

NOTE ON THE PECTORAL FIN OF THE SOLE, *ACHIRUS*
CAPENSIS: ITS ORIGIN AND SIGNIFICANCE.

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(With Plate IV.)

The changes which take place in the body of flat fish in correlation with alteration of the position of the body are of particular interest from an evolutionary point of view. These changes are not so far back in the genealogy of the animal that we cannot hope for some light on the question of their origin, and the more recent such changes are the more instructive they will be. The following case may therefore be of special interest in this respect. It is also suggestive of some wider problems, such as the origin of paired limbs, on which some remarks are made.

The pectoral fins of the soles have lost their original functions of balancing the body, and we find that their subsequent fate has been very diverse. In some species they become very much enlarged; in others they disappear altogether. This is well illustrated in the South African soles, of which there is a great variety. Among these there is a small sole, *Achirus capensis*, which has been described as devoid of pectoral fins. It is common on the sandy shores of False Bay, and as it can readily be kept in confinement, it is a very suitable subject for the study of colour-adaptation to various surroundings. It was while some experiments of this kind were being made that a peculiar action of the branchial aperture was observed, for, in inspiration, not only did the opercular membrane close down against the body, but a small flap of transparent skin was seen to rise from the body to meet it, thus forming a double valve for the closing of the aperture. Other living specimens were examined, and in all this little valvular membrane was found, apparently functioning as an accessory organ in respiration. On one occasion, however, a number of very small soles of this species was procured, and it was observed that the small flap, though present and well developed, lay applied to the body, and did not function in any way in the process of breathing.

This structure may be best examined in an adult specimen. In one,

128 mm. in length, it is readily seen by raising the membranous border of the operculum, which conceals it. It consists of a transparent fold of skin, which at its upper end is continuous with the opercular membrane. It attains its greatest breadth (1.3 mm.) about 2 mm. from the upper angle of the opercular opening, and from this broader part gradually tapers away, the total length being 7 mm. The whole structure is situated over the clavicle, to which, however, it is not attached, and that it represents a reduced pectoral fin is indicated by the presence of six dermal rays, though no traces of other elements (radials) of the limb are to be seen. These dermal rays are widely set apart, and are so arranged as to form a support for the elongate fold. The rays taper off towards the border, near which they end. This border is slightly emarginate between the distal ends of the rays, the emargination being much more marked in movement in the living condition (Pl. IV, fig. *b*). The two halves of each ray are fused together throughout their length, except at the proximal end, where they appear as short stout forks, the function of which in normal fins is to secure the rays to the radials. As these radials are absent in this case, the meaning of the marked development of these forks here may be interpreted as a device for the more effective control of the valvular pectoral in its movements.

The upper and lower ends of this fin may be particularly noticed (Pl. IV, fig. *a*). At its upper end it is distinctly continuous with the margin of the opercular membrane, and but for the presence of the rays the whole structure might be interpreted as an extension of this margin on to the body. At its lower end it is continued as a rayless membrane, gradually becoming narrower. This rayless part is about half its total length, which is considerable, being about a third of the whole opercular opening.

This structure differs very considerably from the normal fin of fishes. The mesodermal supporting elements of the fin have been lost, the dermal rays reduced in length, though comparatively stout; their proximal ends are well developed and spread out. Though the fin is shorter in length, its base is relatively large, so as to form a thin vertical membrane, which is supported by the altered position of the rays. Not only has the structure of the fin been very much altered, but the function is totally different.

We have therefore here an illustration of the appearance of a new organ, which apparently does not occur in any other fish,* and is of comparatively recent origin.

It can be accounted for, as any modification of the body can be accounted for, by a process of natural selection of favourable germinal variations. Such an explanation cannot, however, with our present knowledge of cell structure and function, either be proved or disproved, and we may meantime look round for some other possible suggestions.

* Since this paper was in print, I have noticed a similar fold, but without rays, in some of the Chimaeridae, and that, in the living *Callhorhynchus*, it functions as an accessory valve in respiration.

We may assume that the altered position of the body of the flat fish was not assumed suddenly and by all its members at once, and that it came about probably in correlation with a changing external environment. A change in environment, brought about primarily by a simple change in physical conditions, may be followed by much more complex changes in the actual surroundings of the organism. By way of illustration we may suppose that the first change was a purely physical one, as, for instance, the gradual deposition of mud. Secondary changes would follow, the mud becoming populated by a variety of its characteristic forms of life. These forms in their turn would attract other predatory fish, etc., which feed on them, and so a great many new factors—these and others—would arise which could possibly lead to changes in the ancestral sole. One possibility is suggested by an observation on a particular species of fish, the blenny, *Clinus*, of which there is a great variety at the Cape. It is active in its habits, and preys on other small fish, crabs, etc. Its eyes are well developed, and resemble the motile eyes of the chameleon. In captivity it was seen frequently to seize and devour small mullet swimming above it at the surface, and it was observed that, in order to watch its prey more readily, it frequently lay over on one side, thus directing an eye upwards. It can be readily concluded that if this device is adopted for detecting prey, it will serve equally well for detecting enemies, and may have been adopted by flat fishes; another possible factor is the changed source and changed kind of food, consisting of small animals in the muddy ground. The reason for the change of position need not, however, be considered here, and these possible factors are merely mentioned to indicate how complex the external environment may become. The suggested change in environment by a gradual deposition of mud is also purely illustrative. A change in environment may be brought about in other simple ways, as, for instance, by gradual migration of the animal itself to other localities.

With the change from a vertical to a horizontal position the function of the pectoral fin of maintaining the body in a vertical position would be lost, and, owing to disuse, it would tend to diminish in size. This diminution in size, accompanied probably by more complex physiological changes, would of course appear in the succeeding generation if the identical factors which brought it about in the parent were present, and it follows that if these were more pronounced, as they would be in a changing environment, the effects would be more marked. This process of diminution would be arrested at any stage, in which it began to function in another capacity, as has occurred in the *Achirus*.

It might be suggested that the reduction of the pectoral fin is in co-ordination with the elongation of the body as happens in the case of many fish. This, however, is not the case in *Achirus*, where the body is not elongate, but rather short in proportion to its depth.

If reduction of the fin in length to its present dimensions can thus be accounted for, how can we explain the relative elongation of its base of attachment to the body? Apparently this cannot be explained as an effect of use of this portion of the fin, for, as noted above, in the early stages this feature is well marked, though the organ is functionless. It is then merely a dermal membrane in which rays are not developed. It may be borne in mind, however, that the paired as well as the unpaired fins arise in this way, the membrane being replaced by the permanent fin, whose base of attachment to the body is, as a rule, relatively shorter. The presence of a well-developed though functionless pectoral fin of this nature at an early stage may therefore be accounted for by the facts, or rather the mechanism of development.

A modification of the body acquired in this way by functional and environmental changes would be hard to distinguish from a germinal or "innate" character.

The question as to whether such acquired characters may become fixed in another way, viz. by so affecting the germ-cells that they would be reproduced in succeeding generations, if their original cause were removed, is another though quite legitimate inquiry, namely that of the inheritance of acquired characters.

There are so many pitfalls to be avoided in the discussion of the question of heredity, largely due to the use of terms not strictly defined, that one must walk warily. Thus the word "environment" has been here used in two senses, first as the external surroundings (physical and biological) of the body as a whole, and secondly as the external surroundings of an organ of the body, including the other organs. It is necessary to use the term in the wider sense, for the change in position may not have been in direct co-ordination with a changing external environment, but with some gradual internal change in the organs of the animal itself. With this explanation it will probably be admitted that the acquired characters referred to are transmitted, or rather repeated in succeeding generations, for the same cause acting under the same conditions will produce the same effect. It may even be admitted that the changed environment so defined may become so complex and fixed that these characters will be indistinguishable from hereditary characters, acquired by a process of natural selection of favourable variations which have not been brought about by use and disuse. In this particular case it is not at all obvious that the new organ is of any great advantage to the animal. On account of its accidental position near the ebb and flow of the current of water at the opercular opening it is kept in activity, and, so long as it does not seriously interfere with the normal functions of the body, its continued existence will be tolerated. Other cases apparently of this nature are known in the animal kingdom, and perhaps this may be added to the list.

Whatever the explanation of the process may be, however, there is little doubt but that we have here the reduction of the pectoral fin to a simple fold of the epidermis of the body, lying parallel with and resembling the membranous epidermal border of the operculum. So striking is the resemblance that the idea of their possible homology is suggested, though such resemblance is no proof of homology. The reduction of a pectoral fin to a lateral fold of the body also recalls one of the oldest theories of the origin of paired limbs, and is an inducement to inquire a little further into the matter.

The simplest mechanism of respiration by gill slits would appear to be the establishment of a current of water by ciliated epithelium, as in some of the lowest vertebrates (*Balanoglossus*, Ascidians, *Amphioxus*). In the higher forms, the Cyclostomes, there are gill pouches connected by tubular passages to the exterior, where they open by small rounded apertures, guarded by more or less circular rings of cartilage. In the Elasmobranchs, which are provided with a more expansible pharyngeal cavity for inspiration, there is a simple mechanism consisting of a series of vertical folds which overlap the slit-like external openings of the gills, and act as effective valves, being mechanically closed in inspiration and opened in expiration. These are very well developed in some Elasmobranchs (*Chlamydoselachidae*). In others (*Chimaeridae*) there is a great development of the anterior of these flaps, which grows backwards over the gill openings, and acts as a valve for the whole of the branchial apparatus forming the operculum proper of the fishes.

In bony fishes there is a further elaboration: this enlarged operculum strengthened by dermal bones takes over the functions of inspiration, while the membranous posterior border retains the original valvular function. Further, the bony operculum may come to subserve other functions, chiefly defensive, and, in exceptional cases (*Anabas scandens*), locomotory. We have therefore an illustration of how the simple epidermal flap which covers the external opening of a gill slit may be transformed into a somewhat elaborate organ, modified to perform other than its original functions.

There is some reason to suppose that in the primitive vertebrates the number of gill slits were more numerous, and extended further along the body than in later forms. The reduction in the gill slits began probably in the more posterior; they became closed up, and their gill arches and opercula disappeared, but it is quite possible that some of these opercula may, like the anterior operculum, have become developed into more elaborate organs taking on some other function, and should the evolution of the vertebrate body have been in the direction of a decrease in length and an increase in depth, the function now performed by the paired fins is a likely enough one. How the simple opercular flap could have tided over the critical period when the gill opening which it covered became closed up may be indicated by the

case of the *Achirus*, for it could still perform a valvular function in conjunction with the operculum in front of it, or it may well have been the case that in the primitive vertebrate with its increased number of gill slits, not only the opercular flap of the hyoid arch became enlarged to cover some of the gill clefts, but that this happened also in two of the branchial arches. It need not, however, necessarily find any form of useful activity to justify its continued existence.

It may be significant in connection with this suggested opercular origin of the paired limbs that in the lower vertebrates, such as Cephalochordata and Cyclostomata, in which no opercular flaps are developed, though there are branchial skeletal elements, there is no indication of the existence of paired limbs at any time in their development or life-history.

The origin of paired limbs from such opercula is not a new suggestion, as it is part at least of the hypothesis associated with the name of Gegenbaur, who suggests that the limb-girdle and pterygia are derived from a visceral arch and its rays, and (2) the pinna or distal part from the flaps or external free part of the gill septum. He, however, did not apparently entertain the idea that one of these parts of his theory might be correct while the other might be wrong. Another theory (Graham Kerr) is that external gills were in primitive vertebrates developed on each visceral arch and that these gave rise to the paired limbs. This theory is not inconsistent with Gegenbaur's suggestion that the girdles are derived from visceral arches. A third theory (Balfour) is that the paired limb is derived, not from any external modification of the gill septum, but from an epidermal fold which in primitive vertebrates is supposed to have occurred along each side of the body. It seems to have been generally taken for granted throughout the history of the discussion that this is inconsistent with the derivation of the supporting structures of the limbs from visceral arches, but it is not quite evident that it is necessarily so. It is true that in the elaboration of the lateral fold theory it has been suggested that the differentiation into limb rudiments began at the anterior and posterior regions of the folds, but this is not a necessary corollary of the hypothesis, for the differentiation may have commenced at the anterior extremity in association with a disappearing gill arch, and, on the movement backwards of this combined structure (epidermal fold and supporting visceral arch), the process may have been repeated to give rise to the anterior pair of limbs.

On the other hand, while all three theories look for an external epidermal organ as the origin (in part at least) of paired fins, the derivation of the supporting structures (girdles and radials) from gill arches is not bound up with this origin. Any of the three views in this limited sense are consistent with the origin of these elements *de novo*. Thus even Gegenbaur's or Graham Kerr's hypotheses may be correct so far as the limb proper is concerned, and yet open to question as regards the origin of its supporting structures.

There are many illustrations in the body of how ready the mesoderm is to collaborate with any process initiated by the ectoderm or endoderm, by contributions of muscular or supporting tissues. Examples of this are abundant, for instance, in the elaboration of the nervous system and the sense organs, or, to take a more kindred example, in the provision of the supporting radials for the vertical or unpaired fins. In fact this collaboration and assistance is sometimes carried so far that the mesodermal elements usurp the place and function of the original organs entirely, as, for instance, in the case of the notochord initiated by the endoderm, and perhaps in the apparently primitive pectoral of the Dipnoi initiated by the ectoderm.

The question, therefore, whether or not the skeletal elements of paired fins are derived from the visceral arches or arise as in the case of unpaired fins may be looked upon as supplementary to the question of the origin of fins as such, the origin of radials and girdles being another though interesting and important enough question in itself, particularly in connection with the possible derivation of the skeleton of the pentadactyle limb from that of the fish limb.

If, therefore, we must look to some epidermal structures or superficial modifications of the body as the precursors of paired limbs, we have—(1) external gills whose primary function is respiration, (2) a problematic longitudinal fold of the body with the function, also problematic, of balancing the body, (3) vertical folds of the body, whose function is primarily connected with the mechanism of respiration by gill slits.

With regard to the external gill theory, it may be helpful to keep in view the probable meaning of the external gills or other additional organs of respiration, which appear to have displaced the simple external respiratory organs so characteristic of animals devoid of gill slits. The most obvious significance of the appearance of these simple organs is that the supply of water to the gill slits has in some way or other become partially cut off.

This may occur under various altered conditions of environment, as, for instance, in a prolonged embryonic stage, rendered possible by a more abundant supply of food in the form of yolk. A protecting shell is present in such cases, and this, of course, seriously interferes with the free access of water. In some such cases the yolk and body may become highly vascularised as in the large egg of *Galeichthys feliceps*, which is carried about in the mouth-cavity of the parent and thus has the benefit of its respiratory apparatus, or the egg of the Cape *Bellostoma* in the shell of which there are numerous slit-like apertures. In the pelagic egg of a Cape fish the pectoral fin was observed to be in constant motion—yet another device connected with respiration. Compare the branchial character of the paired limbs in *Ceratodus*.

In other cases, more particularly the embryonic Elasmobranchs, more specialised supplementary respiratory organs are developed in the form of

external gills which project from the gill septum into the surrounding liquid medium. The egg case is constructed so that the water can pass in at one end and out at the other, and, in the somewhat elaborate egg of *Callorhynchus*, there is a very perfect device for providing a current of water, as the long flat tail of the embryo projects into a narrow part of the egg case, and keeps up a constant undulatory movement.

This same diminution of the supply of water may occur in post-embryonic life, and here we find similar devices adopted, both the simple increase of vascular surface and the development of external gills.

Two simple cases of the first which do not seem to have been previously recorded may be mentioned. One is that of a species of Goby (*Trypauchen*) found in masses of mud brought up by dredge off Delagoa Bay on one or two occasions. When alive it was of a bright red colour, which microscopical examination showed to be due to blood contained in a network of fine vessels spread over the whole body under the thin transparent skin. The other is that of the blind deep-sea fish (*Barathronus*), a specimen of which was brought up from a bottom of Globigerina ooze off the Cape. Another example is the highly vascularised skin of the clawed toad, *Xenopus*, which spends most of its life under water.

In post-embryonic stages we may also have the development of external gills, under conditions unfavourable for an adequate supply of oxygen, as, for instance, in the muddy or semi-aquatic environment of the Dipnoi, in which external gills are developed.

It is obvious that a semi-aquatic environment must have been passed through by the numerous vertebrates which now lead a terrestrial life, and these, in all probability, passed through an external gill stage. Further, it is not improbable that migration to the land conditions began as early as migration to the pelagic conditions or at the *Amphioxus-Myxine* stage. (In this connection it may be mentioned that the Cape *Bellostoma* is said to make occasional excursions from its aquatic element.) What more probable than that the primitive limbless vertebrates, equipped with external gills, should, as has been suggested, use these as organs for the support and locomotion of the body under its new conditions of life, and from these the pentadactyle limb be developed?

If the tetrapod limb has been evolved in this way from an external gill, developed in connection with the transition of the primitive aquatic vertebrate to terrestrial life, it can hardly be supposed at the same time that from this organ arose the paired limbs of fishes, developed as organs necessary in the transition to pelagic life, probably in association with the shortening and flattening of the body.

There have been belated attempts among fishes to acquire the terrestrial habits. The most successful, however, such as that of the *Periophthalmus* or *Anabas*, have shown no approach to the acquisition of an organ of terrestrial

locomotion at all similar to the pentadactyle limb. Attempts to trace any structural resemblance between a paired limb of any fish and that of a terrestrial animal cannot be said to have been much more successful.

The theory of the origin of paired limbs from a lateral fold of the body has at least this in its favour—that its suggested function was essentially in the direction of an adaptation for an active pelagic life. The various arguments for and against this theory need not be repeated, and only some points noted which seem to indicate the origin of paired fins from vertical folds rather than lateral folds.

(1) Vertical opercular folds of the epidermis exist in fishes at the present day, and there can be no doubt but that they existed in the primitive vertebrates, in which an expansible pharynx and its associated valvular opercula first appeared, not unlikely before balancing paired limbs suitable for a more pelagic life appeared, whereas, not only does no such longitudinal fold as the hypothesis requires occur in any living fish, but there is no satisfactory embryological or palaeontological evidence that it ever existed.

(2) The function of the vertical folds is an obvious one at the present day, and even a necessity in the first primitive vertebrates, in which the respiratory current of water was drawn in by the mouth by means of an expansible pharynx provided with a framework of jointed branchial arches, whereas the suggested function of the lateral fold, a keel for steadying the body or a parachute-like expansion, are at the best conjectures, the first perhaps not mechanically justifiable.

(3) That such opercular folds may attain greater dimensions is shown in some primitive sharks, and more especially in higher fish, in which they may have assumed the form of large organs taking on other functions, such as assisting in inspiration, acting as defensive and offensive organs or organs of locomotion.

(4) It accounts for the absence of paired limbs in the Cephalochordata and the Cyclostomata in which no opercular folds are developed, and their presence, except when secondarily absent, in all vertebrates in which such folds appear. Gill septa provided with skeletal elements are present in the Cyclostomata as in other fishes, but there are no opercula and therefore (?) no limbs.

A great many objections have been raised to Gegenbaur's theory as to the origin of paired limbs from branchial septa from two points of view, which may be distinguished from each other: first the suggested origin of girdles and radials from the skeletal parts of a gill septum, and second, the implied origin of the distal part of the limb from the gill flap or operculum.

The objections to the first, which appear to be weighty, need not be gone into, but the objections to the second apply equally to the opercular origin and may be considered.

(1) The gill septa with their skeletal elements of the apparently primitive Cyclostomes and Elasmobranchs are fixed, not projecting beyond the surface, and therefore not likely to give rise to external organs like paired limbs. This may be admitted in the case of the Cyclostomata, but it is just these which have no paired limbs. In the case of the Elasmobranchs the opercula are external organs and are well developed in Chladoselachidae and Holocephali.

(2) Another objection to the origin of pectoral fins from vertical folds is that it has been observed in most cases examined that when they arise as folds of the body these are more or less longitudinal in direction, and it is only subsequently that they assume a vertical position, and that by rotation sometimes in one direction, sometimes in another. This certainly does not corroborate this vertical fold origin, but it may be noted that the position of the developing paired limb has not been investigated in many kinds of fish, and that the paired limbs of Elasmobranchs are not necessarily primitive in this respect. In this group and that of the Dipnoi, indeed, the endoskeletal elements seem rather to be taking the place of the primitive fin. In some *Achirus* and in the larval form of a very large South African sole (*Synapturus microlepis*) the rudiments of the pectoral have been observed to be vertical in position.

In this connection, however, another theory of the origin of paired limbs which has been much discussed may be noted, namely, that they arise from a longitudinal lateral fold, not such as Balfour supposed to have occurred in primitive fishes, but as it arises in the formation of the metapleural folds in *Amphioxus* (Thatcher, etc.) These folds now function as a protective covering for the external opening of the gill slits. Evolution of organs is often in the direction of a reduction in numbers in co-ordination with the elaboration of a few, and it is not impossible that with muscular pharyngeal in place of the more primitive ciliary respiration the fold may have become differentiated into valvular opercular flaps for the remaining gill opening. This suggestion is very speculative as is also this theory itself, but it is mentioned as a possibility which might indicate that the origin of paired limbs in ontogeny as longitudinal folds which only later become vertical folds is not so inconsistent with their derivation from opercula as appears.

(3) It is objected that transverse folds across the body, such as the opercula, would rather tend to arrest than to assist in the forward movement of a swimming fish, but it is just for this purpose that paired fins are frequently used, as may be observed in the commonest types of fish in life. With the shortened and deep body assumed by the vertebrates in taking to a free-swimming life there is no such provision for the checking of the forward movement as is found in the more elongate bodies, in which advance or retreat can be effected by a reversal of the undulatory movement of the body and paired fins are necessary for this purpose. This is confirmed by

the tendency in elongate forms for the pectorals to disappear. High speed is usually associated with some means of controlling it.

The checking of forward progress in the primitive limbless vertebrates could be effected by the only available structures, the transverse opercular folds, and it may again be noted that the Cyclostomes which have no such transverse folds or opercula have apparently never advanced to the paired limb stage.

(4) It may be objected that there is no evidence of the free opercular part of the gill septa becoming separated from the more internal part with its supporting skeleton. The evidence against that part of Gegenbaur's theory dealing with the origin of girdles and radials from gill arches and rays is in part a reply to this, and need not be repeated. It has carried so much weight that his whole hypothesis of the origin of paired limbs (from the vertical opercular folds as well as the gill arches) is generally viewed with less favour than the lateral fold hypothesis. His theory might still be partly true, even though the girdles be derived from some one of the other sources which have been suggested—ribs and other organs. (The extra-branchial cartilages, which are well developed in some present-day sharks (*e. g. Odontaspis*) and form the main supports for the gill flaps, are possible sources of the girdles, more especially as they are situated in the somatopleure like the girdles, and not in the splanchnopleure like the visceral arches.) To the evidence already adduced of the possible persistence of the opercula, when gills, gill-clefts and the rest of the gill septum have disappeared, may be added that the operculum of living Teleostei may find other or additional supports, as, for instance, in the *Scleroparsi*, and that in the many cases of reduction of gill clefts the gill arch may be as greatly reduced as the gill cleft.

It might be suggested that the fact that the pectoral fin can become an epidermal fold supports the suggestion that an opercular fold may have become a pectoral fin, as this is merely a reversal of the process. This argument might have had more weight at one time, but recent investigations seem to indicate that such reversals do not occur in the evolution of animal life. This has been inferred from the fact that no clear cases are known, but this inference does not, however, imply the existence of any law, and cannot be advanced as an argument against the above suggestion, if indeed the particular case of the *Achirus* may not point to the possibility of such reversal, at least in measure. The argument, however, is not a good one. It might be used also to indicate that the opercular fold disconnected from the gill septum, for in the case of the *Achirus* the fold has lost its attachment by radials to the shoulder girdle. It might be used also in favour of another suggestion, that paired fins have arisen from median fins, for in several soles the pelvic fin of one side may assume a median position and become continuous with the anal.

Perhaps it may be necessary to note another point of view which has been taken up with regard to this question of the origin of paired limbs. It is pointed out that in development it is the mesodermal elements which seem to take the initiative, that in the origin of the skeletal elements the successive appearance of parts is from within outwards, and that a mere epidermal fold cannot be looked on as the actual origin of limbs, for the real structure of a fin begins only when the supporting mesodermal cartilaginous elements appear. With regard to the first two points, it is true that ontogeny is often a valuable guide in tracing the rise of an organ, but not an infallible one, and with regard to the last, the finished organ is often totally different from its initial phases, as for instance in the case of the axial skeleton of vertebrates. Besides, it is difficult to imagine that an external organ of locomotion originated entirely from an internal structure. It seems, therefore, quite legitimate to discuss the origin of paired fins apart from that of the radials or girdles.

Reviewing the position as a whole with regard to the origin of unpaired fins, apart from the question of the source of their secondary supporting structures, the following hypothesis has been proposed: (1) The external valvular flaps of the gill septum and (2) external gills attached to the gill septum; (3) longitudinal lateral folds of the body conjectures from certain evidences to have been present in some primitive fishes; (4) longitudinal lateral folds such as occur in *Amphioxus*; (5) unpaired fins.

The only one of these which seems entirely exclusive of the others is the last, for which there is little or no evidence. What is suggested is that the paired limbs of fishes arose as modifications of the external gill flaps, called here for convenience valvular opercula, which appeared as separate active external organs in co-ordination with muscular pharyngeal inspiration and expiration, and that these opercula in their turn may have originated as segmental differentiations of a supra-branchial lateral fold, originally used in raising and sustaining the body in the water, and which now appears in ontogeny as more or less disconnected longitudinal folds. This is not opposed to the hypothesis that external gills which are vascularised gill septa may have given rise to the paired limbs of Amphibia and terrestrial animals.

Much more could probably be said in elaboration of the supposed opercular origin of paired limbs. Thus a specially pleasing feature, and therefore perhaps to be regarded with caution, is that it appears to account for the absence of paired limbs in the Cyclostomes which have a branchial arch skeleton but no opercula, and shows that this negative feature is not secondary but essentially connected with one of the three fundamental characters of the Chordata, namely pharyngeal respiration by gill slits: in fact the phylum could be divided into two sub-phyla on the basis of its pharyngeal respiratory system and its derivatives (paired limbs) thus:

(a) CYMNOPLEURA, with simple respiratory mechanism and no opercula nor limbs, including Hemichorda, Cephalochorda, Urochorda and Cyclostomata, each of which might also be rearranged on the same basis.

(b) CLADOPLEURA, with complex respiratory mechanism and paired limbs, including fishes with paired limbs derived from opercula (Tetraptera), and Amphibia, etc., with paired limbs derived from opercula modified as external gills (Tetrapoda).



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