XVI. THE EVOLUTION OF THE CAUDAL FINS OF FISHES.

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(With text-figures 1—3.)

There is ample justification for the assumption that the most specialized of caudal fins among fishes have been evolved from a simple type which formed a part only of a once continuous median fin-system, extending from immediately behind the head on the dorsal side round the posterior end of the body to the vent on the ventral side ; thus there was no caudal fin as a differentiated structure. The whole of this primitive median fin-system was almost certainly provided with similar skeletal elements throughout, probably of the nature of interspinous bones or radials, not unlike those now found to support the dorsal and anal fins of modern fishes. The caudal extremity was therefore perfectly symmetrical both externally and internally, the dorsal contribution meeting the ventral in a line continuous with the chordal axis. Such a type of caudal fin is referred to as ' protocercal.'

Embryology is not of much assistance in verifying the exact details of skeletal structure in the primitive caudal fin, for modifications of this primitively symmetrical type set in very early before skeletal elements are properly laid down. Yet it is reasonable to suppose that no specializations were present in the primitive caudal fin ; the early fishes undoubtedly moved by serpentine action, undulations of the whole body producing a forward motion resembling the progress of the modern eel. Thus the posterior extremity of the body had no special demands made upon it as a propulsive organ beyond those shared by the rest of the body.

Before proceeding further it will be advisable to describe the types of caudal fin now met with among fishes. It is probably quite safe to say that no fish at the present time possesses a protocercal caudal fin ; hence any tail fins which shew perfect symmetry both externally and as regards internal skeletal supports will be secondarily symmetrical, that is gephyrocercal. When, however, it would not be safe dogmatically to assert the primary or secondary nature of caudal symmetry, it is convenient to employ a non-committal term signifying symmetry only ; diphycercal is the term which conveys such a meaning, thus protocercy will be synonymous with primitive diphycercy and gephyrocercy with secondary diphycercy.

Now undoubtedly the protocercal fin is the earliest in evolutionary order ; heterocercal forms no doubt succeeded the protocerca in the ascending scale towards the highly specialized tail fin of the Teleosts. Heterocercy is characteristic of the Elasmobranchs and the Ganoids ; it differs from protocercy in one important feature, *viz.*, that symmetry has been disturbed. In general, the asymmetry affects both the external form and the inner skeleton, though modification of the latter may not always be very strongly marked. The ventral contribution to the caudal fin is larger than the dorsal, and in most cases markedly so, as illustrated in the Ganoids *Acipenser*, *Polyodon* and *Amia.* Associated with this, as would be expected, the skeletal supports of the ventral fin-rays are more strongly developed than those on the dorsal side.

Though often less marked in Elasmobranchs than in the Ganoids, from the base of the fin there is an upward bend of the axis which is continued to the extremity, and when centra are present, they remain distinct throughout this upwardly directed part. We thus see that the main characteristics of the heterocercal tail are (1) an enlarged ventral lobe compared with the dorsal; (2) a bending upward of the axis at its end; (3) the retention of individual centra, when present, to the end of the axis.

Turning now to the homocercal type, there can be no question as to its having succeeded directly the heterocercal form. Reference to the skeletal structure of the caudal fin of *Amia* will readily shew that this particular fin requires but slight modification to convert it into a homocercal form, for homocercy is characterized by (1) external symmetry; (2) strongly asymmetrical internal skeletal structure by which the majority of the fin-rays are always supported by ventral elements; and (3) the presence in the larval or adult stage of a urostyle which represents a much shortened axis.

The caudal fin of *Amia* has always been recognized as deserving of some special distinctive designation, and it has usually been referred to as hemi-heterocercal; however since its distinctive feature is its close approach to the homocercal form, I have elsewhere[1] proposed that a better term would be hemi-homocercal.

It is well known that the earliest fishes of the Devonian period possessed heterocercal tail fins and that diphycercal forms appeared later. Thus the evidences of embryology have been said to be at variance with those of palaeontology; it is true that the evidences mentioned do not agree, but it would seem that there is no ground for denying that the embryological data are indicative of the sequence of forms in the evolution of the caudal fin. Professor Dollo[2] in dealing with the Dipnoi recognized the difference between the embryological and palaeontological evidences and suggested a way out of the difficulty. He argues that since the caudal fins of the earliest fossil fishes found are heterocercal, and later forms diphycercal, these later forms are secondarily diphycercal, *i.e.*, gephyrocercal.

Now gephyrocercy implies the complete loss of the original caudal fin elements, a great reduction of the axis having brought this about; and also that the new tail fin is in reality the result of a "bridging over" of the gap thus produced, by the dorsal and anal fins, each having an equal share in the formation of the new fin. *Fierasfer* is the best illustration of a gephyrocercal fin; the larva is known to possess a long filamentous termination to the chordal axis, which is entirely lost in the

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[1] *Proc Zool. Soc. London*, October 1910, where most of the caudal fins mentioned in this paper are figured.

[2] The Phylogeny of the Dipnoi.

adult fish; in the adult, the dorsal and anal fins have not completely joined round the extremity and the vertebral column has exactly the appearance of having been artificially abbreviated.

It does not, however, necessarily follow that all the symmetrical forms of the tail which follow the asymmetrical have once been heterocercal and that this fin has been lost entirely to be replaced by a gephyrocercal form. It is possible that something of this nature occurred: both the later heterocercal and diphycercal forms were descendants of a primitively symmetrical (protocercal) type; at a certain period, a divergence took place, some forms adopting the heterocercal tendency, while others continued in the line of their ancestors and retained their symmetry. This may be represented by a simple diagram (fig. 1).

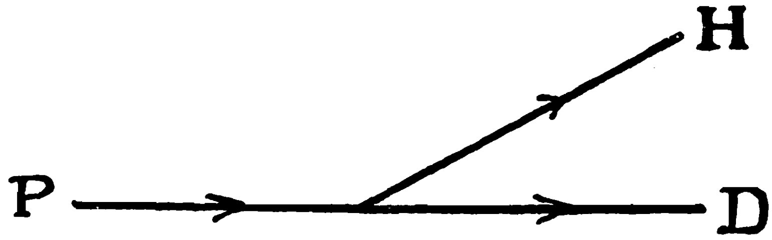

FIG. 1.

It should be noticed that this does not necessarily regard all diphycercal fins as protocercal; a reduction of the terminal axial elements might proceed by which the original caudal element might be eliminated and the dorsal and anal elements made to contribute to the new caudal fin. Thus the question of the symmetrical fin is left open, and the fossil diphycercal forms might be regarded either as protocercal or as gephyrocercal.

This interpretation would appear to be a perfectly natural one; an order of things which might easily have occurred, for the modification of such an organ is only the result of a change in habit; it cannot be expected that all fishes adopted the same form of locomotion in early times, since it is not likely that all adopted the same change of habit.

I have said that the development of heterocercy was due to a change of habit, and it is necessary to enquire what change was consequent on the adoption of the heterocercal caudal fin, or rather how heterocercy could bring about any change. An explanation is not easy even if possible. In this connection we may recall Ryder's theory of the use of heterocercy; he likens the use of the tail fin to the sculling action of the boatman, who propels his boat by a side to side motion of a single oar from the hinder end. The analogy is a good one and explains the use of the tail as a propeller, but it still leaves it uncertain why the axis turned upward and not downward; why the ventral side was chosen for enlargement and not the dorsal. It is a question mainly for the physicist to answer, and innumerable enquiries I have addressed on the point to physicists have all failed to obtain an answer.

It is thought that early fishes were bottom dwellers, and that in the attempt to explore the upper waters there was a mechanical stimulus, the response to which caused the ventral lobe to increase in order to cope with the demand made upon it. The rearing of the trunk to reach upward, causing a bend in the body convex to the bottom, would be accompanied by a lash of the tail; it would be an advantage to have the propelling force more or less in line with the anterior end of the body, and thus the ventral side of the caudal fin would have a greater demand made upon it than the dorsal.

If the fish is represented as rising from the bottom by the bent arrow in the diagram (fig. 2), the broken line will indicate the posterior continuation of the line of progress after the tail has completed a lash; the dotted lines would represent the form of fin useful for this purpose. This is merely a suggestion put forward until a better one is forthcoming, but correct or no mechanically, certain it is that all fishes with heterocercal tendencies developed the lower lobe of the caudal fin and never the upper.

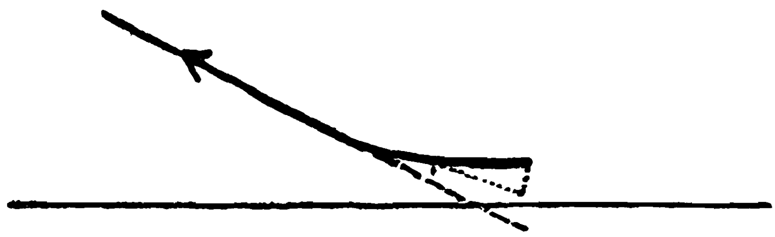

FIG. 2.

Having discussed the probable stimulus effecting heterocercy, there still remains the question as to why it was at all necessary to develop this asymmetry. When we remember that heterocercy is but a stage in the production of homocercy, it is clear that external symmetry was the ideal to be reached; why then was the symmetry of protocercy abandoned only to be again attained? Again the answer is one of mechanics; had the protocercal form been merely expanded, the internal skeletal supports of this fin could not have met the demand made upon them. The epural and hypural elements would have been long and practically parallel with the axis; this in itself would not have been mechanically strong. Moreover, the centre of the caudal fin would have been weak, there being no direct support for the fin-rays in the middle line, and it is here that strength is most needed. An essential, therefore, for a strong caudal fin is a firm support for the dermotrichia forming the greater part of the fin especially near the centre.

It is in the final product of homocercy that one must look for an interpretation of the meaning of heterocercy. The examination of such a caudal fin as that of *Scomber*, well known as one of the fastest of swimmers, shews how the result has been attained; the upturned axis provides the supports of the fin-rays with a firm attachment, and the supports are seen to radiate from a centre which is in line with that of the axis. In the majority of Teleosts the hypurals, which always support the greater number, and sometimes even the whole of the caudal fin-rays, are firmly fused to the vertebral elements. It will therefore be seen that the reason for the heterocercal stage is that the ventral fin-ray supports may be brought into the same line as that of the axis, and at the same time afford a strong attachment for them. It was the only way these ends could be achieved; symmetry had to be abandoned during heterocercy in order again to restore an external symmetry of a more efficient type.

There is still another morphological question that the above evolutionary process involves. What is the true nature of the homocercal caudal fin ? Is it a true modified caudal or is it an anal fin which has come to occupy a relatively posterior position ? If we examine almost any heterocercal caudal fin, such as that of *Acipenser* or *Polyodon*, we see that the greater part of the fin is supported by hypurals some considerable distance from the end of the chordal axis. Should the axis again be straightened, this portion would certainly be regarded as anal fin from its very position. That the vertebral axis of Teleosts, and it may be of all fishes, has been very much reduced in length is certain; the continuation of the spinal cord beyond the last centrum is sufficient proof of this, and with this reduction the original caudal rays have gone too, unless a few dorsal rays associated with the opisthure are the last remnants. The upturning of the chorda therefore almost certainly involved the bringing of a more anterior fin, an anal, into a relatively posterior terminal position.

The question as to whether separate median fins had been yet differentiated need not seriously affect this view, for during development it can be seen that the skeletal elements of the differentiated fins are laid down before heterocercy sets in, and thus differentiated fins might be regarded as having been established during the protocercal condition in some cases at least. Differentiation, however, may not have been developed in all cases, and then it is only a matter of extended growth of a part of a continuous fin. Thus this question is not one of primary importance since certainly dorsal, caudal and anal fins are only names for portions of a once continuous series.

The supporting elements for the caudal dermotrichia are of three kinds : firstly hypurals ; secondly epurals ; and thirdly radials, either dorsal or ventral. These terms are here used according to the definitions given by me in an earlier work,[1] and it may be useful to quote them briefly. A hypural is defined as any hypaxial element having direct connection with the chordal axis, and bearing one or more caudal fin-rays distally ; an epural is the corresponding epaxial element ; a radial is synonymous with 'somactid' and 'interspinous bone.'

One constantly sees statements which refer to hypurals as haemal arches ; Sedgwick writes [2] "In all fishes the ventral part of the caudal differs from the other median fins in the fact that the dermotrichia (fin-rays) are supported directly by the haemal arches." Such a reference is typical of text-books in general concerning caudal fins, but the matter is one deserving of discussion. As far back as 1854 Stannius in his text-book on the Vertebrata clearly stated that the fin-ray supports were compound structures, consisting of arch and radial combined. Ryder[3] in 1884 seems to have come to the same conclusion but this interpretation seems to have been ignored in more recent works.

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[1] Loc. cit.

[2] *Students' Textbook of Zoology*, 1905.

[3] "Evolution of the Fins of Fishes," *Rep. Comm. Fish and Fisheries*, Washington, 1884, published 1886.

Before entering into the question, I would again draw attention to the presence of independent radials as supports of caudal fin-rays. Dorsal caudal radials as I have called them are usually present, and are the bones referred to by Huxley[1] as epurals; ventral caudal radials are also frequently present though much less than their corresponding dorsal homologues. In all Gadidae, *Solea*, *Zeus*, *Gobius* and others, radials persist ventrally.

Now since radials are the normal supports of the dermotrichia in other median fins, we may assume that they once were in the caudal, which is merely a part of the same system. Haemal arches, therefore, cannot be regarded as the original supports of fin-rays, and if they are considered to have taken over this function, they must be regarded as having lengthened and expanded distally with a view effectively to fulfil their new function. On the other hand, radials are the natural supports of fin-rays. It is also interesting to notice which of the two elements, radials and arches, are the more persistent when subjected to eliminating influences. The flexion of the extremity of the chorda affected the dorsal and ventral side of the fin differently; epaxial elements had less room assigned to them, while the hypaxial structures were afforded scope for extended development. The response to this influence is very marked; on the ventral side fin-ray supports have expanded to fill the widening cleft between them, but dorsally suppression has resulted. But which structures dorsally have succumbed to this crowding-out process? Not the radials but the neural arches; as long as dorsal fin-rays remain to be supported, the radials retain their function, while neural arches have disappeared or been reduced. We are forced therefore to regard radials as more persistent than arches.

When the caudal fin became a definitely propulsive organ, more rigid support was required for the fin-rays; to accomplish this there were clearly two ways open; (1) by the transference of the supporting function from radials to haemal spines, and (2) by the mere fusion of the radials with the haemal spines. The first alternative involves, one might almost say, a preconceived purpose on the part of the spines to acquire a new function; they must lengthen, expand and, in so doing, eliminate structures already performing the work they are to take over. Such a change of function is usually accompanied by a stimulus, in response to which the change takes place; but it is difficult to see what stimulus could have been applied to the haemal arches to initiate a change. The radials clearly had a stimulus, a mechanical one, and one cannot avoid concluding that they responded thereto, thus obtaining as it were a start on any other competitor.

It has been shewn that radials are more persistent than arches dorsally; is it likely therefore that in a region where extended scope for development is afforded, as is the case ventrally, that structures already well adapted for the support of fin-rays, and indeed actually fulfilling that rôle, should abandon their function in favour of structures in no way so fitted, especially when, under adverse conditions, as dorsally, they tenaciously retain that function? It is inconceivable, and one is tempted to ask what would happen during the period of transference.

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[1] "On Some Parts of the Skeleton of Fishes," *Q. J. M. S.*, 1859

It is far easier to conceive of the very simple process of fusion of radial with the rigidly attached haemal spine, for this is exactly what would be expected. Without labouring the theoretical aspect further, it may be mentioned that there is abundant evidence among Teleostean fishes, as well as Elasmobranchs and Ganoids that such fusion has occurred; the following examples may be quoted as affording evidence: *Acanthias, Galeus, Heterodontus, Acipenser, Polyodon, Synodontis, Plotosus, Anguilla, Conger, Gadus, Gadiculus, Molva, Motella, Centriscus, Belone* (Stannius' example), *Box, Zeus,* and *Pleuronectes.* In all these cases the line of fusion between arch and radial can still be seen.

There is, however, another aspect worth mentioning; it has been maintained that radials are derived in the first place from neural and haemal arches by segmentation, a view which receives support from the Dipnoi, where the radials rest directly upon the spines. But the most favoured opinion does not lend support to this view since, except for the caudal, in the median fins of Elasmobranchs radials are so far removed from the axis. Were this segmentation theory correct, it might have been argued that the caudal region retains the primitive condition, but in this connection the presence of radials in the caudal fin would present a difficulty. Thus the study of the caudal fin-structure entirely supports the view that radials are elements developed independently of the axial structures.

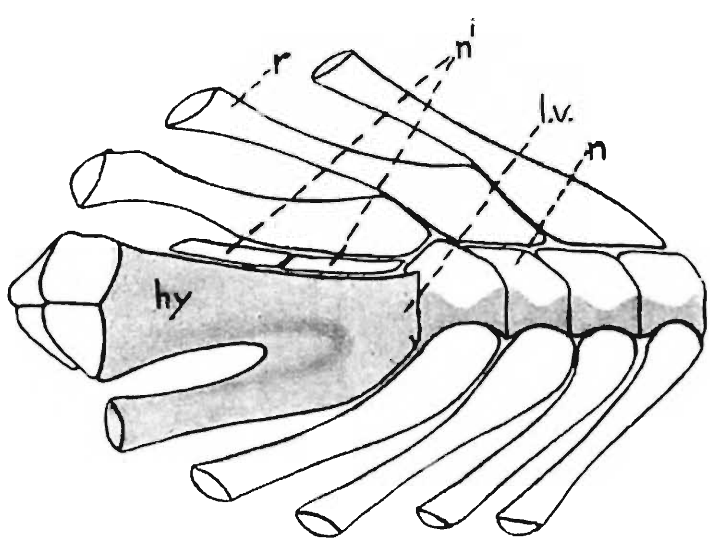

FIG. 3.—Caudal extremity of *Torpedo ocellata.*

hy., hypural; l.v., last centrum; n., neural arch; n'., neural arches of centra now suppressed; r., radial.

In concluding these remarks on homocercy, I would like to refer to the internal structure of the caudal fin of the electric torpedo, *Torpedo ocellata* (fig. 3); this fin has never to my knowledge been previously described, and I have refrained from discussing it earlier, because material has not been available to allow me to examine more than a single specimen. But even if this particular specimen was abnormal, which I doubt, it certainly is extremely useful in shewing that tendencies to the homocercal type may occur among the Elasmobranchs; indeed more than mere tendencies, in fact a homocercy which, had it been found in the Teleostei, would not have been considered strange.

The specimen was dissected by me some years ago and I believe affords the only instance of homocercy yet recorded among the Elasmobranchs. As is well known, the external form of the tail fin of *Torpedo* is symmetrical; internally, however, the ventral fin-rays are directly borne by hypurals, the two terminal ones being strongly developed, fused at their bases both to one another and to the last centrum. Above the last hypural are to be seen the remains of the neural arches of vanished centra, occasioned by the abbreviation of the vertebral column; they are still to be found because they are necessary to provide protection for the terminal portion of the spinal cord. All the ventral supports are hypurals, while dorsally the rays are borne exclusively by radials which have not fused with the neural arches.

It is possible that an investigation into the tail fin of the Rays may prove to be of considerable value; while *Torpedo* thus possesses what may be regarded as a fairly specialized type of homocercy, others may shew a simpler tendency in that direction.