of about 5 meters — admitting that its proportions were not unlike those of the related *Coccosteus*.  The present example shows the hard parts of the animal in fair preservation.  The roof of the head is about two-thirds original: it lacks, unfortunately, the anterior (supraoral) rim.  The specimen is interesting as having been the "first *Titanichthys* found" (Newberry) (in the early eighties): and the jaws appear to have accompanied it.  The plates forming the sides of the eye-openings, are from a second specimen, but of the same species.  The great shoulder-plate probably belonged to the same species.  In spite of possible discrepant details it cannot be denied that the *Titanichthys* as now mounted gives a graphic picture of one of the maximum points in the evolution of the lower vertebrates.  Only once before (by Dr. Eastman in the Harvard Museum) have any of the parts of a representative of this genus been associated.

*Details*:— The present species differs from *Titanichthys agassizi* in having the cranial roof considerably narrower and rounder — a difference which affects the shape of the various plates and the direction of the sensory canals.  These details can be made out fairly well in spite of defects in the fossil, for one side of the head is usually complete.  The mucous canals show several peculiarities.  The canals which pass centralward from the "external occipital condyle" are continuous with the transverse canals which pass medianward, not underlapping these canals as Eastman indicates in *T. agassizi*.  So also we find that the canals which run from the centrals to the preorbitals are not single but are accompanied by several smaller canals more nearly median.  It is further to be noted that on each suborbital there are two canals, not a single one branched, the condition for example in the kindred *Dinichthys*.  These two canals arise close

together near the margin of the plate at its contact with the postorbital, and proceed thence across the suborbital, one following the orbital border, the other soon turning at an angle and passing to the lower and hinder corner of the plate.

As to the peculiarities of the various plates: The pineal plate is almost rectangular, with its long axis transverse, not elliptical as in *T. agassizi*, according to Eastman's figure. The external occipitals have heavier and more prominent condyles. The antero-dorsolaterals are defective: their only genuine parts are in the immediate neighborhood of the articular processes, and the restored portions should have extended further at the sides,— as far doubtless as the line of the outer edge of the marginals, as Eastman's restoration indicates. The postero-dorsolateral is entirely hypothetical, although probably of this shape, judging from kindred "fishes." The dorsomedian is practically unrestored.

The jaw parts, finally, require comment. The splendid "mandibles" are a pair and are believed to have accompanied the present cranium. The rostrognathals are hypothetical — in fact in *Titanichthys* no jaw parts other than the "mandibles" are definitely known: in the present case the left "rostrognathal" is restored, and is actually lighter in color than its fellow, though unfortunately this distinction is not clear in the photograph. The right plate belongs to a *Titanichthys*, and may prove to be placed in its true position, for it has some of the features of a rostrognathal, at least judging by analogies with *Dinichthys*: thus it has a similar rounded eminence at one side, one margin apparently secant, and a similar arrangement in its nutrient canals. On the other hand, it is possible that it represents an "orbitognathal," but in any event the long secant margin suggests strongly that it was apposed to the similar margin of the "mandibles." It may finally be remarked that a rostrognathal (or orbitognathal) might be represented in the imperfect plate which overlies the oval end of the right suborbital. In any event the "anterognathals" as they appear in the specimen may keep their place until more satisfactory material is forthcoming.

In final comment it may be said that the "clavicular" of this species is preserved in the museum but could not well be put in place on the present slab.

The mounting and restoration of this specimen proved a more difficult task than was at first anticipated. It was carried out by Dr. Hussakof with the assistance of Mr. Hermann, and the writer.

1889. **Newberry, J. S.** U. S. Geol. Surv. Mem., XVI, p. 135.
1898. **Eastman, C. R.** Am. Nat., XXXII, p. 763.
1907. " " N. Y. State Museum, Mem., X, p. 140.

## IX.  On the Arthrodire *Trachosteus clarki* Newberry.

A large slab (nearly a meter square) containing the *membra disjuncta* of a "placoderm" was collected by the veteran collector Dr. William Clark from the bank of the Rocky River, near Berea, Ohio, about 1886.  Shortly thereafter it was placed in the hands of Professor Newberry who described it (1889) in his monograph on the palæozoic fishes of America as *Trachosteus clarkii* (pp. 166–168), a new genus and species.  This determination Dr. Newberry based mainly upon the parts of the jaws which he figured, and he reserved the further study of the fossil until "other individuals shall have been found," observing that the general body elements of the specimen "are so confused that it is not possible to describe them fully."  He noted, however, that the tubercular ornament of the plates was peculiar and diagnostic,— high narrow tubercles with traces of a radial pattern at their bases: he figured the round orbital ring, which will serve at once to distinguish the eye of this fish from that of *Dinichthys gouldi*, which occurs in the same beds.  And he summed up the knowledge of the new form in placing it in the family "Dinichthidæ" with closest affinities to *Aspidichthys* of the Huron shale.

Since the time of the discovery of *Trachosteus* more than two decades have passed, but unhappily they have yielded no further specimens of this form.  But, on the other hand, these decades have greatly advanced our knowledge of forms kindred to *Trachosteus*, and from this point of view, that is from the standpoint of comparison, one might venture to reconsider even the defective materials which the type specimen provides.

At the time of its fossilization the soft parts of the "fish" had evidently broken down and the plates scattered.  The heavier elements, including the headroof (hinder portion) and the shoulder armoring probably remained in the more fixed position — seen in the lower right hand corner of the photograph, Plate XLI — the lighter plates, such as suborbitals, jaws, orbitalia, were swept outward and lie dissociated — in the upper and left hand corner of the picture. And the various parts as far as they can be identified are indicated in the tracing which accompanies the plate, *e. g.*, head shield, *HS.*; median dorsal, *MD.*; antero-dorsolateral, *ADL.*; postero-dorsolateral, *PDL.*; antero-ventrolaterals, *AVL.*; suborbitals, *SO.*; pre- and postorbital, *PO., PTO.*; pineal, *P.*; orbitalia, *ORB.*; gnathals, *G.*; rostrognathal, *RG.*  Together with these we may refer to several plates of unknown position, *e. g., X., Y.*

In Fig. 56 a number of these plates have been outlined and arranged provisionally as in kindred Arthrodires.  And this figure, in connection with the photograph of the entire specimen, may serve as a basis for the consideration of the separate elements.
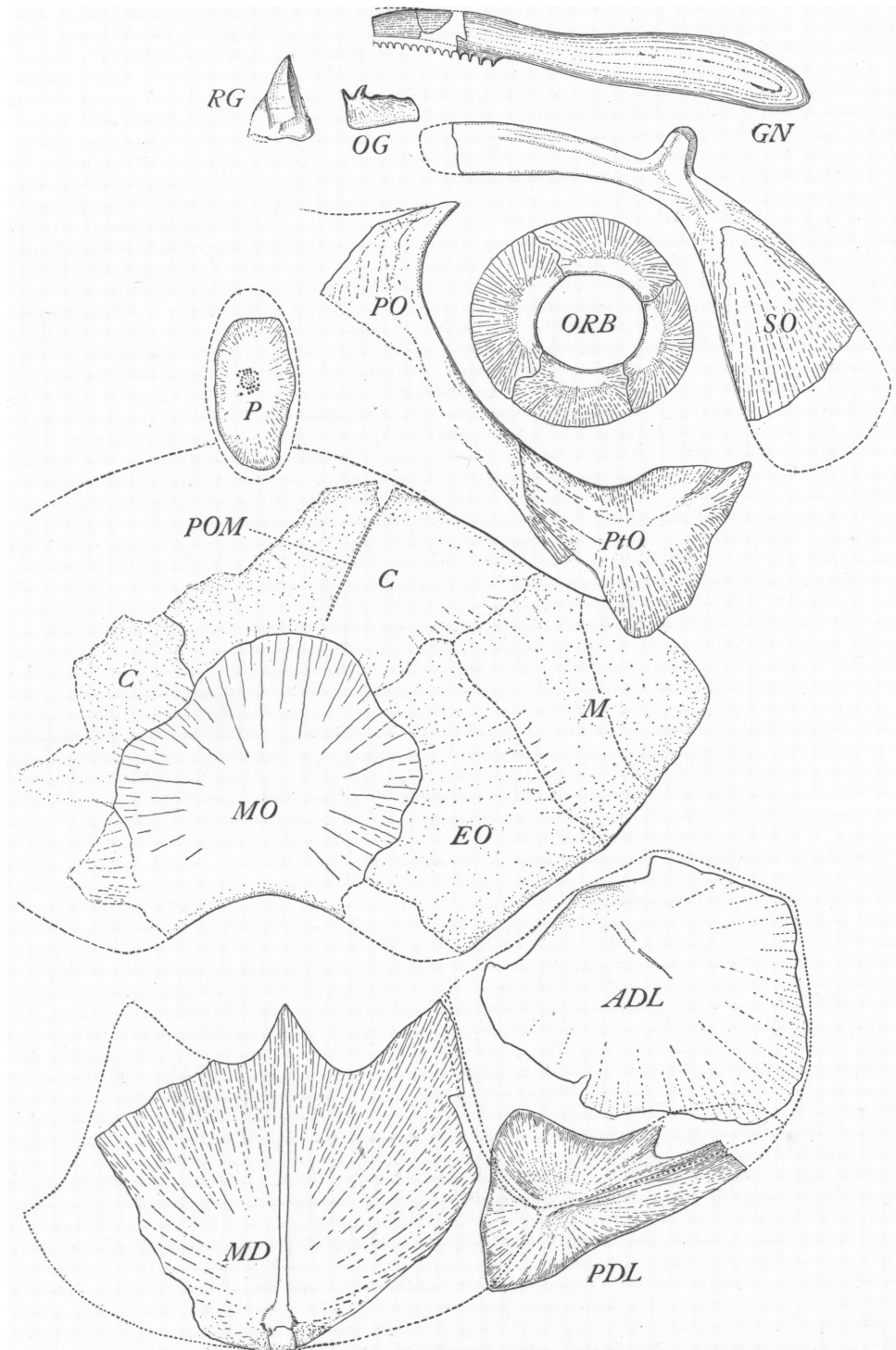
Fig. 56. *Trachosteus*. Reconstruction. *A D L.*, antero-dorsolateral; *C.*, central; *E O.*, external occipital; *G.*, gnathal; *M.*, marginal; *M D.*, median dorsal; *M O.*, median occipital; *O R B.*, orbitalia; *O G.*, orbitognathal; *P.*, pineal; *P D L.*, postero-dorsolateral; *P O.*, preorbital; *P T O.*, postorbital, *R G.*, rostrognathal; *S O.*, suborbital.

The *head shield* is identified from its size, from the radial arrangement of its tubercles, and from its division into component plates. This subdivision, however, is not an obvious one: for in surface view the sutures are obscure,— as they are often indeed in kindred forms. (Indeed the whole head shield was at first regarded by Newberry as "apparently a dorsal plate," *i. e.*, the median dorsal.) The median occipital, *MO.*, is the most clearly indicated of these component elements: it is thickest in its hinder median region, which is the center of radiation of the tubercles, and its proportion suggests rather *Coccosteus* or *Homosteus* and *Titanichthys* or *Dinichthys*: especially noteworthy, as in *Homosteus*, is the fact that the center of radiation of the tubercles is situated well away from the posterior margin of the plate. The external occipital, *EO.*, is imperfectly preserved: its line of suture with the median occipital is vague; its hinder median corner is lacking, and one cannot determine confidently the occipital mucous canal. Scarcely in better condition is the marginal plate, *M.*, whose outer third is probably represented in the fragment of a plate which lies beside it in the slab. The central plates, *C.*, are also defective, but in one of them occurs a line which we interpret as a preorbital mucous canal, *POM*. We note that the apparent line of junction of the centrals is not median, a condition of asymmetry which, however, is not unprecedented in arthrodires.

*Pre-* and *postorbitals* are identified by their finished and thickened orbital rim; and they are united in a suture somewhat as in *Selenosteus*. Save in the orbital region their margins are defective.

The *pineal plate, P.*, shows an area of radially arranged tubercles and corresponds in shape and relative size with that of *Homosteus*.

The *suborbital, SO.*, is relatively straight: its postorbital dilated portion is narrow, and altogether it suggests *Stenosteus*. In the mid-region, however, where a ridge is developed in the suborbital of *Stenosteus*, there is here developed a stout process, downturned.

The *orbitalia, ORB.*, are present in the form of rings, each made up of four plates. One ring is present, admirably preserved: nearby lie separate the four elements of the opposite eye. They do not differ notably from these elements in other arthrodires.

The "jaw," or *gnathal, GN.*, has already been referred to by Newberry. He did not, however, note that in the case of one "ramus" fragments of the distal portion are preserved: these are stout and the blade of the "jaw" was evidently continued a considerable distance before the symphysis was reached. From this condition and from the character of the teeth this element suggests again *Stenosteus* (or indeed *Diplognathus*, with which Newberry early compared it).

The *rostrognathal, RG.*, is unsatisfactorily preserved. It has certainly, however, the general outline and anterior surface contour of the corresponding element in *Dinichthys*. And in the original description, it is figured (pl. xlii, fig. 4) with a series of denticles on one, probably the right side. Unfortunately these denticles are no longer evident in the fossil.

The *orbitognathal* is represented by an element of the right side, *OG.* Its lower border bears two prominent denticles (anterior), whose axes, curiously enough, diverge, and three marginal undulations which clearly represent denticles. The posterior portion of the plate is lacking, but judging from the character of its striation it tapered backward to a distance of perhaps several centimeters. One remarks finally that the plate is of an extraordinary shape for an orbitognathal, and were it not that its hinder part were narrow and tapering one would be inclined to identify it as the missing tip of one of the neighboring gnathals.

The *median dorsal, MD.,* though lacking a large part of its margin, can be identified clearly. Its inner surface is exposed, showing a low median keel, a trace of the hinder knob, and the usual radiating striæ in the structure of the plate. In outline it suggests a median dorsal of *Titanichthys* (*cf. T. agassizi,* No. 7590, Am. Museum, figured by Hussakof (1908) in Bull. Am. Mus. Nat. Hist., Vol. XXV, p. 20). The most remarkable feature of the plate is that it develops a median angular outgrowth on its anterior margin, a line which in the rank and file of well-grown arthrodires is simple and concave, predicating indeed that in *Trachosteus* the head shield could hardly have been widely bent upward, in an elater-like movement, as it certainly could have been bent in such a contemporary form as *Dinichthys terrelli.*

The *postero-dorsolateral* is represented with fair probability by the plate *PDL*; it corresponds with this element in *Dinichthys,* and fulfils the general conditions in size, direction of striæ and outline demanded by association with the median dorsal and antero-dorsolateral plates.

The *antero-dorsolateral* is probably the plate *ADL.* Its margins are imperfect and its identification is based upon its size, striation (inferred from the concentric arrangement of the tubercules) and the presence of a line which may represent a mucous canal.

Of the plates of the ventral armor both *antero-ventrolaterals, AVL.,* are preserved (regarded by Newberry as post-dorsolateral, plate 7). Fig. 57. They are quite typical in shape, their only peculiarity being that the center of the radiation of their striæ is less nearly marginal than in *Dinichthys* or even *Mylostoma.* The *postero-ventrolateral* is possibly represented by the element *PVL.?* Of median ventral elements nothing is definitely known: the plate *AVM.?* may represent the anterior of these: it is of the requisite size, and its "lower" portion corresponds, but the asymmetry of the remainder of the plate, and its salient anterior border are evidence against this identification. It is true that the condition of the median occipital and centrals render it possible that asymmetry is strikingly developed in *Trachosteus*: it is true, also, that the production of the anterior rim of the median dorsal makes it possible that a similar production would occur on the anterior border of a median ventral plate. But for the present at least this speculation is unprofitable.

In addition to the parts of *Trachosteus* above referred to the fossil contains

several plates which are indeterminable. Of tuberculated plates large frag-
ments are present, enough indeed to represent nearly all of the missing elements,
e. g., of the front and left side of the cranial shield, and of the shoulder armoring.
Several small plates are also present whose outlines are fairly well preserved.
One of these, Fig. 57, X., is a stout plate from some lateral position, another,
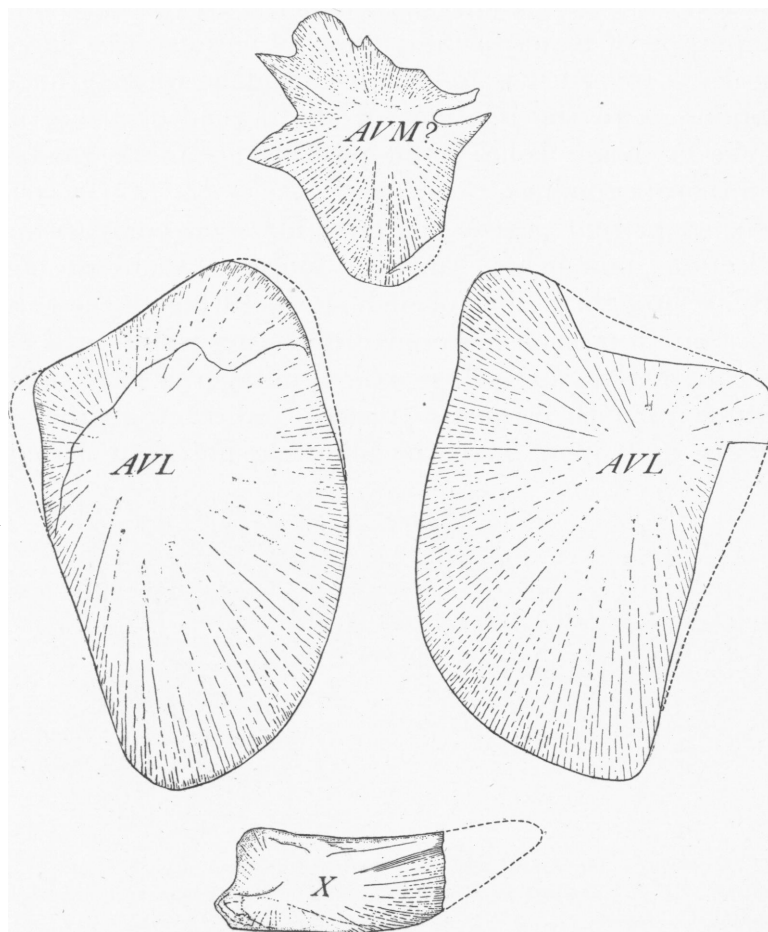Pl. XLI, Y., is probably a "clavicular" ? or rather a part, the lower narrow
part, of this plate.



Fig. 57. *Trachosteus.* Detached plates. *A V L.*, antero-ventrolateral;
*A V M.*, antero-ventromedian; *X*, plate of unknown position.

To sum up our
knowledge of *Trachos-
teus*, I think we may
safely conclude that it
may be taken as the
type of a new family
of arthrodires (as al-
ready suggested in
1901, Mem. N. Y. Acad.
Sci., Vol. II, Pt. 3, p.
120). This would be
defined as follows:—

*Trachosteidæ.* — Arthro-
dires belonging to the order
Arthrothoraci but with the
postnuchal plateless area re-
duced in size (by the produc-
tion of the anteromedian
border of the median dorsal)
and with inconspicuous artic-
ulation of the shoulder armor
to the head, predicating less
mobility in the arthrodiral
joint than in dinichthyids.
Suborbitals narrow and
straight, with conspicuous
process on the ventral border.
Orbitognathal with few large
anterior denticles. Dorso-
median with obsolescent keel and knob, and with a marked anteromedian point or angle.

The closer affinities of the Trachosteidæ are not as yet evident. From the
characters of the dorsal plate and the jaw parts, the family may be placed pro-
visionally near the Titanichthyidæ or better, perhaps, near the Selenosteidæ.

## X. On the Development of Certain Plates in Dinichthys.

Early stages in the development of arthrodan "fishes" will probably never be known. But in some degree at least a knowledge of their growth characters will be derived from a comparison of plates of individuals of various sizes, large and small, of the same species. Indeed it is by this means alone we may hope to obtain some generalizations as to the relations of the dermal elements to other and neighboring plates in these "fishes" and possibly as to the greater problem of dermal plates in their beginnings.

Unhappily there exists at present scanty material for such comparison. Even in the Newberry collection,[1] now in the American Museum, there are but few plates which can clearly be brought in line for such study, although they are enough, indeed, to indicate that from such materials interesting results will be forthcoming. Thus in the case of *Dinichthys* there exist a number of very small (probably therefore immature[2]) mouth elements (rostro- and orbitognathals), suborbitals and dorsomedians, and upon these the following notes are based.
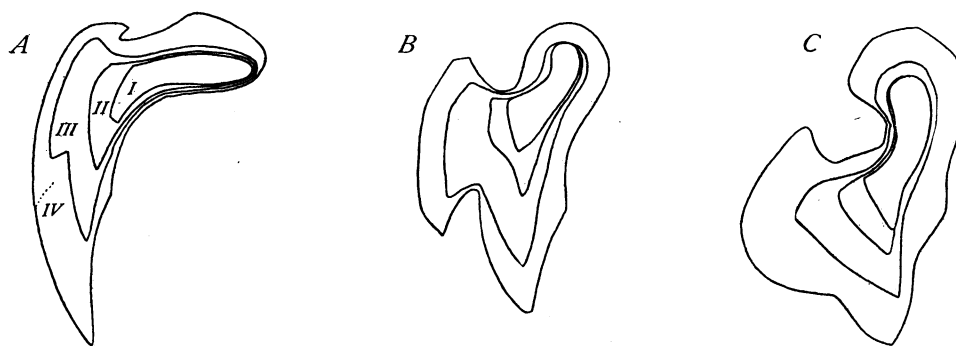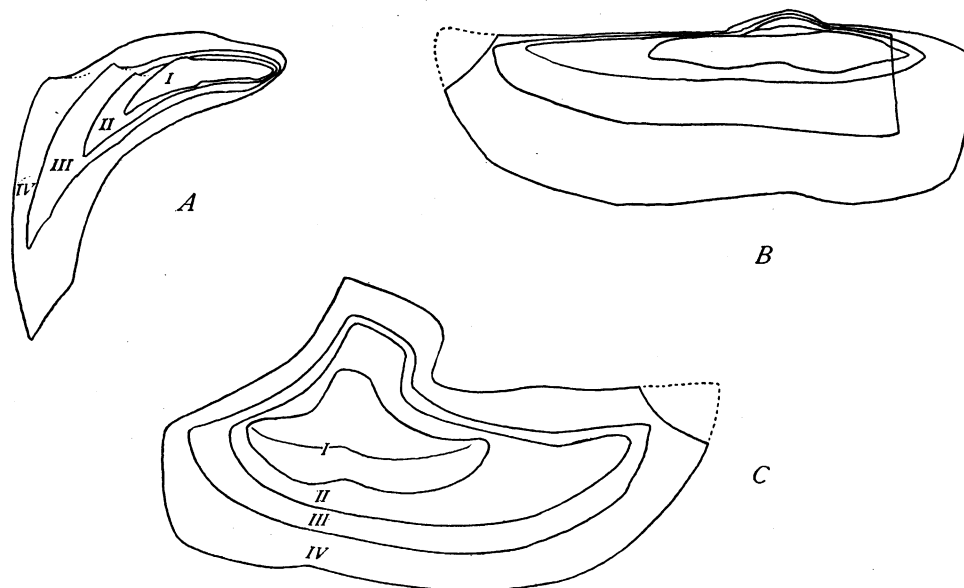


Fig. 58. Rostrognathal plates of *Dinichthys*. Superposed outlines of plates of different sizes, I, II, III, IV: I and II are in all probability immature, III, is identified as *D. curtus?*, and IV, *D. intermedius*. Shown in lateral (A), frontal (B), and dorso-frontal (C), aspects.

In Fig. 58 a series of four (left) rostrognathal elements in *Dinichthys* are represented superposed in such a way that the outlines of the larger elements may be contrasted readily with the smaller ones. And from such a contrast is shown broadly the mode of growth of this plate. Thus it is clear that in this element the greatest proportional growth takes place in the region of the beak-

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[1] In the early collections of dinichthyid material (1866–1880) several immature individuals were brought to light; and of these a few detached plates have been preserved (notably in the Terrell collection now in the American Museum). The remaining parts of these priceless specimens could not be detached from the matrix and were thrown away as valueless!

[2] The conclusion that these small elements are immature is borne out by their coarseness of fibre, and by surfaces which are uneven and unfinished when contrasted with larger plates.

like cutting border of the plate.  In the smallest plate of the series the basal portion makes up three-quarters or more, of the bulk of the entire plate.  In the largest plate on the other hand, these proportions are practically reversed.  It will be seen that a great flange arises from the antero-median rim of the plate and that this extends, coming ultimately to form a ridge growing almost in the opposite direction to that in which its growth began.  In the process of this growth a lobe-like cutting eminence develops medianward, and in the largest plates of the series this has become an exceedingly conspicuous feature: in addition to this a trace of a smaller outgrowth is seen along the lateral (ectal) edge of the plate.  From such a condition one concludes that the rostrognathal plate arose as a flattened dermal element, and that the production of the greatly

Fig. 59.  Orbitognathal plates of *Dinichthys*.  Superposed outlines of plates of different sizes, I, II, III, IV; of these I, is probably immature, II, is of an unidentified species, III, belongs probably to *D. curtus*, IV, to *D. intermedius*.  Shown in profile (A), lateral (B), and dorsal (C), aspects.

down-turned cutting rim was a more modern development.  It may of course be objected that the plates of various size here figured belonged to different species of *Dinichthys*, or that perhaps only one or two referred to the same species, and this objection is frankly a valid one.  But it must be none the less conceded, I think, that the larger plates in their individual development underwent the plan of form-growth here outlined, and that the small figures, if adult, represent more primitive conditions in the line of dinichthyid descent.

*Orbitognathals.*— As in the former, so in the present elements of the mouth, the series of plates indicates that the region of the cutting margin is the later developed (Fig. 59).  In the earliest stage the basal portion of the plate is of greater size, composing two-thirds the outline of the plate, and the cutting margin is not merely small but it extends outward almost in the same plane

as the base of the plate. In the larger plates, as the series shows, the proportional growth is greatest in the cutting flange, and we note furthermore that this flange comes to alter its plane of growth, growing more and more at right angles to its base. This plan of development, as in the case of rostrognathal, suggests clearly that the plate was originally flattened, resembling therefore in its shape and relations a neighboring dermal plate of the head.

Scanty as are the foregoing data we may yet see that the growth characters of the dental plates of *Dinichthys* are unlike those of lung-fishes with which they have frequently been compared. In the lung-fishes it is the denticular cutting portion which is first laid down and the basal is acquired only in latest development. In a word, in the dental plates of lung-fishes the cutting surfaces are relatively large in the young, and small in the old, while the reverse is the case in *Dinichthys*.

*Suborbitals.*— In Fig. 60 are outlined suborbitals of various sizes and from
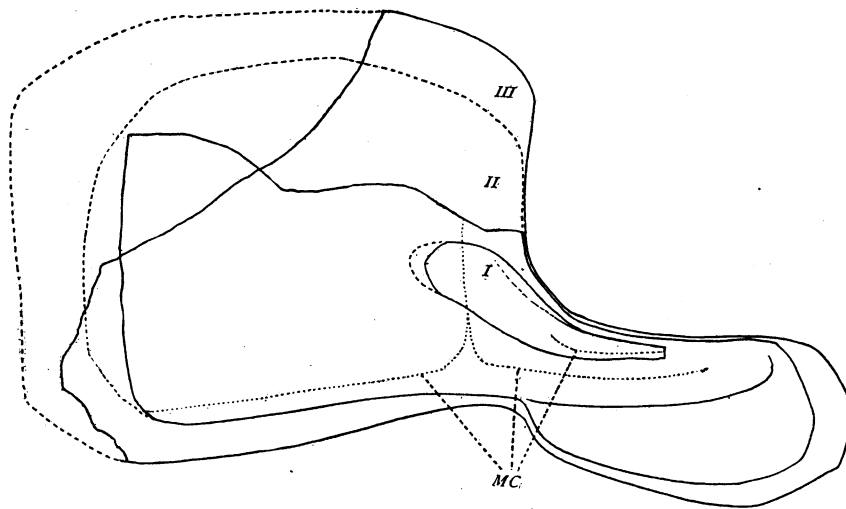


Fig. 60. Suborbitals of *Dinichthys*. Superposed outlines of plates of different sizes, I, II, III. I, is probably immature, II, belongs to *Dinichthys curtus?*, III, to *D. intermedius*. *MC*, mucous canal.

the comparison of these elements one observes that the differentiation of the various parts of the plate is most prominent in the largest plates. In the smallest the distinction is not great between that portion of the plate which lies below the eye and that which lies behind the eye. So also the suborbital region has not yet evolved the suborbital flange which is so conspicuous in the larger plates. It is clear, accordingly, that in this plate we are dealing again with one which in its earliest stage is a simple dermal plate more closely resembling the plates of the head-roof of this form.

*Mediandorsal.*— In Fig. 61 a number of mediandorsal plates are compared and from these one concludes that the lateral flanges of the exposed part of the plate grow with greater rapidity than the median portions. From a pointed

leaf-like expansion the exposed surface widens, forms a transverse anterior margin, and later a deeply concave one.   At the same time the end of the peg-like projection which arises from its posterior border becomes obtuse, and its
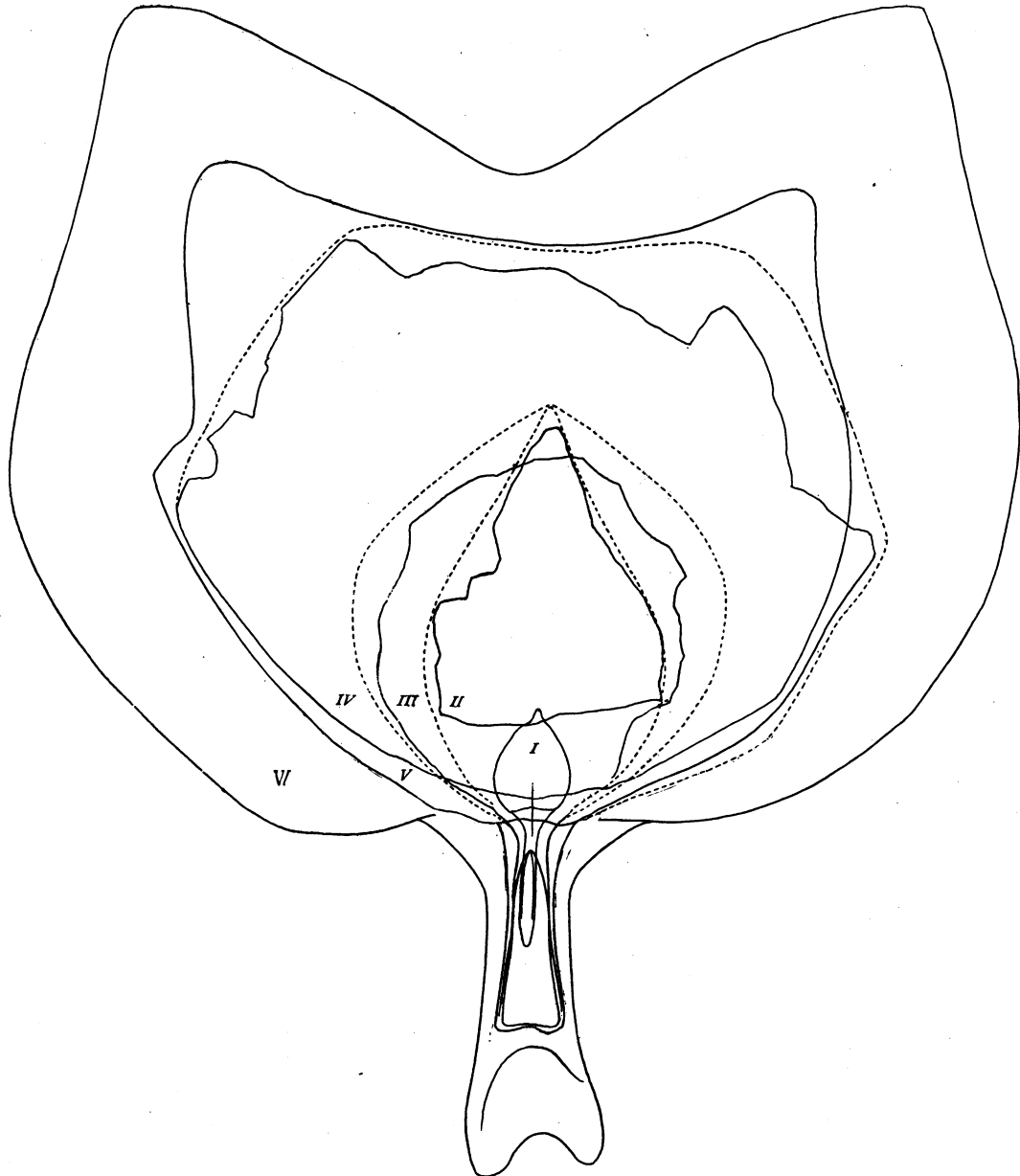


Fig. 61.  Median dorsal of *Dinichthys*.  Superposed outlines of plates of different sizes, I, II, III, IV, V, VI:  I, is clearly immature, II, is of *D. minor?*, III, *D. sp.*, IV, *D. gouldi?*, V, *D. sp.*, VI, *D. intermedius*.

tip deeply excavated.   It is a curious feature in the development of this plate that the median keel and hinder peg are prominent at so early a stage, a condition which suggests that these structures have already attained a high degree of functional importance.   The later growth changes in this plate have been

studied by Hussakof (Bull. Am. Mus., Vol. XXI, pp. 34–35) who points out the tendency of the plate to grow more rapidly in length than in width.

Among the various other immature plates preserved are the median occipital, marginal and probably the antero-dorsolateral; but the material is too meager to warrant comparisons.

The foregoing examination, incomplete as are the materials upon which it is based, is nevertheless interesting as indicating a general line in the morphology of the Arthrognathi. If we admit that the growth stages in the jaw elements of *Dinichthys* represent in their evolution transitional stages from dermal elements more similar to those of the neighboring head-roof we must conclude that the ties of kinship are then to be drawn more closely between the Arthrognathi on the one hand and the Antiarcha on the other, a conclusion which bears pertinently upon the discoveries of recent years.

## XI.— The "Pelvic Fins" of the Arthrodires.

The Arthrodiran "fishes" flourished from the late Silurian to the Lower Carboniferous, and formed a dominant group of chordates. During this time their representatives were numerous and highly diversified,— we already know two dozen genera, representing about a dozen families, and at least three orders, — and their structures are preserved in considerable detail. In spite of all this, however, there exists at the present moment — after half-a-century's painstaking investigation — the most surprising lack of knowledge as to what these fishes really were,— to what group of modern fishes they were most nearly akin, or, indeed, whether they were fishes at all, in the sense in which this group is to-day understood.

There is hardly need in this notice to recapitulate the opinions upon these matters held by the various specialists who have examined the arthrodires. It may be enough to indicate that writers have allied them to sharks, chimæroids, teleostomes, and lung-fishes,— that is, to each and every one of the surviving major groups of fishes, and that others have placed them in a separate class (Arthrognathi), whose relationship is on the one hand with the Antiarcha, and on the other with the earliest gnathostomes (?) (*Lanarkia*, *Thelodus* and their congeners). The only agreement in these diversified views is the belief that the Arthrodira are highly specialized, that they constitute a terminal group, and that only through their earliest members are they to be brought into the class of fishes. The most popular view as to their kinships is that they are highly divergent forms of lung-fishes, a view which was first expressed by Newberry (1875), and is supported to-day notably by Smith Woodward and Eastman. But it should be pointed out that the arguments which have been used in favor of this hypothesis can also be used to ally the arthrodires with the chimæroids.[1] Indeed, if we admit that one of the most salient features of the lung-fish is its type of fin, we cannot fail to feel the weakness of the doctrine of dipnoan kinship. For arthrodires, unlike *Ceratodus*, have not "biserial archipterygia," and their fossils fail to convince us that they even had paired fins at all.[2] The evidence as to the presence of paired fins in the truly piscine sense is based on the pelvics alone. There can be no doubt that Jaekel's restoration,[3] in which shark-like pectoral fins are pictured, is imaginary.

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[1] It is true, however, that the plates of the cranial roof of the Arthrodira are arranged more compactly than we know them in early chimæroids, rather indeed as in the recent (*Neo-*)*Ceratodus*, but this fact is the less weighty since we now know that the remainder of body in the arthrodire is protected by scattered tubercles, very much as in the former group (or sharks).

[2] Eastman in this matter remarks that speculation on the limbs of the Arthrodira, (as to whether they are uniserial or biserial) is futile till their limbs are found. He refers to "obscure traces" of pelvics but believes that there is no doubt as to the presence of a pelvic arch. Am. Journ. Sci., Vol. XXI, p. 142.

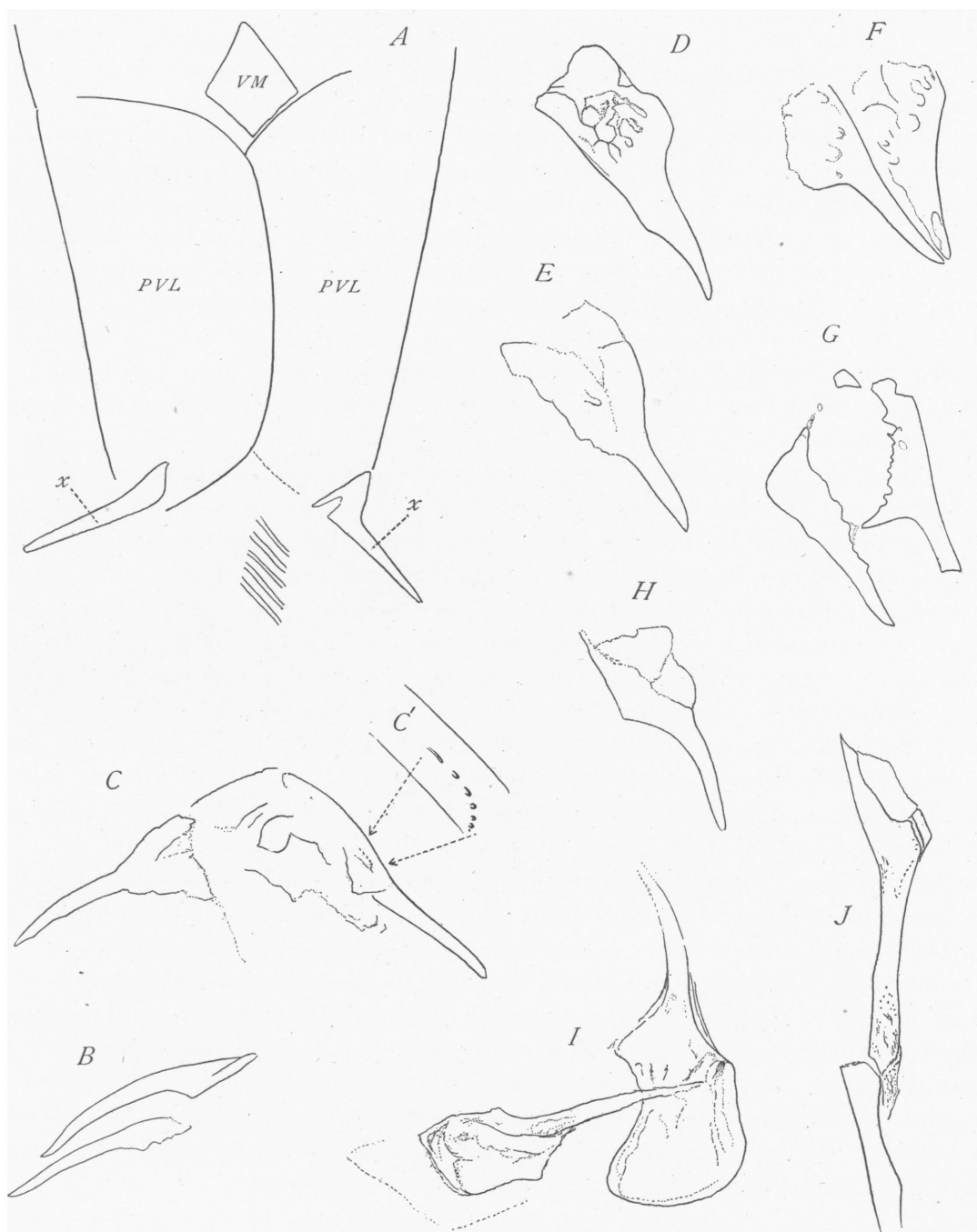[3] 1907, Sitzungsberichte Gesell. Naturforsch. Freunde, Berlin, No. 6, p. 5.

Fig. 62. "Pelvics" of *Coccosteus*. Specimens from (A) Harvard Museum, (tracing kindly made by Dr. L. Hussakof); (B) Museum of Science and Arts, Edinburgh (C) Paris Museum, Jardin des Plantes (D) British Museum; (E), (F) Edinburgh; (G) Harvard (tracing kindly prepared by Dr. Hussakof); (H) Edinburgh; (I), (J) American Museum.

It is clear, therefore, that the region of the "pelvic fins" in the case of *Coccosteus*, the only arthrodire in which these structures can at present be examined, becomes in a sense, the hinge upon which the present discussion of the problem is hanging. For if an arthrodire possessed a pair of fins like those of true fishes one might admit, in view of other anatomical characters, that arthrodires were at least fishes, no matter to what subclass they might later be assigned. But, as we have already pointed out,[1] the pelvic structures in *Coccosteus* are by no means obvious, they may be "displaced elements of the armor plates of the trunk," and in no way related to paired fins.

Accordingly in the present notice the evidence has been brought together bearing upon this detail from various sources. And the result, I think, does not lead us to believe that the "pelvics" in question belonged to paired fins. On the other hand, it must be admitted that we still do not know their exact relationships.

The "pelvics" of *Coccosteus* are not rare. I have examined them in about fifty specimens, in various collections, but in nearly all cases they are so poorly preserved that they show little more than a pair of small irregular elements, with evident traces of calcification, in a position behind the plates of the ventral armoring (postero-ventrolaterals). But good "pelvics" are rare, and very good specimens are superlatively rare,—in fact I know of but four or five which would come under this heading. And it is with these especially that we are at present concerned.

In Fig. 62 are shown outlines of "pelvics" from specimens kindly loaned by Dr. Eastman worthy of detailed comment. In *A*. (from the Museum of Comparative Zoölogy, Harvard) the "pelvics," *x*, appear at the outer and hinder corner of the posterior plates of the ventral armoring; their pointed ends are directed outward and backward, their wider ends cannot be clearly made out, for, unhappily, the plates are bituminized as in the majority of the Orkney fossils. In *B*. (from a *Coccosteus* from Caithness, Edinburgh Museum) the "pelvics" lie parallel to one another, but are defective again with respect to their wider ends. In *C*. (Paris Museum, Jardin des Plantes) the elements are fossilized in the position shown in *A*: and it is of great interest to observe that their wider ends are to a certain degree preserved. Thus one sees that the right and left sides approach one another in the median line, and that although the plates are by no means complete they show a thinness in this region which is not a character of pelvic structures. Then, too, they possess many nutrient canals, similar to those one sees on the inner surface of the dermal plates of arthrodires: We note especially a row or series of nutrient canals at *C'*, enlarged from the region indicated in *C*. In *D* (British Museum, 43,617) is figured the "pelvic" which Smith Woodward has referred to and which has served up to the present as the main support for the usual determination of these structures. Woodward (Cat. Foss. Fishes, II., pl. VII, fig. 2) has fig-

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ured one of these doubtful elements as a "pelvic basipterygium," showing "foramina or pittings" for the pterygial nerves, together with adjacent "cartilaginous rays of pelvic fin." He states (p. 289) that "apposed to the broad end of one of these (pelvic basipterygial) cartilages is a series of four or five short, stout rays, while directly behind the same cartilage are indications apparently of longer rays of a similar character." Accordingly I have examined this specimen with no little care, but I have been unable to confirm the above description. My interpretation, as shown in D, indicates a much larger basal region than Woodward pictures; and his "foramina" are grooves or, indeed, pits on the surface of the expanded portion of the cartilage. There are many cracks in the calcified surface of this element which I believe are artifact. And I certainly find no trace of the fin rays which the above mentioned figure shows. In a word the plate D may very well be interpreted as one of the plates shown apposed in C. In E (Edinburgh Museum, 1893, 107:24), also, is a plate having a greatly extended "basal" end, somewhat fissured (artifact), as in C. (or D.), and showing again, by the way, a groove at one point of its surface. In F (Edinburgh, 1895:190) appear two and perhaps the best "pelvics" I have examined. The broad end of the plate is again present, there are a series of irregular grooves, and there is an indication that the plate was especially large at its wide end — corresponding, therefore, with the condition in C. The elements in G (Harvard Museum, 1409, a



Fig. 63.    Section of plate of the ventral armor of *Coccosteus.*   × 36.

bituminized Orkney specimen) are in further evidence that the "basal" end of the plates was widely extended, and similarly in H (Edinburgh), in which again the wide end of the plate shows a number of fractures. And in I (American Museum, 7585), is a "pelvic" showing a most extended portion of the basal region. In the matter of the structure of these elements we refer, finally, to a specimen, J (American Museum, 7584), a beautifully preserved fragment from Tynet Burn, for in this the texture of the narrow portion of the "pelvics" is retained in detail: in many parts one can follow the nutrient canals, and they suggest clearly the conditions of the visceral side of a plate of the abdominal armor. Cf. Figs. 63 and 64. The texture, in a word, is dermal and unlike that of the calcified tissue encasing the vertebral arches (Fig. 65). The latter has a peculiar crystalline texture and no definite vascular canals. (The arch terminates at the dark area at the upper left hand corner in Fig. 65.)

The foregoing notes make evident, I believe, that the "pelvics" of arthrodires do not correspond to truly pelvic structures. Examination of a large number of specimens, and the best of them, fails to show a vestige of basal or radial structures,— evidence, however, which is negative, and upon which one cannot fairly lay great stress. But on the other hand, as positive evidence, we may now maintain that the "basal" part of the plates was larger than hitherto described, and that the plate was richly supplied with nutrient vessels, and is structurally
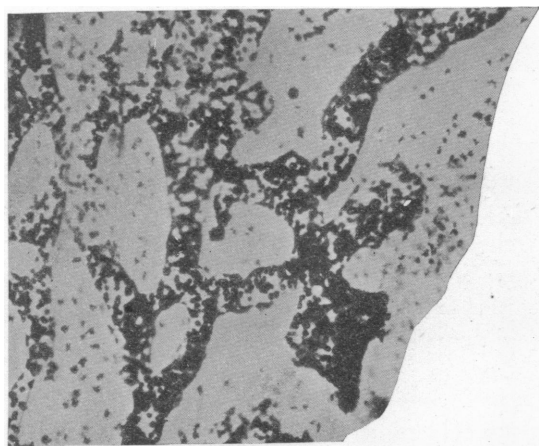


Fig. 64. Section of "pelvic" of *Coccosteus*. × 36.
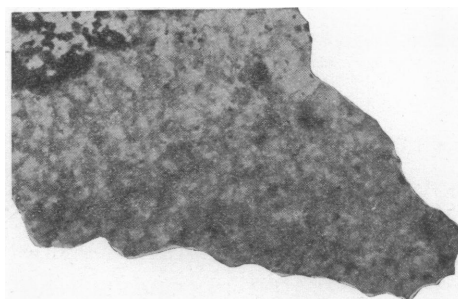


Fig. 65. Section of calcified tissue of vertebral arch of *Coccosteus*. × 36.

identical with the plates of the ventral armoring. We thus conclude that the "pelvic" element was dermal, not cartilaginous, and that therefore it was certainly by no means closely akin to the pelvic structure of any known dipnoan.

The evidence in the entire matter may be summed up as follows: —

*Pro:*

The "pelvics" lie in the relative position in which the elements of the true pelvic arch appear in fishes. They are approximately of the same shape and size,— they have a pitted surface suggesting the appearance of metameral nerves (as in the pelvics of ganoids, etc.).

*Con:*

On closer inspection they have not the shape of the pelvics in any known fish. The "basal" region flares out widely, and is here thin,— the opposite condition to fishes. They are dermal structures, — even their narrow end, which might otherwise be compared to the real pelvic arch which, *e. g.*, in certain ganoids, underlies dermal structures. The pit-like characters are irregular, rather to be interpreted as depressons for muscular attachment, than as foramina for the passage of pterygial nerves. There are no traces of basals, or radials, even where the fossil retains neighboring delicate structures. The presence of pelvic elements, finally, is the more improbable when all admit (Jaekel excepted) that pectorals are altogether wanting. For in no known fishes are pelvics present where pectorals are lost — the pelvics disappearing before the pectorals.

In a word the present evidence does not lead us to affirm that arthrodires possessed paired appendages homologous with pectoral and pelvic fins. This being the case the morphological gap is certainly not lessened between the true fishes on the one hand and the arthrodires on the other.

A                                               B



A. *Cladoselache fyleri* (Newberry).   Type.   Am. Mus. 240.   × about ⅓.
B. *Cladoselache fyleri* (Newberry).   Am. Mus. 7527.   × ²⁄₇.

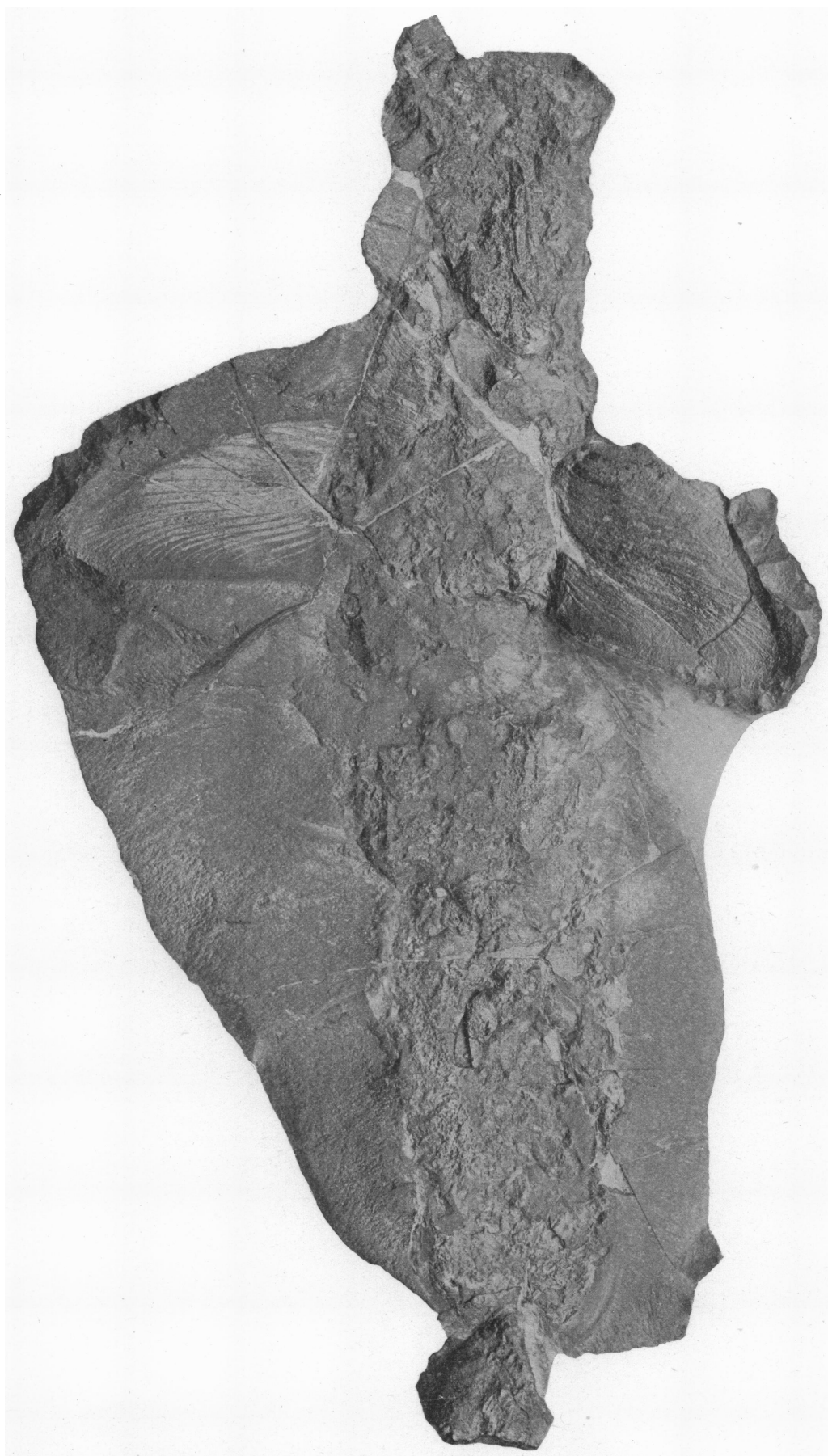*Cladoselachi kepleri* (Newberry) ?.   Am. Mus. 7328.   Head macerated and crushed.   × about ½.

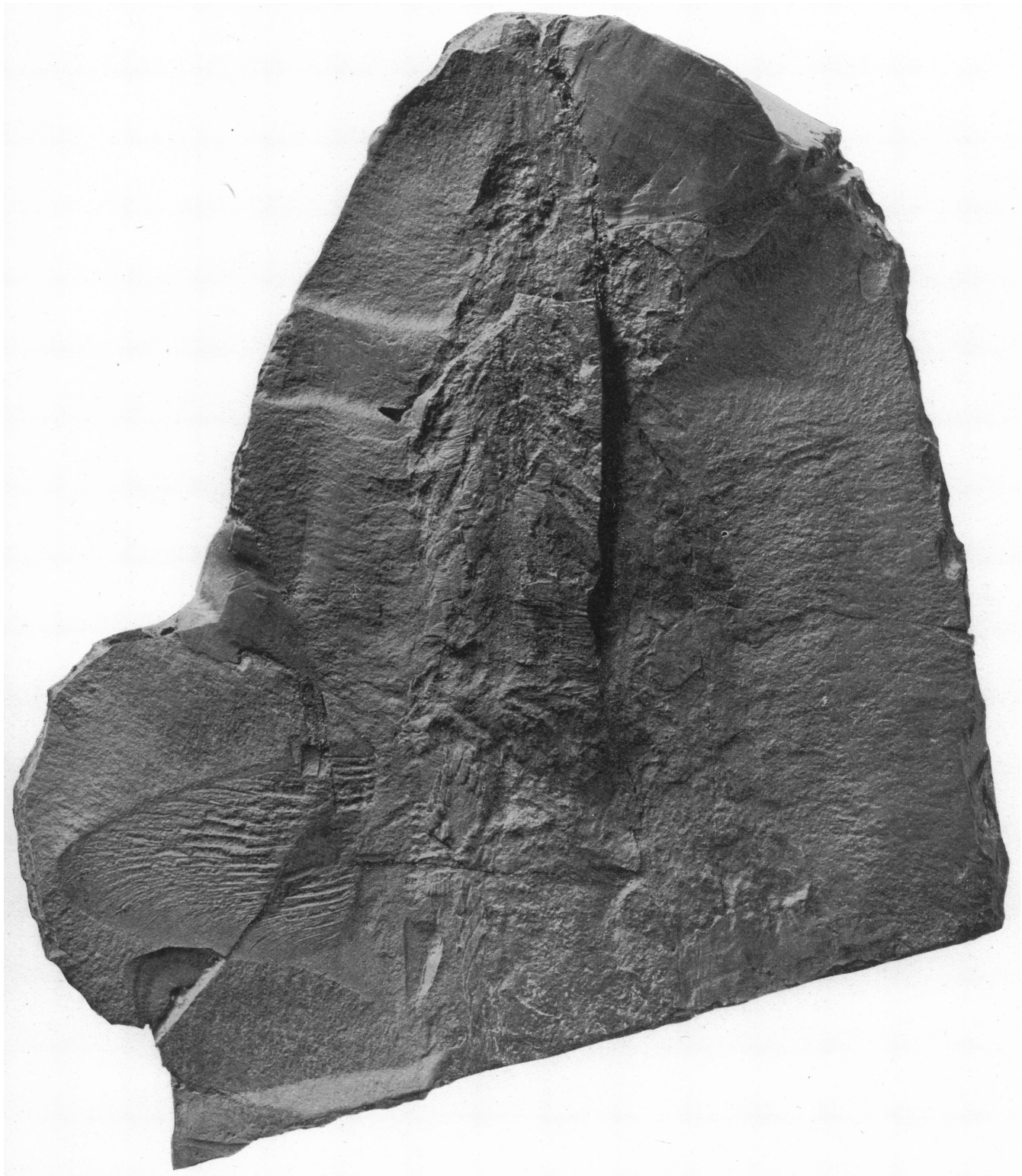*Cladoselache kepleri* (Newberry).    Type.    Amer. Mus. 7317.   $\times \frac{2}{7}$.

*Cladoselache desmopterygius*, n. sp.   Type.   Am. Mus. 7006.   × ⅓.

*Cladoselache newberryi* Dean.   Type.   Am. Mus. 7019.   × ⅔.

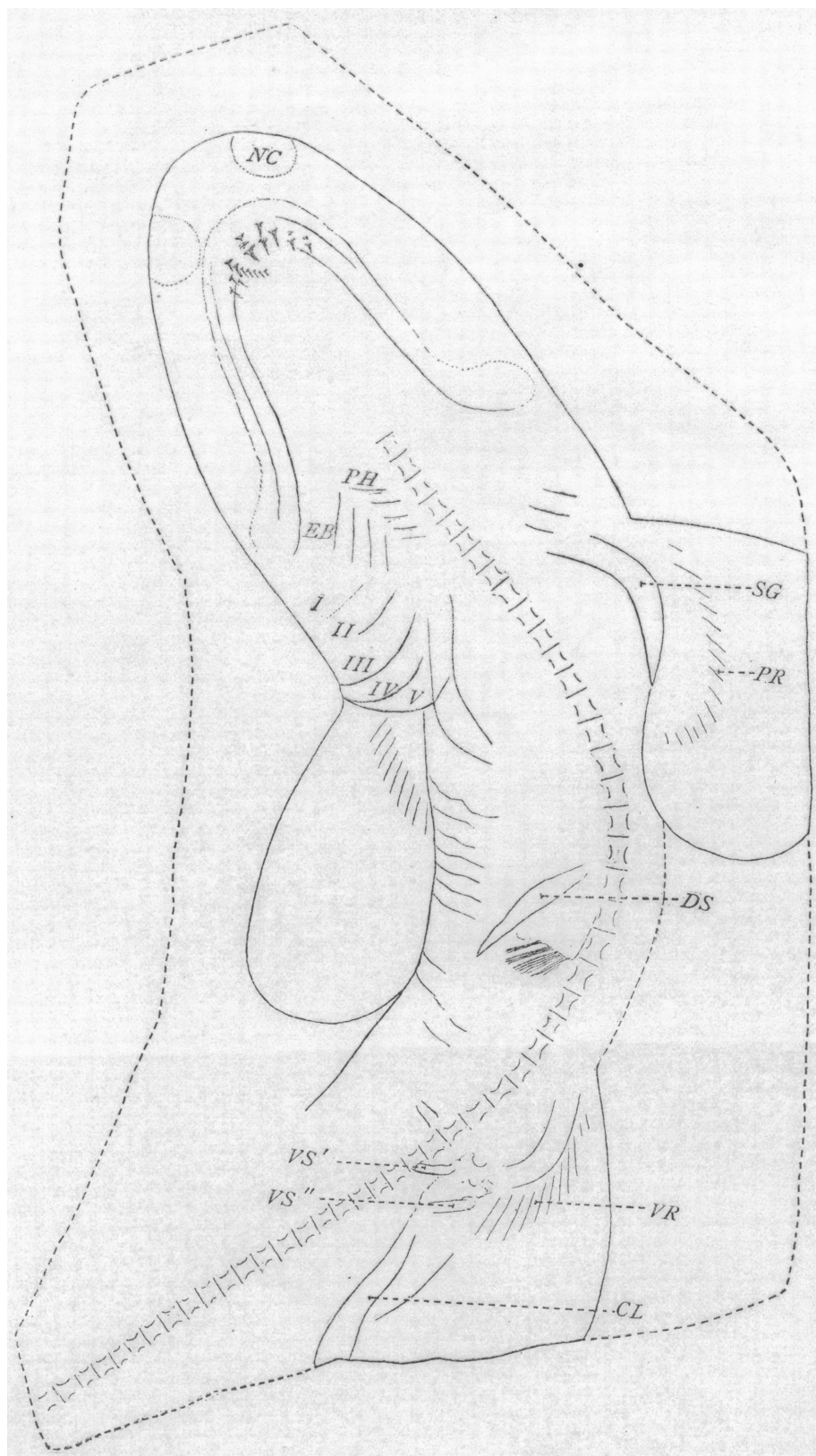*Cladoselache fyleri* (Newberry). Am. Mus. 1670. Showing branchial region. ✕ ¾.
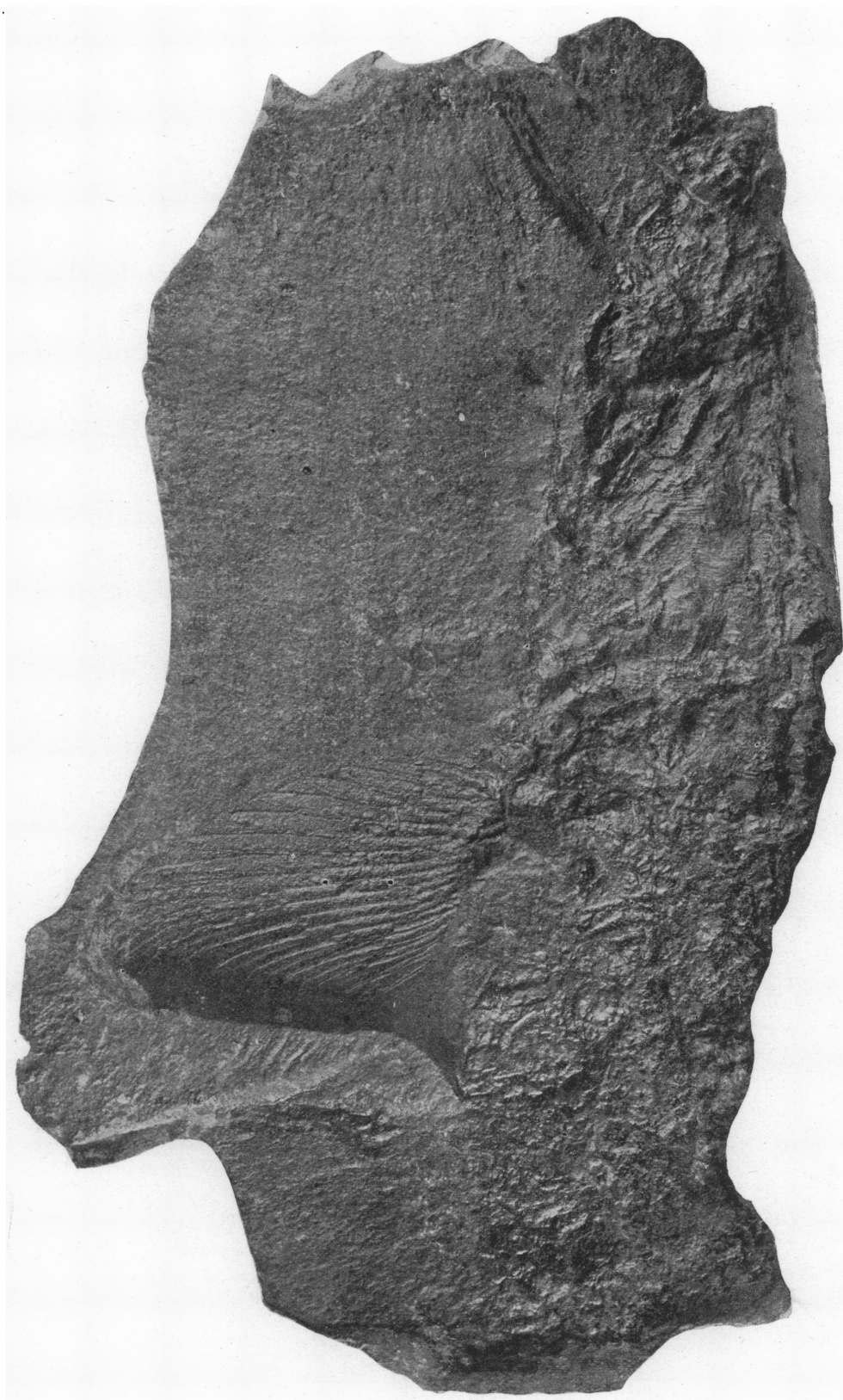
*Cladoselache brachypterygius*, n. sp.   Am. Mus. 7591.   Showing continuation of pectoral fin-web along the side of the body, also gill region.   × ⅘.

*Ctenacanthus clarki* (Newberry).   Am. Mus. 189.   × ¼.

*Palæospinax priscus* Agassiz. Am. Mus. 7085. *CL,* claspers; *DS,* dorsal spine; *EB,* epibranchial elements; *PR,* radials of pectoral fin; *PH,* pharyngobranchial elements; *S G,* shoulder girdle; *V R,* radials of ventral fin; *V S′, V S″,* spines of clasper of ventral fin. I, II, III, IV, V, external margins of gill apertures.
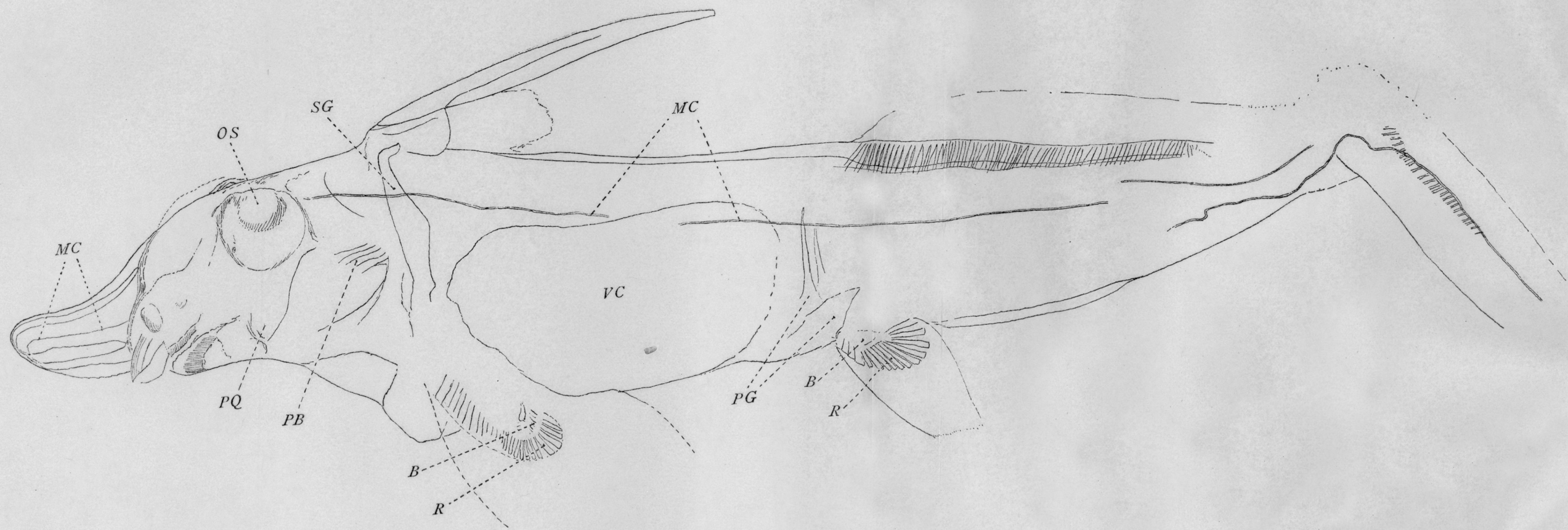
*Palæospinax priscus* Agassiz.   Natural size.

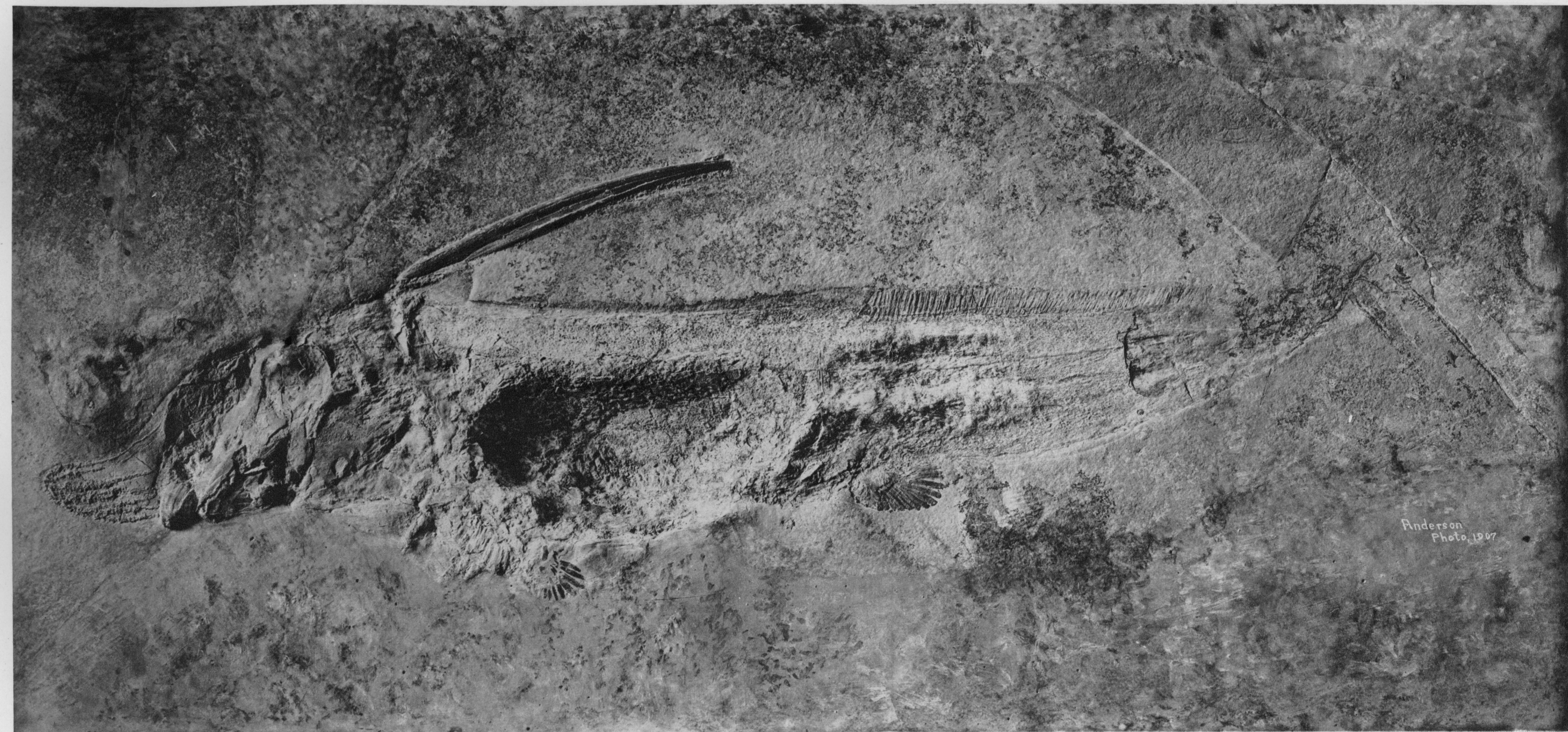*Archæobatis gigas* Newberry. Palatal dentition. Left half restored. Am. Mus. 360. $\times \frac{1}{2}$.

*Ischyodus avitus* (v. Meyer). Am. Mus. 7485. ♀. ×⅜.

B, basalia, MC, mucous canals, OS, orbital septum, R, Radialia, PB, pharyngobranchial, PG, pelvic girdle, PQ, palato-quadrate, SG, shoulder girdle, VC, viscera cavity.

*Ischyodus avitus* (v. Meyer.)

Egg-capsule of a Chimæroid (*Elasmodus?*), from the American Cretaceous.   Natural size.

A

B



*Dinichthys terrelli* Newb.   Mounted specimen.   × $\frac{2}{15}$.   Shown in lateral (A) and in frontal (B) view.

A



B



*Dinichthys terrelli* Newb.  Mounted specimen.   $\times \frac{2}{15}$.  Shown in dorsal (A) and sub-frontal (B) aspects.
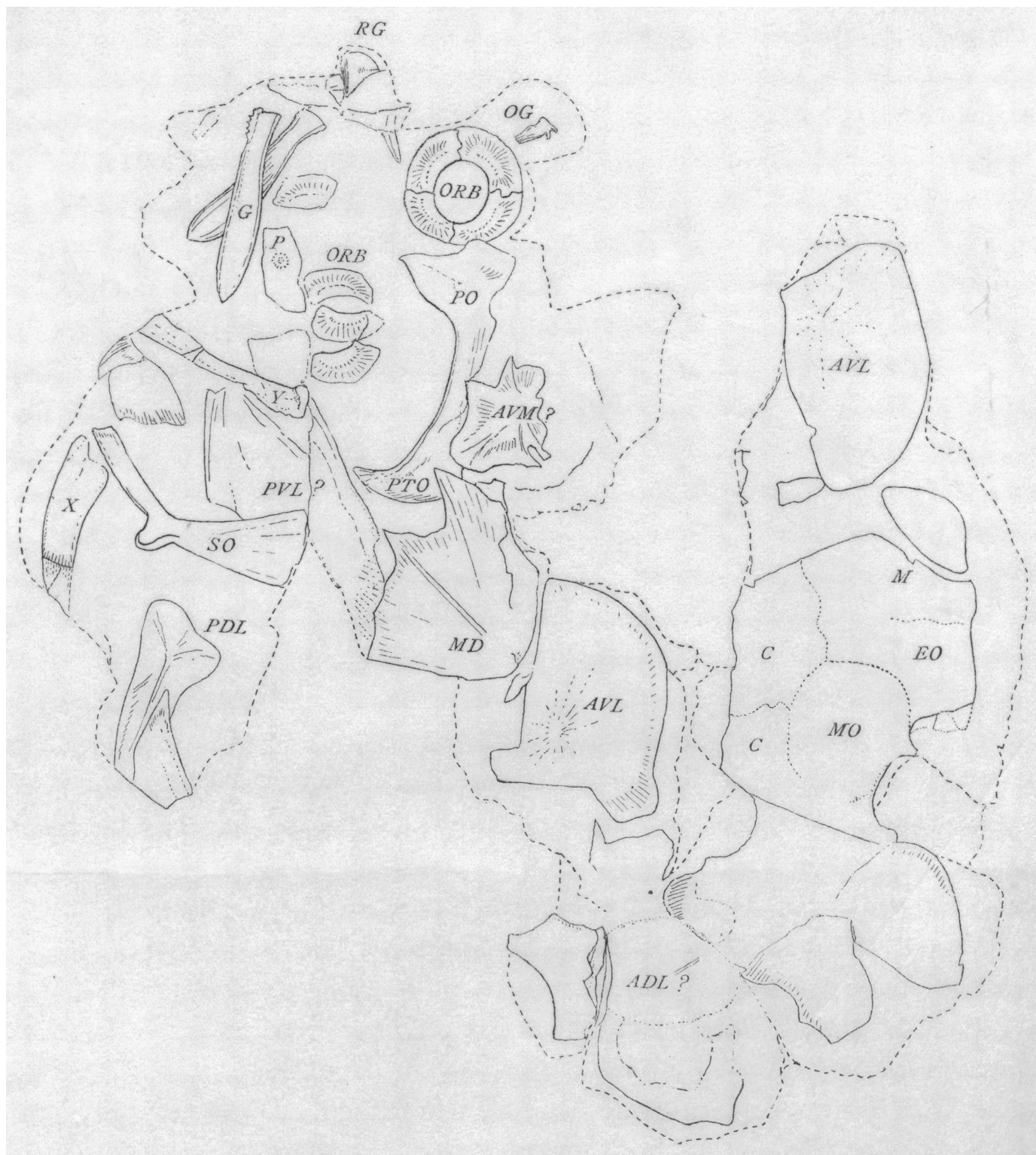
Newly mounted specimen of *Titanichthys clarki* Newberry. The restorations are represented in lighter color, but in the photograph they may best be distinguished by their texture. The mucous canals have been whitened to insure their prominence, and the outlines of the plates have been traced in black (missing outlines dotted). $\times \frac{2}{17}$.

*Trachosteus clarki* Newberry. Slab containing the scattered elements of a single individual. *A D L*, antero-dorsolateral; *A V L*, antero-ventrolateral; *A V M*, antero-ventromedian; *C*, central; *E O*, external occipital; *G*, gnathal; *M*, marginal; *M D*, median dorsal; *M O*, median occipital; *O R B*, orbital plates; *O G*, orbito-gnathal; *P*, pineal; *P D L*, postero-dorsolateral; *P O*, preorbital; *P T O*, postorbital; *P V L*, postero-ventro-lateral; *R G*, rostrognathal; *S O*, suborbital; *X, Y*, plates of unknown position. Type. Am. Mus. 104. ×⅕.

*Trachosteus clarki* Newberry.   Slab showing the scattered elements of a single individual.