

CONTRIBUTIONS TO THE MORPHOLOGY OF CLADOSELACHE (*Cladodus*).

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UNTIL very recent times the Morphology of Elasmobranchs has received few contributions from the study of the earlier fossil forms. It was, in fact, hardly to be expected that uncalcified shark structures should have preserved with any completeness the record of their ancient characters. Fragmentary remains on the other hand have, in many cases, led to confused and contradictory results. It was not until 1888¹ that accounts, in any way satisfactory, were given of the chief features of palaeozoic sharks. In this year there appeared almost simultaneously, a description of the Carboniferous *Pleuracanthus* by Brongniart,¹ of the Lower Carboniferous *Chondrenchelys* and *Cladodus* (pectoral fin) by Traquair,^{2, 14} of a *Cladodont* shark from the Ohio Waverly by Newberry,³ and of the pectoral fin of *Xenacanthus* by Fritsch.⁴ Subsequent papers of especial importance morphologically were contributed by Fritsch,^{5, 6} Döderlein,⁷ Smith Woodward,^{8, 9} Newberry,¹⁰ Wiedersheim¹¹ and Jaekel.^{12, 13}

The sharks discussed at that time by Newberry were received from Rev. Dr. William Kepler of New London, Ohio. They had been collected at Linton, and represented the remains of about six individuals. The remarkable characters they exhibited proved in no small degree puzzling to their describer. The dentition was undoubtedly *Cladodont* and the name *Cladodus* was retained, although it was clearly recognized that a number of genera and even families might be represented by this generalized type of dentition, and that a new genus might be assigned when more material of the type (*Cladodus mirabilis*) should be found. Whether the partial description

¹ The writer must here except the memoir of Cope¹⁵ on *Didymodus* and the earlier studies of Acanthodians.

given by Traquair¹⁴ pertained to *Cladodus*, Newberry was somewhat in doubt. Traquair had ascribed to a shark whose teeth were of the *mirabilis* type, a pectoral fin whose form was a "monoserial archipterygium intermediate between the truly biserial one of *Pleuracanthus* and that of the modern shark."

The writer, basing his observations upon recently discovered material, must, however, follow a suggestion of Smith Woodward as to important differences in fin structure, and regard the shark of the Waverly as entirely distinct from the *Cladodus* of Traquair. Accordingly he regards it necessary to distinguish the American form, and would suggest a new genus, *Cladosclache*.

The material from which this shark type has been studied is in the possession of the museum of Columbia College. It includes the types of Newberry, a number of specimens hitherto undescribed, together with a most interesting and well-preserved example of *C. fylleri*, recently acquired. This specimen is one of an admirable series that Dr. Kepler has succeeded in discovering at Linton, and is the first which has been known to exhibit the tail structure.

At the present time it is possible to consider more exactly the structural characters of this generalized shark type, and they prove of no little interest from a morphological standpoint. The evidence they present as to the origin of paired limbs Smith Woodward⁹ has lately commented upon, regarding their fin structure as the least modified of known forms in which the lateral fold has become divided into its two elements. On the other hand there may be considered in some detail the objections recently urged by Jackel¹² as to primitive characters. This author, for example, would consider the fin structure as of essentially a modern type, ray-like in its specialization to bottom living, in no way, therefore, strengthening the lateral fold doctrine. He assumes, moreover, that the entire posterior portion of the body in the type specimens, which he as well as Smith Woodward had examined in the museum of Columbia College, had been falsely added; although he admits that the presence of circumorbital derm plates is of especial interest phylogenetically (*Acanthodian*).

In the arrangement of his paper, the writer has for convenience, considered questions of relationship under structural headings.

THE AXIAL SKELETON.

The notochord was probably persistent and its surrounding tissue but little calcified. In the trunk no traces of its structures have been found. Its caudal termination is, however, well shown; in this region its substance is compact, finely granular (Fig. 3), lacking the sheath constrictions of *Pleuracanthus* and *Chondrenchelys*.² In the upper lobe of the tail the chorda narrowly tapers, and extends to the extreme tip. As will be later noted, the hypural rod-like supports are here lacking, replaced by an unjointed sub-notochordal rod of semi-calcified cartilage. Of the neural canal in this region little can be learned; its size must have been exceedingly minute, judging from the close origin of the epural supports to the notochord. From the type of chord thus suggested it is not unreasonable to infer that the vertebral arches, of which no traces have been found, must have been of the simplest type, certainly as primitive as those known to occur in *Hybodus*. In no part of the axial skeleton has the writer found the coarse beaded calcifications typical of the 'Ichthyotomi.' In general calcification appears centripetal, is marked in basal fin rays, jaws, skull and shoulder girdle. The head parts appear generally similar in character to those of *Chlamydoselache*. There is no evidence of what were described by Cope as cranial elements in the Permian *Didymodus*,¹⁵ nor of the "parasphenoid" of *Chondrenchelys*. The mouth was terminal, not as large proportionally as that of *Chlamydoselache*. The shape and disposition of the mandibular rami indicate a narrow and pointed snout; at the symphysis, however, their proportions appear to have been heavier than of *Chlamydoselache*. Relatively the nares and eye capsules were slightly further forward. The orbit could have been little anterior to mandibular articulation — and suggests, therefore, a short down-turned suspensorium. From present material there is no evidence of a post-orbital facet for

the first arch. The number of the branchial arches cannot be definitely stated. In one example five gill-slits are to be determined, and a sixth and seventh are certainly suggested. The arches are directed sharply caudad and their distal (ventral) ends could not have been widely separated. The anterior arches were the stoutest and largest; the foremost pair of slits appears to have been connected ventrally by a loose isthmus-flap as in *Chlamydoselache*. In a number of specimens the branchial region is marked by a series of parallel lines, usually transverse, suggestive of fibrous filament bearers, or more probably of supports for loose branchial-flaps. This peculiar character of striation is certainly found in no other portion of the fossils than in the branchial region, *i.e.*, anterior to pectorals and posterior to the region of mandibular articulation. The laminae appear to have been long, and possibly favor the deduction of Garman¹⁷ as to the protrusion of gills in the ancient *Cladodont*.

THE PAIRED FINS, AND THEIR SIGNIFICANCE.

The mode of origin of the paired fins, as most recently stated by Wiedersheim,¹⁰ is in no little way explained by the fin-type of the Carboniferous and Permian genera, *Xenacanthus* and *Pleuracanthus*. In view of the studies upon these forms, the fin-structure of *Cladoseleache* becomes of especial interest as clearly a more primitive form. Wiedersheim, commenting on the studies of Döderlein and Fritsch on *Pleuracanthus* and *Xenacanthus*, notes in summary that the structures of the pectoral fin of these forms are equivalent to those of the ventral of the most primitive of recent selachians (the structure of ventral being of course more primitive than that of the corresponding pectoral), and shows that the ventral in these fossil genera illustrates the simplest of known conditions in a paired fin. In *Cladoseleache* present material shows that the pectoral indicates a more primitive condition than even the ventral of *Xenacanthus*, and offers in a most remarkable way actual proof of the proposition that the ventral in *Xenacanthid*, arranged after the uniserial type, demonstrates that the pectoral too must originally have been of this form.

Smith Woodward⁹ has reviewed the origin of the paired fins in the light especially of the more recent work in palaeontology. He derives them from the crowding of the fin-supports at two definite points, with a tendency towards the contraction of the base of the fin to its narrowest limits, with a subsequent broadening out of the basal portion to become in the pectoral tribasal or polybasal. It is interesting that he has taken the fin of *Cladoselache* into especial account, regarding it as exhibiting one of the least modified conditions of the exoskeleton of the lateral fin-fold that can be expected in any fish in which this fold is already subdivided into its ordinary two remnants. In the pectoral "no fin-basals can be detected with certainty in any of the specimens the writer has examined; and none of the cartilaginous rods that support the fin-membrane are transversely jointed. The most singular feature of the fin consists in the evidence it affords of that crowding and concentration we have already observed in the differentiated median fins of the earlier fishes. Between the extremities of the unaltered parallel bars there are the remnants of similar bars that have evidently been reduced and displaced by growth pressure. Most of the cartilages bifurcate a little distally, but that is a minor matter. The segmentation of the rays, the persistence of one of the middle rays, with the concomitant partial fusion of the still further crowded and reduced bordering rays, would soon, in the writer's opinion, result in the 'archipterygium' of Gegenbaur. It is, moreover, significant that the anterior (preaxial) rays are much more robust than the posterior (postaxial) rays, exactly as in all known examples of 'archipterygium.'"

In this interpretation, however, Smith Woodward is opposed by Jaekel, who had also examined the specimens in the museum of Columbia College. "There is no doubt that the outer clearly-marked fin rays take their origin and diverge from an inner basipterygoid." These rays, he continues, have been mistaken for the supports of an older continuous fin fold. The pectoral fin characters are rather to be reduced to the type of *Xenacanthus*; it is but a *Convergenzerscheinung* of a bottom-living Selachian. The fins, like those of *Xenacanthus*,

are resolvable into a double row of cartilage rods; their structure is the outcome of their living conditions. He thus concludes that *Cladoselache*, if not falsely restored, would be a typical selachian, possessed of all the essential peculiarities of its later kindred.

Before these contradictory views may be considered, the structure of the paired fins should be re-examined in the light of the newly-discovered material.

The pectoral fin (Fig. 1) is remarkable in that its broad base is continuously attached to the body, and that its plane is in the moving direction of the fish. It is a flat triangular plate, directed outward and slightly downward. There can be no doubt that the web-like posterior fin margin was continuous with the trunk integument, and that there was no projecting tip of a lateral Stammstrahl such as Fritsch has figured in the ventral of *Pleuracanthus*, or such as Traquair¹⁴ has described in the pectoral of *Cladodus*. The figure shows clearly the row of parallel cartilaginous rods remarked by Woodward, that appear to take their origin in the outer body wall and proceed directly to the outer fin margin, unjointed. The rays may, for convenience, be divided into three groups of about ten each,—fore, middle, and aft,—which in structure grade imperceptibly one into the other. The first group is of stout bars of cartilage, and includes about half of the fin; its foremost ray is the stoutest, shortest, is directed forward; and the following rays, increasing in size and compacting together, form the stout anterior margin of the fin. The middle rays are the longest, tapering and often forking at the tips. The rays of the final group are narrower, slenderer, and more forked; they decrease in size, becoming more and more posteriorly directed. Noteworthy is the clustering process which these rays appear to be undergoing, as pointed out by Smith Woodward; their bases are so tightly crowded together that the rays have been obliged to form a dorsal and a ventral set, as may be clearly seen at the distal end of the fin where the flattening has given room for the tips of the alternate rays to assume their position in a single plane. The strength of this compact structure is noteworthy; clustered

rays, stout at the base, whose free tips intercalate to weave a stout fin margin. In the posterior fin margin bifurcated tips, as we have seen, often interwedge. Compactness of supporting elements has the effect of making the fin appear thick and immovable, and the inclination of the compressed foremost rays tends to give the entire fin the appearance of being directed forward.

As to the attachment of the fins to the body, — basalia and shoulder girdle: from the specimens earlier discovered but little was to be learned. Newberry asserted the presence of basal plates; but of this interpretation of the fossil Smith Woodward, as noted above, was skeptical. It was clear that the origin of the laterally-placed fin was stout and muscular, giving the latter authority, no doubt, an additional reason for his conclusions as to the lateral-fold character of the fin. Newly obtained specimens, however, showed the present writer that basal plates are unquestionably present, and by careful comparison of his material he was enabled to prepare the accompanying figure (Fig. 1) of the shoulder girdle with its basalia, which he later found, from Fritsch's drawings, readily comparable with the pelvic structures of *Xenacanthus* (female)

There is certainly a series of cartilage plates (basalia) from which the rays take their origin. These, however, are broader and more of a size than those of *Xenacanthus*. They lie within the body wall, and the distal element does not protrude. What in the diagram is termed basal (*Bas*¹) may not improbably correspond with the element proximal to that lettered *Bas*¹ in Wiedersheim's text figure 5a; Basalia one and two are certainly of great interest as possessing coalesced and disappearing fin rays; their arrangement is certainly such as might be expected on the principle of fusion of proximal elements, and clearly suggests the gradual inturning of the anterior end of the line of the basalia. It is further instructive in the general principle of fusion that the proximal basal elements are smaller and decrease in size as they come to be turned towards the median line. Although the present material allows a fairly complete idea of the area and position of the distal basalia, the separation of the caudad elements

must be regarded as doubtful. They are, however, suggested as the writer has indicated in the diagram with dotted lines. Their fusion into a single plate would not prevent them subsequently from becoming conveniently separated or receiving distal increments where their axis comes to protrude from the body wall.

The basal joints of the foremost fin rays may be significant as the first appearance of jointed cartilage rays in a vertebrate extremity—their positions, flanked by an unshifting wedge of cartilage, might seem to suggest a reason for their flexibility and therefore for the origin of the joint. May not the condition here in its beginnings present the advantages of capacity for fusion and for flexibility, which will later be transmitted to the remainder of the fin, and give rise to the stage of its evolution figured by Wiedersheim? It would further appear that the inordinate forking, crowding and coalescence of rays in distal elements would naturally be most marked in the median and hinder portion of the fin when the distal end of the axis (basalia) has come to be external.

It is certain that in *Cladoselache* the fin rays (radialia) in their (unjointed) primitive character proceed directly from body wall to fin tip,—while in *Xenacanthus* and *Pleuracanthus* these have become jointed, often fused by lateral pressure, and reduced proximally to such a degree that more than half of the fin is dermal.¹ Derm rays have certainly, even in these early forms taken the duty of the marginal cartilage rays. It is significant that the cartilage rays in the posterior portion of the fin of *Cladoselache* become delicate and fork in their efforts to combine flexibility and lightness with strength.

It is to be noted that this region when the fin margin becomes membranous delicate striation may be seen,—these lines are parallel to the direction of the fin rays, pass between them, and represent perhaps, the beginnings of dermal rays which margin the fin in *Pleuracanthus*.

The characters of the pectoral of *Cladoselache*, thus described, would accordingly represent a more primitive condition than

¹ 'Dermal' is here used mainly for convenience, for in ontogeny these fin rays have been shown by Ryder to be mesodermic.

that even of the ventral fin of *Xenacanthus* (female). The axis of the basalia in the latter has already emerged from the body wall, has become of the archipterygial type, clustering its radials distally in what Fritsch and Wiedersheim call the *post-axial* Strahlenreihe. This fin type will shortly (as in the pectoral of the same form) proceed to form the biserial archipterygium by the process of ray splitting being continued from the tip to the opposite side (pre-axial of Fritsch) of the fin axis.

One would now naturally look to the simpler structure of the ventrals of *Cladoselache* for further light on the primitive vertebrate extremity. One of the best specimens of these has already been figured by Newberry,¹ but may here (Fig. 2), with slight modifications, again be figured.¹

The ventral is first to be noted as a longitudinal fin nearly three times as long as wide, its length alone suggestive of its archaic fin-fold character. Its plane is that of the pectoral; it is more delicate, and smaller, less by two-thirds in linear measurements; its position is midway between pectoral and caudal. Like those of pectoral its rays are unjointed, proceed from body-wall to fin-tip; the foremost are the smallest, stoutest and most clustered. Unlike the rays of the pectoral they never branch, are distinctly and sharply tapering, show no specialized shapes, are directed somewhat backward, and vary but little in their angle of inclination, save that the posterior rays are directed slightly further backward. The ray concentration at the anterior margin is regularly accomplished. In the median portion of the fin nearly the entire length of the alternating rays, *i.e.*, those whose bases have been compressed into the ventral fin-surface, is to be seen. The sloping, anterior fin-margin is exactly what might be expected if the intervening fin-fold be imagined to have slowly disappeared; its slow disappearance might also account for the concentration of the rays in the anterior margin, whose function now must include that of cut-water. The hind portion of the fin, naturally least modified, seems little more than the actual remnant of

¹ In no specimen are claspers present; sex apparently is not to be distinguished by the shape or character of ventrals.

the fin-fold of the ancestral vertebrate. The anterior fin-margin, like that of the pectoral, is encrusted with denticles of shagreen.

The supports of the ventrals are entirely in accord with the primitive disposition of the fin-rays. The basalia, which in *Xenacanthus* and *Pleuracanthus* have coalesced, are here in a condition of concrescence in the anterior root of the fin, *but are still separate, one from the other, and are still rod-like, homologous in every way with the baseoste of an unpaired fin.* A still more proximal element has not been determined, but it may not unnaturally be inferred, from the very convergent nature of the rod-like basalia, that a pelvic cartilage, — if one existed, — must have been exceedingly small, representing the coalesced axonosts of a paired fin of so azygous a type. It is with some doubt that dermal striation is to be observed in the ventrals.

Returning to the view of Smith Woodward as to the significance of the fins of *Cladoseleache*, it will at once be seen that the discovery of basalia must of necessity modify his general conclusions. The concentration of the rays in the anterior and median portion of the fin might not imply that the process of joint-forming, and of the out-sprouting of an "archipterygium," would here take place; it would seem that these conditions would rather arise in the regular train of evolution exemplified in *Xenacanthus* and *Pleuracanthus*. Concentration of rays would appear a modification of the anterior rim of this primitive fin as a support or cut-water. The compressed nature of the fin-rays (*i.e.*, there appearing to be two layers, the tips of the under layer being only seen) might, moreover, be regarded as a specialized device for strengthening the fin-plate, unless one were to devise an unnecessary theory as to the original derivation of paired fins from double lateral folds. The primitive character of the paired fin, the significance of the radial cartilages, and the manifest homology of paired to median fins, the recent material shows that Smith Woodward has very precisely indicated.

Jaekel, on the other hand, has taken a most conservative view as to the morphological value of the fins of '*Cladodus*.'

He finds in them, if anything, an argument against the lateral fold doctrine. He regards *Cladoselache* as "a typical selachian possessing all the essential peculiarities of its later relations." That the fins were not, according to his interpretation, of dermal fold character is fatal evidence against the atavistic value of the early lateral folds of *Torpedo*.¹⁸ "From the structure of its (*Cladoselache*) pectoral we shall find no possible ground for deriving the paired limbs from lateral folds," but at the same time he admits that there is no ground for asserting the presence of the "archipterygium" of Gegenbaur, and notes that it is of the plan of structure which Fritsch has shown as the stem-form for the paired fins of Xenacanthids, a group whose specialized archipterygium is evolved from its conditions of living. *Cladoselache*, he concludes, shows in the structure of pectoral nothing more than would be seen in an immature fin condition of modern sharks. The rays of the ventral joined to basal cartilages are adduced as an additional ground for the ungeneralized nature of the paired fins.

At the present time the writer would regard the results of Jaekel as hardly to be warranted. Aside from the general primitive characters of the *radials*, as pointed out by Smith Woodward, we now are able to determine from the basalia of the pectoral direct homologies with those of the ventral in the Permian forms,—we find indicated in the ventrals not the "Flossenstrahlen" and "Knorpelspange" that Jaekel uses as an argument for its modern type of structure, but *primitive, unjointed radialia and basalia that are as yet altogether unfused*. In this remarkable basal condition the fin would at once seem more primitive than that of the cartilaginous ganoids,—which Wiedersheim states is below that of selachians, excluding Xenacanthids: the latter, he states, present the most generalized characters because they were lacking in hip girdle, show the fused basalia, and present as many as twenty radials.

Cladoselache now becomes of interest, appearing to foreshadow even these primitive characters. In its ventral it possesses 22–23 radials, as many as nine unfused basals, arranged in a way suggestive of lateral fold, with no axis

protruding from the body wall ; the arrangement of the basalia, moreover, gives ample ground for regarding a girdle as lacking.

That *Cladoselache* is by no means of a modern order of shark Jaekel, himself, has already given one and a very convincing proof, in describing the circum-orbital ring of derm plates, whose acanthodian value might at once have led to a closer scrutiny of fin characters. A final and positive proof as to the claims of this fish to archaic characters is now at hand in the unique structure of the caudal. Jaekel has several times referred to the "painted tails" of the older specimens, figured by Newberry ; these now prove, from an examination of a number of examples, to have been in no way falsely restored—if restored they had ever been—by their collector. The spade-like body terminal, as it was originally figured, appears now to have represented a vertical projection, whose tapering apex represented a portion of the margin of the tail. The length of the specimens (which Jaekel states should be considerably greater) proves to be exactly as Newberry described it.

THE CAUDAL OF CLADOSELACHE.

The structure of the caudal was a remarkable one,—its characters strongly suggestive of *Acanthodes*. The notochord extends to the tip of the upper lobe in the usual elasmobranch manner, but is so sharply upturned that the tail has become widely vertical (Fig. 3). So broadly have the lobes forked that the tail outline has become that of *Xiphias* ; its total breadth equals the measurement from tip to tip of the pectorals. Its posterior margin is not, however, an indented one ; it forms a straight line at right angles with the axis of the fish.

Structurally, the remarkable character of the fin is that the upper lobe is strengthened *only on the neural side* ; it is wanting in hypural rays, and is in this region web-like. Epurally it is supported by a prominent cut-water of well-defined cartilages.

In hypural characters the caudal structures may well be compared with those of *Acanthodes* ; there is a series of

stout parallel rays of cartilage which form the inferior lobe of the tail, but disappear in the hinder web midway from tip to tip. In *Cladoselache* these are about twelve in number, the middle pair being the longest, the remainder extending in graded sizes to and from the lobe tip. They are unjointed; of their connection with the haemal arches no satisfactory determination may be made; it appears, however, that they were attached at no great distance from the notochordal sheath. Rudimentary structures pass caudad; four are seen to be separable as basal supports; a terminal cartilage bar is closely apposed to the chord.

Unfortunately the upper lobe of the tail cannot be compared with that of *Acanthodes*, since the epural structure in the latter is obscured by the crusting remains of shagreen. In the present case nearly two-thirds of the lobe breadth is formed of a compact row of epural cartilages. These supports are readily to be reduced to proximal and distal elements, and indicate as well traces of a second proximal division, making the entire epural structure comparable in its elements to radalia, basalia, with perhaps included axonosts. Of the distal elements about fourteen may be defined, and appear to be curiously homodynamous with foremost radials of the pectoral; thus the foremost are the shortest and stoutest and are directed forward, blunt ended, while those succeeding come to be gradually elongated and directed more and more caudad. The row of basal elements is less readily separable, seven plates perhaps may here be included, although doubtfully; and of the proximal row nothing is positively definable.

The membrane-like posterior margin of the caudal extends between the tail lobes in a straight line from tip to tip; in the upper lobe it reaches proximad to the sub-notochordal cartilage; in the lower it gives the rays a distal derm margin of about $\frac{1}{4}$ inch. It is particularly interesting to note that here again appear the beginnings of dermal rays (trichinosts) extending in the same direction as indicated in recent forms. They are so fine in character that they are scarcely to be seen by the unaided eye (240 to an inch). They exhibit no branching or jointed structure. The actual

margin was slightly crenulate, and bears a coarser type of granular shagreen than that which covered the entire tail. The tail's anterior margin, like that of the other fins, was coarsely shagreened.

There can be little doubt that on either side of the base of the tail there was present a longitudinal derm fold or keel, not unlike that developed in a number of recent fish forms whose caudal outline is similar to that of *Cladoselache*. In specimens whose ventral aspect is preserved (and these are in the majority of instances) the flattened body terminal, exaggerated doubtless by mechanical causes, spreads out like the fluke of a sirenian, the tail itself to be seen in vertical projection as an acutely produced apex; the outline has in these instances been formed by the lateral keels. That this keel was a stout one appears probable, as traces of it are to be found in examples which have preserved the lateral aspect of the tail.

The significance of the caudal of *Cladoselache* is not readily to be determined. At first sight its apparent specialization is not at all in keeping with the peculiarly archaic and generalized character of the paired fins. Its broadly heterocercal tail has appeared to have reached almost the limits of homocercy, — it certainly *seems* more specialized than the caudal of Xenacanthids. The peculiar nature, on the other hand, of the epural supporting plate, and of the dermal margin of the upper lobe leads one naturally to the closest examination of suggested relationships, homodynamous, to paired fins.

The type in this early fin is certainly a pure heterocercal one, in no way approaching the archaic diphyrcy which one might naturally expect in the earlier kindred of Xenacanthus. Diphyrcy as represented in *Ceratodus* has been (as far as the writer is aware) generally regarded as the most primitive condition of the body terminal of aquatic vertebrates.¹ McCoy¹⁹ in 1848 and Cope²⁰ in 1871, in their comments on

¹ Since the above was written, the memoir of W. N. Parker on *Protopterus* (Trans. Roy. Irish Acad., 1892) has been received. His view in this matter, strengthening an earlier influence of Dr. Traquair (Brit. Ass. Rep., 1871), is that "it is impossible to draw any conclusions with regard to the ancestral form of caudal fin in the Dipnoi from a study of adult forms."

diphycercy, have carefully reviewed this primitive condition from the standpoint of the palaeontological material then extant. Ryder²¹ in 1884, treating the subject of fish fins mainly from the embryological side, has given a most important memoir upon the evolution of the tail of fishes, comparing his results critically with those of K  lliker, Vogt, Dohrn and Lotz. He brings out clearly the degenerate stage in the development of the tail, whereby the homocercal is reduced to a diphycercal type which he terms *gephyrocercy*.

Reviewing the matter carefully, in view of the puzzling caudal structures of *Cladoselache*, the present writer is led to suggest that the origin of the caudal of gnathostome fishes is to be derived not through a diphycercal, but through a heterocercal condition. He believes, furthermore, that embryological results might in this way be interpreted. That phylogenetically the heterocercal type itself may have been evolved from some form of diphycercy, wanting, however, in radials, would appear extremely probable.

From the standpoint of palaeontology, there can certainly be little doubt that the heterocercal condition can easily claim priority in time, — heterocercy is represented in all Elasmobranchs (Xenacanthids excepted), in all known Ostracoderms. In recent forms it maintains in chondrosteian Teleostomes, either in adult or young, and in bony teleostomes as a regular embryonic condition. The only fish group whereby true diphycercy can claim antiquity among fossil forms is the Dipnoan, since the condition of caudal in Crossopterygians is generally heterocercal in the most ancient types, *Holoptychiuss*, *Osteolepis*.

If the fins of Xenacanthids are reduced to selachian conditions, why should not the tail, in view of its homologous origin, be regarded as also derivable from a selachian tail type? If dipnoan-like fins in this group are secondarily acquired, why should not also the dipnoan tail structures? If it is shown that the lateral fins of Xenacanthids may be reduced to the more ancient and more primitive type of *Cladoselache*, the tail structure in these forms, simple though it appears, might equally well be regarded as of acquired character.

Diphycercy in its existing conditions, with radials developed, as in *Ceratodus*, is, in the opinion of the present writer, a specialized, perhaps more strictly a degenerate condition, directly comparable with gephyrocercy, as shown in *Echiodon*, figured by Ryder.¹

On the side of embryology confirmation as to the antiquity of heterocercy is singularly clear, if the question of continuous dermal fold and of larval fin hair-rays be placed aside. Certain it is that the cartilage tail supports, radials, occur first on the ventral side, and have here increased to a remarkable size, often fusing, before the epural supports come to be formed.² The stimuli that give rise to this outgrowth of the caudal lobe have been closely followed by Ryder,³ whether or not we accept his views as to the exact manner of causation. That the tendency was from the earliest towards heterocercy is seen in the primitive outgrowth of the lower lobe of the tail, and in the consequent upturning of the fin end of the notochord. That epurally this axis became strengthened by variously grouped neural plates may clearly be seen in the embryos of flounder, salmon, shad, *Amia* or *Lepidosteus*.²² It is further noteworthy that the hypural border of the upper tail lobe tends for a long while to remain rayless, as is well seen in the young of *Lepidosteus* (or of flounder⁴). The free tip of the chord at a later stage is known to become regularly reduced, surrounded by growing and fusing radials or basals, or, in the case of *Chimaera*, curiously filamentous.⁵ It is, perhaps, significant that there seems in every case a stage in development when the heterocercal tail suggests a forking character, though this stage may be quickly outgrown and masked by a bending together of the lobes.⁶ In one of the stages in the development of the flounder⁷ would be represented the actual condition of *Cladoselache*, if

¹ Ref. 21, p. 1098, Pl. VIII, Fig. 3.

² Cf. l. c., Pls. I, II, III, IV and IX.

³ l. c., p. 1057.

⁴ Ref. 21, Pl. I, Fig. 7.

⁵ Balfour and Parker, Phil. Trans., Pl. II, 1882, p. 408.

⁶ Ref. 21, Pl. I, Figs. 7, 8, 9.

⁷ l. c., Pl. I, Fig. 7.

the tip of the chord be upturned, the (derm) rays absent, and a stouter outgrowth of the cartilaginous radials.

Among ancient forms all stages of gradation from heterocercy to diphycercy might well be illustrated in the ancient Crossopterygians, *Holoptychius*, *Osteolepis*, *Gyroptychius*, *Glyptolaemus*. Further degeneration in these forms might result in typical gephyrocercal types, whose transitional stages would be represented in Coelacanthids, e.g., *Coelacanthus*, *Undina*, *Diplurus*, *Macropoma*. From the tail type of *Cladoselache* diphycercy, as shown in *Xenacanthus*, might readily have taken its origin; it would have required merely the continuation posteriorly of the hypural rays and a gradual downturning or degeneration of the tip of the chord,—a condition specialized to environment, which among recent forms is clearly evolved in the case of the eel.

This view as to the derived character of what is accepted as diphycercy certainly assists not a little in closing phylogenetic ties. It adds further evidence for the nearing of Dipnoid as well as of Crossopterygian forms to the stem ancestral of Xenacanthids. It aids, moreover, in the comparison of Xenacanthids with more ancient and more generalized Elasmobranchs.

THE UNPAIRED FINS.

The structure of the unpaired fins of *Cladoselache* would naturally be expected to prove of great morphological interest. The present material, unfortunately, does not permit any satisfactory determinations. In a single specimen is preserved a detached fin of *Cladoselache kepleri* (?) which is entirely different in type from pectoral or ventral, and might, perhaps, be regarded as dorsal.

The specimen (Fig. 4) presents nine fin rays (radials) in a graded series, of which the foremost is the shortest. In this region, as in the other fins, the rays are concentrating and fusing, are most erect, perhaps may even have inclined slightly forward. The caudad rays are most inclined, abruptly tapering and become distinctly hollow in their basal half. It is interesting that each ray at its distal hinder edge has split off a bridge-

like bar which passes over and appears to be attached to its next neighbor, thus forming a cartilaginous margin to the fin web. The rays show a trace (?) of but a single basal support. It is evident that this material is in no way sufficient for generalizations, — *e.g.*, as to the beginnings of unpaired fins, or as to the troubled question of dorsal spines in *Cladoselache*.

One is, however, tempted to comment on the mode of strengthening the distal web margin, which *Polypterus* has so aptly specialized, in all probability as a neomorph. So, too, the foremost rays in their process of clustering might readily be adduced to prove the mode of origin of a dorsal spine. Or the hollow nature of the hindermost (and therefore the least modified) rays might be emphasized as typifying the most ancient form of fin support.

This specimen will become of value when others are found ; — in the present paper it is described as the only known remains of an unpaired fin.

THE SHAGREEN AND DERMAL DEFENCES.

Palaeozoic sharks seem as a rule to have been richly provided with dermal defences ; many and characteristic spines were evolved, specialized in their characters to a remarkable degree, as in the hook-like head spines of *Hybodus* and *Acrodus*, or in the fin spines of *Acanthodes* or *Diplacanthus* ; shagreen was often stout, tuberculate and sculptured, at times 'ganoid' in its outward characters, varying often in its coarseness of texture in different regions. *Xenacanthids*, as well as *Chondrenchelys*, however, appear to have been shagreened with the finest of denticles, a deficiency in dermal defences perhaps of a secondary nature, since in the former instance at least a median spine was present. In *Cladoselache*, it is to be noted that fineness of shagreen texture is unaccompanied by spines, — as far at least as can be positively judged from the present material. In this form the denticles become larger in size at the sides of the head, in the region of the jaw angle (suggestive, perhaps, of *Chlamydoselache*) and in a marked way on the anterior margin of fins and tail. The denticles are usually lozenge-shaped, varying in shape and

stoutness in different regions. Those that have fused together to form the circum-orbital plates have already been commented upon by Jaekel, whose figure, slightly modified by the writer, is here reproduced (Fig. 5). An entire ring of derm-plates as shown in a more perfectly preserved specimen (*C. fylleri*) is also figured (Fig. 6). Their Acanthodian characters have been noted.

Dermal investiture of the fins, as already seen, is as yet specialized in the development of only the most minute rays. These appear to be intercalated between the primitive cartilage rays. In the pectorals they suggest from their extreme fineness of character, the slightest plaitings of superficial derm layer (Fig. 1). In the ventrals, however, they are not to be positively defined. Those of the tail are clearly marked, and have evidently been of a degree of usefulness consequent, perhaps, of the absence of cartilaginous supports in the upper lobe. They certainly agree in arrangement and direction with the firm dermal supports of the upper lobe in modern sharks. It is of especial interest that in the paired fins of this ancient form the superficial rays are intercalated, and not joined on to the endoskeletal part in a fringing line; it is thus suggested that the protrusion of these parts from between the cartilages, which gave them direction as well as support, was the origin of the dermal fin. Where greater rigidity combined with lightness was required, as in the outer posterior border of fin, the cartilaginous radials were obliged to resort to processes of forking, splitting and interwedging their pointed tips, devices which could not long remain in competition with the dermal ridges which now became acquired secondarily. The latter have, in paired fins, developed on the same lines as the older structure, have spread between them, and usurping their functions, have caused their degeneration.

Of lateral line nothing is determinable in specimens that are to be positively referred to the type genus. A portion of a shark from the locality in which *Cladoselache* was found shows clearly a lateral line, which is figured (Fig. 7), although but doubtfully referred to this form. It is especially interesting

that the lateral canal is an open one as in *Chlamydoselache*, and is bordered by stouter and more numerous denticles. The relation of their size to that of those of the surrounding body wall might be looked upon as significant of the primitive mode of encasement of the sensory tract.

THE DENTITION.

Comparison of a series of jaws has rendered it possible to understand the general characters of dentition. The head of *Cladoselache* viewed from below, even in its crushed condition, is strongly suggestive of *Chlamydoselache*, especially in the incurving, fringing teeth of the upper jaw. Like the modern form, its teeth were largest, longest and most acutely pointed symphysially, and shortest and smallest at the angle of the mouth. It has apparently the two anterior rows of the upper jaw separated by a depression, probably toothless, passing inward between. It is impossible as yet to say that there existed a symphysial unpaired row of teeth on the lower jaw to be opposed to this depression. The broad horizontal bases of the teeth were not, however, arranged in fore and aft rows, with alley-ways between.

In *Cladoselache fylleri* each ramus of either jaw was closely studded with about twenty-five (ecto-entad) banks of teeth, each bank containing about eight teeth.

These ecto-entad banks, as already suggested, vary in general character in different regions of the mouth. Each tooth is wedged in between its neighbors of the right and left banks so that one lateral denticle becomes the buttress of the main cusp of its right neighbor, the other denticle often going no further than opposite the lateral denticle of its left neighbor. The general curve of the jaw gives an even and close-set appearance to the dentition. The symphysial rows, though consisting of the largest teeth, have not been satisfactorily determined. Their outermost teeth possess an extremely long principal cusp, whose length is about one-ninth the distance from snout tip to articulation of jaw. These appear to have been greatly incurved, and were notably larger than their succeeding neighbors in the same bank. The lateral denticles were

not marked in the symphysial rows. The development of the lateral denticles, outer and inner, as we pass to the angle of the mouth, leads naturally to a condition that is strikingly hybodont. (Cf. *Synechodus*.) Hybodont, too, is the fact that (1) the marginal rows are the smaller and rounder and more degenerate in cusp characters, and (2) that the greatest wearing line appears to fall upon the middle members of each bank. The teeth typical of *Cladodus* occur in the rows of the anterior third of each jaw; here the length of the lateral denticles is about one-half that of the main cusp. Incurving of teeth is most marked in the front of the mouth, the direction of cusp becoming nearly parallel to its broad base. Underlying teeth appear to assume the *s*-like form. Teeth in the region of the mouth angle, become slightly unsymmetrical. Entire specimens, which represent perhaps young animals, show little abrasion of cusps. The teeth of an entire mouth of a large individual of *Cladodus* (?) *terrelli* indicate that wearing action had been greatest little more than midway from symphysis of jaw to articulation,—the pointed cusps, stout heavy ones in most cases, being ground away to their bases; and the appearance of the entire jaw is in consequence decidedly hybodont, none the less so as the teeth of jaw margin and mouth angle became small and bluntly chisel-like.

There appears to be present in *Cladoselache* no shagreen denticles at the outer margin of each jaw, which might be mistaken for teeth.

Eyes and nares are prominently marked in nearly all specimens. The olfactory capsules were terminal, large, and seem to have been placed quite closely together. The orbits were placed well forward in the head, the capsules appearing to be larger proportionally than those of *Chlamydoselache*.

Chlamydoselache may be looked upon as representing one type of Cladodont dentition. It does not agree with that of *Cladoselache* in a number of important characters. Its teeth, for example, are small, uniform in shape, decreasing in size from the middle line to mouth angle, and from the outer to the inner rows, each row with an alley-way separating it from its neighbor, each lateral denticle almost as serviceable as a

median cusp. In no instance, is the writer aware that the cusps have been found worn by usage. In *Cladoselache*, on the other hand, appears a character transitional to hybodont, — its teeth vary in a marked manner in size and shape. Except in the anterior portion of the mouth, the teeth are larger on the inner than on the outer mouth margin, the outer teeth are reduced in size, lose the prominent character of median cusp but augment in solidity and breadth. They secure solidity by interwedging their broad bases, but lose thereby the ingoing alley-ways; the lateral cusps function principally as neatly fitted buttresses to the central cusp of a succeeding neighbor. Even the longer cusps come in certain parts of the mouth to present a greatly worn appearance, suggestive of permanent character, as Dr. Newberry has already noted.

CONCLUSIONS.

Cladoselache in summary presents historic evidence as to the mode of origin of a number of shark structures. Its archaic characters, to be expected, perhaps, from its early occurrence, appear to allow no other interpretation than that of Wiedersheim as to the derived nature of Xenacanthid fins. It gives, moreover, evidence as to the antiquity of fins strikingly lateral-fold-like in character. As to this evidence, the conservative deductions of Jaekel, even had his observations been justified by the material recently discovered, seem to the present writer exceedingly debatable. Thus, for example, his conclusions as to the morphological value of the embryonic structures of shark and *Torpedo* seem by no means convincing. Admitting that in youngest stages the fin fold of a later derived form, *Torpedo*, may present a condition more archaic, it does not follow necessarily that in sharks there could not primitively have existed a continuous fin fold. On the other hand, in the present stage of our knowledge of the retarding and acceleration of embryonic structures, Jaekel's views would seem all the more questionable. Equally well might the living conditions of the later derived form have selectively evolved a latent ancestral character, which, reacquired, might

be emphasized by very early development. The significance of the heterocercal tail of *Cladoselache* is of especial importance, since this form occurs earlier than Xenacanthid. It suggests that the diphyrcery of existing gnathostomes might be secondarily acquired.

Cladoselache, in view of its generalized characters, might naturally be looked to for more accurate knowledge as to the phylogeny of the ancient Elasmobranchs. Fin and tail structure would appear to indicate that the ancestors of Xenacanthids may not have been widely separated from *Cladoselache*.

Especially interesting is the light that *Cladoselache* gives as to what may have been some of the characters of the Elasmobranch stem, from which the Diplacanth and Acanthodians may have had their origin. Comparison with Acanthodians brings out many points of agreement.¹ Shape and outward proportions were similar, gills were protected by frills of integument, eyes were similar in position and in their protecting ring of bony plates; feebleness in axial parts, and characters of dermal denticles were common to both; in lateral line a correspondence may, with probability, be traced; tail characters were at least similar; similar, too, in these forms appear the myocommata, whose clearly-marked character in fossils might indicate an unusual thickness or compactness of the connective tissue which separated the myomeres. Even the most bizarre characters of Acanthodian, lateral fin spines, are not altogether incomparable, especially when the evolution of the Acanthodian paired fins is taken into account as explained by Smith Woodward.² Thus in this fin the clustering of the unjointed radialia to the anterior fin margin is not unsuggestive of fusion into a single plate, especially as it would appear that the lateral fins functioned as balancers, were incapable of great upward or downward motion. Fusion of the anterior radials might result in a sturdy spine, while degeneration and fusion of the posterior radials, which would leave a free fin web, might be the origin of the basal

¹ General affinities to Elasmobranchs have been summarized by Reis (Sitz-Ber. d. Gesell. naturforsch. Freunde, Berlin, Nov. 15, 1892).

² Ref. 8, vol. II, p. 5.

cartilage figured by Smith Woodward¹ for *Acanthodes* and *Parexus*.²

Dentition, on the other hand, is to a noteworthy degree suggestive of Hybodont; teeth often appear worn; in lateral region tend to become broad and blunt; their grouping is in interwedging banks. In this regard *Cladoselache* differs from *Chlamydoselache*, whose frilling gill integuments seem the only striking point of comparison between modern and ancient form.

In conclusion a modification in the arrangement of the lowest sharks might be proposed. Cladoselachids would naturally be removed from the order Ichthyotomi (including Pleuracanthids), Cope. And, based on the extremely primitive fin girdle and tail characters, which *Cladoselache* and Acanthodian together present, the writer would suggest that these forms might be grouped together at the base of the Elasmobranch sub-class in an order which might be termed Pleuropterygii, in allusion to the fin axis not protruding from the body wall. In such a group Cladoselachids and Acanthodians would take subordinal rank.

This arrangement would have the merit of placing the Acanthodian group, which has proven difficult to adjust on account of its puzzling specializations, in a position where, from its appearance in time, one would naturally expect it, — near the base of the Elasmobranch stem, among more generalized forms.

Divisions might thus be defined: Subclass, *Elasmobranchii*;

ORDER I, PLEUROPTERYGII.

Notochord unconstricted; endoskeletal cartilages permeated with minute granular calcifications; (membrane bones sometimes occurring as in the specialized (Acanthodian) sub-order). Tail broadly heterocercal, lacking hypural supports in upper lobe; paired fins appearing as remnants of the primitive lateral fold, and functioning probably as balancers, directed somewhat downward; the line of basalia imbedded in the body-wall, its

¹ L. c., II, pp. 4, 35.

² The second pectoral fin spine in *Diplacanthus* might be explained on the ground of the approximation of the ventral spine next posterior. Cf. Cope, *Am. Nat.*, 1890, p. 413.

caudad end not protruding; radialia, with little trace of jointed structure, extending from body-wall to fin tip, tending to concentrate and fuse in the *anterior* fin margin.¹ Claspers absent. A circum-orbital ring of derm plates. Evidence of loose integumentary gill flaps. Myocommata often preserved in fossils.

SUBORDER I, CLADOSELACHII.

Membrane bones together with neural and haemal spines lacking. Suspensorium probably short and down-turned. In paired fins concrescence of anterior elements giving rise to specialization of radialia, and tending to rotate and fuse the fused basalia; the anterior fin region therefore becoming the more modified, tending to mask its structural characters: in pectoral the specialization of anterior radials producing a bow-like fin margin; in ventral the foremost basalia as yet unfused: the fins' body angle, anterior and posterior (horizontal), rounded by dermal investiture, the remnant perhaps of the continuous lateral fold. Circum-orbital ring of many derm plates.

FAMILY CLADOSELACHIDAE.

Body fusiform, presenting a horizontal dermal keel at the base of the tail. Fins bluntly lobate: in pectoral the posterior radials often bifurcate. Teeth cladodont. Anal and dorsal probably small, lacking in fin spine (?). Circum-orbital derm plates quadrangular and in concentric rows.

GENUS CLADOSELACHE.

Body bluntly fusiform. Teeth cladodont, p. 106. Shagreen varying in body regions. In pectoral delicate (dermal) rays between radialia, radialia in character as described p. 92. Tail, with basal supports arranged as shown p. 98, exhibiting fine (dermal) ray structure in place of hypurals of upper lobe.

The Acanthodians would then follow as presented by Smith Woodward, but regarded as a sub-order.

¹ In the order Selachii on the other hand, the concentration, splitting and fusing of the radialia is at the posterior (distal) fin end, consequent of the protrusion of the tip of the basalia in this region.

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EXPLANATION OF FIGURES.

FIG. 1. Pectoral fin. $\times \frac{1}{2}$. *Ax.* Axil of fin. *Bas.* Basalia. *BW.* Body wall. *D.* Dermal fin-margin. *Rad.* Radialia. *T.* Trichinost.

FIG. 2. Ventral fin. $\times 1$. *Bas.* Basalia. *BW.* Body wall. *D.* Dermal fin-margin. *Rad.* Radialia.

FIG. 3. Tail. $\times \frac{2}{3}$. *C.* Lateral view of horizontal cut-water. *CH.* Notochord. *D.* Dermal fin-margin. *Ep.* Epural plates. *Hyp.* Hypural rods. *M.* Membranous hypural margin of upper lobe. *SN.* Sub-notochordal rod. *Tr.* Trichinosts.

FIG. 4. Unpaired fin (dorsal?). $\times 1$. Showing conical radial cartilages, whose distal ends split posteriorly to form marginal rim of fin web.

FIG. 5. Circum-orbital derm plates. After Jaekel (drawing slightly modified from fin type-specimen).

FIG. 6. Circum-orbital ring of derm plates ($\times 1$).

FIG. 7. Lateral line ($\times 1$). The arrangement of the dermal denticles indicating the presence of an open groove as in *Chlamydoselache*.

