The Structure and Development of the Tail in the Plaice (Pleuronectes Platessa) and the Cod (Gadus Morrhua).

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With 25 Text-figures.

I. INTRODUCTION.

It is well known that the tail of the Gadidae differs from a typical Teleost tail in its structure, and it is all the more remarkable that, despite the extensive use of the group in zoological teaching, little seems to be known of the development of this tail beyond certain isolated stages briefly described by Agassiz (1) and Cole and Johnstone (6). The present work, to which reference has been made elsewhere (Barrington, 3), was originally planned as an attempt to fill this gap in the literature, but at the suggestion of Professor E. S. Goodrich it was extended to include also a study of the tail of Pleuronectes in order to facilitate a comparison of the Gadoid tail with the normal homocercal type.

The writer is very much indebted to the Director of the Flodevigen Sea-fish Hatchery, Norway, for a supply of specially fixed developmental stages of Gadus morrhua L., to the Director of the Marine Laboratory, Plymouth, for similar stages of Pleuronectes platessa L., to Professor Goodrich for criticism and encouragement, to Dr. G. R. de Beer for kindly supplying some stages of Gadus merlangus L., and to Mr. J. A. Moy-Thomas for the loan of some Victoria blue preparations of Pleuronectes.

II. METHODS.

All the stages were fixed in mercuric-formol, and the majority were stained by the Victoria blue method of van Wijhe, which,
as is now well known, reveals the cartilaginous skeleton with the utmost clarity. These preparations have been drawn with the aid of a Zeiss drawing-prism, and it is therefore hoped that the figures provide as accurate a representation as possible of the development of the caudal skeleton. A few stages were sectioned and stained on the slide with Mallory's stain and with borax-carmine and picro-nigrosin; these sections were reconstructed graphically. For determining the structure of the skeleton of the adult, specimens were dissected in glycerine after treatment with alizarin-red and potash.

III. NOMENCLATURE.

In order to avoid unnecessary repetition later, certain terms will be defined here in accordance with the usage suggested by Whitehouse (17) and more recently by Blanco (4). A hypural may be defined as a ventral element supporting one or more lepidotrichia and making contact with the notochordal axis, being subsequently attached to a vertebra; it is presumed to be composed of a haemal spine fused with a ventral radial. An epural is a dorsal element with analogous relationships, and is presumed to be composed of a neural spine fused with a dorsal radial. A radial is a dorsal or ventral element supporting one or more lepidotrichia, but not making contact with the notochordal or vertebral axis.

IV. THE CAUDAL FIN OF PLEURONECTES.

i. Structure.

The structure of the caudal fin of Pleuronectes (Text-fig. 1), which has been previously described by Cole and Johnstone (6), is of the normal homocercal type in which an apparent external symmetry conceals an internal asymmetry. The web of the fin is supported by a fan-shaped system of twenty dermal fin rays (lepidotrichia), of which twelve are attached to two large, symmetrically disposed hypurals (hyp-y., hyp.), these in their turn being attached to the terminal vertebra (tv.). The axis of this vertebra turns slightly upwards, and this is the only indication of a urostyle in the sense of a structure formed by
the fusion of the reduced terminal vertebrae. This vertebra is also prolonged along both the upper and lower edges of the upper hypural, and it is possible that the upper prolongation (o.) may represent the neural arch of the vertebra. According to Regan (14) the homocercal tail is characterized by the modification of the posterior neural arches into 'uroneurals' which, primitively separate but later fused to the terminal vertebra, functionally replace the corresponding centra and so
lead to their suppression. However, it is equally possible that the prolongation in question is a secondary response to the functional need for a support for the hypural and a protection for the tip of the spinal cord. Whitehouse, it may be noted, interprets a precisely similar structure in Solea (17) as representing a neural arch. Ventral to the terminal vertebra there lies an expanded radial (vr.) which supports three lepidotrichia, while dorsally there are found three more bony elements. The two uppermost of these (dr.2, hyz.) have been regarded by Cole and Johnstone (6) as morphologically dorsal elements, but it will be seen below that the hinder one (hyz.) is morphologically ventral and must, in fact, be regarded as a hypural. It is true that it does not make contact with the vertebral axis in the fully developed fin, and to this extent does not satisfy the definition of a hypural stated above, but the use of this term will be seen to be justified by the facts of development. The third of these three bones (dr.1) is very small, and appears to have escaped previous notice; it will be shown that although it is not concerned in the support of fin-rays, it must be regarded in view of its mode of development as a dorsal radial. These three bones thus provide an excellent example in miniature of the danger of applying morphological definitions without consideration of the embryology of the structures concerned.

The penultimate vertebra (pv.) bears a dorsal (ep.) and a ventral (hyu.) process which again provide a difficulty in nomenclature. Cole and Johnstone draw attention to the fact that each has the appearance of being composed of anterior and posterior regions more or less clearly demarcated from each other, and they suggest that the anterior regions represent respectively a neural and a haemal spine to which have fused posteriorly a dorsal and a ventral radial (an epural and hypural according to their nomenclature). It will be shown later, however, that another explanation is possible, for there is reason to believe that this vertebra bears two neural and two haemal arches, the neural arches fusing with each other and perhaps with two corresponding dorsal radials, and the haemal arches behaving similarly; from the latter is formed the last hypural (hyu.) supporting the last ventral fin-ray.
ii. Development of the External Form.

It has long been known that the homocercal fin of the Teleostei passes through a symmetrical (diphycercal) stage, and later through a heterocercal stage which results from an increasing development of the hypochordal lobe of the symmetrical fin. This appears first to have been recorded by von Baer and was subsequently emphasized by Huxley (11), who pointed out that such a specialized homocercal type as Gasterosteus was 'as heterocercal as an Acipenser, and far more so than a Scyllium or a Squatina'. Subsequently A. Agassiz (2) showed that in the Flounder the tip of the embryonic caudal fin appeared as a dorsal lobe of the developing caudal fin, and that this lobe, which he called the axial lobe, gradually disappeared. The present work adds nothing to his description of the development of the external form of the homocercal tail, but some new illustrations are given in order to facilitate comparison with Gadus. It will be seen (Text-fig. 10) that in the heterocercal stage there is a well-developed hypochordal lobe (hp.) with lepidotrichia (l.), this being separated by a notch from the axial lobe (ax.) which contains only actinotrichia (ac.) and into which the notochord (no.) is continued. The axial lobe gradually disappears (Text-figs. 11 and 12) together with the original tip of the notochord, and the web of the fin comes to be formed exclusively by the hypochordal lobe supported, as will be shown below, by morphologically ventral elements.

iii. Development of the Skeleton.

At the earliest developmental stage available (Text-fig. 2) most of the elements of the caudal skeleton are already represented in the form of cartilages. The largest is the hypural hyv., which is situated at about the point of flexure of the notochord. Behind it the hypural hyv. is seen in the form of a small irregularly shaped cartilage. The two dorsal radials (dr.1, dr.2) and the single ventral radial (vr.) are also to be seen, and in front of these are the first neural arch (nau.) and the first haemal arch (hau.). A curious feature at this stage is that both of these arches appear to be double, unlike any of the succeeding arches (nat., hat.). Unfortunately, this condition appears very
TEXT-FIGS. 2-9.
Development of the caudal skeleton of Pleuronectes platessa
(drawn from Victoria blue preparations).
early and is soon lost, the arches assuming a normal form, so that it has not been possible to shed any further light upon it. There can be little doubt, however, but that it is a phenomenon of the same nature as that referred to by Schauinsland (15) when he describes the base of the cartilaginous arches in fish as sometimes extending backwards; according to him, the caudal part may even be cut off to form a separate cartilage, as in the tail of the Trout, and he regards this as representing a trace of the interdorsal, or interventral elements which are seldom developed in the Teleosts.

During the succeeding stages of development (Text-figs. 3–9) there occurs a general moulding and increase in size of the cartilages already identified. The neural and haemal arches (nau., hau.) gradually extend into what must be regarded, by analogy with the more posterior elements, as a combination of spine and radial; there is no indication of a fusion of a distinct spine and radial such as has been described by Totton (16) in Pleura-gramma. As the hypural hyw. continues its development it shows clear indications of being of compound origin, a point not observed by Agassiz (2). To judge from Text-figs. 6 and 9 three separate cartilages (hyw., hyx., hyy.) have combined in the course of evolution to form this hypural, and even at the latest stage available the boundaries between them are visible as notches in the inner edge of the hypural. There is no analogous evidence of hypural hyv. being of compound origin. Behind the last of this series of cartilages, all of which must, of course, be regarded as hypurals, there later appears (Text-fig. 6) a small cartilage (hyz.) which, to judge from its position, is also a hypural. Remaining separate from the others, it comes to overlie (Text-figs. 8, 9) the tip of the notochord as the latter shortens up, and finally occupies in the definitive skeleton, as has been shown above, a position superficially resembling that of a dorsal radial.

The later stages of development are marked by the fusion of neural arch nau. with neural arch nat., and of haemal arch hau. with haemal arch hat. In Text-fig. 7 these arches are seen to be already very closely approximated; in Text-fig. 9 the fusion has affected the haemal arches but not the neural arches; in
Text-fig. 8, although in its general development an earlier stage, the fusion is complete above and below and is seen to have caused the interruption of the radials associated with the arches, the distal ends of the radials (re.) being left as isolated cartilages. It may be assumed that the remaining length of the radials is involved in the fusion. It is natural to ask whether the arches concerned in this process really represent basalia belonging to distinct segments, or whether the process is a fusion of basalia with interbasalia so that only one complete segment is involved. On general grounds the latter alternative is extremely unlikely, for in the Teleosts interbasalia are commonly either absent or at best represented by transient vestiges of the type mentioned above, and it would be remarkable if they were at this one point as well developed as the basalia of the rest of the caudal region. Several series of sections have been cut in order to determine this point more definitely, but the matter proved to be one of some difficulty. Theoretically, the myotomes and the segmental nerves and blood-vessels might be expected to provide evidence, but unfortunately at the extreme hind end of the body and at these early stages of development, the boundaries between the myotomes cannot be seen, while the nervous system is so attenuated and feebly developed that it is impossible to determine the presence or absence of segmentation in it with any confidence. Text-fig. 16 is a graphic reconstruction of a stage approximately corresponding to that of Text-fig. 6 and it shows the position of the segmental vessels (sv.) which, although also very small, are quite clearly defined in transverse sections; assuming that each vessel represents one segment, their distribution indicates that arches nau. and hau. belong to one segment and arches nat. and hat. to another. It may thus be concluded that basalia belonging to two segments become fused together and associated with one vertebra, this being, of course, the penultimate vertebra. This conclusion is in accordance with the suggestion put forward above in explanation of the peculiar morphology of that vertebra.
V. The Caudal Fin of Gadus.

i. Structure.

The structure of the fin of Gadiculus argentatus has been described by Whitehouse (17), while the same author has more recently (18) drawn attention to certain points in the structure of the tail of Gadus morrhua. This type of caudal fin differs from that of Pleuronectes in extending for some distance along the body, so that its skeleton includes a number of vertebrae (ten in Gadus merlangus, Text-fig. 18). Each of these vertebrae bears an epural (ep.) and a hypural (hy.), the forked appearance of some of these being attributed by Whitehouse (17) to the fusion of additional radials. He argues that 'in the other median fins two radials are present between successive vertebral arches; thus probably the hypurals and epurals of the caudal have already absorbed one radial and the tendency is to effect a fusion of the second also', a conclusion which 'affords one of the strongest cases for the theory that hypural bones are formed by the coalescence of radials with haemal arches'. For the purpose of comparison with Pleuronectes only the posterior of these vertebrae need be considered in detail, and, indeed, only in this region are the supporting elements preformed in cartilage.

The terminal vertebra (Text-fig. 17, tv.) bears a single hypural (hyw.), and is prolonged along either side of the latter as a pair of processes (o.) which are more slender in Gadus merlangus (Text-fig. 18) than in Gadus morrhua. These may be uroneurals, in the sense in which that term has been used above, but whatever their nature they provide a protection for the tip of the spinal cord which runs above the last hypural, and so indicate the inherent homocery of this tail. The only indication of a true urostyle is, as in Pleuronectes, the slight upturning of the axis of the last vertebra.

Lying above the penultimate vertebra (pv.) are two radials (dr.1, dr.2) which are separate in Gadus morrhua but fused together ventrally in Gadus merlangus. This vertebra bears ventrally a single hypural (hyv.), while the ante-penultimate vertebra (apv.) bears, like the succeeding vertebrae, an
epural and a hypural (ep., hyu.). Between hypurals v. and u. there lies a ventral radial (v.r.) which in Gadus merlangus becomes attached to the hypural behind it, and in Gadus morhua to the one in front of it; this doubtless indicates

The mode of development of the tail of Gadus (Text-figs. 18-15) differs in one fundamental respect from that found in Pleuronectes, for at an early stage lepidotrichia begin to
appear both above and below the notochord (Text-fig. 13, l.), and later a dorsal and a ventral lobe grow backwards, maintaining a more or less symmetrical form (dl., vl.). These lobes, in which fin rays continue to appear, enclose between themselves a third slender lobe (ax.) which contains only actinotrichia and the tip of the notochord, and which clearly represents the axial lobe of Pleuronectes. This lobe is progressively reduced

(Text-figs. 14 and 15), and with its final disappearance the dorsal and ventral lobes are able to fuse to form the continuous web of the fin. Thus, whereas in Pleuronectes the web is exclusively ventral in origin, in Gadus it is half dorsal and half ventral. As a result the axial lobe in the latter is median and not dorsal, and, as a corollary of this, the tail cannot be strongly heterocercal. These facts will be discussed later, but it may be noted now that Agassiz (1), failing to discover the axial lobe in Gadus, published a well-known figure of the tail of a 20 mm. Cod which he described as representing a heterocercal stage. It is clear, however, that while the developing

Text-fig. 16.
Graphic reconstruction from serial transverse sections of a portion of the tail region of a young Pleuronectes.
tail does show a slight heterocercal flexure (Text-fig. 14) to say nothing more than this about it is to miss the essential peculiarity of this tail.

iii. Development of the Skeleton.

At the earliest developmental stage available a ventral and a dorsal cartilage are present, the latter being only faintly
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distinguishable. It is probable that these (Text-fig. 19) represent respectively the hypural _hyv._ and the radial _dr._, but it is impossible to be certain as there is no point of orientation. In the next stage (Text-fig. 20), which corresponds with that

**TEXT-FIGS. 19-24.**

Development of the caudal skeleton of _Gadus morrhua_ (drawn from Victoria blue preparations).

shown in Text-fig. 13, all the elements of the skeleton of the last three vertebral segments are present, and six lepidotrichia (_l._) have appeared. In this stage the last neural arch (_nau._) and haemal arch (_hau._) are both double at their base, the former
more clearly so than the latter. This condition resembles exactly the corresponding phase described above in Pleuronectes, and is no doubt to be interpreted in the same way as representing a trace of the interbasalia. As in the latter fish, this condition is a very transient one; only one specimen of this particular stage has been available, and this has been the only specimen to show any trace of this condition, several later stages, corresponding approximately to Text-fig. 21, failing to show it.

The succeeding stages of development (Text-figs. 21–4) involve chiefly, as in Pleuronectes, the appearance of more rays and the further development and moulding of the cartilages already present. The terminal hypural (hyw.) extends upwards and backwards so that the notochord which runs above it is necessarily thrown into a slight heterocercal flexure. (The striking difference between the extent of this flexure in the two fish is illustrated by a comparison of such stages as Text-figs. 11 and 14.) A significant fact which also emerges is that in Gadus this terminal hypural never displays any trace of compound origin; its backwards extension appears only as a simple growth process, its main impingement upon the notochord is at its anterior end, and it is never subdivided by notches.

In the later stages it may be seen that the last neural arch (nau.) and haemal arch (hau.) fuse with the arches in front of them (nat., hat.), a process recalling that described in Pleuronectes. Text-fig. 28 is of a stage in which this fusion has occurred ventrally but not dorsally, while in Text-fig. 22 the fusion is complete above and below. That two arches thus come to be borne upon a single vertebra is particularly easy to demonstrate in Gadus for the extent of the future vertebra is marked (Text-figs. 22, 23, 24) by ridges on the notochord where the latter is least constricted (r.). As with Pleuronectes, it does not necessarily follow that this represents the fusion of neural and haemal arches from two distinct segments, although the extreme improbability of interbasalia being as well developed as basalia at this one point alone applies equally strongly here. Text-fig. 25 is a reconstruction from serial transverse sections.
of *Gadus merlangus* in which the position of the segmental vessels, the only segmental structures distinguishable, suggests that these arches do, in fact, belong to two distinct segments. Unfortunately, the form of the definitive vertebra concerned, which is the ante-penultimate one (Text-fig. 17, *apv*.), sheds no further light, for the only peculiarity comparable to the abnormal structure described in *Pleuronectes* (apart from the forking

![Diagram](image)

**Text-fig. 25.**

Graphic reconstruction from serial transverse sections of a portion of the tail region of a young *Gadus merlangus*.

of the epural and hypural, which has been seen to occur also in the more anterior vertebrae) is a foramen subdividing the neural arch in *Gadus merlangus* (Text-fig. 18, *f.*) and not found in the other vertebrae. Since, however, this division is not to be found in *Gadus morrhua* it may be no more significant than the other slight variations of structure which occur between the two species. It can only be concluded, therefore, that it is probable, but not certain, that these fusing arches represent basalia belonging to two distinct segments.
VI. Discussion.

The present work, while adding nothing to the account given by Agassiz (2) of the development of the external form of the tail of the flat-fish, gives a more complete account of the development of the caudal skeleton. It has been shown, firstly, that a series of reduced hypurals develops beneath the upturned tip of the notochord; of these, the most posterior persists as a small independent element which has not previously been recognized as a hypural, while the succeeding two become merged with the larger one in front to form the upper of the two hypural bones finally borne by the terminal vertebra. In the less specialized homocercal tails such as that of Clupea (Whitehouse, 17) there are as many as seven hypurals associated with the terminal vertebra, and it has always seemed likely that the transition from this stage to the more specialized condition of two large hypurals was accompanied by some degree of fusion of the primitively more numerous and smaller elements, rather than by a complete disappearance of the apparently missing ones. Agassiz failed to detect this fusion in the Flounder, but Totton (16) showed that in Pleuragramma antarcticum the upper of the two large hypurals developed from the fusion of two rudiments. In the tail of Solea lutea, which in its general morphology, as is to be expected, resembles that of Pleuronectes, this fusion of hypurals is apparently never completed, for Whitehouse (17) describes the terminal vertebra as bearing four firmly united hypurals; the fourth, of course, would correspond with the lower of the two hypurals of Pleuronectes, and this shows no trace of compound origin.

The second point which has emerged from this work is that during development the penultimate vertebra comes to bear two dorsal and two ventral arches, probably representing the basalia of two segments, a fact which can still be detected in the abnormal structure of this vertebra in the adult. There is nothing inherently novel in this situation; on the contrary, the terminal vertebrae of Teleosts appear to be much subject to such abnormalities, no doubt as a result of the considerable amount of secondary modification which must have been in-
volved in the fashioning of the homocercal fin, and of which the fusion of the hypurals is merely another example. Thus, the corresponding penultimate centrum of Pleuragramma bears double neural and haemal arches, but the resemblance to Pleuronectes is only superficial, for Totton (16) describes this condition as resulting from the splitting of originally single rudiments. He observes that similar phenomena are to be found in other fish, and points out, as is indeed illustrated by the present comparison, that they may be produced by quite different causes.

The third point is the double nature of the last neural and haemal arch at their first appearance, a condition, it may be noted, which is quite distinct from the fusion of arches which occurs later. It has already been pointed out that this probably represents the transient appearance of interbasalia.

Passing now to the tail of Gadus, it becomes possible for the first time to estimate its relationship to the specialized homocercal type in the light of the facts of embryology. The interpretation of this tail has always been a source of some controversy, for while it has been generally recognized that it departs from the normal Teleost type, the extent of this departure has never been satisfactorily decided; indeed, from time to time it has been suggested that the differences are merely superficial and that the tail is to be regarded as belonging to the normal homocercal type (Agassiz, 1; Dietz, 7; Whitehouse, 18). Agassiz's argument was based upon his well-known figure of a 20 mm. Cod larva in which the notochord is clearly bent upwards; this led him to assert that the Cod passed through a heterocercal stage in its development, and that this was, in fact, essentially the same as that of the Flounder. He admitted that 'the separation between the embryonic and permanent caudals is never distinctly indicated—at least, not in the specimens I have had the opportunity of examining—by an indentation or a sharp notch, as in other species', but he ascribed this to the early appearance of numerous dorsal and ventral 'accessory fin rays', and, despite this difference, inferred from the apparent heterocercal nature of the developing fin that 'the tail of Physicus and of Gadus therefore ... do not in reality differ
from the tails of other bony fishes'. The description of the
development of the tail of Gadus given here, however, has
shown that this conception cannot be maintained, for not only
is it possible to identify the axial lobe of the fin, but the identi-
fication makes it clear that this lobe occupies not a dorsal but
a median position, and that it is suppressed between a dorsal
and a ventral lobe which, developing at the same rate and of
approximately equal size, ultimately form the web of the
definitive fin by fusing together behind the axial lobe which is
itself lost. Thus the heterocercal flexure described by Agassiz,
while genuine enough, is only slight in extent, for normal
heterocercy is a result of the exaggerated development of the
ventral (hypochordal) lobe. Such a normal flexure, although
it must have occurred in the ancestors of the Gadidae, cannot
occur now because it is automatically reduced as a result of the
newly evolved method of formation of the fin web.

It is now necessary to compare the structure and development
of the skeleton of these two fins. It seems reasonable to homo-
logize the penultimate hypural (hyv.) of Gadus with the
hypural hyv. of Pleuronectes, as did Agassiz, for in their
development they are correspondingly situated at the point of
flexure of the notochord. The terminal hypural (hyw.) in Gadus
cannot, however, be strictly homologized with the hypural
hyw-y. of Pleuronectes, for the former shows no indication
of compound origin; it must, therefore, be homologized with
the most anterior of the three hypurals which contribute to
hypural hyw-y. in the latter, and if this is correct it follows
that the posterior hypurals (hyx., hyy.) have disappeared in
Gadus. It could, of course, be urged that they had not actually
disappeared but had rather become merged with the hypural
hyw.; but it is on the whole unlikely that this could have occurred
without leaving some trace of compound origin in the develop-
ment of that hypural, as is seen in Pleuronectes. Thus
Agassiz's proposal to homologize the two symmetrical hypurals
of the Flounder with the last two hypurals of the Cod is in-
correct in detail, although sound in principle. If this assumed
disappearance in Gadus of the most posterior hypurals be
accepted, it can easily be accounted for, for these elements,
although ventral in origin, are concerned in Pleuronectes with the support of the dorsal part of the web of the fin, a function taken over in Gadus by morphologically dorsal elements developing in the new dorsal component of the fin. Thus these particular hypurals become redundant.

Dietz (7), in an attempt to relate the Gadidae to such specialized Teleosts as Cyclopterus and Liparis, has argued that the terminal hypural in Gadus could be derived by the fusion of the two symmetrical hypurals of the specialized homocercal tail, accompanied by a reduction in size. It is apparent that the facts described here afford no basis for this suggestion, for it is scarcely conceivable that such a fusion could have occurred and yet have left no trace in the development of that hypural.

A consideration of the remaining cartilages suggests further resemblances between the two tails. In both there are to be seen, in front of the hypurals which have already been dealt with, two dorsal radials and a single ventral radial. The neural and haemal arch immediately in front of these are in both forms double at their first appearance, while in the later stages of development they fuse with the arches lying anterior to them. The nature of the arches involved in this fusion has been discussed above, and it has been shown that there is an element of doubt as to their interpretation. The question of whether or not the phenomenon is identical in the two forms is not, however, of the first importance, for it has already been pointed out that the terminal vertebrae of the tail of Teleosts may develop superficially similar abnormalities by quite different means, and only a knowledge of the conditions in a variety of different forms would make it possible to determine if any phylogenetic significance attached to any particular situation. The conclusion which does seem to emerge is that an abnormality in the developmental history of the arches in this region is a peculiarity which the tail of Gadus shares with the normal homocercal type. One other such resemblance is the presence of bony processes, possibly uroneurals, lying above the terminal hypural and forming a protection for the tip of the spinal cord.
One difference between the two fins must now be noticed. In Gadus the penultimate hypural (hyv.) becomes attached to the penultimate vertebra, whereas in Pleuronectes the corresponding hypural (hyv.) is attached to the terminal vertebra, and there is a corresponding discrepancy between the arrangement of the associated cartilages. The effect is as though the terminal vertebra in Pleuronectes included the penultimate as well as the terminal vertebra of Gadus, and this may well be so, for the evolution of the homocercal fin has been accompanied by a reduction and fusion of the vertebrae which primitively (e.g. Salmo) extend to the tip of the notochord along the upturned axis. It thus becomes possible to argue that the tail of Gadus was derived from a homocercal tail of a type less specialized than that characteristic of Pleuronectes; from a type, in other words, in which the terminal vertebrae were less reduced than they are in this genus. Such a conclusion would be in harmony with the opinions of such authorities as Regan (13) and Goodrich (8) who have considered the Gadoids to be an essentially primitive group standing rather by itself and perhaps taking its origin from some remote ancestral Teleost.

If these comparisons are well-founded, it is to be concluded that the tail of Gadus resembles in various details both of its structure and development a normal homocercal tail of a type rather less specialized than that of Pleuronectes, and that it is to be derived from such a tail by the backward growth of a dorsal fin lobe which has resulted in the disappearance of the most posterior hypurals, which, already reduced in the homocercal tail, become redundant in Gadus when their supporting function is taken over by dorsal elements. It is true that there is no proof that these comparisons are, in fact, correct, and it is admittedly very hazardous to draw phylogenetic conclusions from a region of the body so much subject to adaptive change as the tail. But if comparisons are to be made at all the ones made above seem coherent and plausible, while if they are to be rejected on the grounds of lack of final proof then any attempt to analyse the tail of Gadus from the standpoint of embryology must be futile.
It remains to add that the fact that so many vertebrae contribute to the support of the Gadoid tail indicates that a median ventral fin-fold has also made an extensive contribution to the final structure, the ventral lobe of the developing tail including, in other words, more than the hypochordal lobe. For such a tail the term 'pseudocaudal', used by Goodrich (8), appears to be appropriate. He has suggested (9) that 'either the true caudal has extended forwards, or it has combined with the posterior part of the median dorsal and ventral fins', and of these two alternatives the latter appears much more likely, for it satisfactorily accounts for the backward growth of a dorsal lobe which has been seen above to occur during development. Thus the homocercal fin of the ancestor of the Anacanthini became absorbed into a continuous fin-fold, such as is still found in the Macruridae, the process involving a loss of the tip of the homocercal axis, as represented by the most terminal hypurals but not to the extent assumed by Boulenger (5) who regarded the homocercal extremity as having been lost, with the result that a new caudal fin had been formed. Gregory (10) has suggested the term 'hypocercy' for this condition, regarding it, however, as being derived from homocercy by coalescence of the caudal with the prolonged anal fin, the conjoined ventral fins being then pulled out into a long pointed tail fin to give rise to the condition found in the Macruridae. This hypothesis, of course, is incomplete as it omits the dorsal contribution described here. For the caudal fin of Gadus (as also for that of Anguilla and Simenchelys) Gregory has suggested the term 'isocercal', and he regards this as being derived from homocercy or from hypocercy by atrophy of the pointed tail and development of a new fan-shaped tail around the stump of the old one. If this represented the actual course of events, however, it would be surprising to find the tail of the modern Gadidae resembling the homocercal type in such respects as those suggested above. In any case it is to be expected on general evolutionary grounds that the Gadidae would have branched off soon after the establishment of the continuity of the fins and without passing through the more specialized condition of an attenuated tail. Such a conception, of course, need not
disturb the interpretation of the Macruridae as the more primitive members of the Anacanthini (Regan, 13).

VII. Summary.

1. The structure and development of the tails of Pleuronectes platessa L. and of Gadus morhua L. are described, with some reference to Gadus merlangus L.

2. In Pleuronectes: (a) seven hypural cartilages are identified, the most posterior becoming a dorsal element in the definitive tail while the next three fuse to form the upper of the two hypural bones borne by the terminal vertebra; (b) the penultimate vertebra comes to bear two dorsal and two ventral arches, probably basalia, as a result of their fusion during development; (c) the last neural and haemal arch bear traces of transient interbasalia at their first appearance.

3. In Gadus: (a) the tail resembles that of Pleuronectes in certain respects, including the general arrangement of the dorsal and ventral skeletal elements, the appearance of transient interbasalia in connexion with the last neural and haemal arch, and the fusion of two dorsal and ventral arches, although these come to be borne by the ante-penultimate vertebra instead of by the penultimate vertebra; (b) the embryonic axial lobe of the fin is median (instead of dorsal as it is in Pleuronectes) as a result of the upper half of the definitive fin being formed by the backgrowth of a dorsal fin-fold.

4. The two types of fin are compared, and it is concluded that the Gadoid fin could have been derived by the fusion of a homocercal fin, of a type more primitive than that of Pleuronectes, with a dorsal and ventral fin-fold, accompanied by the loss of the most terminal of the hypurals characteristic of the normal homocercal fin.

VIII. Bibliography.

2. —— (1878).—“Development of Flounders”, ibid.