ON THE VALUE OF THE FIN-RAYS AND THEIR CHARACTERISTICS OF DEVELOPMENT IN THE CLASSIFICATION OF THE FISHES, TOGETHER WITH REMARKS ON THE THEORY OF DEGENERATION.

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As stated by me in various notices heretofore published, *the most primitive arrangement of the rays of fishes is a continuous one, such as is permanently retained by the Dipnoïns.** Since this conclusion has been reached, further investigation and comparison has shown that in the most primitive types of the fins there are no interradial spaces, such as are found between the rays of the fins of Teleosts. This general truth, completely verified by embryology, seems to lead to results of some significance in taxonomy. For instance, the two groups, Dipnoï and Holocephali, which have the least differentiated system of rays in the fins, are also amongst the lowest and most archaic in their organizations, for in neither are there any true interradial spaces such as are found in the members of the Ganoid and Teleostean series.

The Dipnoï, as respects the fins, are nearer to the Teleostei than to the Squali, because their membranous fin-rays (horn fibers of authors), or actinotrichia, properly speaking, are in a single series on either side of the mesoblastic core of the fins, the same as in Teleostean embryos, and are not made up of several superimposed rows, as in the Sharks.

Since the foregoing was written, a memoir† of the greatest value, by Dr. Meyer, has appeared on the development of the median fins of Elasmobranchs, in which it is also shown that in the embryos of this series there is but a single row of actinotrichia on either side of the

*1. An Outline of a Theory of the Development of the unpaired Fins of Fishes. Am. Nat., Jan., 1885, pp. 90–97, 8 figs.

2. The Development of the Rays of Osseous Fishes. Am. Nat., Feb., 1885, pp. 200–204, 5 figs.

3. On Certain Features of the Development of the Salmon. Proc. U. S. Nat. Mus., 1885, pp. 156–162, pl. XII. (The word *actinotrichia* was proposed for the first time in this paper as a general term for the "horn fibers" or embryonic fin-rays of fishes.)

4. On the Availability of Embryological Characters in the Classification of the Chordata. Am. Nat., Aug. and Sept., 1885, pp. 815–819 and 903–907.

5. The Archistome-Theory. Am. Nat., Nov., 1885, pp. 1115–1121.

6. On the Origin of Heterocercy and the Evolution of the Fins and Fin-rays of Fishes. In press. 12 plates.

N. B.—The new terms which will be met with in the following are defined in the context. Fuller definitions will be found in the author's papers cited above.

†7. Die Unpaaren Flossen der Selachier, von Paul Meyer. Mitth. aus der zoolog. Station zu Neapel, VI., pp. 215–281, pls. 15–19. (Dated latter part of May, 1885.)

unpaired fins. It follows, therefore, that the superimposed rows of actinotrichia found in the fins of many of the Sharks is an advance upon the primitive single-rowed arrangement seen in Dipnoï, Holocephali, and Teleostei. There have, therefore, been two lines or routes of specialization in the development of actinotrichia, viz, (1) that characteristic of Elasmobranchia and (2) that distinctive of Teleostei.

Only amongst the Rays and Skates do we find an approximation to the arrangement met with in Dipnoï and embryo Teleostei. In the Rays, however, the actinotrichia are quite rudimentary—embryonic—in the paired fins, so much so that they are confined to a very narrow marginal portion of the pectoral, for example, not over an eighth of an inch in width in specimens a little over a foot in length. This shortness and rudimentary condition of the actinotrichia in the paired fins of the Rays is correlated with the great length of the actinophores or cartilaginous rays supported by the pro-, meso-, and metapterygium, themselves formed by the fusion of the proximal ends of actinophores.

The only fins found in the Teleostei which retain the primitive features of the continuous ones of the Dipnoï are the so-called "adipose fins" of Salmonoids, Nematognaths, Characinids, &c., but in them a primitive structure is retained by the posterior dorsal only. But these "adipose fins" are part of a discontinuous system of vertical fins, a portion of which is developed to the degree characteristic of Teleostei with interradial spaces. The adipose fins represent, in fact, the survival of a Dipnoän character as a part of a Teleostean organization.

The theory according to which such a survival was brought about seems to be the following: Inasmuch as "adipose fins" are embryonic in structure, just in the same way as the radii of the fins of Dipnoï are permanently embryonic, we are forced to infer that such fins, co-existing as they do with others in the same fish, having well developed membranous, radial interspaces and ossified rays, have been retarded in development so as to retain embryonic characters. The degeneration, or rather retardation, of development of the second dorsal, which is apparent in the Salmonoids, has been completed in the Cyprinoids, a group which has entirely lost the posterior soft dorsal, retaining only the anterior dorsal, with bony rays of the Teleostean type. The Cyprinoid series has, however, acquired other structural specializations, such as the development of a system of auditory ossicles, coincidently with which the anterior portion of the vertebral column has been modified. Turning now to the Nematognaths, a majority of them have retained the "adipose" second dorsal, supported by actinotrichia, while they have acquired two new structures not met with in the less modified and older Salmonoid organization, viz, the system of maxillary, mental, and nasal barbels, supported even in the embryo by cartilage, and ossicula auditus, and often a peculiarly modified air-bladder, bifurcate anteriorly and coming into close contact laterally and anteriorly with the skin in the fore part of the body-cavity, so as to ap-

parently form a kind of tympanic membrane on either side just behind the scapular arch.

It is thus rendered evident that the mutations of development of three or four structures may be sufficient to supply characters of ordinal value to the taxonomist; that, in fact, we may get a far greater variety of small differences between the many species belonging to the orders, founded on such a small number of prominent characters, than might be supposed possible if it was assumed that a permutation of the number of characters used in the ordinal definitions would give the number of species to be included by the supposed orders, for each character is capable, within very wide limits, of infinitely small amounts of variation, which may serve as the marks of species or varieties. We are thus forced to infer that in the "genesis of species" we are dealing with a permutation, the exact number of terms in which, and in which the capacity for the variation of each term is unknown, so that it would, if all the structural characters of a group were given, be impossible to predicate how many species or possible combinations of characters that group was capable of yielding under the stress of environing influences competent to produce changes in the relative development of parts.

For instance, the one feature which *Cyprinus* and *Amiurus* retain in common is the possession of a barbel at the angle of the mouth, yet the one has no cartilaginous basis and appears late, whereas the other has at first a cartilaginous support which afterwards ossifies at its base. Now it is absolutely no proof whatever that these structures in the two forms are not indicative of affiliation, if we assume that this is so, because in the one there is no skeletal support, while it is present in the other. Because, if we attended to the development of both forms we might find reasons for the belief that what had failed to develop in the one was nevertheless possibly as salient a feature in the ancestor of *Cyprinus* as in *Amiurus*, and that the tendency to suppress or retard the development of the barbels in the one and exaggerate them in the other was due to the operation of the very forces which we found capable of producing a complex series of permutations. This idea may be rendered somewhat clearer if we bear in mind that it seems to be a frequent embryological rule that structures which are disappearing in an organism disappear part by part in an order just the reverse of that in which they are normally developed to their fullest importance.

This principle in embryology may be very clearly illustrated by the succession of events in the course of the development of the rays of the median fins of a few types in which the gamut of changes traversed by the process of development is analyzed.

(1) Taking the Dipnoï as the lowest and simplest type, it seems that the following is the method of development of the median fins which will be found to exist: First, a perfectly cradiate, lophocercal, median fin-fold, into which mesoblast is proliferated, between which and the epidermis a single row of actinotrichia are developed on either side of

the continuous fin which extends uninterruptedly along the back, over the tail, forward to the vent. No interradial spaces ever developed and no further differentiation of the actinotrichia, except augmentation in size and strength, and vastly more numerous than the serially arranged actinophores or interspinous elements. The latter are cartilaginous, with a membranous osseous investment, while the actinotrichia are purely membrane and not cartilage, as asserted by Günther. No sign of atrophy of any part of the azygous fin-system is evident unless it may be that there is an anterior portion of the dorsal and a preanal portion which disappears.

(2) The Holocephali, during development, probably approximate the preceding type up to a certain point, when they diverge by differentiating atrophied intervals, especially between the dorsal fin and the epaxial part of the caudal, and in some species the tail-fold seems to atrophy over the posterior portion of the chorda, so as to give rise to a nearly cylindrical appendage without rays extending beyond the true tail, and which may be called an opisthure. (See No. 1.*)

(3) The next grade of differentiation of the fins is that seen in the Elasmobranchs, in which, instead of there being a single row of actinotrichia under the epidermis on either face of the fins, there are several superimposed. A tendency to form true permanent rays is also apparent in large specimens, though the simpler Dipnoän arrangement of the actinotrichia is very apparent in very young specimens and in cases where those have become rudimentary. There is also a less obviously wide and continuous median fin-fold than in Teleostean embryos, and a pronounced tendency to differentiate a caudal, dorsal, and anal fins, with intervening atrophied intervals between them.

(It is very remarkable that Parapodoid structures should exist in the embryos of *Scyllium*, as noted by Meyer (No. 7, pp. 219–229), whose figures also show that there is at first an archicercal terminal part of the embryonic axis projecting beyond the point where median fin-folds are developed, thus giving rise to a degenerate worm-like tail, such as has been described by me as an opisthure (No. 1, p. 94). Such data as Meyer has presented are sufficiently conclusive, it seems to me, to add great force to some of the conclusions reached by the writer in No. 5, pp. 1119–1121, but which were formulated still earlier upon other grounds by Dohrn.†)

The fourth grade of radial development in which several salient characters appear for the first time is represented by the Chondrosteans, Holostei, Crossopterygians, and Teleostei, which form a very natural group for other reasons, in like manner based on data which embryological investigation has supplied.

* The papers cited will be referred to by number.

†8. Studien zur Urgeschichte des Wirbelthierkörpers. VI. Die paarigen und unpaaren Flossen der Selachier. Mitth. zool. Stat. Neapel, V, 1884, pp. 161–195, pls. 8, 9.

The new features which appear in the differentiation of the rays of these forms are four in number, viz:

(*a*) The atrophy of a number of actinotrichia at the bases or along the whole width of the fin-folds, as a result of which absolutely eradiate interradial spaces are formed.

(*b*) The coalescence of a number of actinotrichia and their fusion within a membranous matrix in order to form a basis for the ossification of the "soft rays" or malacopterygian type of fin-ray.

(*c*) The dichotomy of the soft rays due to the manner in which the actinotrichia are fused and drawn together antero-posteriorly at their proximal ends.

(*d*) The segmentation of the soft rays, the segments increasing in number with age, so that it seems that the segmentation is due to a kind of transverse fracture during their development due to use in swimming, as would seem to be indicated by a microscopic examination of the articulating ends of the segments, which seem to be widened terminally by the pressure on alternate sides brought to bear upon them.

Another advance is made in the development of the acanthopterygian type of fin-rays or "spines," which are mainly confined to the Physoclistous types of Teleosts, where they develop in more or less clearly distinct epiblastic pockets in advance of the continuous fold which gives rise to the malacopterygian, dichotomous type of rays. Good examples of this style of development of spinous rays are seen in *Lophius* and *Gasterosteus*. It is doubtful if spinous, simple rays are developed from actinotrichia at all, but from membrane formed by the mesoblast and molded upon the inner walls of epiblastic pockets.

While the Teleostean series, as a rule, develops a lophocercal stage, there are notable exeeceptions, and it frequently happens that when the median continuous fold is formed the actinotrichia are not developed simultaneously throughout its whole extent. Only in types which are apparently primitive, such as the Salmon, do the actinotrichia of the entire fold develop so as to be visible along its whole extent. But the continuity of the fold is soon interrupted by the atrophy of the intervals between the median fins.

It is thus made obvious to the discriminating student that embryology is just as capable of supplying data of taxonomic value as a study of outwardly palpable features or as a study of the anatomy of a series of forms. But the obvious disadvantage under which anatomy labors is that it cannot safely surmise what genetic relations are indicated by the morphology of the completed or adult organism, for the reason that it cannot indicate the order and method according to which the various parts made their appearance. The blundering on the part of anatomists in this respect is notorious, and is only excelled by the careless taxonomist who is in search of differences for the sake of discriminating new species, while he is in absolute ignorance of how such differ-

ences arose. Happily such taxonomic methods are becoming a matter of the past, and it will not be long before it will not be the misfortune of the conchologist to name the "spat" stages of the oyster as distinct species, or for the ichthyologist to erect "families" upon the characters presented by larval fishes.

The truth is, that if embryological, internal or external, anatomical characters are each taken separately they will lead to diverse results, and just in proportion to the superficiality of the characters upon which names are based in just that proportion will there be uncertainty as to the relations of the discriminated forms in the minds of subsequent investigators who may have other forms to compare or better specimens to study. So it will not be by means of embryology through a study of a single character or group of characters or with the help of external or of internal anatomy alone that we can be guided, but by all three combined, with such help from distribution in space as may be accessible in the case of living organisms. The method of the palæontologist is necessarily different, but even that does not afford an apology for the treatment of now-living forms according to a widely prevalent but fundamentally wrong method.

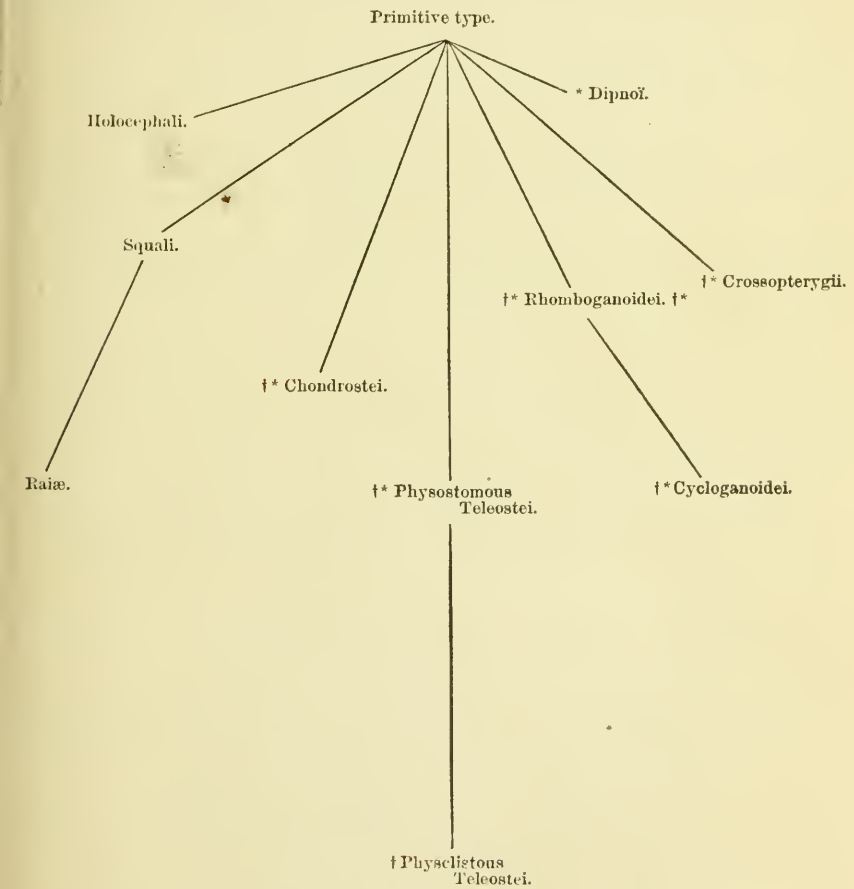
To cite an instance in illustration, most persons would suppose that there was no reason to suspect that the ventral fins of a Sea-robin or a Toadfish had not always been inserted in advance of the pectoral. There have been theorists who have thought differently, Owen amongst the number, but it was not until the embryological observations of A. Agassiz put us in possession of the data from which to formulate it as a fact that in some instances at least the ventral fins of the embryos of Physoclist fishes originate behind the pectorals, and are suddenly shoved forward, below and in advance of the pectoral. This information gained, we are in a position to state with positive certainty that the relative position of the paired fins of Physoclist fishes was preceded in time by one in which they were more nearly in the same relative position as in the existing physostomous forms. No possible construction of the facts of the anatomy of the adults could have given such conclusive evidence in favor of what becomes an obvious truth in the light of ontogenetic investigation. Moreover, the facts of the anatomy of Physoclists become at once of greater interest, for the crossing of the nerves which supply the paired fins is satisfactorily explained.

To return, however, to the discussion of the fact that parts of structures vanish in an order exactly the reverse of that in which they appeared, we may recur to the Salmon, in which the preanal fin-fold atrophies or disappears in a manner exactly the reverse of that presented by its appearance. During its outgrowth it slowly widens or becomes higher, while during its atrophy it becomes gradually lower and narrower, until all outward evidence of its existence vanishes.

Where new complications of development occur, when new structural details are added to pre-existing ones, as in the case of the fins, it is very clear that this process is often actually accompanied by one of atrophy,

for it is found, in the first place, that, as a rule, the median fins, for example, begin their development as uninterrupted folds. Only one type, the Dipnoï, has retained this pre-eminently embryonic character, all other fish-like branchiferous Chordata (not considering the Leptocardians and Marsipobranchs) very soon show a tendency to depart from such a primitive condition. In consequence there is atrophy of certain portions of the fold, while others hypertrophy, and the included actinotrichia become involved, and new features arise from primitive ones, some being actually superimposed upon older ones.

It is difficult to arrange the groups of fishes in a satisfactory way by the help of any one character or group of characters, and it is especially difficult to indicate by the help of an ideal tree what seem to be their actual genetic relationships. The best way to indicate changes in the grade of development would be to consider the most embryonic form nearest to an ideal type from which there has been divergence and specialization in various directions, thus:



The groups indicated by an asterisk are physostomous, and in the diagram the length of the diverging lines is intended to show the de-

gree of morphological differentiation of the fins, or the approximate extent of departure from the primitive type in reference to this one feature. The groups indicated by the mark † are those in which true interradial spaces are developed, these being the least prominent in the Chondrostei, which therefore depart least from the still more primitive Dipnoï. Objections may be raised as to the plan of this diagram as indicating relations, but it seems to me to be far more in keeping with legitimate scientific method to refrain from indicating phyletic relations until our knowledge is comprehensive enough to include an analysis of *all* the characters of a series of groups, so as to be able to represent their true relations. This diagram aims only to illustrate the relations which appear to subsist between ten of the major groups of fishes, as indicated by the development and morphology of the fins and fin-rays.

The Rays have been placed higher than the Sharks in the diagram because their horn-fibers or actinotrichia are degenerate in the paired fins and their organization otherwise specialized. If, however, I were to consult the mode of outgrowth of the other elements of the paired fins in the Rays, during which these organs maintain their primordial relations to a greater extent than in other Elasmobranchs, I would be obliged to rank them much lower than the Sharks. If, therefore, we take development as a guide, we are often forced to admit that one set of organs has advanced in organization or has remained stationary, or even may have become more or less degenerate and thus reverted in that feature to an older and more embryonic type. The question which then arises in estimating the value of such characters in taxonomy is in which one of these three ways the characters of the forms under consideration have arisen.

This is not always an easy matter, as we will find if we turn for a moment to the consideration of the three above-specified methods, according to which single organs and groups of organs are developed in some given form.

(*a*) Taking the first case, or that of advancement, we may find that a process of *evolution* has specialized one feature, which in turn has clearly exerted a stunting influence, or one of *retardation*, upon another, or the reverse. In this way new features arise upon which new species may be founded.

(*b*) In the second case no evolution, accompanied by the addition of new elements of complication to already existing, fully-developed, or partially degenerate organs, is taking place, and we may designate such a state as one of fixity or *stable equilibrium*. Such an attained equilibrium of the working of the life forces of an organism as a whole, as is shown by adult forms, enables the naturalist to discriminate *species*, otherwise a taxonomy would be logically impossible, because there could then be no such thing as *species*. An orderless, lawless variation of organisms would then make an end of all taxonomic method.

(*c*) The third case is one which is often difficult to distinguish from a case of *evolution* or one of *stable equilibrium* for reasons presently to be given. This case is often designated by the terms *degeneration*, *degradation*, *retrogressive development*, *retardation*, and other like words and phrases. But at the very outset we may be confronted by an inquiry as to how such degeneration arose, and also be asked how we know that it is an actual degeneration. A study of development indicates that anatomists have often used the terms indicative of degeneration hastily and in an ill-considered sense. In order that my meaning may be made clear it will be necessary to consider the possible ways in which degeneration, real or apparent, may arise, and in this quest embryology will be our best guide. In order to make our meaning the more directly applicable here the illustrations used will also be drawn from studies upon fins and similar processes of the bodies of fishes. What holds there is applicable as a general principle elsewhere. As it is, it is evident that there are several types of degeneration, so called, some of which cannot be properly included under the one same term.

(*aa*) True or *actual* degeneration may be defined as that sort which is witnessed when, for example, the preanal fin-fold of the Salmon is developed to the protopterygian stage, with a row of actinotrichia on either side, but is soon after absorbed so as to disappear completely, and long before the animal is fully developed. Another illustration is that of the suctorial disk of *Lepidosteus*, which disappears in like manner, leaving but very slight traces of its existence in the adult. Such a method of degeneration, which involves the total atrophy of a structure, embraces, for the most part, in the range of its action only so-called larval characters. This type of degenerative action is operative within the life-time of an individual.

(*bb*) The next subtype of apparently retrogressive development is probably not actually retrogressive, if it is intended to apply the expression in its strictly literal meaning, but is only apparently so, at least in many cases. An instance of that is the "adipose fins" of fishes. These have developed as far as to the stage represented by the fins of the Dipnöi, but have been arrested at that stage and have advanced no farther. It would therefore be pure hypothesis, unsupported by any evidence whatever, to assume that that type of fin had been derived by *degradation* from a dorsal in which there were wide interradial interspaces between true bony rays. Far rather let us suppose that the development has been so *retarded* in its advance toward the evolution of the Teleostean type of fin as to preserve the older Dipnöan condition. The term *retardation*, so often used by Cope, expresses the facts of the case far better than to say *degeneration*. This applies, however, so far as we can see, only to individual development, beyond which embryology, it must be admitted, does not afford anything more than hypothetical clews.

In many cases degradation of some structure has, however, certainly occurred. A most notorious case of this kind is that of the Whales, which have lost their functional hind limbs. On investigating the condition of the *vestiges** of these limbs we find that the skeletal parts have actually been arrested, as to the *extent* of their development, at a point corresponding to an early embryonic stage, beyond which they fail to advance. We are now ready to ask where this curtailment of development began, and we find that there is logically no way out of the difficulty except to admit that the retrogressive metamorphosis must have begun after birth in each and every one of the series of individuals constituting the race, because there could be no equilibration between extrinsic forces on the one hand and intrinsic or organic forces on the other as long as the fœtus was protected and incapable of free movement *in utero*. I see no escape, therefore, from the conclusion that the second sort of *degeneration*, designated by the word *retardation* for embryological reasons, has actually arisen in many instances through a very slowly acquired undoing of development or loss of parts through an extended series of adults which have as slowly transmitted these increments of loss or degradation, which so far as we can see is now tolerably stable, though far less so than the development of functional structures, as has been shown by the researches of Struthers.

The distinction between the type of degradation under *aa* and that under *bb* is that in the first the atrophy or loss of a part is an *ontogenetic* process, while in the other the degree of degradation of a part is acquired and becomes fixed by hereditary transmission, and is therefore presumably a *phylogenetic process*, because we see no evidence of any gradual atrophy of such parts in the course of the ontogeny of the animal.

Another illustration of the use of the method of embryology is found amongst the Catfishes. The genus *Noturus* has the adipose dorsal fin adnate and continuous with the caudal, while in the genus Amiurus there has been a decided advance upon the former arrangement, for the reason that in it the adipose dorsal is separated by a wide interval from the caudal. *Amiurus*, during its development, actually recapitulates very closely the stage represented by *Noturus*, which indicates that the latter is taxonomically lower in rank than the former. And just in this instance we also have a very good illustration of a principle of development which ought to make anatomists cautious in the use of the word "degeneration." While I see no evidence whatever of degeneration in *Noturus*, I do see very obvious evidence of arrest or retardation of development of its adipose fin at a point corresponding to a transient stage in *Amiurus*. That is to say, this fin in *Noturus* has been perma-

* Structures which are disappearing should be called *vestiges*. Structures which are still imperfect but are appearing ought to be called *rudiments*. As it is, the word rudiment is usually misapplied, so far as concerns its literal sense, when speaking of "rudimentary organs." Such a distinction it seems to me is important.

nently arrested and held at a certain point in the developmental scale of *Amiurus* without any very obvious signs of concomitant atrophy. The phylogenetic as well as ontogenetic modes of degeneracy are therefore both obvious in the adipose dorsal of *Amiurus*, but neither mode is more than faintly evident in that of *Noturus*, where the fin in question is large, and permanently, or almost perfectly, retains its embryonic proportions.

The median fin-folds of the lowest Chordata, viz, *Branchiostoma* and *Petromyzon*, are not supported by actinotrichia, but in the last, especially, by dichotomous median cartilaginous rods wholly of mesoblastic origin in the median tract. The Amphibia agree with them so far as to have no actinotrichia, as far as known, in the median fin-folds of the larvæ, and are without cartilaginous supports for the same parts. Whether the actinotrichia have degenerated in these last or not it is now impossible to decide, because if they are totally wanting, as they seem to be, it is now quite impossible to prove that they ever existed in their ancestors from any evidence based on now living species, unless the fossil remains of this type may have preserved evidences of their presence in the older and presumably more fish-like forms. If the Amphibia arose from some generalized type which gave rise to the fishes also, or to the most generalized of the latter, then it would seem not unreasonable to expect to find traces of the most primitive of all the types of fin-rays, namely, actinotrichia, preserved in some of the Permian or Carboniferous Amphibian remains.

A structure may, however, be completely suppressed, and for so long a period in some forms that their development will no longer recapitulate the complete story of their phylogeny. This is illustrated for Physostomous as well as for Physoclistous forms in the genera *Gambusia* and *Hippocampus*. Both of these last named genera have tended in fact to revert very early to what I have called the archicercal stage, the latter the most completely so of all known fishes except, perhaps, *Chimœra monstrosa* and *Gastrostomus*.

With this I may conclude the presentation of the evidence in favor of the use of embryological characters in the classification of fishes. Such characters, it appears to me, may be used with just as much propriety as any others; in fact with more, because the only possible way in which the genesis or origin of any and all characters can ever be properly understood is through a study of development. I have heard it stated by systematists that embryological characters were of little or no value in taxonomy; in fact I once thought so myself, but upon a wider acquaintance with the phenomena of development in certain groups I believe I am warranted in saying that just in proportion as our knowledge becomes more detailed and exact in reference to the small groups, just in that proportion will we be able to avail ourselves of such characters in taxonomy, and to appreciate exactly what is meant when we speak of degeneration or specialization.

It will be noticed that the results arrived at in respect to the taxonomic value of the characteristics of the development of the rays of fishes of the different groups are essentially in accord with the views of the best American authorities on the subject. The results here given re-enforce, it seems to the writer, in a remarkable way the views of Gill and Cope as to the systematic relations of the larger groups, and serve at the same time to indicate that the group Palæichthyes of Günther must be looked upon as a thoroughly unnatural assemblage of forms.