XXXVII.—ON THE ORIGIN OF HETEROCERCY AND THE EVOLUTION OF THE FINS AND FIN-RAYS OF FISHES.

By John A. Ryder.

"Alles Gewordene, im Reiche der Natur, wie in der Geschichte, ist nur durch sein Werden zu begreifen und die Entwickelungsgeschichte ist in diesem Sinn für den Naturforscher vollkommen dasselbe, was die Weltgeschichte für die Menschheit."—Bruch: *Wirbeltheorie des Schädels*.

INTRODUCTORY.

The following paper is the outgrowth of scattered observations made during the last four years on the development of fishes, and in order to make the results available, it has been thought best to bring them together in a permanent form. The portions which do not seem to the reader to bear directly upon the theory of the fins, which it has been sought to establish, may be regarded merely as collateral or supplementary, and are introduced to further illustrate the kinetic or mechanical hypotheses of evolution of structural differentiation through the voluntary or habitual movements of animals, which the author has previously advocated in other publications in relation to other sets of organs. Abstracts of some of the special results here published in full have already appeared in another place.*

The views here put forth in relation to the way in which the morphological differentiation of the fins of fishes has occurred, rest partly upon facts of my own observation, but I must express my great indebtedness to the researches of L. and A. Agassiz, especially the latter, and Vogt, Dohrn, Th. Lotz, Balfour, W. N. Parker, Huxley, and Kölliker, whose labors have prepared the way for me to co-ordinate many of the known facts and establish doctrines founded upon the theory of ontogeny, respecting the origin and differentiation of the fins, both paired and unpaired. Acknowledgments are also due from me to Professor Baird for the loan of valuable material from the collections of the National Museum, and to Dr. Bean and Mr. G. Brown Goode, who have called my attention to specimens which would otherwise have been overlooked. Finally, I must express my thanks to Professor Gill for the interest he has shown in calling my attention to extremely specialized types of fins in rare or aberrant forms, and for aid in obtaining information upon the literature of the subject.

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*1. An outline of a theory of the development of the unpaired fins of fishes, Am. Naturalist, 1885, pp. 90-97.

2. The development of the rays of osseous fishes, Am. Naturalist, 1885, pp. 200-204.

I.—TERMINOLOGY.

The names applied by different authors to the initial or larval stages of development of the Teleostean tail differ so greatly in their etymologies and their implications, that it is desirable not only to consider the terms hitherto proposed, but also, in order to be more precise, to add certain ones in order to designate phases of development and conditions of structure which have not been heretofore recognized.

The term *archicercy* and its adjective form *archicercal* will therefore be introduced here in order to define the cylindroidal, worm-like caudal end of Ichthyopsidous larvæ before they acquire median fin-folds.

Jeffries Wyman* in 1864 proposed the term *protocercal* to designate the larval condition of the tail of *Raia* when it had acquired median fin-folds. This term seems to imply that this primary form of the tail of larval fishes precedes in the order of time the subsequent conditions, or that it is the first stage of the evolution of the caudal fin. This term was adopted in the same sense by Wilder in his article, "Gar-pikes, old and young," Popular Science Monthly, XI, 192, 1877, where the condition of the tail of the larvæ of *Lepidosteus* was considered.

A. Agassiz† in 1877 considered the subject anew, and in an essay *On the development of the tail*, which is of great value from an embryological standpoint, proposed the term *leptocardial* for the same condition implied by the word *protocercal*, for the reason that young fishes in this stage showed a uniform and continuous development of the median fin-fold over the end of the body, very similar to the condition which is permanently characteristic of the vertical fins of the Leptocardians. If it is true, however, that the median fin-folds of the latter contain rudimentary cartilaginous basal rays or their representatives, the comparison and the choice of the name are slightly at fault, and is really not as appropriate as the one previously proposed by Wyman. Inasmuch, therefore, as the terms *diphycercal*, *heterocercal*, &c, refer to definitely understood structural conditions of the tail in adult forms, it seems not inappropriate, undesirable as it is to add another to the number of existing terms, to propose a new one to designate the symmetrical, eradiate condition of the continuous or discontinuous median fin-fold or folds of larval fishes, and which, like the terms applied to the description of the tail of the adult, shall have reference solely to structure and not imply anything as to an hypothetical parallelism with a lower type, nor anything respecting a supposed order of evolution. Such a term it is not difficult to choose, if we bear in mind that the earliest form of the caudal fin is little or nothing more than a fold of the skin which is composed entirely at first of epiblastic tissue, and that it does not include rays even of the most rudimentary kind. The term, therefore, which

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* Observations on the development of *Raia batis*, Mem. Amer. Acad. Arts and Sciences, 1864.

† On the young stages of Osseous Fishes, Proc. Am. Acad. Arts and Sciences, XIII, p. 123.

will not only describe this larval condition, but also be in harmony with the terms descriptive of the adult tail, will be, *lophocercal* and its derivative, *lophocercy*, which will imply that the membranous tail is formed merely of a fold of skin or epiblast, continuous with that on the axial part of the tail, and that the inner surfaces of this fold are more or less nearly in contact.

The next term will apply to the next stage of development as indicated by the most undifferentiated median fin-system as seen in *Ceratodus*, *Protopterus*, &c. *Diphycercal* and *diphycercy* will therefore imply a condition in which the end of the axial column bears not only hypural, but also epural intermediary pieces which support rays, as defined by Huxley. *Diphycercy* may coexist with *heterocercy*, and does not completely vanish until all of the rays of the caudal are supported by hypural spines only, or when an ideal *hypocercal* condition is attained.

The next stage of caudal development is attained in the *heterocercal* condition, when the hinder end of the vertebral axis is flexed upwards, and the words *heterocercal* and *heterocercy* throughout the present paper will invariably mean that such an upbending has happened, even if it involves the modification of but a single terminal vertebra.

The words *homocercal* and *homocercy* will merely express the epaxial and hypaxial symmetry presented by the fan-shaped caudal of Teleosts and other fishes. It is the final stage of the evolution of that fin.

Gephyrocercy and *gephyrocercal* are terms which will apply to the type of caudal structure appearing normally in only a few forms, such as *Mola* and *Fierasfer*. The end of the urosome in these forms, together with the posterior end of the chordal axis, is aborted. In consequence of this, the hinder epaxial and hypaxial tissues concerned in the formation of rays and their supports are approximated or swung round over the rayless interval existing over the stump of the axis, and by such a secondary process of growth the caudal fin-rays are formed, together with their interspinous supports. The interval between the vertical fins bridged in this way leads to the formation of gephyrocercal tail.

In the discussion of the neural and hæmal arches of the caudal vertebræ of heterocercal forms, it is also expedient to use some convenient terms which will indicate without circumlocution what is meant in speaking of the structure of these greatly modified elements. They will be spoken of as spineless if they are without dorsal or ventral spines, or as dorsally spineless, or as ventrally two or three spined, as in the case of the concrescent hypural bones, or as dipla- or triplacanthous.

The caudal part of the axial column may be perfectly *monospondylic*, that is, each of its vertebræ may have its dorsal and ventral spine, or every alternate vertebra may have these aborted, and thus become reduced to a centrum only, or become *diplospondylic* in the terminology of Von Jhering, or every alternate centrum may be said to be spineless.

The meanings of the terms *epural* and *hypural*, as applied to indicate the position of the caudal apophysial elements in reference to the centra, are used in the sense in which they were first used by Huxley in 1859 in his discussion of the development of the tail of *Gasterosteus*.

The word *opisthural* applies to apophysial elements in contact with the under side of the urostyle, but separated from the hypural pieces by an interspace, as in *Amiurus*.

The whole of the body of fishes from the vent backwards to the end of the tail will be frequently spoken of as the *urosome*. The exserted, or rather the degenerated, portion behind the urosome, as found in *Stylophorus*, *Chimæra monstrosa*, and the larva of *Lepidosteus*, will be called the *opisthure*, because it is behind the true or secondary caudal, which is developed after the former has begun to lose its function through the substitution of the latter. The word *opisthure* is by no means synonymous with *urostyle*, because it includes more, as in some of the cases mentioned above. It comprises the end of the chorda around which the osseous urostyle is developed; bands of muscular tissue on either side, which are frequently rudimentary or imperfectly formed myotomes or muscular segments, beside connective tissue, the whole being covered externally by integument, which is continuous with that over the rest of the body.

In the case of a perfectly lophocercal form an imaginary horizontal plane cutting longitudinally through the center of the notochord will divide the urosome of a larval fish into an inferior and a superior half, and these halves may, roughly speaking, be said to be the dorsal and ventral counterparts of each other. All of the skeletal elements above the notochord may therefore be said to be *epaxial*, those below it *hypaxial* in position. This also applies to the median skeletogenous tract, the parts of which may be spoken of as epaxial and hypaxial in position.

The *skeletogenous tracts* of fish embryos seem to be largely intermuscular or intersegmental, perichordal, hypaxial, and epaxial, so that it is possible to trace the segmental development of the median and paired fins in early stages, and leads us to suspect that such a segmental arrangement may be effected from such *loci*, and thus determine the relations and serial arrangement of the rays and basal pieces of all of the fins. While the development of the rays and their proximal supports is often obscured by processes of coalescence, degeneration, and shifting, due to growth, future ontogenetic studies will unquestionably place the theory of all of the fins upon some such solid basis of observed fact. When the *skeletogenous tract* is spoken of here it is used with such implications.

The *embryonic skeleton* is at first mainly cartilaginous, and around or in this cartilage—usually the former—ossific deposits are laid down in a peculiar homogeneous kind of membrane which invests the cartilages (*Teleostei*). This sort of a *homogeneous membrane* may appear in the skeletogenous tracts of definite regions nearly as soon as cartilage, as in the case of the membranous rudiments of the shoulder-girdle of Teleosts.

The development of the *rays* seems to begin peripherally in the fin-folds in membrane and approaches the *basilar interneural* elements from without, these latter being the most peripheral of the median series, which are developed in true cartilage from mesoblast. The rays are therefore sub-epiblastic, though their proximal ends may embrace nodules of cartilage of epaxial and hypaxial mesoblastic origin. The words *peripheral*, *distal*, and *proximal* will, therefore, be occasionally met with as used above.

The words *concrescence*, *coalescence*, are usually synonymous here as applied to describe the blending of series of bars of cartilage. The terms *homonym* and *homonomous*, *segmental*, and *metameric* are nearly synonymous in some cases. *Homonomous*, *homonomy*, *homodynamous*, and *homodynamy* are used in the sense defined in Gegenbaur's Elements of Comparative Anatomy. The term *serial homology* (Owen) is equivalent to the last of the above-mentioned words. *Metamerism* refers to the segmented condition of the vertebrate embryonic, and even, in fishes, to the adult axis, in which we find similar successive segments or *somites*. The word *urochord* is used a few times to designate the membranous part of the axis of the embryo when it is exserted beyond the hypural cartilages, to distinguish it from the ossified urostyle of the adult.

The term *protopterygian*, to designate the stage when the embryonic fin-rays first appear, was chosen to designate that condition when it may be said that true fins first appear. *Pterygoblasts* refers to the protoplasmic bodies from which the embryonic fin-rays are developed. The word *orthaxial* is used to designate the archaic straight type of vertebral axis, which is not bent upwards at its posterior extremity.

The word *actinost* as used by Gill applies only to the distal cartilaginous or bony elements of the limbs of fishes, which support the rays, or those more especially of Teleosts and Ganoids resembling them, and, inasmuch as these elements are clearly those from which their isomeral equivalents are evolved in the higher forms by concrescence, their homology throughout the *Lyrifera* becomes apparent, though very frequently fusion has occurred to form elements called the pro- meso- and metapterygium. Regarding the whole of the mobile axial skeleton of the limbs of the *Lyrifera* as essentially homologous, I will call the distal parts which directly support the true rays *actinophores*. While the Teleosts have had these elements much shortened as compared with the same parts as found in the Rays amongst Elasmobranchs, such a shortening is merely the result of extreme specialization growing out of adaptation. The basilar interneural and interhæmal nodules in this terminology become median epaxial or hypaxial *actinophores*.

II.—THE THEORY OF THE DEVELOPMENT OF THE MEDIAN FINS.

The median fins of fishes normally present five well-marked conditions of structure, which correspond to as many stages of development, which in typical fishes succeed each other in the order of time. A sixth exceptional form is developed in consequence of an extensive degeneration of the chordal axis and hinder end of the urosome, unaccompanied by the upbending of the axis, as in the case of heterocercy. The most archaic stages, or those found to appear during the younger phases of growth of fishes, are approximated by the structure of the fins of some of the most ancient Devonian, Triassic, and Jurassic forms, and by such living forms as *Chimæra*, the Dipnoans, Leptocardians, and Lampreys, but the parallelism of the development of the tail of young fishes with the successive modifications of caudal structure found in the forms of successive geological periods is not exact, as we shall presently show.

(1.) *Archicercy.*—The most primitive modification of the urosome is that which I will call *archicercal*, and which is characterized by the absence of any fin-fold whatsoever. While it is true that only a few degenerate or specialized forms of true fishes, such as *Hippocampus*, *Nerophis*, &c., permanently approximate such a condition, it must be admitted that the fins are acquired structures, and that the folds from which they are developed have been acquired in the course of the evolution of the ancestry of the fishes. The probability is that the history of the lateral fins is similar; that is to say, inasmuch as the paired fins of the lower types possess a greater number of rays (basalia) derived from the ends of the buds thrown off from the lateral somites than those of the higher forms, it would seem that the lateral folds which led to the differentiation of the pectoral and pelvic limbs were at first much longer than at present, possibly continuous with each other; such a conclusion would be favored by the presence of the large homodynamous series of cartilages which enter into the formation of these fins in Dipnoans and Elasmobranchs. The archicercal condition justifies such a conclusion, for during its persistence in normal forms there is little development of the rudiments of the paired fins; notwithstanding this, however, a noteworthy objection may be raised against this conclusion, which I have stated elsewhere.

When a young fish is developing in the egg its tail grows out at first as a blunt prolongation backwards of the body, which is for a time wholly without fin folds, and is cylindrical and vermiform in general appearance, with the muscular somites clearly marked.

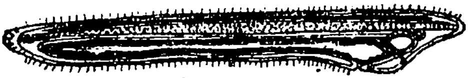


Fig.1.

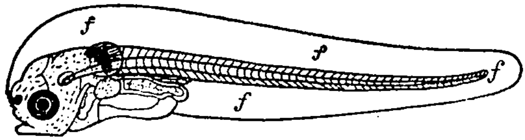
The larva of *Branchiostoma* (Fig. 1) is without median fin-folds, and that of *Petromyzon* seems to be without them during the very early stages, and, while we must make due allowance in both these cases for the effects of degeneration, we may, I think it probable, look upon these types as possessing at one stage a typically archicercal and vermiform tail. The solitary urochordate forms or Ascidians pass through an archicercal stage of development of the urosome, according to the observations of Kowalevsky on *Phallusia mammillata*, and of Kupffer on *Ascidia mentula*. In the course of further development the Ascidians never seem to pass beyond what I have called the second or lophocercal stage, when the tail is absorbed in the caducichordate forms, but persists in the same stage in the perennichordate *Appendicularia*.

The Elasmobranchs seem to pass through an archicercal stage, while the Amphibians do not usually exhibit it in so pronounced a way, very soon becoming lophocercal, though the larva of *Dactylethra* has the anterior part of the urosome, with high median folds, while the termination is somewhat like that of *Chimæra monstrosa* (Fig. 2), but tapers more and is typically archicercal. After the absorption of the lophocercal tail of an anurous amphibian larva has been in progress for some time, it seems to tend to lose its median folds somewhat and revert to the archicercal condition. This is also the case with the young of most *Urodela* as they approach maturity.

Fig. 2

(2.) *Lophocercy.*—The second stage of development of the median fin system of *Ichthyopsida* is what I have called lophocercal (= protocercal, Wyman; = leptocardial, A. Agassiz) when it consists of continuous (Amphibia, Elasmobranchs, Teleosts, &c.) or exceptionally of discontinuous folds (*Siphostoma*, *Gambusia*), which do not include true permanent rays, but may at about the close of this phase contain the numerous fine embryonic rays of what may be called the protopterygian stage of development of the permanent fin-rays. The continuity of the median fin-fold in embryo fishes, as shown in Fig. 3 in the embryo cod, seems to depend somewhat upon the extent to which the permanent fins are approximated so as to form a more or less completely continuous system in the adult. Several forms amongst the Clupeoids develop an expanded eradiate caudal fold, with the chordal axis dividing it into equal moieties, which thus anticipates the outwardly homocercal tail of

Fig. 3.



the adult. Beyond the lophocercal condition the typical fishes at once diverge from the rest of the *Chordata* and *Urochorda*, in that they develop groups of permanent rays in definite regions of the median finfold or continuously throughout its entire extent, and thus give rise to the distinct or continuous fins of the adult. The intervening parts of the fold in the first case atrophy, thus locally reverting to archicercy, the materials for the formation of the rays and their supports being supplied by the mesoblast which proliferates into the median fin-fold. The disposition of the materials for the development of the permanent rays of the unpaired fins seems to be under the control of heredity, which determines their permanent location or position in the primitive folds, which may be considered the matrix of the permanent fins.

In the formation of rays and their supports and musculature there is clearly a close correspondence between the number of ray-bearing somites of the body and the one, two, or three rays and supports which are developed to each segment, and this is manifested even when heterocercy and its accompanying degenerative processes manifest themselves in the caudal region of the most specialized forms. We find, in fact, that where apparent coalescence of two hypural elements has occurred, two corresponding mesoblastic thickenings of the caudal fold are developed, which extend from the lower end of the hypural pieces to the margin of the fold, and in and upon which the future permanent ray is molded. This segmental proliferation of mesoblast is possibly favored by the intersegmental disposition of the blood-vessels.

(3.) *Diphycercy.*—The most primitive disposition of the median fin-rays is a continuous one, as is indicated by the embryological evidence of the existence of a multiradiate protopterygian stage, and is hypaxial from in front of the vent in many cases, extending backward over the end of the tail, thence epaxially and forward dorsally (*Cœlacanthi*, *Placodermi*, *Dipnoi*, Fig. 4). Another archaic trait which also marks a phase of the ontogeny of the Teleosts is the cœlacanthus (hollow) condition of the bony portion of the neural and hæmal spines and the interspinous elements. Fishes with a long, eel-like body have tended to remain diphycercal, while those whose bodies have been abbreviated have tended, with the exception of such forms as the Flounders, or *Heterosomata*, to develop discontinuous median fins, which have been derived from hypertrophied portions of a continuous series. This hypertrophy in some cases involved the whole series, e.g., *Platax*. The primæval diphycercal condition is followed by the next stage, which grows out of the former in the course of further local degeneration and specialization, with a secondary upbending of the hinder end of the chorda. This view is fully substantiated by the development of the caudal skeleton of the eel, in which, in spite of its slight heterocercy, the diphycercal continuity of the fin series has remained prac-

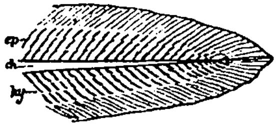


Fig. 4.

tically unimpaired, thus affording the necessary proof of the *serial homology* of the entire series of median fin-rays and their intermediary supports. Previous authors failing to attack this part of the problem by the light of the ontogeny of a diphycercal, eel-like type, have missed the solution of one of the most important minor parts of a rational theory of the median fins, since it is otherwise impossible to prove the existence of such a homology in forms with atrophied intervals between the vertical fins. The existence of the protopterygian stage also tends to prove this view to be correct. The skeletogenous tract, from which the whole of the median fin-rays and their supports are developed, is continuous in the median line of the urosome, above, below, and over the end of the chordain fish embryos; such continuity affords an explanation of why the median fin-rays form an uninterrupted series in the case of perfectly diphycercal forms, or where the archaic has not yet been replaced by a specialized mode of development. Such an archaic condition is actually retained with but slight impairment by the embryo of the salmon, which has a nearly continuous series of embryonic fin-rays.

(4.) *Heterocercy.*—Heterocercy affects only the end of the chordal axis which is bent upwards (Fig. 5), as a result of which it and the later formed terminal vertebral segments are consolidated into a urostyle (in many *Teleostei*), above and below which epaxial and hypaxial elements are formed, of which the former are, however, often aborted and the latter widened as supports for the caudal system of rays. This condition appears to result from two causes, (1) great activity of growth in the terminal hypaxial part of the primitive fin-fold, in consequence of which the chorda is shoved upwards, and (2) by the actions of the animal in using the resulting expanded hypaxial caudal ray-bearing fold in swimming; the strokes of the fin in action, owing to the resistance offered by the water tend to throw up the somatic axis, just as an oar tends to be thrown upwards when used in sculling.

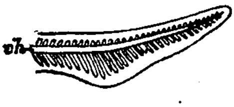
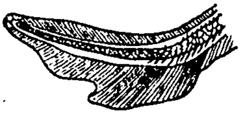


Fig. 5.

Since the hypaxial fold may be developed at some distance from the end of the tail, in the more specialized forms (*Lepidosteus*, *Gasterosteus*), a more or less free portion of the lophocercal caudal axis is left to project during the growth of the true caudal, as shown in Figs. 6 and 7. This part of the larval axis, which may be called the *opisthure*, subsequently degenerates, or it may persist as a prolongation of the

Fig 6.



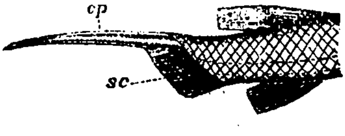


Fig. 7

chordal axis, as in the diphycercal *Chimæra monstrosa*, or, as in heterocercal *Amiurus* (Fig. 8), it may, at an early stage, have the chorda exserted beyond the last hypural cartilages, and at some distance behind them have another hypaxial cartilage developed, which may be called opisthural, as it probably represents the remnant of proximal hypural pieces, which were developed in some more archaic ancestral form, in which diphycercy was more pronounced or even perfect. Where the caudal ray-bearing fin-fold is developed nearer the end of the chordal axis (*Apeltes*, *Siphostoma*, *Gambusia*) heterocercy is not so pronounced, as the urostyle is shorter, and only a part of the terminal vertebræ are involved, whereas in other cases (*Salmo*, *Lepidosteus*) more terminal vertebræ may be implicated by degeneration. In archaic forms of heterocercy there may be some epaxial rays and intermediary supports developed, while the hypaxial supports and rays extend to the end of the upwardly bent termination of the axial column. This trait may possibly differentiate the archaic type of heterocercy (*Palæoniscus*, *Platysomus*, *Acipenser*) from the more recent or specialized form (*Amiurus*) now prevalent amongst Teleosts, and which have for the most part a more or less well-developed urostyle, but with a very short or included opisthure (= dorsal lobe, Agassiz), and with epaxial spines of the urostyle displaced, rudimentary, or aborted. Outwardly homocercal Palæozoic fishes (*Dapedius*, *Pycnodus*) probably had an opisthural filament developed in their larval stages, which subsequently aborted, as in *Lepidosteus*, but in others (*Platysomus*, *Pygopterus*) the terminal part of the chordal axis doubtless became segmented, the segments bearing hypaxial caudal rays and few or no epaxial rays, so that the opisthure was probably rudimentary.

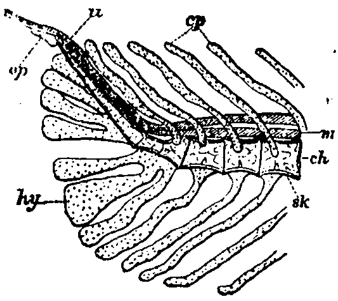


Fig. 8.

It thus becomes evident that the development of modern Teleosts presents only a partial or inexact parallelism with that of the Palæozoic *Rhomboganoidei*, for few, if any, of these forms show the urostyle so distinctly developed or the hypural pieces so extensively co-ossified as in existing Teleostéi. The *Rhomboganoidei*, *Crossopterygia*, *Cycloganoidei*, and *Chondrostei* show a more decided tendency towards the development of a continuous dorsal and ventral or only ventral series of caudal rays, and thus trend more towards a diphycercal condition than the existing *Teleostei*, which may be said to be verging towards *hypocercy*, when all of the caudal rays will be of hypaxial origin, with frequently a rayless hiatus behind the last hypaxial pieces and the end of an exserted urostyle. These are some of the marks of progress which distinguish the Teleosts and supplement the significant fact of their well-ossified skeleton. It is probable that we have no remains of the larvæ of Palæozoic fishes preserved in the rocks, so that we have no means of contrasting their early phases with those of existing forms, but it is certain that none of the most simple forms of the Palæozoic fishes, in respect to their skeletal structure, even approximate such a primary condition as the lophocercal stage. Of modern forms, the only trait which they possess in common are continuous median fins, in the first, containing permanent rays, the latter without them, but at most provided with embryonic fin rays only. When we know the larvæ of *Ceratodus, Polypterus, Lepidosiren*, and *Protopterus* as well as we know that of *Lepidosteus* we may have a more comprehensive understanding of the main features of the larvæ of Palæozoic fishes.

The evidence in favor of degeneration of the caudal region is the existence of a permanent archicercal opisthure in *Chimæra monstrosa* and *Stylephorus chordatus;* the extensive development of a temporary opisthure in *Lepidosteus;* the concrescence of the hypural pieces; the ventrally diplacanthous and even triplacanthous caudal vertebræ or their coalesced representative, the urostyle; the existence of hypaxial opisthural elements; the abortion of the epaxial spines of the caudal vertebræ, and finally the abortion or extreme modification of the last muscular somites of the caudal region.

(5.) *Homocercy.*—This merely expresses the condition of epaxial and hypaxial symmetry presented by the fan-shaped caudal of Teleosts, and is the final term in the evolution of the growth of the rays of that fin, in consequence of which the archaic symmetry of perfect diphycercy becomes again restored though the structure of the tail is heterocercal.

(6.) *Gephyrocercy.*—This type of tail appears to be normally met with in only two forms, of Teleosts, namely, *Mola* and *Fierasfer*. The primitive opisthure or end of the urosome in these forms is apparently aborted in the first case, in the course of larval existence; in the other, during post-larval life. As a result of this a hiatus is left between the epaxial and hypaxial rudiments of the median fins, and in the center of this hiatus the axial column ends abruptly as if cut or bitten off. The hinder hypaxial and epaxial tissues concerned in the formation of rays and their supports are then approximated and developed later than the other median fin-rays, and the interval so bridged by a secondary process of development leads to the formation of what we may call a gephyrocercal* tail.

III.—ON THE DEGENERATION OF THE POSTERIOR PART OF THE AXIAL SKELETON OF FISHES.

There is undoubted evidence of the extensive degeneration and consequent modification of the caudal part of the vertebral axis of fishes. This is apparent upon making a study of the tail of the entire series of

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* γέφυρα, bridge; and κέρκος, tail.)

Teleosts and one of the *Holocephali*. The complete absorption of the tail of the larval *Anura* is also interesting in this connection, and, as already suggested by Huxley, may account for the development of the styliform, unsegmented urostyle which terminates the vertebral column in adult *Anura*, as an ossification of the proximal part of the chordal axis of the tail of larva.

It may be that the intestine terminated much farther posteriorly in the most primitive forms of the *Vertebrata*, when they were more worm-like, with a terminal anus. With the degeneration of the body-cavity, and its specialization anteriorly, the caudal region probably became rudimentary, and was either partially absorbed, or became specialized into a portion of the body the sole office of which was to aid in locomotion. With this acquisition of a new function the degenerating tail has passed through a remarkable series of changes, which left the posterior axial elements to atrophy more or less, while their hinder appendages, which were more or less well preserved, became intermediary supports for appendicular rudder-like organs or a fin-skeleton developed in the skin. *Polypterus** shows how far back and near the tail the body-cavity may extend. As extremes of the opposite kind may be cited the entire group of the *Heterosomata* and the case of *Orthagoriscus*, fully discussed in another place. This last-named case of extreme reduction or degeneration surpasses even the specialized condition found to obtain in the tail of *Hippocampus*.

In *Gastrostomus* we meet with a condition of the vertebral column resembling its condition in the allied form *Eurypharynx*, writing of which it has been said by Vaillant that its body seemed in its progress to the tail to lose its bones and be converted into a sort of tough and gristly appendage. While such a statement is hardly true of *Gastrostomus*, the caudal portion of the axial skeleton is exceedingly degenerate, the vertebral segments long but without distinct upper and lower arches, and so little ossified as to consist of very little else than the membranous notochord, which actually does appear to constitute the extreme terminal part of the axis of the body. This condition therefore recalls the structure of the tail of *Chimæra monstrosa*, with its caudal axis prolonged as a filament, or that of the singular type called *Stylephorus* by Shaw.† The caudal filament of *Stylephorus* is, however, twice the length of the body, or 22 inches. The "caudal" fin consists of five epaxial spines, if Shaw's figure is trustworthy. The form therefore has no true hypaxial caudal rays, as in nearly all Teleosts; in fact

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* *Polypterus* also has the ribs passing outward through the lateral muscles to the skin anteriorly, somewhat as in the sharks, while they girth the body-cavity posteriorly, as in other fishes. The character which Balfour insisted upon as one which distinguished the sharks from Ganoids and Teleosts, therefore, has no great taxonomic value, unless this trait of *Polypterus* should be found to be characteristic of all of the Crossopterygians and not be found in any other fishes.

† Shaw's Naturalists' Miscellany, VII, Pl. 274.

Shaw's figure shows that there are absolutely no hypaxial rays developed, nor does the accompanying description mention them. The form therefore contrasts morphologically with *Gymnotus*, which has no dorsal or epaxial system of fin-rays.

Dohrn* has lately published some interesting and important speculations upon the phylogenetic origin of the paired and unpaired fins. He lays particular stress upon the presence of a postanal gut in fish embryos as determining the abortion of the preanal unpaired median fin-fold, and its division into two ventro-lateral folds, which he thinks it conceivable were derived from the parapodia of a worm-like ancestor. The abortion of the postanal section of the gut in vertebrate embryos has permitted the approximation or coalescence medially of these primitive lateral folds or metameric series of papillæ from which parapodia have been evolved in worms, and which led to the differentiation of paired fins in their vertebrate offshoots. Since Dohrn's investigations have undoubtedly shown the archipterygium and cheiropterygium hypotheses of Gegenbaur and Huxley to be utterly untenable, as had been pointed out before by Balfour, there are still some difficulties in the way of Dohrn's own conclusions, which seem to me to be serious enough to be worthy of passing notice. What is here referred to is the presence of preanal unpaired fin-folds in certain forms of fish embryos, as in *Alosa*, *Pomolobus*, *Salmo*, *Coregonus*, *Cybium*, *Lepidosteus*, &c.,† and which would indicate that the presence of the intestine in these instances had not exerted the influence which he has suggested. In *Alosa*, *Pomolobus*, and *Lepidosteus*, this preanal fold, contrary to what is found in Elasmobranchs, is especially well developed. It is therefore evident that Dohrn's view of the origin of the median folds does not hold for all of the *Ichthyopsida* without some modifications.

Dohrn is right, however, in the view that what I have called the urosome is a structure secondarily developed, for, as he points out, we know from the researches of Goette on *Bombinator*, Kowalewsky and Hatschek on *Amphioxus*, and Balfour on the Elasmobranchs, that there exists an open communication between the primitive neural tube and the intestine by way of a *neurenteric canal* and *postanal gut*, and that while such a relation is obscured somewhat in Marsipobranch and Teleostean embryos, traces of it nevertheless exist even in those types. The tendency to develop an anal opening considerably anterior to the end of the tail after the archicercal or worm-like condition is passed over, while the postanal section of the gut atrophies instead of developing a quite terminal anus after the manner of many worms, is very significant, and would indicate that we have here an instance of degeneration manifesting itself at a very early period. This process of degeneration by which in reality an advance is made upon the more prim-

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* Studien zur Urgeschichte des Wirbelthierkörpers, Pt. VI. Mitth. zool. Sta. zu Neapel. V. Hft. I, 1884, pp. 174-189.

†A contribution to the Embryography of Osseous Fishes, § 18, p. 67.

itive worm-like plan recapitulated by embryonic development, leads to the differentiation of the anterior or cephalic and somatic parts of the form from the caudal part. Such a differentiation really leads to the production of a number of very important morphological and physiological changes, but it also at the same time affords embryological evidence of the fact that the theory of serial homologies founded on the tail of the eel is correct.

The degeneration—possibly specialization—which we have observed to occur in the course of the development of the tail of embryos is followed by other degenerative processes of considerable significance. The most important of these are, of course, those which lead to the evolution of heterocercy and the formation of a urostyle, but the instances in which we observe degeneracy to be so palpable that we cannot deny the fact of its existence are apparently those of *Chimæra monstrosa*, *Gastrostomus Bairdii*, and *Stylephorus chordatus*, in which a long *opisthure* has been formed, which at a very early period was vermiform and practically without developed median fin-folds. This almost useless *opisthure* results from the failure of the animals under consideration to develop in this region, during their early stages, well-marked myotomes, or if they ever did develop they subsequently degenerated more or less completely, leaving little or nothing behind except the chorda invested by connective tissue and integument.

If, as it is possible to conceive, the original form of the vertebrate body had more segments than it now has in even such comparatively simple forms as heterocercal Teleosts, it is not unreasonable to suppose that the failure to fully develop the terminal myotomes actually helped to lead to the initiation of heterocercy, for the reason that not sufficient material was built up into muscular segments at the tip of the tail to supply the muscular bundles for the formation of the flexors and divaricators of the caudal rays of heterocercal forms, the musculature of which has been really derived by differentiation of certain antepenultimate myogenous segments. This failure of the myogenous tract to develop in the last segments may have resulted partially from the sufficiency of the more anterior part of the urosome for purposes of propulsion in a watery medium, so that its posterior part failed to become functional from disuse, and was from such a cause atrophied, owing to a diminishing blood-supply which must have supervened.

I am also aware that the number of myotomes found in Teleost embryos before the body becomes free anteriorly and posteriorly from the yelk varies in different families, so that the preceding argument must be qualified by just so much as such variations in the number of larval somites developed may be supposed to affect the number in the adults of different groups. This larval variation actually depends upon the number of segments functionally developed in the adult, as is shown by the development of *Belone* (*Tylosurus*), by *Fierasfer*, and the Leptocephalid stages of certain marine eels, when contrasted with the young stages of the higher Teleostean forms possessing a shorter somatic and caudal region with fewer somites and a much modified heterocercal tail.*

Such forms as *Stylephorus*, *Chimæra*, *Gastrostomus*, and *Eurypharynx* would throw a great deal of light upon this subject, if we knew their embryonic history as well as we know that of *Fierasfer* and *Echiodon* so ably worked out by Carlo Emery.† The morphological and embryological evidence of caudal degeneration in *F. acus* is most complete, for the chorda with a blunt rounded posterior end (Fig. 4, Plate VII) abuts directly against the integument which covers the end of the tail. In *F. acus* the terminal caudal vertebræ are most imperfectly developed, while in *Echiodon dentatus* (Fig. 3, Plate VII) there is a more complete development of the last vertebral body, that vertebra manifestly not being the last one which would have been developed had the chorda persisted. In the first form there are no interneural cartilages developed as in the latter; these facts, therefore, taken together with the more pronounced persistence of the chorda in *F. acus*, show that the latter has retained a more embryonic condition of the tail than *E. dentatus*. *E. dentatus* is typically gephyrocercal, while *F. acus* has not developed the tail so completely as even to attain the condition of gephyrocercy, so that *it is absolutely without a true caudal fin.* On these and other grounds, Dr. Gill thinks it proper to distinguish these forms as separate genera. The young of *E. dentatus* has a very long and flagelliform tail which seems to be more prolonged than that of *F. acus* in the relatively younger "*Vexillifer*" stage, and which is either absorbed or even possibly lost in some other way, but it does not matter from what cause the tail is lost, the fact remains that in *Echiodon* the caudal, or what represents that fin in other fishes, is formed by the coalescence of a short posterior section of the dorsal and ventral series of rays into a terminal fin having the same function as that found in heterocercal types.

If both the heterocercal and homocercal types of the tail show in a great number of instances that the caudal extremity has been at one time provided with a more or less well-developed opisthure, and if such an opisthure does not in some cases even bear a fin-fold, but is merely the terminal part of the original urosome of the larva, it would seem that such forms had descended from types at one time possessed of longer tails with well-developed myotomes extending to their very ends, and that they were at first lophocercal, as are the larvæ of existing fishes. The enfeebled or degenerated posterior part of the urosome, which we designate as the opisthure, may not have contained sufficient muscular tissue to flex it from side to side, and that condition may have been brought about during development. In fact, less meso-

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* See my paper on the Development of the Silver Gar (*Belone longirostris*), Bull. U. S. Fish Commission, I, 1881, p. 293, Fig. 11, Pl. XX.

† Atti R. Accad. dei Lincei, VII, 1879–'80. Fierasfer. Studi intorno alla sistematica, l'anatomia e la biologia delle specie mediterranee di questo genere pel dott. C. Emery.

blastic blastema may have been laid down in the primitive terminal somites, so that the urosome was slender and weak from the embryonic period onward. This might readily lead to the degeneration of the caudal fin-fold, for the reason that no surplus of mesoblast was previously laid down in the vicinity which could be proliferated into the terminal fin-folds, consequently no caudal rays, apophyses, or even fin-folds were developed. Degeneration would then assert itself in the higher forms by the development of a transient opisthure; in the lower forms either a persistent opisthure would be formed, or the whole tail would become slender, weak, and flagelliform, as in the Rays and in *Gastrostomus.*

With the loss of mobility, or rather of muscular power, owing to a lack of well-defined muscular segments, it would result that no vertebral segments or only very imperfectly differentiated vertebræ would be formed, such as we actually find to be the case in *Gastrostomus*. Converse reasoning from another set of facts leads to a similar conclusion. In every case where a well-marked urostyle is developed from the point of axial flexure it is unsegmented when fully formed, as in *Amiurus*, or it is unsegmented at its posterior extremity only. The degenerate posterior extremity of the chorda often becomes covered by a continuous osseous investment which renders it inflexible, a condition which could not have been established if the musculature on either side had been well enough developed, and the end of the urosome had retained its archaic or straight form. When, however, heterocercy was developed the musculature of the tail became subordinated to a new function, viz, flexing the powerful caudal rays upon the hypural bones; the forces competent to induce segmentation of the urostyle are therefore absent, as it is usually found that the segmentation of hard parts corresponds pretty closely in the lower forms to the points of segmentation or to the points of origin and insertion of the muscles. With the advance in the differentiation of the muscles, as in the limbs of mammalia for example, this correspondence is less marked, being obscured by secondary adaptation.

The evidence in favor of the doctrine that many of the recent Teleosts, as well as the recent and fossil Ganoids, have descended from an ancestry the urosome of which was more prolonged or contained more segments than the urosome of existing species, is therefore quite conclusive, and that what has led to this decrease has been the further functional specialization of the caudal fin. In fact, a survey of the Vertebrates, taken as a class, leads to the conclusion that in almost all orders there has been a tendency in the course of their phyletic histories towards a degeneration of the caudal part of the axial skeleton.

The remarkably uniform tendency of nearly all of the *Lyrifera* to become heterocercal, involving the degeneration of certain parts which enter into the tail, would indicate that similar causes were operative amongst such a diversity of forms, productive of such similar morphological effects. The interaction between the Lyriferous type and its environment must have been pretty uniform in its character, because that environment—water—has been constantly about the same as respects its density, penetrability, and the resistance it would offer to the movements of the fish-like organisms immersed in it, so that in form and organization these latter have within certain limits remained pretty constant in their general conformation, widely as they differ in morphological details. Such a uniformity of tendencies shows that the forces competent to effect their initiation have not been haphazard, or fortuitous, or dependent upon chance variations to favor their operation, but have been fixed by determinately acting energies, the effects of which the writer has sought to trace. The embryologists have afforded us the clew to the origin of vertebrate bilaterality from structures which have been functional in the lowest Metazoa, and if this bilaterality so inherited has the significance which it appears to possess in determining further modifications, such as the differentiation of the vertebrate skeleton and metamerism in general, we are probably not far from a possible solution of most of the problems which confront us in the simple organization of the fishes, which foreshadows the far more complicated organizations of the higher types.

We have seen that the weak, lophocercal tails of young fishes frequently did not contain the materials for the complete differentiation of the axial and median distal appendicular parts of the skeleton. Then, as the upper and lower lobes of the caudal fin are developed, the tendency to develop the second anal or "lower lobe" of authors to a greater extent than the upper, there has been a tendency to push the tip of the chorda upward, or to push its ventral parietes inward (*Alosa*) for some distance in front of its hinder end. This hinder extremity then degenerates, or extensive anchylosis of the imperfect caudal segments of the axis and their appendicular elements supervenes, which aids in carrying the degeneracy of the chorda still farther at this point. The principle is the same, as we find upon careful analysis, which obtains in both the most primitive types of fishes and in the early stages of development whereby the rays become located and developed anteriorly to the end of the chorda, so that what has followed is mainly the result of the acceleration in the development of the lower or ventral part of the median fin-fold, from which what is morphologically a second anal is formed, in a position in which there is no corresponding dorsal lobe developed as its dorsal antitype, in consequence of which there is a lack of balance on either side of the end of the chorda in respect to the mode in which work is done by the tail, especially by the ventral lobe, which then becomes a kind of oar or sculling organ. In action this ventral lobe, when moved from side to side, encounters resistance from the water, and as it is alternately flexed in an oblique direction to the line of greatest resistance, the resultant of the antagonistic forces will pass obliquely upwards and across the axis of the tail; this obliquity of action of the resultant forces being alternately reversed as often as the tail is vibrated in opposite directions, will tend to throw up the end of the axis of the body, and thus produce a heterocercal condition, or one in which the end of the notochord will at least tend to be bent upwards. In case the dorsal and ventral rays of the tail are equally developed, there is no disturbance or upward displacement of the notochord, as may be seen in the cases of *Chimæra*, *Protopterus*, and *Ceratodus*, because here the interacting forces, if their lines of action are traced, may be shown to have a tendency to promote a preservation of the original or lophocercal symmetry, in which the chordal axis is straight posteriorly.

The extent of the development of the ventral lobe is highly variable, but it usually presents the greatest amount of surface laterally if the line of curvature of the urostyle, which is the true caudal axis, be used as the line dividing the ventral and dorsal lobes, and the curvature of this line is the index of the degree of heterocercality. It follows from this principle also that there is a correspondence between the proportion of the dorsal and ventral lobes to each other, and the degree to which the extremity of the chorda or axial skeleton is bent upwards posteriorly, if the principle of mechanical evolution here traced has any meaning.

An examination of a large series of types beginning with the *Chondrostei*, *Selachii*, *Crossopterygii*, *Rhomboganoidei*, *Cycloganoidei*, and ending with the most highly differentiated members of that series, the Teleosts, shows that the second anal or lower lobe of the caudal is not serially in the same relative position in different types; that in some forms it arises near the end of the axis of the embryo, in others a long distance in front of the termination of the axis of the body. Upon the location of the lower lobe, therefore, depends the number of segments in the dorsal or axial lobe of the tail from the point where it is flexed upwards to its termination. In *Alopias* there are about two hundred segments in the long dorsal lobe of the tail, and in some Teleosts there may be no vertebræ at all developed behind the point of upward flexure, as in *Gasterosteus*, for example, where the axis of the dorsal lobe is represented only by the urostyle and modified posterior half of the last vertebræ. The range of modifications which the tails of fishes undergo is, therefore, largely conditioned by this variation in the position of the ventral lobe, which may be placed near the end of the axis or far in front of it, and thus involve a smaller or larger number of the terminal segments of the axis in the upward flexure of its terminus.

The point of flexure of the chordal axis ought, if the mechanical hypothesis here outlined is at all probable, to begin at the anterior margin of the lower lobe, which is what we find to be the case. From the type in which the caudal axial skeleton is not flexed, as in *Ceratodus*, to the extremest type known, namely, *Alopias*, this rule holds. The cases of *Anguilla* and *Cnidoglanis* are somewhat difficult to reconcile, yet in truth their heterocercy is but slight, the caudal being reduced to eight dichotomous rays in *Anguilla*, Fig. 4, Pl. 4, and it would seem that the apodal condition and the elongate body had reacted so as to prevent the development of heterocercy, or it may be that this form has descended from a type which began to be heterocercal, but which lost that condition to some extent in the course of becoming apodal, when the tendency to preserve the tail in its primitive form began to assert itself and prevented further caudal degeneration, and that loss of terminal segments which we have seen has occurred to some extent in the course of the evolution of the fishes.

Kolliker,* as a result of his investigations, proposes the following provisional scheme of classification for the structural conditions found to obtain at the hinder end of the axial columns of fishes:

A. The end of the vertebral column incompletely or entirely unossified.
  I. The end of the vertebral column without a spinal canal, but consists—
    1. Of the chorda alone, *Esox*.
    2. Of the chorda principally, which is, however, covered by a short more or less complete cartilaginous sheath, *Salmo*, *Alosa*, *Elops*.
    3. Of a complete cartilaginous tube which incloses the end of the chorda, *Cyprinus*.
  II. The end of the vertebral column consists of a cartilaginous sheath, which incloses both the ends of the chorda and the spinal cord, *Polypterus*, *Lepidosteus*, *Amia*.
B. The end of the vertebral column completely ossified.
  I. The end of the column is not segmented, but consists of a longer or shorter bent bone (*urostyle*, Huxley), which is to be regarded as an ossification enveloping the chorda, and which resembles, more or less, anteriorly, a vertebral body. All (?) *Acanthopteri*, *Malacopteri* in part.
  II. The vertebral column ends with a simple vertebral body, *Plagiostomi* with a fully ossified vertebral axis.

These histological and morphological results of Kölliker's researches are of great interest, but they throw but little light upon the questions which we are attempting to elucidate on the basis of embryological and mechanical hypotheses, until they are viewed through the medium of the latter. The facts given in the table above merely show, as all of our studies have shown, that all the types of caudal differentiation found in fishes are stages tending toward the concentration of the caudal skeleton towards a point in advance of the hinder end of the chorda. The differences observed in the details of structure at the posterior end of the chorda are such as merely indicate phases of specialization. This is quite clearly demonstrated by the fact that a series of conditions might be picked out from this table which would roughly correspond with a series of the stages of development of a young fish.

IV.—THE SERIAL HOMOLOGY OF THE HYPAXIAL AND EPAXIAL ELEMENTS OF THE CAUDAL FIN.

Huxley has held that the hypural pieces of *Gasterosteus* were in reality composed of hæmal and interhæmal pieces, as indicated by develop-

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* Ueber das Ende der Wirbelsäule der Ganoiden und einiger Telostier. 4to. Leipzig, 1860.

ment.* An investigation of the structure of the caudal fin of *Anguilla*, Fig. 4, Pl. IV, very young individuals being used for the purpose, shows that this view of the structure of the tail of fishes is probably the true one, for reasons which we will now present.

In the first place, the Eel seemed to us to be especially well suited to clear up any doubts upon this question, for the reason that, if there was any actual serial homology to be found throughout the extent of the unpaired fins, such a condition ought to be apparent in this type, in which the dorsal, anal, and caudal are serially confluent, and the mode of transition from the one to the other ought consequently to be apparent. This, I am glad to say, was found to be the case, as had been anticipated on morphological grounds.

An exact drawing of the relation of the last interspinous pieces of the dorsal and anal fins shows that these pieces are not confluent with the neural and hæmal spines, but the first true hypural process is sharply bent backward at a point which is serially on the same level with the break in the continuity between the hæmal arches and every alternate interhæmal piece of the anal in front of it, as seen in Fig. 4, Pl. IV. A slight flexure of the same kind is visible in the next hypural piece. From this circumstance I infer that the hypural pieces are not simply hæmal, as held by Balfour, but are, as held by Huxley, composed of at least both hæmal and interhæmal elements, and that the point where the abrupt flexure of the first hypural piece is found marks the point where there was formerly a separation between the hæmal spines and the interhæmal pieces. That the distal parts of the hypural pieces of the heterocercal part of the tail of the Eel are not hæmal is proved by their exact serial relation to the interspinous pieces pertaining to the anal in front of them, the hæmal arches being abbreviated so as not to extend as far out or so near to the margin of the muscular mass, dorsally and ventrally, as does the terminal portion of the hypural pieces. The complete separation of the interspinous cartilages from the hæmal arches shows that the former cannot be medially fused pleurapophyses, but must be hæmapophyses and interspinous elements together. Moreover, at no time can it be shown that the distal parts of these hypural pieces in the Eel arise from the fusion in the middle line of distinct cartilaginous rudiments homologous with ribs, any more than it could be demonstrated that the interspinous pieces were so formed. Of other young fishes and embryos the same may be said; yet I admit that, if the truth of the theory of caudal degeneration and specialization which I have sought to establish is well founded, it may be that the lateral halves of the median, proximal, neural, and hæmal elements fail to develop, for the reason that the process of degeneration has affected their primitive mode of formation. Yet even this, for evident reasons, would not necessarily vitiate the conclusions

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* Quar. Journ. Mic. Sci., 1859.

arrived at respecting the serial homology of the epural and hypural bones in the tails of *Holocephali*, Ganoids, and Teleosts.

An examination of the tail of the Eel has, as already stated, led to the belief that a part of the hypural bones are the homologues of interspinous bones; but we find that even in this case they are present as a pair of successive appendages on the inner side of the ultimate and penultimate vertebræ. The next step in our inquiry will therefore be the following: What is the probable cause of such a duplication or multiplication of median appendicular elements on the under side of the posterior end of the vertebral axis? The antepenultimate vertebra, which has nothing to do with supporting the caudal lobe, has a single neural arch and two hæmal arches, and to these correspond two inferior interspinous elements. This would seem, therefore, to indicate that the double hypural elements of the penultimate and ultimate vertebræ were in part, or at least distally, the homologues of interspinous elements.

The neural arches of the penultimate and ultimate vertebræ are wanting, and there are no superior interspinous pieces which belong to the two last vertebral segments. This implies a degeneration and complete atrophy of the dorsal interspinous pieces pertaining to the caudal vertebræ, while it is evident, from what has been said above, that the inferior homologues of the suppressed upper pieces are present.

The inferior elements, or true hypurals, of the Eel are present as four hypaxial apophyses formed in cartilage and ensheathed in membrane bone in the young animal. In the old animal these four elements are reduced to two, because of the fact that the sheaths of membrane bone investing the two successive two in the young become co-ossified.

Further possible conclusions are derivable from a study of the structure of the tail of the Eel. The penultimate vertebra bears two inferior arches, which are hæmal, but it supports only one neural arch. This may imply that at one time this vertebra was compound, or double, and that it is now fused into one, having lost one of its neural arches. Such a duplication of centra occurs in the caudal part of the axial column of *Amia*, but here the appendages of the alternate segments are suppressed.

The concrescence or crowding together and fusion of the proximal ends of the epural and hypural elements, so frequently noticed, seems, however, to be really due to the tendency of the heterocercal caudal structure to incline toward the development of that of the gephyrocercal condition, as pointed out in another place.

The diplospondylism of part of the caudal axis of *Amia* is not apparently due to a process of concrescence, but to the elision of some of the skeletal appendicular parts of alternate segments. At the other extreme the excessive multiplication of epaxial arches to a single segment in *Lophobranchii* is an instance of the acquirement of supernumerary arches, which it is difficult to account for unless it be supposed that the single myotomes of the adults of the existing forms represent several primitive myotomes fused together, the septa between the latter having supplied the materials for the arches in excess of those demanded by the number of existing myotomes. But investigation again shows that such a view is not tenable, because the number of myotomes in the larva of *Siphostoma* are not in excess of those in the adult, so as to justify the hypothesis just outlined; so that it is evident, in this case at least, that the number of homonomous appendages of a segment may form a series which may be a multiple of the homonomous segment. Such results throw considerable doubt upon the legitimacy of the inference that the primitive cartilaginous rays of the paired fins of Elasmobranchs are each homonomous with a single segment.

The hypural pieces are really composed in many if not in most heterocercal forms of several median appendicular pieces fused together, and are usually not a little expanded at their distal ends, so that one of these processes frequently gives a basis of support to a number of caudal rays. In *Gasterosteus* and *Scomber*, for example, the fusion and expansion of the hypural pieces have proceeded so far that they are present merely as two fan-shaped pieces in the former, while in the latter the last vertebra is expanded posteriorly so as to present but one process which can be considered as the homologue of the series of hypural bones of other forms. In still other forms, such as *Lophius*, the process of specialization of the caudal end of the axial column proceeds so far as to involve vertebral segments in advance of those supporting the caudal rays. In this way it results that a number (about three) of the caudal vertebræ in this genus become fused together by synostosis.

There is a tendency in heterocercal forms for the neural arches to become more or less suppressed or aborted, apparently for the reason that the upturning of the posterior end of the chorda, when heterocercy is in process of development, encroaches upon the position which the posterior neural or epural arches originally occupied in the unmodified diphycercal type of tail. This pushing upward of the end of the chorda within the caudal fold seems therefore to really occur, and to play an important part in the evolution of the specialized caudal of Teleosts. In the Eel there are three hypural processes, which have no epural homonyms. Even when the epural pieces are developed as far as the cartilaginous condition, as the serial homologues of those in advance of them, they often have their direct connection with the chorda or urochord more or less sundered, owing to the degenerative influence of the upbending of the end of the latter, as may be seen in the course of the development of many forms. Sometimes the epural arches, or antitypes of the hypurals, are completely suppressed, as in *Amiurus*.

The tendency toward suppression of the epural pieces and that of the hypural pieces to become distally widened are correlative, and are evidently to be ascribed to the same causes. While the epural elements are being suppressed by the upturning urochord, the development of their cartilaginous beginnings even being interfered with, the hypural elements have been given more room for development in an antero-posterior direction distally. In consequence of this they have been frequently much widened at the distal extremities. This expansion of the hypural cartilages has then influenced the subsequent development of the membrane in which ossification occurs and also extended or expanded its development.

In *Amiurus* there is a small somewhat bent cartilaginous nodule found just at the apex of the urostyle, Fig. 1, Pl. IV, *op*, or at the extreme tip of the chorda in a still younger stage. This nodule is evidently an almost suppressed member of the once more extended series of hæmal arches. It is separated by a considerable interval from the last hypural piece in the young fifteen days old, and belongs to a system of arches which were doubtless well developed farther back in time in the ancestry of this form.

The position of this nodule in relation to the hypural pieces and to the end of the chorda and the extremity of the spinal cord, which here extends backward beyond the end of the notochord, would seem to prove that there probably was a time during the phyletic history of the Catfishes when the tail was longer and more nearly approached the most primitive diphycercal condition. The extension backward of the spinal cord beyond the end of the urostyle is also strong evidence in favor of the probability of the existence of a diphycercal condition which preceded the present one.

The sigmoid flexure of the end of the spinal cord *ms*, in Fig. 1, Pl. IV, is also evidence in favor of the theory of the upbending of the chorda which was defended above. The suprachordal portion, over the urostyle, has been bent up, but the part extending behind the end of the urostyle has not been bent upward at the same angle, but is very much less inclined to the plane of the axis of the body than the portion immediately in front of it. So it appears that the upturning of the chorda seems to affect the upbending of the spinal cord to the same extent as itself only as far as the two structures coincide in their relative positions of parallelism with each other.

The exserted end of the spinal cord in *Amiurus* rests ventrally upon the opisthural piece *op*; it, like the end of the cord, has not been so extensively pushed upward distally as the more anterior, ultimate, hypural piece, the axis of which has been shifted through at least ninety degrees from the position it occupied in the old diphycercal type in which it first appeared.

V.—DEVELOPMENT OF THE MEDIAN AND PAIRED FINS AND THE EFFECTS OF CONCRESCENCE.

The structure of the tail and of the median fins of fishes has been described by a number of eminent authorities, but it is only within a few years that we have been furnished with the kind of embryological knowledge which has enabled investigators to reach any general and harmonious conclusions regarding this subject. The researches of A. Agassiz* upon the mode in which the tail of the most highly specialized fishes is developed are the most important and extensive, but it is to be regretted that his illustrations do not give the outlines and relations of the hypural chondrifications in greater detail for all of the species which he has considered, his object being apparently to identify the forms and trace their metamorphoses without entering too much into elaborate minor details.

For the relations of the embryological structures involved we are still mostly dependent upon the researches of Balfour, Oellacher, Lotz, Swirski, Dohrn, and myself.

Since Balfour's discovery that the paired fins are apparently developed, at least in the Elasmobranchs, from continuous lateral folds of the epiblast into which the mesoblast proliferated to form the vascular, axial, radial, and muscular systems of the limbs, there has been a large amount of evidence gathered which shows that the history of the paired and unpaired fins of Teleosts is very similar. Oellacher† was the first to trace the origin of the axial substance of the pectoral limbs of the Trout to the mesoblast. Since Oellacher's observations have been published, Dohrn‡ has reconsidered the development of the paired and unpaired fins ontogenetically, and has fully confirmed and greatly extended Balfour's original conclusions, so that we now have a secure foundation upon which to found a theory of the fins which does not rest upon hypothetical assumptions, but upon observed facts.

Dohrn holds essentially the following views respecting the origin of the paired fins, viz: (1) As shown by Balfour, they are derived from continuous, inferior, horizontal, lateral folds of epiblast, into which muscular and other mesoblast proliferates. (2) The muscular somites then throw out ventral buds which are thrust into the fold, in segmental order, when they become constricted off from the somites, *mb*, Fig. 9, Pl. X. (3) These segmental muscular diverticula then divide into dorsal and ventral processes, which give rise respectively to the inferior and superior muscles of the actinosts and rays. (4) The *actinophores* are then formed by a gradual chondrification of the loose mesoblastic tissue between the divided diverticula of the muscular segments. (5) As the paired fins become longer and more pedunculate, the primitive actino-

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* The development of Lepidosteus. Part I. Proc. Am. Acad. Arts and Sci., XIII, 1878, 65–76, 5 pls.

On the young stages of Osseous Fishes. I. Development of the tail, Proc. Am. Acad. Arts and Sci., XIII, 1877, 117–127, 2 pls. II. On the development of the Flounders, Proc. Am. Acad. Arts and Sci., XIV, 1878, 1–25, 8 pls. III. On the young stages of Osseous Fishes, Proc. Am. Acad. Arts and Sciences, XVII, 1882, 271–303, 20 pls.

† Beiträge zur Entwickelungsgeschichte der Bachforelle. Vorläufige Mittheilung. Ber. d. nat.-med. Ver., Innsbruck, 1879, pp. 141–143.

‡ Mitth. zool. Sta. Neapel, 1884. V. Die paarigen und unpaarigen Flossen der Selachier, pp. 161–189.

phores, which correspond to the segments whence the muscles are derived, coalesce at their proximal ends to form the basipterygial cartilaginous plate, Fig. 8, Pl. X, which subsequently segments to form the pro- meso- and metapterygium. The antero-posterior constriction of the horizontal peduncles of the pectoral and pelvic fins is greatest from behind, so that a fold of skin is pushed in behind the basipterygial plate, shoving it outwards and freeing it posteriorly from the sides of the body to thus give rise to the uniserial limb of these forms. The innervation of these fins is also segmental. The pectoral and pelvic girdles, according to Balfour, are at first integral anterior parts of the basipterygial plate and become segmented off afterwards from the basipterygium. The coracoid and pubic are then developed still later in a proximal direction as continuations of the scapula and ilium. Dohrn's researches therefore enable us to complete the theory of the paired limbs of Elasmobranchs, and lead us to the conclusion that such a biserial limb as that of *Ceratodus* is merely the result of the concrescence of primitive segmental rays or embryonic actinophores from behind and from before instead of from behind only, or possibly the middle or axial actinophore is composed of the bases of a lateral series fused together and secondarily segmented. At any rate, it would not be surprising to find that when the development of *Ceratodus* is known that it had almost continuous lateral fin-folds, along the whole length of which actinophores were developed, one actinophore of the series in each paired fin being accelerated in growth longitudinally to form the axis of the limb, and, as the fin gradually became pedunculate, carried its anterior and posterior serial fellows outwards along with it. The primitive character of its skeleton, the cœlacanthous structure of its median arches, interspinous bones, its cartilaginous biserial and multiradiate paired fins, and its simple skull are remarkably embryonic in every particular, and contrast in the most remarkable way with its specialized breathing apparatus. Some such manner of development as described above, if it somewhat exaggerated that which is figured by Balfour (Comp. Embryol., II, 505, Fig. 348) as obtaining for the pectoral skeleton of an embryo of *Scyllium stellare*, might lead to the evolution of a fin like that in *Ceratodus*, without any very extensive anterior coalescence of the segmentally-arranged actinophores of the fin-fold and lead to the formation of a biserial limb. At any rate, I would expect to find the lateral fin-folds of greater relative length in *Ceratodus* embryos than in most of those of the *Squali*, Crossopterygians, or Chimæroids, thus contrasting, but not quite so decidedly, as the fin-folds of these latter contrast in length with the short, paired fin-folds of Teleosts. This last contrast is in accord with the conclusions to be drawn from the facts of embryology generally, as to the highly specialized character of the Teleosts when compared with other groups of fishes. Pronounced reduction in the length of the lateral fin-folds of Teleosts has occurred, so that we should not expect to find in their embryos any evidence of continuous fin-folds as I have already urged elsewhere,* so greatly does heredity influence and directly mar the potency of remoter ancestry, so as to induce a defective repetition of the phyletic history in the course of ontogenetic development.

The posterior paired fins or ventrals of Teleosts also develop from horizontal folds (*Salmo*), and there is no evidence to show that their plan of evolution is much different from that of the pectorals; at any rate, no elaborately-contrived archipterygium or ichthyopterygium hypothesis can give us the slightest aid in settling what must be determined by actual investigation. While there is much reason to regard not only the pectoral but also the pelvic fin of *Ceratodus* as very archaic, it is not certain that its very primitiveness may not be correlated with the primitive character of the median diphycercal fin system, and there is much reason to regard the Elasmobranch paired fins as more specialized, while those of the Ganoids and Teleosts are even more so, since the latter rarely have a prolonged peduncle, but, on the contrary, a very short one, the osseous elements of which are much more decidedly included by the soft parts of the body walls. The pro- meso- and metapterygial elements (fused actinophores, or the separate actinosts of Teleosts) which are the undoubted partial homologues taken together of what is the basipterygial plate in Elasmobranch embryos, which afterward subdivides into the three proximal pterygial pieces, which are evidently related, not to as many somites, to judge from what we know of their evolution, but each consists of several coalesced elements derived from as many somites. Not so in the case of the actinosts of Teleosts, which evidently consist, perhaps exclusively, of derivatives of far fewer somites than the basipterygium of the Elasmobranch embryo, as we know from the fact that so few somites enter into the formation of their paired fin-folds. While it is true that a secondary segmentation of the pterygio-coraco-scapular plate occurs in Teleosts during a late stage there are forms in which it retains the form of a chondrified plate, which does not develop either an osseous scapula or coracoid, but persists, as in the larva, as a cartilaginous lamina, with which the pectoral rays articulate directly (*Gastrostomus* and ? *Eurypharynx*). It is therefore clear how deplorably hopeless the attempt must ever remain to determine such homologies by consulting adult structures alone, if it is desired to follow the metamerism of the embryo as a basis for their determination.

We may now glance backward and see what conclusions we may legitimately draw from the foregoing discussion of the facts. It is evident, in the first place, that there is a metameric relation between the actinophores of the fin-rays of the paired fins. In the second place, it

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* Development of the Spanish mackerel (*Cybium maculatum*), Bull. U. S. Fish Commission I, 1881, pp. 160-161; Contrib. to the Embryography of Osseous Fishes, Rep. U. S. Fish Commission, 1882, p. [64] or 518.

is evident that various displacements have occurred,* due to growth, accompanied by a coalescence in the peduncular region of the basal actinophores of the paired fins, which has obscured the homologies of their parts and also developed the coalesced series of paired nerves so as to develop the plexuses which innervate the limbs.

The evidence of metameric or serial homology in the unpaired fins is too palpable to need serious discussion, for we find one spine bearing accessory radii to correspond with several somites (dorsal of *Polypterus*), or one spine or ray to each somite, or two or even three or even more to a single somite. This is the clearest possible proof, and goes far to supplement the ontogenetic evidence respecting the metameric origin of the basipterygial elements of the paired fins.

The case of the dorsal of *Polypterus* is a remarkable one, and has puzzled me greatly until recently, when I noticed that the strong, bony, anteriorly enamel-covered spines, with their posterior accessory rays, were probably not homonomous, or all derived from a single segment, but probably homodynamous, as Gegenbaur would express it, or serially homologous, according to Owen. This becomes evident in the light of the ontogeny of the basipterygium, as worked out by Balfour and Dohrn, for we find that the principal spines are homonomous with about every fourth vertebral spine, so that about three intervening spines do not apparently support rays or spines, and are thus without homonyms; but in view of the way in which the principal spines support accessory jointed radii posteriorly, it is probably fair to conclude that these accessory rays are the homonyms of the intervening apparently spineless segments between the great spines, and that in the course of development the bases of the accessory rays have been shoved forward out of their original relations with these segments, as the posterior actinophores of the pectorals of Elasmobranchs have been, and crowded up against the principal anterior ones and carried up and away from the body as these grew in length. The process is therefore one which in all probability is perfectly parallel with that involved in the production of the so-called archipterygium, so that the primordial continuous system of median dorsal homodynamous rays has been interrupted in *Polypterus* so as to develop discrete dorsal finlets by a process of proximal concrescence of sixteen short series, consisting of about four to five rays each. The foregoing hypothesis of the true nature of the dorsal of *Polypterus* we may, I think it probable, confidently expect to be confirmed by ontogenetic research.

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* See my remarks upon the rotation of the pectoral of *Gadus* upon its base (Contrib. Embryog. Osseous Fishes, pp. 66, 67). It is evident that such a rotation does not take place so soon in Elasmobranchs. The base of the fin in them permanently occupies a more primitive position or one which is much less different from the direction of the original fold. This is especially noteworthy in the Rays, in which the base of the pectoral of the adult undergoes almost no alteration of position in relation to the position of the fold from which it is derived. (See Wyman's memoir on the development of *Raia batis*.)

Supplementary evidence of the occurrence of serial concrescence of the radial supports may be found in the median fins of other fishes, as it is very strongly marked in the dorsal and anal of the adult of *Mola*, in which both neural and hæmal spines and interspinous elements are crowded together and pushed forward posteriorly and backward anteriorly so as to condense these fins in an antero-posterior direction, so that their bases are little more than half as wide as they would be had no such distal approximation of their supports occurred. In consequence of such concrescences the primitively-continuous median fins are shortened, as in this case, or interrupted in other cases, in the same manner as the lateral ones have been by the concrescence of their anterior and posterior segmental elements into a pectoral and ventral fin. This fact does not, of course, discountenance the actual abortion of some of the segmental radial elements which so frequently occurs, as any one knows who has noticed the wide eradiate intervals between the caudal and dorsal and the anal and caudal in the skeletons of numerous species of Teleosts.

This same kind of proximal concrescence occurs in the tail of Salmonoids, according to the investigations of Lotz (Pl. III, Fig. 4), where certain hypural elements originally distinct are shown to be in the act of coalescence. While it is true that in many cases actual concrescence of the hypural elements does not occur until ossification has been established in the course of nearly completed development, I believe that the origin in part of the diverging system of hypural bones and radial elements of the caudal of heterocercal Teleosts is to be rationally accounted for on the basis of this principle, just as the diverging system of rays of the paired fins is obviously to be similarly explained. It may be that in the case of the Teleosts the urostyle, which is included by the soft tissues of the tail, may be exserted beyond the hypural bones for this reason, as seen in Salmonoids (Pl. III, Figs. 1-4); that in fact the more posterior hypural elements, as they are successively developed from chondrifications which take place in the median skeletogenous tract, are shoved closer together basally than distally, so as to leave a longer portion of the end of the chorda projecting than would have projected had the bases of the hypural pieces been enabled to maintain their normal position in the straight condition of the chorda. This, I think, will be evident to any one who will take the trouble to compare the stages of development of the Salmon (Pl. II, Fig. 3) with the condition of the tail of the adult (Pl. VI, Fig. 2), copied from Lotz.*

According to this view the notch marking the distinction between the dorsal and ventral lobe of fish larvæ in the act of becoming heterocercal acquires a new significance. The epiblast is, in fact, shoved in at this point somewhat in the same way as the post-pectoral epiblast is shoved in at the hind part of the pectoral fold of Elasmobranchs, so as

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* Ueber den Bau der Schwanzwirbelsäule der Salmoniden, Cyprinoiden, Percoiden und Cataphracten. Zeitschr. wiss. Zool., XIV, 1864, pp. 26, Pls. X-XII.

to crowd the actinophoral elements together to form the basipterygium. This gradual crowding together of the hypural elements and the proximal ends of the rays is well shown in seven figures of the young of *Atherinichthys notata*, Günth., given by A. Agassiz in Part III of his paper *On the Young Stages of Osseous Fishes*, Plates X and XI, where the advance inward of the dermal fold just spoken of is also well shown.

There are instances, however, in which so much of the dorsal lobe projects posteriorly as to really constitute what we have called an opisthure, as in *Lepidosteus* and *Gasterosteus aculeatus*, Linn., where the terminal caudal somites, with their included metameric skeletogneous tracts, are wholly absorbed, whereas in most Teleosts what corresponds to the opisthure of the preceding species is included more or less completely by the tissues which enter into the formation of the permanent tail. It thus happens that most of the primitive hypural elements in most forms are permitted to develop, but are much crowded together proximally so as to leave the urostoyle to project, in many cases permanently, and in almost all species during the very early stages, in the form of the upturned end of the chorda, which might, in its membranous condition, be called the *urochord.* In many instances amongst Teleosts degeneration or suppression of hypural elements has occurred, but even in these cases the loss in number has been small.

Those forms, such as the Salmonoids, which have the upturned end of the caudal vertebral axis more or less extensively segmented (Pl. VI, Fig. 2), are apt to develop rudimentary epural spines, which are homodynamous with the more anterior normal neural spines, as has been conclusively shown by Lotz. Distinct in their cartilaginous condition, they are finally covered with perichondrium, which becomes confluent, and ossifies to become the lateral "grosse Deckstücke" of Lotz. Such epural rudiments consequently become displaced more or less upwardly and laterally, apparently for the reason that the urochord is bent upwards so as to be shoved in between their homonomous basal halves.

In those forms which do not have the axis distinctly segmented beyond the bend of the urostyle it would seem that no epural spines are developed even as cartilaginous rudiments. J. P. McMurrich's criticism of Lotz, in his *Osteology of Amiurus* (Proc. Canadian Inst., Vol. II, No. 3, p. 298), as based on the latter form, is therefore entirely gratuitous, as there are never any epural cartilages developed on the urostyle of *Amiurus*, as in *Salmo*, as may be learned by examining Fig. 1 on Pl. IV, taken from the completely chondrified caudal skeleton of an embryo of *Amiurus albidus* fifteen days old.

What is true of the pectorals the writer has found to be true of the ventral fins of Teleosts in a number of widely-separated genera. In *Amiurus* the material of which the axial portion of the pectoral is formed consists of mesoblast continuous with the spongy connective tissue of the larvæ. In like manner the medullary substance which fills the epiblastic fold, from which the anterior dorsal is developed in

Amiurus, is continuous with the mesoblast of the skeletogenous investment of the notochord, by way of a thick band of mesoblast, which thus fills up a wide space between the lateral muscular laminæ of the opposite sides of the body. So far as it is possible to decide from very thin sections ($\frac{1}{1600}$ inch thick), no part of the epiblast takes a share in the formation of the primitive blastema, from which the proximal axial elements of the fin are derived, the corium, Malpighian, and epithelial layer not being involved in the formation of the basal actinophoral elements; the basal cartilages of the proximal ends of the rays, as well as the rudiments of the basilar interneural and interhæmal pieces of Cope, or median actinophores, being evidently laid down from mesoblastic rudiments.*

This evolution of cartilage actually occurs before the development of the ribs in cartilage and contemporaneously with the formation of a cartilaginous basal plate in the pectoral fold, upon which the divided osseous sheaths of the rays are afterwards superimposed. This basal or basipterygial plate *bp*, Fig. 5, Pl. X, becomes segmented distally into at least the basal cartilaginous nodular portions of the rays, there being no long basipterygial bar formed in the Teleosts, as in Elasmobranchs, but the proximal portion of this plate is thickened in some Teleosts, and this thickening doubtless represents the basipterygial bar of cartilaginous fishes.

The continuity of the tract from which the axial portion of the vertical fins are derived, with the skeletogenous investment of the notochord, shows that the mesoblast from whence the fin-rays and interspinous pieces are derived has a common origin with the former in the embryo.

The vertical epiblastic folds from which the unpaired fins are derived, are at first, throughout the whole fin-bearing series of the *Vertebrata*, as well as the larvæ of Amphibians, almost devoid of mesoblast; that layer being insinuated into the folds secondarily, either to furnish the material for the limiting walls of vessels or else to supply the material of which the basilar and all of the medullary substance included by the rays is formed. How much of the rays themselves are formed from without or by the epidermis, it is difficult to say, but the deposition of new material, we would, on account of the relations of the vessels, expect to occur from within or on the internal faces of the opposite halves of the rays. So that after all it is not so clearly demonstrated that the rays of osseous fishes are wholly of dermal origin, though their outer

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*It may also be here stated that the medullary substance of the barbels of embryo Catfishes consists of mesoblast, and that shortly after the barbels have appeared, or about the sixth day of development, they contain a central cartilaginous rod, which appears contemporaneously with the cartilaginous elements of the larval cranium. The presence of cartilaginous internal supports in the barbels of larval Catfishes, as well as their extremely early appearance, as compared in these respects with the chin barbel of the Codfish and the labial barbels of the young Carp would indicate that these barbels of the *Nematognathi* appeared very remotely in the past in the ancestral form whence the modern forms are derived.

surfaces lie immediately against the epidermis, except at their bases, where it is apparent that more or less mesoblast intervenes between the ends of the proximal halves of the rays and the epiblast. Such is the case at least with the pectoral rays which are first laid down as dense homogeneous membrane, in the same way as the primary rudiments of the cranial membrane bones. A cartilaginous nodule (median actinophore) is also included by the proximal ends of the dorsal, ventral, anal, and pectoral rays, while the cartilaginous part in the caudal rays is the margin of the expanded hypural cartilages, which betray in the arrangement of the nuclei a tendency toward the separation of homologous nodules at certain nodal points near the ends of these pieces, though they probably never become discrete in consequence of the reduction and specialization which the elements of the caudal fin have suffered in the most specialized fishes. It is therefore evident that if the tract from whence the interspinous elements are formed is mesoblastic and cartilaginous, and at the same time continuous at one time with the nodules at the bases of the rays, that those basal elements are not truly of dermal origin. These facts, at least, indicate that the whole ray is not of dermal origin; or that only its lateral osseous halves developed in membrane can ever have had such an origin in the Teleostei.

The marginal bands of cartilage *b* Fig. 1, Pl. IV, at the ends of the hypural processes, and which are indistinctly differentiated by nodal aggregations of nuclei which resemble in appearance the arrangement of these bodies in the basibranchial plate or in the hyomandibular and symplectic bar at a time when the segmentation or sundering of these pieces into distinct elements is about to occur, is a striking fact, and one which leads me to think that the hypural processes are not simple. These nodal aggregations of nuclei are also found at the tips of the neural and hæmal spines of such Teleosts as do not have the dorsal and anal confluent with the caudal, and I am inclined to regard these terminal cartilages also as epiphysial elements, or rudimentary median actinophores which at one time were separate, but which have in consequence of a process of degeneration been suppressed. These rudimentary elements of the spines anterior to the caudal may be regarded as representing the nearly suppressed basilar interspinous elements, while those cartilaginous borders which we find to terminate the hypural pieces may be considered with some show of probability to represent the basal nodules or basilar interspinous pieces of the other developed median fins, for we find that the proximal ends of the caudal rays clasp this part of the hypural processes somewhat after the fashion in which the proximal ends of the dorsal and anal rays clasp the basal cartilaginous actinophores in the embryo.

The method of development of the parts of the segments of the median or unpaired system of fins is therefore very similar to that of the paired fins, as displayed in the course of their outgrowth. The continuity of the coraco-scapular cartilaginous plate with the basal cartilages of the longer rays or actinophores of the pectoral shows how close this parallelism is.

The relation of the epaxial and hypaxial arches, in the course of their development, to the chorda, and the similar close relation of the paraxial processes, the ribs, to a spongy and reticular mesoblastic tract which invests the chorda and brain, and also extends upwards and downwards between the lateral musculature of the body in the middle line, and even shows itself in the vicinity of the pectoral at the time of its outgrowth, demonstrate very clearly that the belief in the doctrine that the whole skeleton is derived from an interstitial mesoblastic tract which is developed as a continuum over the chorda, the cerebro-spinal axis and also invests the muscular system, is securely founded upon observed fact.

Evidence of the occurrence of the process of concrescence, as observed in the limbs of higher forms, also exists, as may be gathered from the longitudinal section through the basal portion of the hind limb of a chick of the sixth day. The segments *s h l*, which afford the nerve supply and muscles for the hind limb, are evidently concrescing, as shown in Fig. 1, Pl. X. The sternal ends of the thoracic segments *s t* also exhibit such a tendency and seem crowded forwards. Other evidence on this point may be gathered from a paper by Miss Alice Johnson.*

Investigations such as these promise great results when applied to human and mammalian development generally. If the outgrowth of the limbs can be traced by means of microtomy through a sufficient number of stages, remembering also that more or less twisting or rotation of the limb-rudiment occurs during its outgrowth, we may be able to trace the nerves, blood-vessels, and muscles to their proper embryonic segments, formerly denominated protovertebræ, but now generally spoken of as somites by the more recent and more exact embryological writers. By the use of this method we may probably yet be able to say that the subclavian artery represents one of the intersegmental vessels of a young fish; that the complex muscular system of the limbs of higher forms is derived, as in the fishes, from the myotomes.

If also it is true that the proximal skeletal elements of the limbs of the lower forms are derived from a series of chondrifications belonging to successive metameric segments, then, inasmuch as it is probable that the higher forms have descended from the lower, the proximal elements of their limbs, humerus and femur, have probably also been derived from an originally compound structure made up of a series of metameric elements. This idea is to some extent countenanced by the existence of a separate series of proximal and distal epiphysial centers of ossification in the humerus of man. The epiphyses of the bones in higher

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* On the development of the pelvic girdle and hind limb in the chick. Quar. Journ. Mic. Sci., and in Studies from the Morph. Laboratory Univ. of Cambridge, II, 1884, pp. 13-25, Pls. IV, V.

forms are probably suppressed axial segments of the limbs, which were probably functional in the limbs of lower forms. This view is further sustained by the fact that there is a tendency toward synostosis of many other elements of the skeleton in the higher forms, whereas their homologues in the lower ones remain distinct through life. In the light of such embryological research it will also become less difficult to understand the possible origin of a manus with more than three phalanges in each digit, as found in some Cetacea, of the development of which we know little or nothing relating to the bones of the limbs.

VI.—ON THE PROTOPTERYGIAN STAGE OF DEVELOPMENT OF THE RAYS IN THE FINS.

As stated in another portion of this paper, it was proposed to discriminate a so-called lophocercal stage following that designated as the archicercal and characterized by the want of fin-rays as understood in speaking of the adult condition. A very remarkable kind of rays are, however, developed during the lophocercal stage of Teleosts which become most clearly marked just at its close, or when the permanent fins are about to be developed. These *embryonic fin-rays*,* as A. Agassiz has called them, were observed by C. Vogt about 1840 (and are alluded to) in his essay entitled *Embryologie des Salmones*, but they were positively shown to be connected with the formation of the permanent rays about twenty years since by Theophile Lotz† in a paper not devoted to the rays themselves, and the fact has therefore been apparently overlooked that to this author properly belongs the credit of having first pointed out that the filamentous embryonic rays stand in a genetic relation to the permanent rays which are derived from them. A. Agassiz nowhere in his several papers intimates that such a relation exists between the embryonic and permanent rays, although he has found the former in a great many genera of osseous fishes besides those in which they have been found by the writer, so that it seems probable that such rays will be found in the embryos of all *Teleostei*. Lotz found them in the young Salmon just after hatching immediately underlying the larval integument of that part of the median fin-fold which is destined to become the permanent caudal, but he says nothing of their more extensive distribution in other fins. It now remains for me to state (1) that these rays are first developed just beneath the epidermis of the fin-fold, Fig. 9, Pl. IX; (2) that there are two series, one under the right and the other under the left epidermic wall of the fold with some mesoblast insinuated between the two series, Figs. 4, 5, 6, and 7, Pl. IX; (3) they are, as pointed out by Lotz and Agassiz, very much more numerous

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* Since this has gone to press the necessity of giving these elements a single name has become manifest to me, and in a later paper I have therefore named them *actinotrichia.*

† Uber den Bau der Schwanzwirbelsäule der Salmoniden, Cyprinoiden, Percoiden und Cataphracten. Zeitschr. wiss. Zool., XIV, 2. Hft., 1864.

than the permanent rays, as shown in Fig. 1, Pl. IX; (4) these structures are found at about the close of the lophocercal stage in both the paired and unpaired fins and in the same relation to the integument in both, and form a perfectly continuous series when the folds are continuous; (5) they either atrophy together with the atrophied portions of the median folds, or they persist as in the adipose fins of *Salmo*, *Amiurus*, &c., or they coalesce and become enveloped by a homogeneous substance (Fig. 10, Pl. IX) to form the permanent rays, or they become more or less covered by the mesoblast, and some finally atrophy; (6) they are perfectly homogeneous, as shown in Fig. 11, Pl. IX, and are in every respect similar, optically and histo-chemically, to the perichondrium as developed around the chorda, cartilaginous ribs, and spines, or the homogeneous hyaline membranes in which the membrane bones of fishes form and calcify.

The fact that these fibers coalesce proximally to form the matrix of the permanent rays in Teleosts is positive proof of the fact that the numerous horny fibers found in the fins of Chimæroids, Sturgeons, Plagiostomes, and Dipnoans, are almost exactly homologues of the osseous rays of the first mentioned, supplemented as such a conclusion is by the fact that in all of these, as shown by evidence gathered by Balfour, Günther, and myself, the relations of the fibers to the epidermis and mesoblast is fundamentally the same in all; that is, the fibers occupy exactly the same place in respect to the other tissues in the fin-fold as do the two halves of the rays of the fully-developed fins of Teleosts. The fibers being parallel, numerous, and developed in a form which develops a skeleton in a cœlacanthous manner at first, which in its later cartilaginous condition at the close of the lophocercal stage resembles more than any other the condition which is permanent in *Protopterus* or *Ceratodus*, leads me to the conclusion that this stage of the larvæ of osseous fishes may very appropriately be called the *Protopterus* or *Protopterygian stage* on account of the remarkably close resemblance of its fin-system to the archaic type of fins possessed by the Dipnoans, which unquestionably preceded the Teleosts in time.

We thus get a more satisfactory notion of the relation in which these forms stand to each other. And we must now, for obvious reasons, regard the rays of Teleosts as merely a more highly specialized condition which ontogeny has shown must have arisen from a stage which is permanent in the Dipnoans, forms strangely advanced in some respects while they have remained singularly embryonic in almost every other. We thus find that the parallelism which has been insisted upon as existing between Palæozoic forms on the one hand, and the young stages of osseous fishes on the other, by L. Agassiz and Vogt, and also by A. Agassiz, is warranted in its main features, when all of the facts are produced which ontogeny has to offer, though it is true that it will not do to push the comparison too far. We are also enabled to say with some certainty that the distal cartilages of the paired fins upon each side of which the fibrous rays of the protopterygian stage terminate proximally are in all probability homologous for reasons which will presently be given. The theory that certain portions of the primitive median fin-folds degenerate in those forms which have intervals between the permanent fins, as insisted upon in another part of this paper, is now conclusively demonstrated by the fact that in the preanal fin-fold of the embryo Salmon, just after hatching, we find the fin-fibers of the protopterygian stage present, though this fin never develops, but is gradually lost, nearly vanishing after about four weeks. This fact indicates that the Salmon has descended from a form which had an unpaired fin in front of the vent, and that the development of rays went no farther in this fin than the formation of the two series of fin-fibers. I have not found any evidence amongst recent fishes, of the existence of preanal fins, though *Balistes* seems to have the ventral fins coalesced into what might at first be taken for a preanal fin, were it not that its rays are alternately elements of the pelvic fins of opposite sides, as shown by their close relation anteriorly to the falcate and greatly prolonged pubic bones.

The larvæ of *Chondrostei* are represented as having preanal fin-folds with embryonic rays, but the Elasmobranch larvæ which I have been able to examine do not seem to possess them. Inasmuch, therefore, as they are not constantly present in the larvæ of all fishes it is probably premature to insist that they indicate anything more than this, namely, that the preanal fin-folds have been inherited from forms in which they were functional; what these forms were we do not know.

The pectorals of young Rays (? *R. stellata*) one and a half inches long do not seem to contain any horny fibers, though they are abundant in all of the fins of young Dog-fishes (*Squalus*), considerably smaller, where they are present as very short fibers in the marginal part of the fins beyond the point to which the cartilage protrudes. In young Lampreys four inches long I have found no traces of them, the vertical fins in these being supported by branching rays consisting entirely of cartilage which extend nearly to the margin of the fin-fold. In prepared sections of Tadpoles three-eighths of an inch long no horny fibers are apparent in the median fins. The *Amphibia* and Marsipobranchs are accordingly excluded from that category, the larval stages of which are characterized by the possession of horny fibers in the fin-folds, since a protopterygian stage is found only in *Dipnoi*, *Chondrostei*, *Elasmobranchii*, *Holocephali*, and *Teleostei*.

The *Leptocardii* are also excluded from the above assemblage of forms since the development of their so-called fin-rays is entirely different from that of any of the branchiferous Vertebrates possessing fin-rays, according to the account given of their development by Kowalevsky.* They arise in this form from aggregations of cells which become thrust apart centrally by the appearance in their midst of a vacuole filled with

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* Entwickelungeschichte des Amphioxus lanceolatus. Mém. l'Acad. imp. des sciences de St.-Pétersbourg, VIIe sér., t. XI, No. 4. (See especially p. 12, Pl. III, Fig. 39.)

fluid, so that the development of the rays is similar to that of the chorda dorsalis of the animal. They are probably of mesoblastic origin, while the fine embryonic fin-rays, the protopterygian stage of other Vertebrates, are interposed between the epiblast externally and more or less mesoblast internally. The development of the rays of the Marsipobranchs offers more analogy with that of *Amphioxus* than that of any of the other ray-bearing Vertebrates.

In most anatomical hand-books it is explicitly stated that the permanent rays are integumentary in their origin. Since I have again taken up the subject with the object of finding out the true state of the case by the help of more refined methods of investigation, I have reached a conclusion which, in some respects, is opposed to the one generally accepted. My sections of Salmon embryos show that while the embryonic rays are at first interposed in a single layer between the epiblast and mesoblast which has wandered outward into the epiblastic fin-fold, at a late period relatively these embryonic rays become invested by the cells of the lower layer of the integument formed from the mesoblast, seeming to sink into the latter as its cells multiply and surround these rays externally. But the phenomena which occur prior to the formation of the embryonic rays themselves are even more conclusive as showing that the larval integument or epiblast has little or nothing to do with the formation of the permanent rays.

If sections through the tail of an embryo fish are prepared at about the time that the lophocercal stage is almost fully developed, of *Lophius*, *Belone*, *Fierasfer*, and *Alosa*, for example, it will be found that the vertical fin-folds are filled with an homogeneous substance, as pointed out by Emery, which shows no traces of cellular structure, and contains no cells whatever, except sometimes a few in the basal part of the fold and near the axial mesoblast (see Fig. 10, Pl. X). Such cells evidently have wandered outwards. In the tail, however, where the embryonic fin-rays first appear, there is already an abundance of mesoblast, on either side of which the layer from which the embryonic rays are formed is placed. This layer seems at first to be very thin, as in Fig. 7*h*, Pl. X, and a product of mesoblastic secretion, in part at least, even should it be shown that what I have called pterygoblasts in the tail of the embryo Cod have no real genetic relation to the embryonic rays, which I am strongly inclined to think they must really sustain, on account of their form and relations to surrounding tissues, Fig. 3, Pl. IX.

The embryonic rays are therefore clearly dependent upon the mesoblast for their development, since it can be demonstrated beyond any doubt that as fast as they appear in the more anterior portions of the vertical fin-fold their advent is preceded or accompanied by the outgrowth of mesoblastic cells into the latter. The layer from whence the embryonic rays are formed seems almost homogeneous, and only as growth proceeds does it seem that the filamentous embryonic rays are differentiated from it. The pterygoblasts first disappear at the basal part of the fold, and it would thus seem that the embryonic rays were formed from within outwards or in the direction of the migration of the tissue from which they are formed, which seems to be converted into the thin, nearly homogeneous membrane already spoken of, before these rays become distinctly differentiated as fibers which present a remarkable homogeneity of structure. Fig. 5, Pl. IX, shows how deeply the membranous rudiments of the permanent rays may become imbedded in the mesoblast at their proximal extremities.

The development of the embryonic rays between the epidermis and mesoblast of the folds which give rise to the paired fins is precisely similar to that which occurs in the folds from which the unpaired fins are developed, as may be gathered from a glance at Figs. 3 and 5 on Plate X.

VII.—What is it that constitutes a fin-ray?

As may be gathered from what has preceded upon the origin and development of the fin-rays, it becomes pertinent to inquire what it is that constitutes a true fin-ray. It may be said that true fin-rays, which are embryologically the homologues of each other, are formed only in the group distinguished under the name of *Lyrifera* by the most recent taxonomists, a group embracing the *Selachii*, *Holocephali*, *Chondrostei*, *Holostei* (and *Ganoidei* generally), *Dipnoi*, *Physostomi*, and *Physoclysti*. It is also a fact that the development of the first traces of the rays is approximately the same; that is, they are first formed just under the larval integument or epiblast (the epidermis of the adult) in all of these forms. In no case are they certainly known to develop in cartilage. The apparent exceptions to this statement, such as the cartilaginous radii found in the fins of the Rays, it must be borne in mind are in no sense the homologues of the horny rays of a form even so closely allied to them as the Sharks, because these radii of the pectorals, for example, in the Rays, are the exact homologues of the cartilage cut across in the Salmon's pectoral, *bp* in Fig. 5, Pl. X, or that of the pectoral, Fig. 3, *cr*, Pl. X, of *Scyllium*. The *cartilaginous rays or actinophores of the Lyrifera develop in the central, axial, or medullary mesoblast of the fin-folds in both the paired and unpaired fins.* These elements may be segmented into basilar interneural, interneural, basilar interhæmal, and interhæmal elements in the paired fins, or even be partially or wholly wanting where the morphological differentiation of the fin has not advanced much beyond an embryonic condition, as in the case of the adipose fins, for example; or they may be more or less suppressed by other causes, such as degeneration in the caudal region, and fused together, as elsewhere stated. In *Polypterus* the dorsal finlets show evidence of concrescence and a tendency towards the formation of a uniserial structure with a loss of the basal elements of the concresced rays. In the paired fins of *Dipnoi* these axial cartilages may be reduced to a single tapering multisegmented bar, as in *Protopterus*, with a few short lateral elements articulating with its basal portion. In *Ceratodus* they are the biserial cartilaginous axis of the limb. In *Polypterus* they are the anterior and posterior basal elements of the limb with intercalated elements intervening. In *Chondrostei* they are the segmented cartilaginous basal plate which subdivides distally into six bars.* In *Elasmobranchii* the axial plate of the paired fins is more complex, and usually consists of three well-marked subdivisions arbitrarily named pro- meso- and metapterygium,† external to which there is a greater or less number of segments resting upon the preceding three pieces, with a more or less parallel course, though often diverging and dividing, as in the Rays, for example. The Torpedo has a so-called cephalic fin resting in part upon antorbital processes and partly on the cranial rostrum. These are the principal forms of the axial skeleton of the paired fins. They are the most primitive and embryonic representatives of the limb skeleton found amongst Vertebrates, as embryological research has shown.

In the Teleosts, where great specialization and even loss or shifting of the posterior fins have taken place in some forms, still greater reduction has occurred. The axial‡ basal elements of the pectoral may be present as a single plate (*Gastrostomus*), or, at most, be represented by a few short (usually three or four) actinophores, often supporting a greater number of rays. The group *Actinopteri* of Cope (*Teleostei* of this paper) is thus defined by its author: "Derivative radii few in the fore-limb, sessile on the scapula; wanting or very few and rudimental on the hind limb, so that the dermal radii rest on the axial element." It is therefore evident that the Teleosts represent the extremest term of specialization attained by the limb-skeleton in fishes, and that in the pelvic limb, at least, the whole limb is sometimes represented by true rays only. *In all of the Lyrifera the axial skeleton of the paired fins is developed from the middle or medullary part of the mesoblast, which is thrust out into the primitive epidermic or epiblastic lateral fin-folds,* just as in the case of the unpaired fins, but there is not that palpable continuity of the skeletogenous tract of the paired fins with that investing the chorda, as in the case of the same tract in the unpaired fins.

The next point of great morphological and theoretical importance in the definition of the true rays is their primordial relation to the axial skeleton of the fins. We found that the latter originated in the central parts of the mesoblastic substance of the embryonic fin, whereas the true rays we find to originate in the superficial part of the same layer,

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* Vide Günther: Memoir on Ceratodus. Philos. Trans., II, 1871, p. 533.

† Vide Huxley: Anatomy of Vertebrated Animals, p. 38.

‡ The term *axial elements* is here used to signify the endoskeleton of the whole of the mobile portion of the limb, and not to signify the endoskeleton which forms the proximal elements or segments of the pectoral and pelvic limbs of fishes, as implied by Cope in the phrase "axial series" in his paper in Proc. Am. Philos. Soc., May, 1877, and Report of State Commissioner of Fisheries of Pennsylvania for 1879 and 1880, pp. 67, 68. This explanation has been thought desirable in case the reader might be led to compare this memoir with those by Cope.

or that next the epidermis, or simply between the latter and the underlying mesoblast, especially the distal and least modified portions of the rays at the margins of the fins. This relation of the rays to the primary embryonic layers has led writers to speak of them as exoskeletal in contradistinction to the other portions of the skeleton, named endoskeletal, for the reason that the stratum which they at first overlie subsequently becomes the corium and a part of the adult skin. But it so happens that very young or larval fishes have no corium or true deep layer of the skin developed, and that proximal portions of the rays soon become quite as deeply imbedded in the mesoblast, even below what can ever become corium, as a considerable part of the clavicle, for example, the membrane of which also lies at first very close to the epidermis in larval fishes. It is thus made evident that the distinction between the rays as exoskeletal as distinguished from the other hard parts called endoskeletal is really a forced one. Furthermore, phylogeny and embryology both indicate that the embryonic fin-rays are in reality the membranous representatives of the more numerous rays once possessed by the most ancient fishes.

The composition of the embryonic rays is the same chemically as that of the membranes in which membrane bones are formed, as is shown by the way in which they stain. A good many of the embryonic rays also atrophy, especially the ends of those lying at the bases of the fin-folds, in the intervals between the points where the permanent rays appear. This last fact is a further illustration of the common occurrence of the reduction of the number of homologous parts with the advance in specialization or evolution. The embryonic fin-rays are never distinctly developed as fibrils till the mesoblast has proliferated into the epiblastic folds from which the fins are developed, which is quite enough evidence to prove that they have as much right to be called endoskeletal as any other portion of the skeleton which develops in membrane imbedded in mesoblast.

The superficial or dermal position of the rays is, however, an important character, and one which is in striking contrast with the position of the axial or cartilaginous skeleton, but not so important when contrasted with the position of the points of origin of many membrane bones, which develop in a quite superficial position, such as the dentary and the upper part of the clavicle.

Another character, which is of some importance, is the proximal extension of the true rays. They uniformly terminate near the edge of the fins distally and proximally just over either side of the distal end of the axial skeleton in both the median and paired fins. Their mode of connection with the axial skeleton is also approximately the same in both kinds of fins; that is, the distal nodular elements or actinophores of the axial or basal cartilages become invested on their right and left sides by the basal ends of the right and left halves of the rays when the latter have been completely differentiated. In the case of those forms, such as the Chimæroids and *Dipnoi*, in which the muscular and osseous segments are far less numerous than the homonomous rays, the inclusion of the distal nodules spoken of cannot be so complete. Such a condition also renders the muscular specialization much less marked and more like that observed in embryo fishes at the time the embryonic rays are formed. The erectores and depressores spinæ muscles are therefore not so distinctly differentiated as at a later period, as must obviously occur to the reader.

True fin-rays, as found in the *Lyrifera*, are never preformed in cartilage, and, widely as they differ in extent of development, the actinosts, as they have been called by Gill, as found in the pectorals of Teleosts, are homologous with the greatly developed pro- meso- and metapterygium of the Rays, together with the very elongate, numerous, often dichotomous, multisegmented cartilaginous radii which they support, provided they have in both cases been developed from the same number of serially homologous segments or somites, which are removed to the extent of the same number of segments from the occipital somite. This may be gravely doubted in some instances, as, for example, in the case of *Gastrostomus*, where the pectoral in the adult is homonomous with a segment or segments separated by at least fourteen from behind and beyond the occiput.

In the unpaired fins of Teleosts there is the clearest evidence that the rays are homonomous with the somites, and that from one to five or six rays are developed to a single somite, each ray involving the coalescence of a number of embryonic rays or fibrils which were developed in the embryonic fin-folds. This concrescence of fibrils, the evidence of which is given in Plate IX, is found to occur in all of the fins of all of the *Lyrifera*.

A fin-ray of the lowest of the *Lyrifera* may be formed of only two primitive fibrils to as many as twelve or even more, so that in the highest types the greatest number of primitive fibrils or embryonic rays enter into the formation of a permanent ray, so that the rays of the highest and lowest forms only differ in being respectively more or less complex in this regard.

The definition of a fin-ray, which will hold for all of the *Lyrifera*, will be as follows: A horn-like or osseous rod formed beneath the embryonic integument (epiblast), and at first composed of fibers, a greater or less number of which become directly or indirectly blended to form a permanent ray, lying distal of the axial cartilaginous or osseous support of the fin in the superficial mesoblast, and invariably consisting, when ossified, of membrane bone, and always of more or less clearly defined right and left halves, formed in the right and left sides of the fin-fold, except when fused together into a hollow rod in the middle line of an early stage. More superficial ossifications may become blended with some anterior rays, as in *Nematognathi*, and lead to the development of spines exaggerated in thickness by synostosis with such superficial hard or bony structures.

The term *horn* or *horny* as applied to the embryonic fin-rays is not justified even in the case of *Chimæra* and *Ceratodus*, or in the other instances where the embryonic rays retain their primitive character, as, for example, in the adipose fins of Salmonoids and *Nematognathi*. In *Chimæra* and *Ceratodus* we might naturally expect to find that the fin-rays exhibited embryonic features, when we bear in mind how embryonic and cartilaginous the skeleton has remained. *Ceratodus* seems, in fact, as if it were an embryo *Teleost* which had been permitted to lose its yelk-sack and grow large, meanwhile losing none of its embryonic skeletal characters, though acquiring others, such as a more differentiated respiratory system, but with the development of its tail arrested at a point nearly coincident with the end of the lophocercal the stage of the Salmon. Such an arrest of development gives to fin-skeletons of *Dipnoi* and *Holocephali* their peculiar traits, which so closely parallel the embryonic condition of Teleosts, so that their fin-rays, while partaking apparently of a horny nature, in reality have no very close resemblance to horn. As already stated, the horny fibers (embryonic rays) are similar to perichondrium histologically; it follows that the rays of *Dipnoi* and *Holocephali* are simply this perichondrium-like substance, which has grown in volume and suffered little or no calcification. Another reason why the rays of these forms, as well as those of embryos, are not comparable to horn is that the epidermis has little or nothing to do with their formation, while truly horny structures, such as nails and hairs, arise, in great part at least, by the direct cornification of the epidermis

The persistence of embryonic rays in the adipose fins of Physostomes is doubtless correlated with that other more embryonic condition of theirs, namely, the possession of an open pneumatic duct, which shows them to be less highly differentiated than the Physoclists, a group which, it should also be borne in mind, embraces the most specialized *Teleostei*, such as the *Lophobranchii*, *Hemibranchii*, and *Plectognathi*, the latter embracing the *Moloidea*, in which the caudal skeleton is more highly specialized than in any other fishes.

VIII.—SPECIAL MODIFICATIONS OF THE DEVELOPMENT OF THE FINS.

In order to bring forward some of the forms of development of the fins or fin-like organs which it is difficult to account for, it has been thought advisable to devote a few paragraphs to certain modifications which are characterized by their exaggeration or extremely specialized mode of development.

The development of *Fierasfer*, which has been worked out by Emery, illustrates in a striking manner the statement that an extremely specialized but transitory structure may be developed in connection with the anterior part of the dorsal fin-fold. On first hatching an interruption appears in the front part of the dorsal fin-fold, which is occupied by a papilla; by the sixth day this has been prolonged into an appendage nearly as long as the tail of the larva. At its base it consists of a short, rigid, vertical portion, to which is attached a long flexible filament, to the sides of which are appended alternately three ovate, flattened, pigmented bodies, of which the terminal one is largest. In the vexillifer stage, before the final metamorphosis into the adult, this flexible portion of the dorsal appendage may support as many as ten of these now nearly acuminate, flat, pigmented bodies. The base of this singular appendage consists internally of a rigid, homogeneous axis of connective tissue, in which no ossification ever occurs. In the vexillifer stage it finally has its base attached in front of the permanent dorsal, and disappears when the adult condition is reached.

It is clear that the development of this appendage is similar to that of a fin, being a very elongate diverticulum of the epiblast, into which pigment and connective tissue are proliferated from the mesoblast.

A somewhat similar development of long dorsal and ventral filamentous appendages or rays, bearing opposite bract-like processes placed at intervals, occurs in the case of the young of *Trachypterus*, two to four inches long, which seem to be aborted and lost during later life. In *Fierasfer* the vexilliferous appendage is not the rudiment of a true ray, but in *Trachypterus* the basal portions of these filaments seem to be retained as rays.

The development of the tail of *Trachypterus* is, however, not a little singular. In the young of the size mentioned above, it is homocercal, and, if the existing figures are reliable, it is structurally heterocercal. Subsequently, however, the longest rays of the caudal assume an upright direction at right angles to the axis of the body, while a few short hypaxial rays arise from the hinder and ventral border of the knob-like swelling which terminates the tail. The development of the tail of this group is evidently widely different from that of other forms, and it is not a little singular that the change of direction of the principal rays of the caudal should apparently occur during the post-larval period of growth.

The remarkable *Stylephorus chordatus* must also be considered in this connection, since it presents the peculiarity of having a body only 11 inches long, with a caudal band-like appendage 22 inches in length. "The caudal is directed upward, and has its rays connected by a rather firm membrane; the tail terminates in a narrow band-like appendage, about twice as long as the body." (Günther, Cat. Fishes Brit. Mus., III, 307.) This "band-like appendage" is undoubtedly homologous, as far as one is enabled to judge from Shaw's figure,* with the caudal filament of *Chimæra monstrosa*, or, in other words, the opisthure of *Stylephorus* is 22 inches long. This appendage of *Stylephorus* is below the upright five-rayed caudal, which it seems to me is not such, but prop-

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*Naturalist's Miscellany, VIII, pl. 274.

erly the last portion of the dorsal, which is differentiated into three portions. There seem to be no anal rays developed.

The development of the Goose-fish or *Lophius*, according to the account given by A. Agassiz,* is one of the most extraordinary yet known to embryologists, and throws a great deal of light upon some of the problems which this study has suggested, especially in relation to certain questions which arise in the consideration of the genesis of the ventral or pelvic fins and their genetic collocation with certain mesoblastic segments posterior to the pectorals, and far behind those with which they are in apparent relation in the adult.

In the youngest stage figured by Agassiz the pelvic fin arises as a flat, lobate fold, some distance behind the pectoral fold, Fig. 1, Pl. XI, of nearly the same form and nearly synchronously with it. In the next stage, Fig. 2, it is represented as arising below the base of the now widened pectoral, as an elongate, spatulate process, arising from the side of the yelk sack, with a blunted, somewhat swollen tip. In the next stage it has become somewhat longer, more swollen at the tip, and its base more advanced, Fig. 3. As development proceeds its base advances a little more in front of the point of insertion of the base of the pectoral. The single first ray of the pelvic fin then buds out a second ray near its base, and the first ray, which is now more elongate, becomes somewhat geniculate and swollen in the vicinity of the bend. Its rays by this time, Figs. 4 and 5, far surpass in length those of the pectoral, which are now only beginning to develop. The rays of the pelvic fin now continue to precociously lengthen until the outermost one is nearly twice the length of the animal from the snout to the end of the tail, the total length being 30^{mm}. The bases of the pelvic fins are now clearly in advance of the bases of the pectorals.

This change in the position of the bases of the pelvic fins, if we keep in mind the successive events which are mentioned above, would seem to be due to an actual shifting forward of these fins from their original position in close homonomous relation with mesoblastic segments behind the pectorals. The jugular position thus assumed by the pelvic limbs of *Lophius* during its early stages might readily affect their final relations with the spinal nerves, and become innervated by pairs anterior to those which appertain to the segments in direct relation with its first rudiment when that was still behind the pectoral. Haswell's† foot-note, in his paper on the Elasmobranch skeleton may, therefore, lose its force if the preceding view is well founded. He says: "I have ventured (On the structure of the paired fins of *Ceratodus*, Proc. Linn. Soc. N. S. W., Vol. VII, p. 10) to make the very obvious suggestion that the derivation of the pectoral and pelvic plexuses from a number of spinal nerves was a strong piece of evidence in favor of

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*On the young stages of Osseous Fishes. Part III. Proc. Am. Acad. Arts and Sci. XVII, 1882, pp. 280, 285, Pls. XVI, XVII.

†Proc. Linn. Soc. New South Wales, IX, 1884, p. 82.

Balfour's theory and against that of Gegenbaur; but I am now inclined to think, in view of certain facts observed by Fürbringer (Morphologisches Jahrbuch, IX) as to the origin of the nerves supplying the pelvic fin in some *Teleostei* with thoracic or jugular pelvic fins, that the portion of the spinal nerves from which the plexuses are derived is too plastic a factor to support any wide generalization at all." At any rate, the only way to settle this question now is to investigate some such form as *Lophius* and trace the genesis of the innervation of the pelvic fin by the embryological method, to see if the nerve supply of that fin is derived from the segments with which its first rudiment was homonomous, or whether its nervous supply originates from segments in advance of those from which it was derived. There is, for obvious reasons, little hope of settling this point by the method of comparative anatomy or the comparison of the morphology of adult forms.

Agassiz' figures also show that there are at most but four myotomes interposed between the early rudiments of the pectoral and pelvic fins, a number which is far less than in the case of the Salmon, where there are about sixteen, or four times as many. We thus find that the tendency to develop the pelvic fins is in some cases conspicuous at a very early stage. In *Gadus* the rudiments of the thoracic pelvic fins evidently do not appear until after the yelk is absorbed, judging by the results of my investigations on the early stages and those of Agassiz on the later ones. In *Motella* (*Onos* of Ayres) the development of the pelvic fins is about as nearly synchronous as in *Lophius* according to Agassiz, and the translocation forwards of the base of the pelvic fins probably occurs in much the same way.

In a larval pelagic form of Flounder from the Mediterranean, named *Peloria rüppelii*, by Cocco and studied by Emery,* the pectoral is remarkably pedunculate before asymmetry begins to show itself, and the ventrals are pushed forward in advance of the base of the former. The four anterior rays of the dorsal are also free at the ends and much exserted, a condition which appears to be evanescent, as in the case of the young of *Trachypterus*.

The embryological data so far acquired seem to indicate that the rudiments of the pelvic fins of the embryos of forms with permanently abdominal fins are not translocated forward during development, while in those forms which have thoracic or jugular fins such a translocation actually occurs. While nearly all of the Palæozoic Ganoids had the pelvic fins abdominal in position, some, as *Blochius*, for example (if that form is really a Ganoid), had them almost jugular, which would seem to indicate that such a translocation of the pelvic limb occurred relatively late in the history of the evolution of the fishes. The *Physostomi* also being the most primitive type of Teleosts, have mostly retained the pelvic fins in the archaic abdominal position, whereas the more highly

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* Contrib. all' ittiologia. Reale Accad. dei Lincei. Classe di scienze fisiche, math. e naturali, XIV, 1883.

specialized *Physoclisti* have either generally had the rudiments of the pelvic fins translocated during development, until in some Ophidioids they are submental in position, or have had them quite aborted. The development of the pelvic fins, as well as that of the air-bladder in the *Physoclisti* indicates that they are more differentiated forms than the *Physostomi*, from which they have probably been evolved.

It may also be pointed out that the shifting of the position of the hindermost pair of fins is quite in harmony with the views of Balfour and Dohrn, and the mode in which the antero-posterior concrescence of homodynamous elements occurs at the bases of the fins, as well as their more or less extensive rotation, apparently over their own insertions, goes very far towards giving us an insight into the way in which the complex brachial and sacral plexuses have been developed by the anastomosis through the antero-posterior concrescence of paired spinal nerves.

We now come to the consideration of another set of phenomena which are of great importance in the development of a theory of the fins. What is now referred to is the peculiar way in which the spines or unjointed rays of certain forms develop. It is unfortunate that we are not familiar with enough forms to enable us to generalize with more certainty; but, thanks to the researches of A. Agassiz, we are enabled in the cases of two species which have the anterior dorsal spines forming a disconnected series, namely *Lophius* and *Gasterosteus*, to reach the interesting conclusion that such spines are developed in a great measure independently of the continuous folds and in a special way, that is, by the precocious outgrowth of a hollow terminally blind diverticulum of the epiblast, in which such spines are formed from the mesoblast.

In *Lophius* the first spine of the anterior dorsal appears as a depressed conical mesoblastic thickening overlying the front end of the spinal cord, as in Fig. 1, Plate XI. In the next stage the epiblastic diverticulum is pushed out and the first indications of the first dorsal ray have appeared, as in Fig. 2, Plate XI. The vertical median fin-fold now atrophies more and more, and in the next stage, Fig. 3, Plate XI, the medullary portion of the process seems to be differentiating in which subsequent ossification is to occur. In the next stage, Fig. 4, Plate XI, two dorsal rays are visible, and in the next, Fig. 5, four may be distinguished.

In *Gasterosteus aculeatus* the researches of Agassiz show that the rigid anterior spines are also formed as more robust distinct papilliform outgrowths of the epiblast into which mesoblastic tissue is at once pushed out, while the hinder rays of the dorsal are formed in a continuous fold in the usual way, embryonic rays being first formed. The spines, however, do not in either *Gasterosteus* or *Lophius* seem to be preceded by embryonic rays. Such spines are therefore probably developed from the basement membrane, which doubtless forms in the mesoblast which grows into these epiblastic papillæ or diverticula, and ossifies directly. The anterior dorsal spines of *Gasterosteus* do not seem to be preceded by a median fold, the latter having atrophied before the papillæ which develop into the dorsal spines have begun to grow out. In *Cyclopterus* also no median fin-fold seems to precede the anterior dorsal; a thick, low, hump-like outgrowth in front of the dorsal fin-fold, leading to the development of the anterior dorsal directly. Embryonic rays may possibly precede the formation of the permanent rays of the first dorsal in *Cyclopterus*, judging from Agassiz's figures.

It will thus be seen that the modes of development of the anterior dorsal spines of *Lophius* and *Gasterosteus*, and the vexilla of *Fierasfer* are similar, and that such a specialized mode of ray-development tends to bring about the suppression of the fore part of the more archaic, dorsal median fin-fold; that it also tends to lead to the suppression of the embryonic fin-rays, which in all probability take no share in the formation of the anterior spines in such forms, but retain such a relation to the permanent rays only in the posterior dorsal, anal, and caudal, and the soft rays of the pectoral and pelvic fins.

The rays of the pelvic fin of *Lophius* are in like manner evidently not derived from embryonic rays, but seem to be formed like those of the anterior dorsal.

These extreme forms of specialization lead us to anticipate other equally singular modes of ray-development, which will probably only differ in detail, because we find after all that the principle upon which both kinds of rays develop, namely, the separate form and those conjoined by a membranous investment, is essentially the same. The first are formed in distinct epiblastic pockets of the skin, the latter in continuous or confluent ones, or in what I have throughout this paper called folds.

I have already referred to the peculiar way in which the rudiment of the pelvic fin is pushed forward in *Lophius*, but I must also call attention to the fact that an actual pushing forwards of the anterior dorsal also takes place in this form, as a result of which the first dorsal ray is finally brought to rest upon the frontal bones of the skull in the adult. In *Malthe*, according to Gill, who has called my attention to the fact, the anterior dorsal is shoved still further forward than in *Lophius*, this peculiarity being recognized as a family character by Gill in these words: "Anterior dorsal ray in a cavity overhung by the anterior margin of the forehead." In Fig. 1, Pl. XI, the rudiment of the first dorsal ray of the embryo of *Lophius* appears above the anterior end of the medulla spinalis and behind the medulla oblongata, but in some way it is slowly advanced until, in Fig. 5, its base is above the mid-brain. A new dorsal ray, according to Agassiz, next appears more anterior to the one first formed, which may explain in another way how the advance forward of the most anterior rays of the dorsal is accomplished by their development as later, single, and more anterior outgrowths. There is, nevertheless, positive evidence that the originally formed dorsal rays have been pushed forward in the young, though the most anterior dorsal rays resting on the head of the adult above the snout may have been developed during post-larval life. This peculiarity of development is approached by the fore part of the dorsal of Flounders, in the young of which, as development proceeds, the anterior dorsal rays are advanced so as to occupy a more anterior position in the adult than in the very young. Such examples of the displacement of structures forwards in the course of development would probably lend support to Gegenbaur's interpretation of the cephalic fin of Torpedo as a part of the pectoral which has been advanced and acquired support from the antorbital processes of the skull secondarily.

IX.—ON THE TRANSFORMATIONS OF THE TAIL OF MOLA.

(See Plate VIII.)

In 1870 F. W. Putnam* described the anatomical peculiarities of *Molacanthus nummularis* (Walb.), Gill, as compared with the young of *Mola rotunda*, Cuv. In the latter, Putnam states that he found "the neural spines of the fifth to the fifteenth vertebræ closely packed together with the interneural spines and extending backwards to support the dorsal fin, while the hæmal spines of the tenth to the sixteenth vertebræ are in close connection with the expanded interhæmal spines supporting the anal fin. The sixteenth vertebra gives off large neural and hæmal spines, the former having five interneural spines anchylosed [in contact] with it as in the adult, while the hæmal spine supports [or is in contact with, posteriorly] nine interhæmal spines, the lower one of which belongs to the anal fin, while the others are of the caudal chain. In the adult only seven interhæmal spines are connected with this hæmal spine. The seventeenth vertebra in the adult lies in the caudal chain of interspinous bones, and from its being separated from the vertebral column has been as often considered an interspinous bone as a vertebra. In the young specimens this vertebra, though separated from the column as in the adult, has in close connection with it two bones above and two below, probably indicating that this vertebra is in reality the consolidation of two vertebral bodies, the seventeenth and eighteenth, while two other small (neural and hæmal) bones posterior to this free vertebra indicate that a nineteenth vertebra existed at an earlier stage. These six neural and hæmal (three each) bones disappear in the adult, and with them the central rays of the caudal fin, and they and the seventeenth, eighteenth, and nineteenth vertebræ are represented only by the free or 'floating' seventeenth vertebra, which lies in the chain of *interspinous* bones of the *caudal*. This is the only instance of a vertebra existing as distinctly separated from the vertebral column, known to the author." * * *

"The skeleton of *Molacanthus* shows the interspinous bones of the dor-

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* American Naturalist, 1874, IV, 629–633.

sal in connection with the neural spines of the fourth to the seventeenth vertebræ, and those of the anal with the hæmal spines of the tenth to the seventeenth vertebræ. The vertebral column in *Molacanthus* terminates abruptly with the seventeenth vertebra, and no caudal chain of interspinous bones can be traced. The liver is small, when compared with that of the young [*Mola*], and is composed principally of a large right lobe overlying the stomach. The stomach is small and the intestine is short, making but two turns like the letter S, while in [*Mola*] it is long and has five or six turns or coils. The arrangement of the muscles and bones of the head is in general about the same as in [*Mola*]."

These extracts from Mr. Putnam's article embody essentially all that he has added to our knowledge of the morphology of the young stages of *Mola rotunda*, as we will show all of them to be in accordance with the views of Lütken, Steenstrup, and Günther, but the position of those authors will be here fortified by conclusions based on another series of comparisons and on the general principles of development, which may be depended upon to clear up many facts of very uncertain significance when viewed merely in the light of the comparative anatomy of the adults.

Mr. Putnam does not seem to have thought of the fact that the differences which he had indicated as existing between *Molacanthus* and *Mola juv.* were just those differences which another investigator would seize upon, guided by the light which embryological principles would afford him, in order to show that *Molacanthus* was only a younger stage of *Mola*. Nor does it seem to have occurred to any one to look and see if the generative organs of *Molacanthus* were developed to maturity, or whether they were present only as *genital folds* or ridges of the peritoneum in the upper posterior part of the abdominal cavity, and therefore in an immature or larval condition. The recognition of *Molacanthus* as an adult form, therefore, rests on pure assumption, and cannot be demonstrated with the help of the anatomical data now at our command.

On Mr. Putnam's investigations the embryologist may very evidently base conclusions diametrically opposed to those entertained by that author. For example, in *Molacanthus* the intestine is short, and has but two bends, or is sigmoid in its course, while in the form thought to be the young of *Mola* the intestine is long and has five or six turns or coils. This is what should have been expected on embryological grounds, for the intestine of young fishes is always straight at first, and only becomes bent so as to develop more coils or loops as the form approaches maturity. The liver also develops unsymmetrically in many young fishes, and to urge its relatively smaller size in *Molacanthus*, as compared with *Mola juv.*, where it is more symmetrical and relatively larger, is simply to ignore the light which embryology might have thrown upon the matter, when all difficulty on this point would have immediately disappeared.

In the same way the differences observed in the arrangement and relations of the interspinous bones of the dorsal and anal fins of *Molacanthus* and *Mola juv.* may be shown, without any doubt, to merely represent stages of development of the median pieces which support those fins. Tabulating the relationship of the interspinous neural and hæmal elements, as given by Mr. Putnam, this will become apparent.

Dorsal interspinous bones connected with spines of fourth to seventeenth vertebræ in *Molacanthus;* with spines of fifth to fifteenth vertebræ in *Mola.*

Hæmal interspinous bones connected with spines of tenth to seventeenth vertebræ in *Molacanthus;* with spines of tenth to sixteenth vertebræ in *Mola.*

The extension of the dorsal and anal fins posteriorly in *Molacanthus*, so as to be brought into relation with two more neural spines and one more hæmal spine than in *Mola juv.*, is very readily explained by the fact that these fins are, as a whole, apparently more posterior in position in the specimens of *Mola* still younger than the one figured as *Molacanthus* by Putnam, and that there is an apparent but not real wholesale shifting of the bases of these fins in a forward direction in order to reach the condition found in the adult, due to the outgrowth posteriorly of the caudal, in consequence of which the dorsal and anal are shoved apart. This line of argument is shown to be in the very highest degree the correct one, from the fact that in a very small pelagic fish, which has been called *Ostracion boops*, and now regarded by Lütken, Steenstrup, and Günther as a still younger stage of *Mola* than that represented by *Molacanthus*, the dorsal and anal fins are very closely approximated over the end of the body, so as to appear almost like the forked tail of a normal Teleost.

One apparent difficulty now presents itself with respect to the apparent shifting backwards of the dorsal fin of *Mola* to the extent of one neural spine farther to the rear in front, so that the first ray of the dorsal seems at first sight to be in relation with the spine of the fifth dorsal instead of the fourth dorsal as in *Molacanthus.* This difficulty, however, disappears at once when we find that in the adult the interspinous piece belonging to the fourth vertebra is really present, but is so closely appressed to that of the fifth as to seem at first as if it were a part of the latter. The dorsal spine of the fourth vertebra does not reach back to the corresponding interspinous piece, but is greatly depressed and lies partly in close contact with the upper side of the fifth vertebra in almost a horizontal position. It is evident that the interval between the posterior end of the spine of the fourth vertebra and its corresponding interneural piece has arisen in the course of growth, and is primarily due to the fact that the body grows rapidly in length anteriorly after the *Molacanthus* stage has been passed, so that the intimate connection of these elements would be sundered, so as to give rise to the interval between them as observed in the adult.

It is evident, therefore, that not a single one of these anatomical characters which have been supposed to differentiate *Molacanthus* as the type of a family, subfamily, genus, or species distinct from *Mola* has the slightest taxonomical value, and much as the writer would desire to agree with Dr. Gill's* views in relation to these matters, he is forced, after carefully weighing all of the evidence before him, to arrive at a conclusion directly opposed to that of the above-mentioned distinguished authority.

That the little fish described by Sir J. Richardson† as "*Ostracion boops*" is in all probability the young of some form of *Mola*, or of a type closely allied, cannot be questioned, from the fact that the spines, while not as numerous as those distributed over the skin of the *Molacanthus* stage, yet agree to a certain extent with those on that form in their relative position, and also in the fact that they, as in the latter, have raised carina radiating from their apices, which are surmounted by rows of diminutive secondary spines. Certain it is at any rate that the form is not an *Ostracion*, because the two posterior fins are manifestly to be regarded as anal and dorsal, and not as "anal and caudal," as supposed by Richardson, for his figure 21 shows that there is a narrow interval between these two fins which is the homologue of the interval between the two corresponding fins of the *Molacanthus* stage.

Richardson's description of "*O. boops*" may be profitably reproduced in this connection:

"Radii: C. [D.]12; A. 14; P. 14 (Dr. Hooker). Being unwilling that any of the novel forms of fish sketched by Dr. Hooker should be altogether lost to science, though the specimens from which they have been designed have perished, we here present an Ostracion, in which the chief novelty appears to be the want of a dorsal fin. Dr. Hooker has given four views of this little fish in different positions, viz: [Pl. XXX, fig.] 18, a lateral view, [fig.] 19, a view of the back, terminated at each end by a long spine, and with two smaller intermediate eminences, which seem to replace the dorsal fin. Fig. 20 shows the under surface, when the fish is turned so as to bring the mouth and frontal spine into view, and [fig.] 21, the posterior surface, looking from the vent over the anal and caudal [dorsal] fin to the long caudal spine.

"*Hab.*—Taken in the Southern Atlantic in a tow net."

It is not stated in the original description by Richardson how much the figures are enlarged, but Günther says (Introduction to the Study of Fishes, p. 175) that Richardson's figure 18, which we have reproduced in the accompanying Plate VIII, Fig. 1, is "much magnified;" information which he may probably have obtained from Dr. Hooker himself. The great size of the eye would also indicate that the specimen was very young, and would lead the writer to think that the figure must have been drawn considerably larger than natural size. The front and top

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* Synopsis of the Plectognath Fishes. Proc. U. S. Nat. Mus., 1884, 411–429.

† Voy. Erebus and Terror (Ichthyology), p. 52, Pl. XXX, Figs. 18–21. (Drawn by Dr. Hooker.)

views given by Richardson also show that "*O. boops*" is very thick in proportion to its length and height, much more so in fact than it is in either the "*Molacanthus*" or *Mola* stages of development; a fact which would also favor the conclusion that this represents a much younger stage, and therefore a smaller fish than the two latter. The two upper rows of spines on "*O. boops*" can be pretty closely homologized with those in the same relative position in the *Molacanthus* stage, but the three median ventral spines present along the median ventral aspect of both the *Molacanthus* stage and the very young *Mola* are absent in "*O. boops*."

This close agreement in the distribution of the spines cannot be considered otherwise than indicative of the very close ontogenetic relationship of the three forms in question, and such a conclusion is still further strengthened by the fact that in all three the spines are apparently of cuticular origin. They are characteristic and persistent until the young *Mola* reaches a length of about two inches, when they drop off, leaving the skin nearly smooth, as in the adult, though the scars with raised borders where the spines were originally attached remain and occupy the same relative position in respect to each other as in still younger stages and that phase represented by *Molacanthus*.

The interval between the dorsal and anal fin of "*O. boops*" shows that even in this early condition of growth the *Molina* have no true caudal fin, or, at least, a caudal developed with intermediary neural and hæmal supports, such as are found in normal Teleosts. Yet it is clear that in the *Molacanthus* stage the first signs of what represents a caudal in *Mola* appear as very short rays included by a narrow fold of epiblast or skin, which grows in height as the rays lengthen, and approach the condition which they present in the young of *Mola*. But the development of the median caudal rays to a length exceeding twice that of the rays above and below them in young specimens of *Mola* shortly after they have passed the *Molacanthus* stage is very remarkable, since, as the fish increases in size, this tail-like extension of the middle rays of the caudal disappears, so that the margin of the whole tail-fin assumes a moderately convex or gently rounded outline when viewed from the side. This prolongation of the central rays of the caudal in the young *Mola*, however, assumes a striking significance when compared with another closely related adult form pertaining to the *Molina* first described and figured by Bleeker* and now known as *Masturus oxyuropterus* (Blkr.) Gill, which has the central rays of the caudal very much prolonged and slightly divergent, as in the young of *Mola*, the backwardly projecting central part of the tail being also armed with a pair of dermal plates. This condition of parallelism in the development of the central rays of the tail of the young of *Mola* and of the adult *Masturus* would indicate that the latter has retained in the course of its evolution a characteristic which is only a transient feature of the evolution of *Mola*.

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*Med. d. Kon. Akad. Wetenschappen, 2de Reeks, Deel, VII, Amsterdam, 1873.

The prolongation of the central rays of the caudal of the young of *Mola* looks at first as if it represented the lophocercal prolongation of the somatic axis of the larva, but a careful examination shows that there is no prolongation of the chorda, nor is the skeleton extended in any way into this median projection of the caudal. If such is the case, sections alone could be depended upon to clear up the question, though I am very decidedly of the opinion that even sections will not show any evidence of rudiments of the chorda in this median posterior prolongation of the caudal fin. If any rudiments of a prolonged somatic axis are present, it is most probable that the chorda will be found present. This is a point which my researches cannot determine with certainty, since it is desired to preserve the materials now in my possession without mutilation for reference. Very careful examinations have convinced me, aided as I have been with an excellent triplet, that the embryonic axis or chorda is not prolonged into the central prolongation of the tail, already described, because this median extension is a secondary formation, and not a part of the primitive larval axis.

The morphology of the tail of the *Molina* cannot, however, be understood without making certain assumptions, which are unequivocally justified by the structure of the tail of the adult. We find, in fact, that the tail of the *Mola*, when full grown, is constituted of rays, which are supported entirely by interneural and interhæmal pieces, and not directly by any hæmal and neural spines. These, however, are indirectly brought to serve as supports for the interneural and interhæmal elements in a way which is without a parallel amongst Teleost fishes. The sixteenth vertebra has its neural and hæmal spines greatly prolonged, and the interneural and interhæmal elements of the caudal fin of *Mola* are proximally in contact with the spines of the penultimate vertebral segment.

The larva of *Mola* is not known, and it is therefore premature to do more than surmise, on the basis of the principles of comparative morphology, what that larva must be like. We find that the vertebral column of *Mola* ends abruptly with a "floating" vertebra, which is cylindrical in form and evidently does not represent the last bony segment as in normal Teleosts. The vertebral segments of *Mola* do not gradually become less in diameter in so striking a manner as in other Teleosts, so that the column does not terminate in an acuminate upturned urostyle, or in an attenuated extension of the chorda, as in normal forms. In *Masturus* it is not improbable that evidence of the greater posterior extension of the vertebral column will be found, as would be indicated by its longer caudal fin. It is evident, nevertheless, that a part of the larval axis of *Mola* has been suppressed, for the reason that the last vertebral centrum is but slightly smaller than the penultimate one, and has evidently been formed in the skeletogenous investment of the chordal axis of the larva far in advance of its posterior extremity in the youngest larval stage of development. The presumption, therefore, is that the larval axis was relatively much longer than that of the adult, and that it possibly had a lophocercal tail, or at least a caudal prolongation which was probably absorbed at an early period, somewhat after the manner of the tail of the tailless Batrachians, and for this reason the end of the primitive caudal axis has not become the support for the caudal fin as in other *Teleostei*. The development of a special mode of support for the caudal has consequently occurred, which has apparently been caused by the abortion of the posterior end of the primitive axial skeleton. This view of the facts is demonstrated beyond any doubt whatever when we find that the interneural and interhæmal pieces which support the caudal of *Mola* are serially homologous with the interspinous pieces which support the dorsal and anal fins, though the interspinous elements of the caudal are shoved out of position and are arranged in two confluent series above and below the osseous axis at right angles to the rows supporting the dorsal and anal. In Fig. 7, Plate VIII, I have attempted to show the caudal of *Mola* somewhat as it would appear if developed normally; the elements which now exist are represented in black, while those which have been suppressed are represented by shaded outlines. The extension of the chordal axis posteriorly beyond the "floating" vertebra is shown in dotted outlines, while the suppressed myotomes and skeletogenous material of the median vertical portion of the urosome is limited in front approximately by the two heavy, curved, dotted lines, with the arrows alongside. Four more interhæmal elements are shown to be developed, in the young, below the line of the vertebral axis than above it.

This diagram represents the structural condition with which we have to deal in clearing up the question of the origin of the tail of *Mola*. If the eleven inferior and the seven superior interhæmal pieces are now swung forward in the direction of the arrows and along the course of the heavy dotted curved lines, the interhæmal pieces will have their proximal ends brought against the posterior face of the neural and hæmal spine of the sixteenth vertebra. This must have been the case, for we have shown that the posterior portion of the axial skeleton has been suppressed, but the superior and inferior margins of the urosome have evidently been preserved so that the interhæmal and interneural pieces belonging thereto have developed, but no remains of the corresponding neural and hæmeal arches are to be found, so that we have the anomalous condition of the interneural and interhæmal supports of the caudal resting upon the neural and hæmal arches of a vertebra in advance of those which would have been developed with their corresponding homodynamous spines, had the posterior and axial part of the tail not been suppressed.

The hæmal and neural supports corresponding to the seven superior and the eleven inferior interspinous bones have failed to develop, apparently, because the skeletogenous tract from which they are normally developed was suppressed, together with the posterior part of the caudal axis. The preservation of only a part of the marginal portion of the median skeletogenous tract from which the hindmost interspinous supports for the caudal are developed is without a parallel, except *Fierasfer*, so far as the author is aware, amongst fishes. These supports sometimes fail to develop, but the layer whence they are derived is present, as in *Chimæra*, for example.

How far is the foregoing theory of the structure of the caudal fin of *Mola* justified by what is known of the development of this fish? Since we have satisfied ourselves that *Ostracion boops* is merely a stage of the development of *Mola*, it is clear that that form has already advanced far beyond the condition of the larva which *must* be assumed to have had some traces of a complete caudal axis, for it already exhibits a condition approaching that of the *Molacanthus* form, with its two developed dorsal and anal fins, which have a slight interval between them.

The youngest *Molacanthus* stage hitherto figured has the dorsal and anal more approximated than the specimen figured by Putnam, or the one in the United States National Museum, which would indicate that a metamorphic process was in progress in the interval between *O. boops* and *Molacanthus*. This view is supported by the fact that the fin-fold, which appears in still older *Molacanthi*, is very narrow or low, and the fin rays which it includes are very short and feebly developed. In the next stage, Fig. 5, this fin-fold between the dorsal and anal has become higher, and the first indications of the production of the middle lobe, such as is found in the next older stage, begin to be apparent. It is thus made very evident that the development of the caudal in these fishes is a progressive process, and that it is remarkable and even unique in this one respect, viz, that all of the unpaired fins do not develop simultaneously as is usually the case with young Teleosts. This can only be explained on the theory already suggested, that the posterior part of the primitive axis has been suppressed, so that in order to develop a caudal at all a secondary and indirect mode of development has been necessary, in the course of which the remnants of the anterior median ventral and dorsal parts of the urosome still preserved have supplied the materials for the growth of the interspinous bones which support the caudal rays, but these portions of the primitive urosome have been drawn forward and included between the anal and dorsal. Then as the caudal grows out it manifests another singular tendency, viz, to develop a certain number of soft rays in its central prolongation which are subsequently suppressed in the adult fish, which is simply additional evidence in favor of the belief that these rays belonged to a dorsal and ventral series, at one time developed along the upper and lower margins of the urosome of some ancestral form, but on account of the suppression of the latter, have been carried toward the end of the persistent part of the axis of the existing derivative form in excess of the number which are permitted to persist as permanent rays.

Dr. Gill seems to lay especial stress upon the statement made by Putnam that there is no caudal chain of interspinous bones developed in *Molacanthus*, and that their absence justifies him in recognizing the form as distinct from *Mola*. Unfortunately this character becomes as completely valueless in the light of embryology as all the rest which have been used to define *Molacanthus* as a form worthy of family rank. As we have already shown, *Ostracion boops* has no developed caudal; while *Molacanthus* has only traces of it as very short and feebly developed rays; and inasmuch as interspinous bones are always developed upon cartilaginous bases in the form of bars, and since fin-rays may be developed while the interspinous cartilages are still very imperfectly formed, there remains no shadow of doubt in the mind of the writer that the interspinous bones or their cartilaginous matrices were still undeveloped in *Molacanthus*, or at least so imperfectly developed in Mr. Putnam's specimen as to be undiscoverable or very readily overlooked. It thus becomes very easy to regard *Molacanthus* as merely a stage of the growth of *Mola*, in which the development of the tail has been retarded owing to the extraordinary and unique modifications which the type form has undergone. I am, therefore, fully convinced that the absence of developed caudal interspinous bones in *Molacanthus* is merely a transient embryological character and absolutely worthless in taxonomy. Of this I am so certain, that I will venture to predict that when an examination is made by a competent anatomist, a condition of things approximately like that which I have described will be found to exist.

Fortunately, I have been able to verify the foregoing prediction, which was written as it now stands a week since. Upon cutting open the skin at the edge of the tail of a specimen of *Molacanthus* with extreme care, so as not to otherwise injure the specimen, I found the axial skeleton in place, and carefully exposed its parts. I found, as stated by Putnam, the interspinous bones, which support the caudal fin, very feebly developed, if not absent. The spines of the seven caudal vertebræ were developed, but the vertebræ themselves, as well as the spines, were feebly ossified, their bony matter being developed, as usual in young fishes, in a perichondrial and perichordal position, wholly dissimilar from the adult condition. The terminal or floating vertebral centrum is developed, and is very short and bluntly pointed, ending just within the margin of the fleshy part of the caudal fin, and so very near the base of its ray-bearing marginal fold that it is difficult to see how there would be room for caudal interspinous pieces. Yet from my examination I am not certain that when a specimen is examined with the more accurate and thorough method of microtomy, they may be found as minute cartilaginous elements. They must necessarily be minute, for the narrow triangular area occupied by them in *Molacanthus* is not quite a millimeter wide and five millimeters long. To judge from the very rudimentary condition of the caudal fin in the *Molacanthus* stage, we should expect these elements to be rudimentary, or even wanting; but they doubtless primarily develop in cartilage, as in other forms. Their development has evidently been belated or retarded as compared with the other vertical fins.

The vertebral axis of *Molacanthus* is apparently very oblique and about parallel with the base of the dorsal, the interval between them being but two millimeters; the distance from this axis to the extreme ventral margin of the abdomen is seven times as great; so that here we have a character strong enough for the most enthusiastic taxonomist to avail himself of as a family character. But let us see if even this is of any value. The fact is that the axial column of *Mola* gradually assumes a more ventral position, *i. e.*, the abdominal contour becomes less prominent with the advance in age, so that the axial column is apparently shoved downwards, as may be seen upon comparing together figures of the skeletons of the different ages. This pushing down of the vertebral column is, however, more apparent than real, the fact being that the abdomen diminishes in height, as a result of which the vertebral axis seems to be pushed downwards. During this process the obliquity of the axial column also diminishes, so that its anterior is lowered more than its posterior end.

During the *Molacanthus* stage the skeleton of the tail bears every evidence of immaturity. It is soft and flexible, and not ossified as flinty bone, as in the adult. The chorda comprises the bulk of the axial column, and one can easily make out that the vertebral segments are only just distinctly formed. The part of *Molacanthus* which is comparable with what is the tail of the young and adult of *Mola* is very rudimentary; and since we now know that the volume of this part of *Mola* actually increases with the advance of age, we have here a remarkable instance of post-larval effort to regenerate a part which has degenerated and been absorbed during the larval period of existence, as we have already pointed out in another part of this paper. The figure of the caudal skeleton of *Molacanthus* in place shows that it is an exceedingly small part of the whole fish, while in the young of *Mola* it becomes wider, and in the adult still wider anteroposteriorly, while it has increased greatly in thickness and changed the form of its posterior contour. These are some of the facts upon which I rest my thesis that, *there actually occurs in Mola a secondary development of the tail, by which that organ is, so to speak, redeveloped from traces of epaxial and hypaxial tissues which had not been absorbed at the time the tip of the larval axis degenerated.* Taken altogether, the tail of *Mola* thus presents us with one of the most interesting chapters known to me in the whole range of vertebrate morphology, and it has been my real purpose to reconcile it with the general theory of the development of the caudal fin developed in this memoir, constituting as it does an extremely aberrant form, which had to be very thoroughly examined with that object in view, and not, as I fear it may be supposed, merely to demolish the grounds upon which the *Molacanthidæ* have been recognized as a family.

A remarkable reduction in the number of caudal rays occurs in *Mola* during the period of growth intervening between the time when it is about two inches long and the time when it is full grown. In the young two inches long there appear to be about twenty-three caudal rays developed; in the adult, on the other hand, if Wellenbergh's figure is to be relied upon (Fig. 9, Pl. VIII)—and it is seemingly very accurate—there are only thirteen caudal rays. This elision or loss of rays seems to occur in the central part of the caudal, while those rays which are distinctly epaxial and hypaxial in position seem to be preserved. The tail-like process in the center of the tail-fin of the young, together with its six nearly simple filamentous rays, appears to be entirely absorbed and suppressed. To what extent the filaments represented by Putnam extend beyond the margin of the caudal of the young I am unable to say; but of this I am certain, that the epaxial and hypaxial caudal rays are not simple, as figured by Putnam, but are dichotomous and soft, having three to four terminal branches. The specimens which I have in my possession for study do not show the radial filaments or their divided ends exserted to anything like the extent represented by Putnam, and I am very much inclined to believe that the specimens which are before me are normal, and have never had any such naked projecting filaments.

It is certain, however, that the dichotomous character of the caudal rays of the young of *Mola* does not persist, but entirely disappears by about the time that they assume their final condition in the adult, and that what with their reduction in number to thirteen and the loss of their dichotomous character and the retreat of their apices from the extreme margin of the caudal fin, the fin, as a whole, undergoes even a tertiary metamorphosis in passing from the young form distinctly recognizable as *Mola* to the adult condition. We thus find that *Mola* presents the most extraordinary series of transformations in respect to the development of its caudal rays to be found anywhere amongst Teleost fishes, the origin of which we can explain only upon the ground that the abbreviation of the tail of the larva and the suppression of the primitive terminal somites of the body have been more extensive in this instance than in any other. Additional morphological and embryological proof of the position which I have taken will hardly be necessary, but it may be well to call attention to the fact that the remarkable arrangement of the muscles of this family of fishes is also unique, yet it is not impossible to explain even this modification according to the general theory of development, as will be seen in the sequel. When we remember that the vertical fins of *Mola* are moved by a series of powerful muscles, the substance of which comprises almost the whole of what corresponds to the lateral muscular masses of normal Teleosts, we must conclude that what is ordinarily developed in other forms into segmentally arranged muscular somites, in this instance becomes subservient to producing the movements of the vertical fins. Upon dissecting a very large specimen we find that the somatic musculature is divided into bundles, which radiate for the most part in a backward, upward, and downward direction, and in a semicircular series to the dorsal, caudal, and anal, into the bases of the rays of which they are inserted by powerful tendons. There are two series of these bundles, with their tendinous terminations, one on the right, the other on the left side of the body, corresponding to the muscular masses of the right and left sides of normal fishes. The tendons are round and lustrous white, and pass through a mass of very tough, elastic tissue, almost cartilaginous, which extends along the bases of the vertical fins, long tubular openings being excavated in the basal cartilage-like substance, through which the long tendons glide. In this way a muscular apparatus is developed on the one side of the body which opposes that on the other, and which most effectively moves the high vertical fins from side to side; and the two series of muscles and tendons inserted into the caudal move it from side to side, very much like the rudder-chains of a ship move its rudder. There is also this resemblance between the caudal of *Mola* and a rudder, that the strip of compressible elastic tissue at either side of the base of the tail acts as a sort of hinge, upon which this thick, rigid, truly rudder-like organ swings from side to side. A slightly similar arrangement is found in *Ostracion*, but the modification is not carried to anything like this extraordinary degree of specialization.

Now, what is the meaning of this modification? Simply this, that almost the whole of the lateral muscular masses have been converted into bundles of muscles terminating in tendons, the function of which is to move the vertical and caudal fins. And how is this change from the normal condition to be explained on embryological grounds? If we examine the developing tails of normal Teleosts we find that the caudal musculature is developed from the last somites of the body; that in fact almost the whole of the muscular somites of *Mola* are used up in order to form the flexors of the caudal and vertical fins alone; whereas in normal Teleosts only a very few of the terminal muscular segments of the urosome are used up or transformed into the musculature of the tail and the vertical fins. This, I infer, may be regarded as the final proof that the tail of *Mola* has had a large part of its urosome aborted, as already urged, so that it was necessary to modify the more anterior series of muscular segments and subordinate them to the function of flexing the tail.

This metamorphosis of the myotomes of *Mola* into flexors of the fins is doubtless due to the fact that the skin of the animal, in large specimens, is quite half an inch thick, thus constituting an almost rigid covering over the body, which would either induce muscular degeneration or metamorphosis.

I do not see that it necessarily follows that the centrum of the seventeenth vertebra of *Mola* consists of two consolidated vertebral bodies, because it has three elements above and three below it, which Putnam, it seems to the writer, erroneously regards as neural and hæmal arches. They are evidently nothing but interspinous pieces, shoved into this strange position by the process of development already described. They apparently disappear as soon as the fish becomes adult. We are not told whether they are forked proximally, as neural and hæmal arches should be when in contact with so large a centrum. In the adult there is good reason to suspect that these "floating" interspinous elements referred to above have been co-ossified so as to form apparently a single element, if we may place full confidence in Wellenbergh's figure* of the adult skeleton. They seem in Putnam's figure of the skeleton of the young of *Mola* to be simple bars or rods, separated by an interval from the last "floating vertebra." It is much more probable that they are merely interspinous elements, like the remainder of the chain. They cannot, at any rate, be homologized with the epural and hypural processes of normal Teleosts, which consist, as we have shown elsewhere, of neural, hæmal, interneural, interhæmal and basilar interneural and basilar interhæmal elements.

Measurements of the height and length of the principal stages of growth are interesting, and show that the metamorphosis from *Ostracion boops* to *Mola* proceeds progressively, as shown by the gradual changes in the proportions of these two dimensions. The proportions of the length to height in *Ostracion boops*, measuring from between the anal and dorsal forwards and above the eye for the length, and for the height obliquely across the eye, are in—

Fig. 1, length to height as 1 to $1\frac{1}{2}$.
Fig. 2, *Molacanthus*, length to height as 1 to $1\frac{1}{2}$.
Fig. 3, *Molacanthus*, length to height as 1 to $1\frac{3}{7}$.
Fig. 4, *Mola*, length to height as $1\frac{2}{5}$ to 1.
Fig. 5, *Mola*, length to height as $1\frac{1}{2}$ to 1.

This will conclude the arguments which we have presented in favor of regarding *Molacanthus* as merely the young of *Mola*. What differences the corresponding stages of growth of such a form as *Ranzania* or *Masturus* might present in contrast with the known stages appertaining to *Mola*, it is impossible to say in the absence of sufficient material for comparison; but it is safe to assert that no amount of additional evidence will be at all likely to break down the reasons here given for the incorporation of *Molacanthus nummularis* (Walb.) Gill, with *Mola rotunda*, Cuv., as one and the same species, for the reason that it is perfectly safe to predict that when such additional evidence is forthcoming it will probably confirm the position which has been here assumed.

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*Observ. Anatomicæ de Orthagorisco Mola. Diss. Inaug. P. H. J. Wellenbergh. Lugduni-Batavorum, MDCCCXL.

It now remains for me to suggest that the true larval condition of *Mola* should be sought for amongst the surface trawlings taken during marine explorations, and I will venture to say that when that larva is found it will very probably differ as much in general appearance from *Ostracion boops* as the latter differs from *Molacanthus* or *Mola*. It is very probably provided with some rudiment which represents the tail of normal fish larvæ. The eggs of *Mola* are very probably pelagic, the larvæ having the same habit.

X.—DISCUSSION OF THE SERIAL HOMOLOGY AND THE INFLUENCE OF HEREDITY ON THE DEVELOPMENT OF CONTINUOUS FIN-FOLDS.

The *Ichthyopsida* or *Anamnia* constitute the lowest portion of the vertebrate phylum. In contradistinction to the more developed types, they possess, almost without exception, at some stage or other, an eradiate dorsal and ventral fold of epiblast, which serves as an organ of propulsion through the medium in which they usually live, either temporarily or permanently. This is characteristic of the group, from *Branchiostoma* to the highest Batrachians, and all the exceptions which are known amongst existing forms are readily explicable on the ground that these have specialized modes of development, which either abbreviate the latter process or induce precocious degeneration of this particular structure. The entire piscine series possess in some form or other this mesial propelling organ, supported in the adult by simple or dichotomous segmented osseous, or by cartilaginous rays, or by fibers. In contrast to this series the median fins are more or less transitory or larval in the Amphibian series, and unprovided with rigid axial supporting organs.

The only Vertebrate which still retains a more primitive system of locomotive organs than the median system of fin-folds, characteristic of the larvæ of the rest of the *Ichthyopsida*, is *Branchiostoma* while it is still in the archicercal or vermiform stage, when most of its epidermis is still clothed with vibratory appendages or cilia.

The lophocercal eradiate stage of development of the azygous epiblastic—really epidermic—fold on the dorsal and ventral aspects of the body seems, therefore, to be eminently characteristic of most fish-like forms during an early stage of their growth. The multiradiate diphycercal condition, which replaces it by a process of natural evolution in *Ceratodus* and *Protopterus*, is primitive, and permanently approached and represented only by the numerous distal branches into which the rays of many Teleosts subdivide at their tips, where traces of the distinct primitive fibers or horny filaments are often clearly marked, even in the most specialized forms, such as *Scomber* and *Xiphias*, or the Mackerel and Sword-fish, along the margin of the caudal fin.

Ceratodus and *Protopterus* are examples of an imperfect embodiment of the protopterygian stage. In these some of the primitive horny fibers or fin-rays have fused together to the number of as many as three, usually not over two; in other fishes many of these fibers become involved to form a single ray. *Chimæra* and its allies are also very primitive, their fin-rays attaining but a slight advance in development beyond what I have denominated the Protopterygian stage of the embryos of Teleosts; yet even in *Chimæra* the rays are not absolutely simple, as in the embryonic condition, traces of their coalescence being present. And I would here insist that the material of which the primitive fibers consists in all fishes, be they Elasmobranchs, Dipnoans, Ganoids, Chimæroids, or Teleosts, is similar in its nature and origin and its relations to the primary embryonic layers; that the point where the fin-rays join or overlap their cartilaginous supports in the embryo is homologous throughout the entire phylum of the fishes, and constitutes, for the pectorals and ventrals at least, a starting point of equal value with the articulation of the proximal elements of the limb to the shoulder or pelvic girdle, for the purpose of determining the homologies of the bones or cartilages which form the true axial skeleton of the limbs.

Dr. Günther, in his valuable monograph on *Ceratodus** (p. 530), says: "The dermo-neurals of *Ceratodus* are not articulated to the extremities of the interneurals, but overlap them for a considerable distance of their length. The shape and arrangement of the dermo-hæmals is exactly the same as that of the dermo-neurals. No ossification takes place in either of them; they consist entirely of cartilage, in which numerous spindle-shaped cells are imbedded, many of these cells being produced at both ends into a very long process (Pl. XXXVI, Fig. 7)." These dermoneural and hæmal elements, as Dr. Günther calls them, are the exact homologues of the horny fibers of fish embryos, and cannot, I regret to say, be regarded as cartilaginous either in origin or histological character. They are allied in constitution to the material in which the ossification of membrane bone occurs.

Dr. Günther also remarks of the fin-rays of *Ceratodus*: "They are exceedingly numerous, four or five or more corresponding to a single vertebral segment, and form a double series, one series on each side of the fin. This peculiarity, which *Ceratodus* has in common with *Lepidosiren*, reminds us of those fin-rays of Teleosteous fishes which can be more or less completely split into a right and left half."

This quotation becomes remarkably significant in the light of the facts of development, since we now know that the right and left halves of the rays of Teleosts actually develop in part from the double series of embryonic fin-rays which underlie in a single layer the right and left dermal wall of the fin-fold. The large number of fin-rays to a single segment in *Ceratodus* likewise no longer appears strange; this condition being simply indicative of the fact that the specialization and the fusion of the embryonic fin-rays into powerful rays has not gone so far as in the more developed and specialized Teleosts, which have all the

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*Philos. Transactions, Pt. II, 1871, pp. 511-571.

other parts of the skeleton well ossified. The embryonic condition of the fin-rays of *Ceratodus* is in perfect keeping with the development of the rest ot the animal's skeleton, which is very largely cartilaginous, so that in a general way it closely resembles in the degree of its development that transitory stage of the Salmon embryo when the embryonic rays are still distinct and parallel with each other. To find such a parallelism existing between an embryo Teleost and the adult of *Dipnoi* is, to say the least, very suggestive of the thought that the Teleostean and Dipnoan phyla are remotely affiliated. On no other ground are we enabled to understand why it is that a Teleost should recapitulate so closely in the course of its development conditions which are permanent in the *Dipnoi.*

Protopterus resembles *Ceratodus*, according to Wiedersheim,* in the structure of its median fin-system, and presents the same dorso-ventral symmetry of the upper as contrasted with the lower half of the tail. The main difference which these forms present when compared with the lophocercal condition of the caudal end of the body of fish larvæ is the presence of partly osseous neural and hæmal spines, interneural, interhæmal, and basilar interneural and basilar interhæmal elements, which support numerous rays nearly equivalent to the embryonic fin-rays.

The tail of the Crossopterygian *Polypterus* exhibits a tendency to become heterocercal, hardly, however in proportion to the extent to which ossification has proceeded throughout the entire column. The persistency of the axial symmetry of the caudal fin we must therefore regard not necessarily as symbolical of its degeneracy or completed evolution, but rather of the persistence of conditions which have not disturbed that symmetry. That the condition of dorso-ventral symmetry found to obtain at the posterior part of the chordal axis of fish embryos generally is the most ancient is conclusively shown by the evidence derived from all known types of fish-larvæ.

As already indicated by competent observers, the lophocercal condition precedes the heterocercal, which is itself followed by the outwardly homocercal condition; yet there are instances known in which this rule is violated to some extent, as I have already pointed out elsewhere. These are where (1) the median fins are not developed from a continuous median fold, as in *Siphostoma*, *Hippocampus*, and *Gambusia;* and (2) where a truly lophocercal homocercy precedes the structurally heterocercal stage of development, as in *Alosa*, for example. In both of these instances, however, there is no reason to believe that we have any embryological principles contradicted, but that in reality those principles are confirmed by these apparent exceptions.

It is therefore noteworthy that the primitive embryonic rays in the tail of the embryo of *Alosa* have a perfectly symmetrical disposition above and below the caudal axis, as shown in the dotted lines in Fig. 2, Pl. II.

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* Vergleichenden Anatomie der Wirbelthiere, Jena, 1883 and 1884.

This proves conclusively that the diphycercal condition so perfectly preserved in *Ceratodus* is actually recapitulated by the larvæ of existing forms, since the primitive embryonic rays undoubtedly represent almost exactly the permanent rays of that form.

Taking the examples of *Siphostoma* and *Hippocampus*, both are highly specialized types of Teleosts; in the former a dorsal, anal, and caudal are developed directly in special discontinuous folds in the situations where they are permanent, though an abnormal specimen shown me by Dr. T. H. Bean has a small second anal developed in an intermediate situation, where it is readily conceivable that it was derived from a part of the continuous tract which in other fish embryos gives rise to all of the median fins. This specimen must, therefore, be regarded as an example in which there has been a very imperfectly successful attempt at reversion towards the most ancient and primitive condition of the caudal skeleton, which is permanent in *Ceratodus* and *Protopterus*. The tail of *Siphostoma* is, however, developed in much the same way as in other forms, though the *dorsal lobe*, or tip of the lophocercal condition of the tail is very feebly marked.

Hippocampus, unlike the last-named genus, has passed through a still more extreme series of modifications, and in consequence not only develops its median fins in separate or discontinuous folds, but the tail, in consequence of the acquisition of a prehensile function, has also almost lost all trace of a median caudal fold, this fin altogether failing to develop at any subsequent stage, Fig. 3, Pl. IV. With other types this form contrasts in the most remarkable way, since it is the only form in which the cartilaginous axis of the body is bent and coiled upon itself ventrally, or in a direction just the reverse of the usual one in the larvæ of fishes. From the remarkable manner in which this fish swims, with the body in a nearly erect position, and the use of the tail as a grasping organ, it is fair to assume that this part of the animal has suffered degeneration as far as the absence of a caudal fin is concerned, and specialization, in consequence of its development into a grasping organ, which has involved the modification of the caudal muscular somites into special flexor muscles having a ventral position.

In *Gambusia* the failure to develop a continuous median fold is rather remarkable. It is possible, in consequence of its viviparous development, that the development of the median fins has been abbreviated and followed a more direct path, as just noticed in the *Lophobranchii*. Since the young of *Gambusia* are developed within the body of the parent female till they are nearly like the adult in form, it may be that the usual method of development of the fins has given place to a much more direct one, influenced possibly by inclosure within the ovary of the parent, as a result of which hereditary influences would be intensified. At any rate, it is certain that the condition of development reached at the time of the first appearance of the median fins as separate folds is no more advanced in other respects than in an embryo Salmon or Shad, in which there is a continuous median fin-fold still present.

In *Alosa* the median fin-fold is continuous and high, and at an early period there is a slight vertical expansion of the caudal portion of the median fold, which is the prelude to a fan-shaped condition, which is attained while the caudal is still eradiate and the chorda is straight at its hinder extremity. In this condition the tail is outwardly homocercal, but really lophocercal, because it is still without any other than faintly developed embryonic rays. In this form there is no outgrowth of a distinct ventral lobe, but, on the contrary, the tail of the adult is developed directly from this symmetrical larval tail, the mesoblast of the tail wandering outward directly into the caudal fold, where it is transformed into the substance of the hæmal pieces and medullary substance of the rays. This in like manner is an example of abbreviated development, though it occurs in a Physostomous form, which is manifestly more primitive, because it possesses a perforate pneumatic duct, than those Physoclistous forms which pass through that stage of development of the tail which is permanent in the fishes of the Devonian age.

The causes of the failure to develop a stage in *Siphostoma* and *Hippocampus* with a continuous median fold, such as is found in other forms, are readily explicable on the ground that they are extreme modifications of the ordinary Teleostean type, but when we consider the two cases of *Alosa* and *Gambusia* amongst the Physostomes, with the modifications of development which the one presents in respect to all of the median fins, and the other in respect to that of the caudal, we are bound to admit that they present singular and striking exceptions to the rules governing the development of the tails of fishes first laid down by L. Agassiz and C. Vogt. Fortunately these exceptions are very few, and they therefore do not affect the general principle upon which these authors insisted as much as might be supposed upon first thought, because after all, in the most important exception, *Alosa*, the tail finally becomes heterocercal in structure just as in almost all other Teleosts, the symmetry of the caudal of the larvæ being simply an acceleration of the process which ordinarily occurs, together with an apparent elision of some of the stages which usually accompany the transformation of the lophocercal tail of the larva into the homocercal or heterocercal of the adult, as the case may be.

The writer has elsewhere expressed his views in relation to the continuity or discontinuity of the median and paired fins, and has suggested the probable reasons for the existence of such differences between embryos of a similar age, in the following words: "*Hippocampus* never develops a caudal fin, so that we would naturally not expect to find the natatory fold prolonged over the end of the tail; but the posterior position of the early rudiments of the pectorals in *Cybium* and *Parephippus*, it appears to me, is a very strong argument against their origin from a posterior branchial arch (a conclusion since reached by Dohrn); indeed, it is the strongest yet offered against that doctrine by any data derived from a study of the development of the paired fins of Teleosts. In other words, since we now know that the natatory fold, from which the unpaired median fins are developed, is sometimes discontinuous, I see no reason why we should not expect to find the lateral fin-folds discontinuous, as there are more reasons why they should be so in the Teleost than in the Elasmobranch embryo. In fact, it would appear that the greater the longitudinal extent of the unpaired fins, in proportion to the length of the body of the adult, the more likelihood there is of finding a continuous dorsal and ventral natatory fold developed in the larva, and *vice versa*. The longitudinal extent of the paired fins of Teleost fishes is less, vastly less, in respect to the number of supporting rays than those of the Elasmobranchs, and in consequence of this difference alone we should not be surprised to find lateral fin-folds of considerable extent in the former. Viewed in this way, we may prove too much for the doctrine of the origin of the paired fins from lateral folds."*

The principle stated by Balfour in the following words, "*the limbs are the remnants of continuous lateral fins*,"† may possibly need qualification, if the preceding view is justified. The case of the embryo *Torpedo*, in which the continuous lateral folds are especially well developed, does not seem to me to be conclusive for the reasons urged above, because that form and its allies *Narcine*, *Hypnos*, &c., have developed in the adult condition what has been denominated a cephalic fin. It thus turns out that we here have the influence of the principle verified which is palpably operative in the case of the embryos of Gadus and the Flounders. Both of these having the median fins of the adult approximated, the tendency would naturally be toward the development of a continuous median fin-fold in their larvæ, such as we find to be actually the case. It thus becomes evident that heredity may directly affect the mode of development of the young. The opposite condition of discontinuity in the *Lophobranchii* is similarly explicable.

Whether the cephalic fins of *Torpedo* were primitively a part of the pectoral or not, as Gegenbaur would urge, is immaterial, for the great extent of the lateral fin-system in the adult must obviously affect the development of the early rudiments of the limbs in the embryo, and tend to cause their first appearance as uninterrupted folds.

In the adult *Torpedo* the cephalic fin does not possess all the traits of a paired fin with straight, parallel cartilaginous supports (see Gegenbaur, Das Kopfskelet der Selachier). In *Hypnos subniger*, on the other hand, the supporting rays of the cephalic fin, according to Haswell,‡ are present as nearly parallel bars, resting in part on a pair of anterior

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*Development of the Spanish mackerel (*Cybium maculatum*). Bull. U. S. Fish Commission, I, 1881, pp. 160, 161.

†Monog. on the Develop. of Elamosbranch Fishes, p. 102.

‡Studies on the Elasmobranch skeleton. Proc. Linn. Soc., of New South Wales, Vol. IX, 1884, pp. 105, 107, and 116.

divergent basal bars, supported by the antorbital cartilages, partly on the sides and ends of the cranial rostrum. By what process these bars came to assume such a relation to the chondro-cranium of *Torpedo* is not clear, unless we assume, as supposed by Gegenbaur, that a part of the anterior end of the propterygium became detached from the pectoral and was secondarily affixed to the antorbital process of the skull. This is an explanation, but is it the one which will be finally accepted? This may be doubted, for even supposing that this view is the true one, it is rather singular that the cartilaginous rostrum in *Hypnos* should divide into three lobes, each supporting rays, while on either side of it accessory rays should be found. What seems to be the difficulty is this: Why must it be supposed that the rostral rays are not directly developed in the connection in which they are found? An answer to this question can scarcely be expected until the development of the cephalic fin of *Torpedo* or one of its allies has been actually traced.

The peculiarities of development of greatly specialized forms evidently do not furnish safe criteria upon which to base general conclusions in respect to the development of all affiliated forms, as the preceding cases would seem to indicate. As another instance of this may be cited the fact that the single vertebral centra of *Lophobranchii* support a number of neural arches, which in certain regions are certainly first laid down in cartilage. The usual rule is a single neural arch to a single centrum, though in the tail of *Amia* this rule is violated in another way, only alternate centra supporting arches in this case. In Elasmobranchs still another arrangement of arches and centra obtains.

In *Siphostoma* it is stated by McMurrich that a distinct fibrillation takes place in the fin-folds of the embryos, "which, increasing, leads to the formation of horny rays."* A similar remark applies to the development of the rays of *Hippocampus* in the pectoral, anal, and dorsal fins. McMurrich's statement, however, that the anal of *Siphostoma* aborts after developing embryonic rays, must be denied, since the anal is present in adults of both sexes of specimens of the same species which have been examined by the writer. The interspinous cartilages are also much more complex in the embryo of *Hippocampus* than in *Siphostoma* of nearly the same age as those figured by McMurrich. The erectores and depressores spinæ muscles terminate as tendons which are as long as the elements which I have elsewhere called *basiradial cartilages*.† These basiradial elements are cartilaginous, and each one at its distal end supports a small cartilaginous nodule or actinophore, which is the representative of a basilar interneural piece. Consequently the cartilaginous bars, the whole of which McMurrich calls interspinous, are only

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* On the Osteology and Development of Syngnathus peckianus (Storer). Quar. Journ. Mic. Sci., XXIII, pp. 623-650, 1883.

† A contribution to the development and morphology of the Lophobranchiates (*Hippocampus antiquorum*, the sea-horse). Bull. U. S. Fish Com., I, 1881, pp. 191-199, 1 plate.

partially homologous with the interspinous bones of normal forms, for at the proximal ends of the basiradial cartilages there is a constriction at the point where they are continuous with the neural spines proper, which become suddenly larger proximad of the constriction. Moreover, these bars bifurcate at the proximal ends, the bifurcation passing over either side of the spinal cord, and the ends finally rest on the upper aspect of the chorda, thus constituting the true neural arches, of which there are evidently several to a single centrum. We therefore have in the young sea-horse neural arches, interspinous and basilar interneural elements represented in cartilage as the supports of the dorsal, which are in no sense to be regarded as "rays," but as epaxial vertebral arches and their distal appendages. The interspinous portions of the extremities of the successive arches are fused together, as observed by McMurrich in *Siphostoma* of a similar age, but just proximal to the basilar interneural cartilaginous nodules or actinophores there is a general flattening of the cartilage cells and a tendency to indicate that an articulation is in process of formation between the interneural and median actinophoral elements.

The structure of the distal part of the anal of the young of *Hippocampus* is exactly similar to that of the dorsal.

It is interesting to note, also, that the neural arches in both *Hippocampus* and *Siphostoma* correspond in number with the rays, which in other forms are often in excess, together with their homonymous interneural pieces, of the number of homonomous neural spines. Here the neural spines are in excess of the number of vertebral centra by about five to each centrum, only about three centra underlying the dorsal of *Hippocampus*. In *Siphostoma*, on the other hand, nine vertebral centra afford arches to support the rays of the dorsal, which number about thirty-five, or an average of about four rays to each centrum. Each vertebral centrum of these Lophobranchiate genera therefore develops a number of distinct neural arches. Their number seems to be about five to six to each centrum. The vertebræ of these types may therefore be said to be *penta-* and *hexacanthous* dorsally.

Proximally these arches, in *Hippocampus* and *Siphostoma*, tend to concresce or be drawn closer together in an antero-posterior direction. In the first genus all of the neural arches are thus drawn together proximally, the effect of this concrescence being most visible in the oppositely inclined position of the anterior and posterior neural elements, respectively. It follows from this that we may possibly be justified in assuming that the dorsal at one time, in some ancestral form of *Hippocampus*, was supported by more centra than at present. In *Siphostoma* this tendency toward proximal concrescence is manifested by the group of neural arches belonging to single centra of the series which afford the dorsal fin its support.

The fin-rays of both these forms probably originate in mesoblast, as I have shown to be the case in *Salmo*. What lends additional probability to this interpretation is the circumstance that the tendons of the muscles which move the rays are attached, not to the "nodules" or basilar interneural cartilages, as stated by McMurrich, but to the membrane of the bases of the rays enveloping these nodules. Such a continuity of muscular and tendinous substance with the membrane of the rays, in which ossification subsequently occurs, obviously points to the conclusion that all of these tissues arose from the same primitive blastema, *i. e.*, the mesoblast.

Balfour and Parker* have recently asserted that in the ventral limb of the caudal of *Lepidosteus* there are no interhæmal pieces developed, as there are in the dorsal side of the urostyle, and that the rays which lie below the caudal axis lie against hæmal pieces. They therefore urge that the caudal is not serially homologous with the anal or the dorsal. They also urge that in *Anguilla*, according to Huxley, while outwardly there is an apparent serial homology of the dorsal and anal rays over the end of the tail, such is not really the case, but that structurally the tip of the tail is truly hetorocercal, some rays resting directly upon hæmal pieces. In *Polypterus* this is the case, as well as in most homocercal Teleosts, though it is, perhaps, unfair to urge this argument to extremes, for, while the dorsal part of the caudal in *Polypterus* and some Teleosts is undoubtedly serially homologous with the dorsal, there are cases among *Nematognathi* and Scomberoids where the interneural pieces in this part of the caudal fin are suppressed, or so reduced and co-ossified as to be obscured.

Not only is this true, but there is also a certain amount of evidence to show that some traces of interhæmal pieces or their representatives are present in the tails of Salmonoids as interspinous cartilages, or as small nodules of cartilage at the tips of the hæmal spines; that with the advance of specialization suppression of certain elements is not only probable, but is also, as we have seen above, supported by the facts of the probable presence of rudiments of interhæmal elements. Interhæmal elements are probably developed about cartilage in most Teleostean forms, certainly in some, and in a few forms they never develop much beyond a cartilaginous condition, as in *Gastrostomus*, for example. Why interhæmal or interneural pieces should apparently not be present in the caudal is not any more difficult to understand than that the basipterygium is reduced, and the rays more nearly sessile in the Teleosts than in most of the other members of the piscine series. In *Gastrostomus*, for example, a specialization of the pectoral has been reached, as a consequence of which the rays are sessile upon the coraco-scapular plate of cartilage, so that a condition is here preserved which is transitory in fish larvæ. In all these cases suppression of the intermediary pieces has evidently occurred as general specialization has proceeded. If we regard *Ceratodus* as exhibiting the most primitive type of caudal; if it has not, in fact, been affected by a general tendency to exhibit a

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* On the development of Lepidosteus, Philos. Trans., 359-442, 1882, pls. 21-29.

biserial repetition of parts correlatively, such as is apparent in the pectoral and ventral fins, then I think it is fair to regard this as the oldest, most unmodified, and nearest the condition of an archetypal caudal from which all the other modifications of the tail fin have been derived by descent with modification.

The Dipnoan *Ceratodus*, with its powerful pectoral and ventral limbs, which exhibit such a singular biserial and segmented arrangement of the elements of the limbs—even the muscles partaking of the last character, so that they are in part segmented, according to Davidoff, in a manner somewhat similar to the myotomes of the body—have had a powerful influence in retarding the modification of the tail; for in no Teleosts, with the exception, perhaps, of the *Pediculati*, do the muscles of the appendicular skeleton extend so far outwards as to form a pedunculate limb. In *Ceratodus*, however, we must not be too hasty in concluding that the segmented musculature of the paired fins is correlated with the segmented musculature or myotomes of the tail or urosome. Since we know that metamerism begins to be developed from within outward in the body, if we examine this condition as to its origin in the limbs of *Ceratodus*, we will reach a similar conclusion. Embryology has proved that both the muscular and skeletal tissues of the limbs are at first unsegmented; from the mode of differentiation of the muscular buds thrust into the limb folds from the primitive somites (gut-pouches), we may get an inkling of how the segmental arrangement of the flexor and extensor muscles of the limbs of *Ceratodus* arose. Our view is necessarily only tentative, because the development of the form is not known, but it is certainly not venturing too much upon hypothetical ground to suppose that the mode of outgrowth and concrescence of the muscular buds of the somites which entered into the formation of the musculature of the limbs gave rise to the segmentation of the axial cartilage of the limb, which, as in other forms, must have been a continuum at an early stage, just as the chorda remains unsegmented so long as no osseous or distinctly chondrified tissues invade or replace it, so as to make it rigid, and thus give rise to the necessity for the existence of segments or vertebral centra, in order to make the axis of the body flexible and under the control of the forces exerted by the muscles.

XI.—THE TENDENCY OF HETEROCERCY TOWARDS GEPHYROCERCY.

The general principle that the changes wrought by organic evolution are progressively developed, is illustrated in the most forcible way by the morphological history of the caudal fin of fishes. In the tail of *Mola* we have the extremest expression of gephyrocercy, while at the opposite extreme of undifferentiated, primordial, embryonic caudal development we must place the Dipnoans, Marsipobranchs, and Leptocardians. Taking a glance at our figures, we may readily verify the fact that heterocercy seems to be tending towards gephyrocercy as the final term of caudal differentiation.

On Pl. I, Fig. 1, the archicercal filament of *Chimæra monstrosa* shows that there is a tendency in one of the lowest types to abort the end of the caudal axis and develop the true caudal farther forward. Turning now to a representative of the *Teleostei* the same thing is repeated in *Gastrostomus Bairdii*, in which the tail is actually lophocercal at the tip in a specimen one-third grown, and with no epaxial or hypaxial rays developed for a considerable distance in advance of its termination. This last type is, however, archaic in some respects. Turning now to *Polypterus* (Pl. V, Fig. 2), the chorda is exserted posteriorly, and does not support neural or hæmal arches for some distance behind the point where the development of vertebral bodies is discontinued. The tail is roundly fan-shaped; some proximal concrescence of the hypurals is evident. The young of *Lepidosteus* (Fig. 6, Pl. V) shows that the termination of the chorda does not develop inferior and superior arches. Yet the embryonic rays are developed in the fin-fold posterior to the last arches. In the next stage the opisthure (Fig. 5, *op.*, Pl. V) is fully developed, the evidence of degeneration which it affords being complete. In Fig. 3, Pl. V, of the adult tail, the end of the unabsorbed remnant of the still more degenerate urochord extends into the dorsal portion of the caudal fin. Concrescence or crowding together of the proximal ends of the supports of the rays is evident. In *Platysomus* (Fig. 4, Pl. V) the end of the chorda is more massive, more persistent, with a less marked proximal crowding of the bases of the rays, contrasting strongly in this respect with the primitive caudal skeletons of *Coccosteus*, Fig. 1, and *Centrina*, Fig. 8.

Turning now to the contemplation of the changes which go on during development, as shown on Plate I, the evolution of the heterocercy of the Flounder's tail displayed in Figs. 3 to 10, after Agassiz, shows that the crowding from behind forward of the proximal ends of the epaxial and hypaxial pieces keeps pace with the gradually increasing heterocercy. On Plate III, illustrating the formation of the caudal skeleton of the Salmon, the same thing is again shown, actual concrescence or blending of two hypaxial elements being in progress in Fig. 4.

In the caudal skeleton of adult Teleosts, that of *Barbus* (Pl. VI, Fig. 3) illustrates the proximal crowding referred to. In *Salmo fario* (Fig. 1, same plate) and in *S. salar*, this is illustrated again, but the urochord or urostyle is not so extensively exserted as in Fig. 3. *Salmo salar* also has the end of the chorda more sharply bent upward, and the crowding proximally of the hypural pieces is more pronounced. The hinder epural pieces, *ep′ ep′*, are slid backwards somewhat in consequence of the markedly upbent urostyle, so that if the latter were now aborted a structurally gephyrocercal tail would result, because the epaxial and hypaxial elements would then form a confluent series. In the caudal skeleton of *Cottus* (Fig. 1, Pl. VII) a more specialized type of heterocercy is shown, in which, as in *Gasterosteus*, *Anguilla*, and *Fistularia*, the number of hypaxial processes are reduced. The urostyle in these is almost suppressed, but enough of it still remains to compel us to regard this type of tail as still truly heterocercal. In *Perca* (Fig. 2, Pl. VII) we have a stage intermediate between *Salmo* and *Cottus*.

The next phase in the evolution of gephyrocercy is that shown in Fig. 4, Pl. VIII, in *Fierasfer acus*,* where the process has been a direct one without a previous tendency to the development of heterocercy. The straight, probably partly archicercal, caudal filament is absorbed or lost in some way and the blunt end of the chorda abuts abruptly against the integument at the tip of the tail. The rays are not developed all the way round over the end of the caudal axis, so that there is an actual hiatus, *h*, between the last epaxial and hypaxial fin-rays. In *Echiodon*, gephyrocercy is more pronounced, as shown in Fig. 3, Pl. VII, because the last epaxial and the last hypaxial rays have been swung round so as to be nearly in contact and parallel, the abruptly terminated vertebral column being included so as not to come into contact posteriorly with the integument. This mode of the development of gephyrocercy was not preceded by the evolution of heterocercy, but it is nevertheless easy to see that in those heterocercal forms where the urostyle tends to be aborted or where it is greatly bent upwards it would need little more than the degeneration of the latter to produce the same or a similar result.

The Eel, while it has a structurally heterocercal tail in the adult, in the young (Fig. 4, Pl. IV) the caudal skeleton presents more nearly its embryonic condition, and it is noteworthy that the urostyle is so shortened and reduced as to be practically included by the surrounding parts, so that the last epural interspinous piece and the last hypural process become approximated much more perfectly than in any of the heterocercal forms hitherto discussed, and a near approach is thus made to a truly gephyrocercal caudal fin. Moreover, the last two interspinous bones if slightly prolonged forward would rest with their proximal ends upon the posterior face of the neural spine of the antepenultimate vertebra, thus simulating the arrangement found in *Mola*.

While *Amiurus* exhibits certain primitive traits, such as the possession of an adipose dorsal and a pneumatic duct, the tail is highly differentiated and strongly heterocercal. The hypural cartilages, however, show evidence of proximal concrescence, while at least six epural arches or spines have been lost; nevertheless, the tendency towards gephyrocercy is undisguised, and the opisthural element *op* in Fig. 1, Pl. IV, shows that the ancestry of *Amiurus* during a remotely bygone period possessed more hypaxial bones than the existing species. This

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*Dr. Gill kindly called my attention to this type of tail, which resembles that observed by us jointly in *Labichthys*, a new genus of Nemichthyoid eels. Something of the same sort is said to occur occasionally in *Macrurus*, but Dr. Bean thinks that its development in this instance is due to injury or accidental loss of the lash-like end of the tail, because this mode of development of the caudal extremity is not constant in the same species of this genus.

opithural piece has apparently been left behind, as the chorda has bent upwards, and the seven hypural cartilages have been carried with it, their proximal ends having been at the same time crowded forwards, so that seven of them correspond to but three indistinctly marked segments of the urostyle.

The total suppression of the caudal rays of *Hippocampus*, as shown in the figure of the tail of its larva in Fig. 3, Pl. IV, is due to the new function acquired by the tail as a prehensile organ. How marked the influence of the atrophy of a part in the adult may be in determining its failure to develop in the young may be gathered from Fig. 2, Pl. II, of the tail of an embryo of *Alosa*. Here traces of five hypural cartilages have shown themselves, while in front and behind them none have yet appeared. On the upper side of the chorda no epurals have appeared, even in relation to the same segments which bear the rudiments of hypural cartilages, but the archaic gephyrocercal condition is clearly expressed even here, for we may note that the embryonic rays are continued round the end of the chorda as a confluent series. This condition we may denominate *protopterygian gephyrocercy.*

Turning now to the form in which gephyrocercy has been expressed in the most pronounced way, we need not do more here than call attention to the development which it attains in *Mola*, as shown on Plate VIII, which illustrates how the hiatus between the dorsal and anal seems to be filled up by a new outgrowth of rays, as indicated by the stages covered by Figs. 1 to 5, while a no less remarkable metamorphosis occurs in the passage from the condition shown in Fig. 5 to that of Fig. 9, or that of the adult. No evidence of the existence of heterocercy at any stage of the development of *Mola* is in existence, unless we may infer that its Plectognath ancestry was heterocercal. Gephyrocercy, here as in *Echiodon*, was directly developed, if we may legitimately infer that Fig. 1 is really the young of this or a closely allied form.

The constant tendency in the evolution of the caudal skeleton of fishes has been to either indirectly or directly abort the termination of the chorda or axial skeleton, and in the first instance to develop an upbent urochord, as in Elasmobranchs, with epural and hypural pieces resting on the whole of its upper and under faces; this same urostyle in higher forms became more and more shortened, reduced, and included by adjacent structures; while, in the last instance, the hinder terminus of the chordal or vertebral axis is wholly suppressed either in a very early larval stage (*Mola*), or persists for a longer or shorter post-larval period, as in *Echiodon* and *Fierasfer*. The tendency of all of these processes, however, is to bring about an approach towards a confluent series of epural and hypural arches or spines. The development of heterocercy always tends also to suppress the last epaxial arches, as in *Amiurus* and *Salmo*, so that if gephyrocercy were in these cases developed by an absorption of the urostyle, the supports of the caudal fin-rays and the rays themselves would be hypaxial in their morphological relation to the caudal axis.

XII.—ON THE INFLUENCE OF MUSCULAR METAMERISM ON THE DEVELOPMENT OF THE AXIAL AND APPENDICULAR SKELETON OF FISHES.

Herbert Spencer,* in a discussion of the origin of the form of the vertebrate skeleton, has, largely upon *a priori* grounds, attempted to account for the origin of vertebral segments. The hypotheses which he put forward were in the main justified by the facts then known, but are not quite in accord with the ontogenetic evidence since worked out by a number of embryologists. He says (p. 201): "It follows from the mechanical hypothesis that as the muscular segmentation must begin externally and progress inwards, so, too, must the vertebral segmentation." In defense of this view he instances the fact that the development of the truly osseous skeleton is centripetal, or from without inwards, the peripheral parts ossifying first. He supposes, in fact, that vertebral segmentation is entirely due to the flexures of the body produced by the contractions of the lateral muscles of fish-like forms during their movements through the water.

Such an hypothesis cannot now be unqualifiedly accepted, since the tendency amongst embryologists at the present time is to conclude that the muscular segments are derived from a centrally-placed archenteron, from which their rudiments grow out as hollow diverticula.† The effect of such a view, founded upon observed facts, as in the case of *Amphioxus*,‡ upon the hypotheses suggested by Spencer, it will be readily seen, is important, though it may be positively affirmed that while considerable modification seems necessary, the essential elements of the great principle of the mechanical genesis of vertebral segments suggested by the English philosopher remain true. The embryologists show, in fact, that the evolution of the muscular system proceeds from within outwards in the vertebrate embryo, instead of from without inwards, as is assumed by Spencer, though this does not impair the efficiency of the lateral musculature and what other muscles are derived from it in the fins in producing segmentation of axially-placed skeletal structures consisting of cartilage, bone, and membrane.

Sections cutting through the axis of a young Vertebrate, such as that of the Catfish, for example, show that the fibrous septa between the muscular segments end internally at the point where two successive vertebræ articulate with each other. The points where the muscular fibers begin and end therefore coincide with the points where segmentation of the skeletogenous tract, from which the vertebræ are developed,

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* Principles of Biology, II, Chap. XV, pp. 192–209.

† *Cf.* Adam Sedgwick, On the origin of metameric segmentation and some other morphological questions. Studies from the Morphological Laboratory of the University of Cambridge, II, Pt. 1, pp. 77–116. Also O. Hertwig, Die Cœlomtheorie, Jena, 1881.

‡ *Cf.* Studien über Entwickelung des Amphioxus, von B. Hatschek. Arb. aus dem Zool. Inst. d. Universität Wien, 1882.

will occur, and where alternate compression and extension or even sundering of the continuous axial, skeletogenous, tubular membrane must occur, owing to the simultaneous contraction of an extensive series of successive muscular segments, entailing a pronounced bending of the whole body. In some such manner we are, it seems to the writer, bound to infer that the segmentation of the axial skeleton of the vertebrate body was initiated, for the reason that the segmentation of the muscular precedes that of the skeletal system—nay, that the mesoblastic myogenous layer of tissue from which the muscular segments develop is subdivided into segments even before it can be said that there is otherwise the slightest evidence that their component cells will become muscular fibers.

These facts seem to me to strongly re-enforce the conclusions of Hertwig and Sedgwick that the origin of the structures which led to the development of vertebral metamerism may be traced as far back as a little above the gastrula, and it may even not be too bold a procedure to assume that the lateral gut-pouches, whence the muscular segments of Vertebrates are probably always developed, have been derived in the course of the progress of evolution from the folded enteric walls of a diploblastic or two-layered cœlenterate ancestry, as held by the latter and Dr. E. B. Wilson,* now that structural bilaterality may be predicated of many *Actinozoa*, as is distinctly shown by the investigations of these authors and Milne Marshall. If such is the true explanation of the origin of vertebral metamerism, as it seems we have many weighty reasons for believing, it is only a step beyond this to apply the doctrine to the whole of the fin and limb skeleton of fishes—an expansion which it has already practically attained through the ontogenetic researches of Anton Dohrn upon the Elasmobranchs, already alluded to elsewhere, though the relation of the anterior muscular somites to the pectoral limb in Salmonoids amongst Teleosts was first indicated by another author.†

Examining longitudinal vertical sections of embryo Teleosts, the observer is struck by the fact that the vertebral spines and interspinous elements of the vertical fins originate almost exactly in the intermuscular septa which separate the muscular segments, while the muscles which move the fins are quite as clearly derived from the upper and lower extremities of the successive muscular segments corresponding in position with the successive interspinous intervals. In the Elasmobranch embryo the correspondence between the successive muscular somites and the diverticula of their upper ends, which they push upwards on either side over the spinal canal into the base of the dorsal fin, is even more clearly marked in sections of embryo Dog-fishes than

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* The mesenterial filaments of the Alcyonaria. Mitth. aus d. zool. Sta. zu Neapel, V, 1. Hft., pp. 1-27, 1884.

† Jos. Oellacher: Entwickelung einiger Organe der Forelle. Ber. d. nat.-med. Ver., Innsbruck, 1878, p. 141.

in the Teleosts, showing that the muscular metamerism at the base of the dorsal is directly dependent upon the metamerism which is observed in the lateral muscular system, which, as we have already noticed, has determined the metameric arrangement of the interspinous or intermuscular cartilages and the erectores and depressores spinæ muscles which erect and depress the rays of the vertical fins of the Teleosts. The muscular bundles which vibrate or abduct and adduct the rays of the anal of Teleosts have a similar origin, and in fact seem to develop from the bundles which also give rise to the erectores and depressores spinæ, and therefore exhibit a similar metameric order of arrangement.

Turning now to the consideration of the *recti abdominales* muscles of fishes, these are metamerically segmented, the segments corresponding to the lower end of the thoracic muscular segments, as is shown in longitudinal sections of embryos of several species (*Amiurus*, *Alosa*). The musculature of the pelvic fin, which is closely affiliated serially with the history of the *recti*, does not in the stages which I have examined show clear evidence of its origin from the muscular segments above it, but such is doubtless the case. The lower ends of those broad membrane bones, the coracoid and clavicle of *Amiurus*, develop in the septa between and above and below the muscular segments of the isthmus, which are clearly the serial homologues of the segments of the recti muscles alluded to above. The hinder coracoid element of the pectoral girdle in *Amiurus* develops in cartilage; the clavicular portion in membrane below the three first segments of the isthmus, the perichondrium of the coracoid above the fourth and fifth muscular segments of the isthmus, counting from in front of to behind the hyoid arch.* It is thus rendered evident that muscular metamerism influences the formation of even the shoulder girdle; and when we bear in mind the fact that such a metameric order was already established during the enterocœlous stage of development, or just a little beyond the gastrula, when the muscular somites were being constricted off from the hypoblast, we may realize how far back in the life-history of an embryo we may begin to trace the influences which determine the ultimate form of the vertebrate skeleton. We saw, for example, that the interspinous cartilaginous bases of what afterwards become the osseous interspinous pieces bear a relation to muscular metamerism; that, in fact,

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* In the Salmon the supraclavicle develops as a membrane bone in the septum between the third and fourth muscular segments behind the auditory vesicle; the post-temporal appears in membrane above the post auditory segment, just beneath the skin. The muscles of the pectoral, that is, its abductor and adductor, it appears to me, probably develop from the lower ends of the third and fourth post-cephalic somites. A slender slip of muscle, which is developed from the lower inner side of the upper end of the first post cephalic muscular somite, passes obliquely back from the hinder aspect of the auditory vesicle to be inserted into the upper end of the clavicle. The adductor and abductors of the pectoral are pushed out on either side of the cartilaginous pectoral plate and inserted on its anterior and posterior faces, resembling the arrangement which is permanent in *Gastrostomus*.

these and other elements tended to be formed in the septa between the muscular somites. These septa are evidently "points of rest," so to speak, where chondrification seems to be favored and where the prochondral elements of Strasser* first become defined when a bone is to be preformed in cartilage, or where the basement membrane of membrane bones first appears.

Passing now to the end of the vertebral axis of fishes, we find the same thing verified again. We find the hypural elements, the anterior ones at least, presenting this intersegmental relation to the muscular segments, and finally we discover that the proximal ends of the mesoblastic thickenings which are sent out from the hypural bones towards the margin of the fin-fold, in and about which the permanent rays are developed, rest upon such traces of muscular septa as are not obliterated at the time the permanent tail-fold is formed. Nor does this metameric influence end here, for we find that in the development of the permanent rays a large number of filamentous embryonic fin-rays are fused together by a material analogous to perichondrium, which the embryonic rays themselves simulate, in order to afford the basis for the ossification of the permanent rays. So far-reaching, therefore, is the influence of this metamerism that we are actually enabled to trace its effects even to the formation of the fin-rays.

XIII.—THE MESENCHYME OF VERTEBRATED EMBRYOS.

As Hertwig has shown that the connective tissue cells in certain forms (*Pseudocœlia*) are split off from the walls of the cleavage cavity of the blastula or gastrula stage, we may say that after the genesis of the myotomes a somewhat similar sundering, partly proliferation, of connective tissues from the myogenous and somatopleural tracts of the vertebrate embryo occurs and gives rise to the indifferent tissues, blood, cartilage, and, later, bone. The character of this indifferent tissue is commonly spongy, and is late in developing, just in proportion as the skeleton is retarded in its growth or development. The indifferent stellate cells of this layer, which forms a sort of matrix or envelope for the other tissues, here become metamorphosed into cartilage; then into fibro-membrane; at other points into the endothelium of vessels, &c., so that it gives rise not only to the hard supporting structures of the organism, but also affords the materials for the construction of the channels for the conduct of the functions of irrigation, respiration, nutrition, secretion, and excretion. Its part in embryonic development is thus evidently very important; it, in fact, forms the bond between the other structures—not only affords the means for sustaining the latter mechanically, but also physiologically. It develops secondarily after the triploblastic stage has been passed over in the vertebrate embryo,

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* H. Strasser: Zur Entwickelung der Extremitätenknochen bei Salamandern und Tritonen. Morph. Jahrb., V, 1879.

instead of directly from the primary layers during the earlier diploblastic stage, as in the *Pseudocœlia.*

The metameric arrangement of this secondary mesenchyme between and in relation, above and below them, to the myotomes, is also, to a certain extent, a merely mechanical or physical phenomenon, because the outgrowth of the gut-pouches in the primitive *Bilateralia* must have given rise to the existing metamerism of *Vermes*, *Arthropoda*, and *Vertebrata.* The bilateral symmetry of the myotomes and their antimerism are, however, not always exact, as may be seen in both the young and adult of *Branchiostoma.* This gives rise to disturbances in the symmetrical disposition of the secondary mesenchyme.

The blood of all animals is evidently a mesenchymal tissue; and it is noteworthy that while the yelk of meroblastic vertebrate embryos is to be affiliated with the hypoblast, in many cases the peculiar way in which it is absorbed during development renders it mesenchymal. The corpuscles originating from the metamorphosis of the yelk substance are actually transferred from a subhypoblastic position to a mesoblastic one. This, as a number of observers have shown, is effected through an indirect or direct communication between the heart and the surface of the vitellus, from whence many if not all of the first blood corpuscles are proliferated.

XIV.—ON THE STIMULI DETERMINING THE OUTGROWTH OF THE LOWER LOBE OF THE CAUDAL FIN.

The hypural lobe of the tail during its outgrowth has a tendency to displace the chordal axis upwardly, as we have noted in the case of the developing hypural cartilages of *Alosa.* Here the development of the hypural elements is accompanied by a pressing inward of the ventral wall of the chorda (Fig. 2, Pl. II). To what extent the upturning of the chordal axis may be due to the deposition of material below it during the development of the ventral lobe, which would tend to displace that axis in an upward direction, it is not possible to state, but it is fair to infer that the energy of growth in effecting displacement here should be considered. But a hasty analysis of this question leads to the conclusion that we are not merely to consider the effects of the outgrowth of the caudal hypural lobe, but the causes which led to such a local hypertrophy of the median fin-fold as to originate this lobe, which we have reason to think must represent a second hypaxial fin which was derived by specialization or hypertrophy from part of a continuous hypaxial series of rays, some of which were also atrophied.

The development of this lobe is essentially similar to that of the other median fins, the medullary portion of which we found was derived from the mesoblast, some of which was pushed outwards into the primitive median fin-fold of the lophocercal stage of development. As further specialization was attained the local suppression of ray-bearing elements has taken place, so that those remaining have been exaggerated in length and strength, to apparently compensate for this local suppression. Upon further examination we find that the portions which have been retained are situated in the most advantageous positions in respect to their effectiveness as organs of propulsion. This is pre-eminently true of the lower lobe of the caudal, which has been shifted into a position which is lineally in a plane with the vertebral axis. The *mechanical selection* which is here implied, has doubtless led to reduction, just as use and effort or impacts and strains have led to a similar selection of certain axially situated digits in the limbs of Ungulates, whch have thus been hypertrophied, while the extra-axial digits have been atrophied in consequence of disuse. The reduction of the fin-rays and interspinous pieces of fishes has, it seems therefore highly probable, followed from the working of the same principle as I have indicated in my discussion of digital reduction. This general principle is confirmed by every morphological condition which we may choose to select, even if an extreme one is chosen, such as that presented by *Mola*, in which a degeneration and complete loss of part of the caudal axis have led to the assumption of the office of the caudal fin by a series of rays which primitively belonged to the dorsal and anal series. Here the flat, nearly discoidal body, no longer flexible, must develop some new mode of progression. The result is that, as in the above-named genus and the trunk fishes, an extreme modification of the lateral musculature has occurred by which this no longer subserves the use of flexing the body, but the fins only, to which the entire system of myotomes are subordinated, powerful tendons passing outwards to be inserted into the bases of the rays of the median fins.

The evidence in favor of local degeneration or atrophy accompanied by local hypertrophy, which in some cases involves a great change of function in some part, is complete, and we may assert with confidence that such changes must produce great displacement or rearrangement of homologous parts with relation to each other, so that there may arise in this way forms which diverge in the most extraordinary way from what would be considered the typical structure of a group.

Development has rung a great many changes in the evolution of the caudal fin, as we may learn if we take even a very hurried survey of the structure of this organ as found in the different groups of fishes. In some the termination of the chorda has suffered but slight modification or abortion; in others a large amount of the chordal axis has suffered degeneration, as in *Lepidosteus*, and many fossil genera. The development of centra sometimes occurs in some of these forms behind the point where the axis is bent upwards, but in others it ceases abruptly at the point of flexure. In the Salmonoids and *Nematognathi* the development of centra passes beyond the point of flexure, but in these there is a point beyond which almost total degeneracy of the caudal axis asserts itself. This degenerate portion is therefore exserted to a variable extent in the different forms, and by just so much do they differ as regards the point where the ventral lobe of the caudal grows out even in the embryo, so that traits appear very early in the development of the caudal which serve as marks which characterize the species. The hypertrophy or local outgrowth of mesoblast to form the lower lobe is variable in position to a very great extent, so that the point where displacement due to growth occurs, also varies in position in respect to the end of the chorda. This variation may be well seen in the figures of embryos given by A. Agassiz and other embryologists.

The development of the lower lobe of the caudal by the proliferation of mesoblast and hypertrophy of a part of the hypaxial fin-fold has led to the final elision or suppression in some cases of the larval opisthure, due to a substitution of a secondary or permanent caudal so developed. The localization of the energy of growth in advance of and below the end of the chordal axis has brought about the abortion of the opisthure or what must primitively have formed all of the tail of the ancestral type. But the stimulus which led to the hypertrophy of some part of the hypaxial median-fin-fold must have been the penultimate efficient cause of the development of the opisthure, which becomes rejected or elided by change of function or functional substitution. That stimulus was applied locally to the hypaxial fold, and the hypertrophy which followed was a natural result of use and effort, which very probably arose from the continually-repeated efforts of the animal to rise to the surface to get away from the bottom, and maintain itself right side up, as a result of which the growth of the ventral fold was stimulated and extended ventrally.

This view of the matter is strongly favored by the theory of the median fins which has been defended throughout this essay. The continuous system of median rays found in a perfect condition of diphycercy or the protopterygian stage would be available for a starting point, from whence subsequent heterocercy might arise. The Chimæroid fishes realize this condition, as was well stated by Balfour and Parker,* as follows: "The tail of *Chimæra* appears to us to be simply a peculiar modification of the typical Elasmobranch heterocercal tail, in which the true ventral lobe of the caudal fin may be recognized in the fin-fold immediately in front of the filamentous portion of the tail. In the allied genus *Callorhynchus* this feature is more distinct. The filamentous portion of the tail of *Chimæra* constitutes, according to the nomenclature adopted above, the true dorsal lobe, and may be partially paralleled in the filamentous dorsal lobe of the tail of the larval *Lepidosteus*."

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How near these authors were to a clear comprehension of the true nature of the tail of *Chimæra* may be gathered from the foregoing extract, but I would take exception to their calling the tail of this form *heterocercal;* that it is not, for the chordal axis has not suffered upward

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* Structure and development of Lepidosteus. Philos. Trans., Pt. II, 1882, p. 408.

flexure, but the form of the terminal ray-bearing lobes resembles very considerably those of Elasmobranchs, and doubtless some such form anticipated the caudal of the latter.

Their recognition of the caudal filament, or the opisthure of our nomenclature, as homologous with the dorsal lobe of A. Agassiz is also right only in part, because the fin-folds are absent in this case, but present in larval fishes in the lophocercal stage; moreover, the opisthure becomes dorsal in position in the heterocercal forms very soon, but not in a perfectly diphycercal form like *Chimæra monstrosa*, where it is literally post-caudal, being, as a matter of fact, opisthural in position and almost perfectly archicercal in character.

The forms of the lobes of what may be recognized as the true caudal epaxial and hypaxial fins of *Chimæra* agree in their general outline somewhat closely with those of Elasmobranchs, but by no means exactly, yet it is easy to derive the Elasmobranch caudal from the Chimæroid tail, as follows: (1.) Let the opisthure be aborted; (2) lengthen the inferior rays anteriorly, and shorten the superior caudal rays; and (3) flex the caudal axis upward, and we have the heterocercal caudal of the Sharks, provided the neural and hæmal arches or spines are supplied. At any rate, the course followed by the process of evolution in this instance, which leads up to heterocercy, is clear. The diphycercal ray-bearing part of the tail of the Chimæroids is evidently differentiating in the direction of that of the true *Squali*, and that it represents a phase of the evolution of the caudal in the latter is rendered all the more probable from the fact that *Chimæra* is more primitive and more embryonic in many of its characters than the latter. Let the whole axial skeleton of *Chimæra* become more differentiated, and it would doubtless veer towards that of the Sharks in many of its features.

As was remarked before, there is manifestly some stimulus to growth tending to widen the hypaxial caudal lobe and lengthen its included rays. That stimulus seems to us to be use and effort exerted in the course of existence or during life, and through which the local activity of nutritive processes is modified through the fluctuations of blood-supply needed in carrying on nervous and muscular action. The sculling action of the flat tail of *Chimæra* in rising toward the surface would necessitate the greatest exertion of effort by the lower lobe of the caudal, and thus initiate such a differentiation as is demanded by the foregoing hypothesis. For reflex activity or response to stimuli begins to be manifested not in the finished metazoan organism as a whole, but has its ultimate source in the histological elements or cells of which such an organism is composed, an opinion with which I think it probable most careful embryological students who have studied much live material will agree, as it is not meant here that what are known as reflex actions involving molar movements of masses of bone, muscle, &c., include all that is truly comprehended by reflex activity, which may in reality be exhibited by the tiniest speck of protoplasm. In fact, all the reflex actions of higher animals are finally reducible to molecular disturbances and more or less spasmodic exhibitions of contractions of aggregates of plasmic bodies in response to nervous stimuli or impulses generated at the periphery as sensations and finally sent back from the nervous centers as motor impulses of the organism which regulate and co-ordinate the contractions exhibited in the course of vital work in the struggle for existence. All of the energy so exhibited is not dissipated in the visible movements of the animal, but some of it is unquestionably consumed in inducing morphological alterations or adjustments, in maintaining a physiological equilibrium, in other words; or, as happens in a mechanical device, some force is consumed in overcoming friction. This kind of an equivalency between a certain residual part of the energy expended by an organism and the energy needed to be used in the acquirement of new organs is clearly correlative and conservative. The acquisition of new organs may therefore very probably be viewed as a problem of physiological dynamics, in which a certain equivalency between the work done, the bulk of the living mass, the distance through which movement is made, and the duration of the effort exerted will be taken into account so as to get at a residual element of potential and dissipated energy used up in maintaining and readjusting the organic aggregate to new conditions. The development of new organs is evidently a progressive process, as our study of the evolution of fishes' tails has shown, for it is hardly possible to conceive that the ascending order of differentiation indicated by ontology and palæontology can be in error, since that order is approximately as follows: archicercy, lophocercy, diphycercy, heterocercy, homocercy, and gephyrocercy.

When an aggregate of plasmic units or an organ, such as a muscle, is stimulated to contract for the first time in response to a new or extraordinary effort, increased waste follows, which must be made good by increased nutritional activity in that part. More blood is therefore sent to such parts momentarily, the remarkable vaso-motor system of nerves being involved in effecting this in higher organisms. In simpler organisms, however, no provision of vessels and vaso-motor nerves exists, and the acquisition of pabulum may be effected in some cases by its mere transfer from cell to cell, as is the case in many processes of embryonic growth. The very remoteness of the peripheral plastids from the nutritive and respiratory centers in higher organisms has led to the evolution of the vaso-motor and vascular systems, so as to provide for the reflex exhibition of the needs of remotely-situated groups of plastids when extraordinary exhibitions of effort are in progress in such groups, and thus enable their immediate wants to be supplied. Such systems are beyond the control of the will as expressed and exerted under the guidance of the rational faculties, and they minister to the demands of the aggregate of the wills, so to speak, of aggregates of remotely-situated plastids calling in this way for oxygen and food. This cellular volition is the exhibition of the low protozoan grade of reflex action when possibly the nucleus was the center receptive of external impressions, the reflex energies being in turn propagated from it. While all of the foregoing is speculation only, it helps us greatly to understand some of the phenomena encountered in the course of the development of new organs, and aids in giving us a somewhat clearer comprehension of what is meant by such terms as "automatic" and "voluntary actions." Enlarging upon what has been said above, it may be said that automatism is pronounced in certain organs directly in proportion to the grade of specialization attained by the animal, and that the automatism of tissues is due to the survival not only of the protozoan grade of differentiation of their elements, but literally to the survival of elements that are in detail structurally comparable to *Protozoa.*

It will thus be seen that an action which had its origin, we will say, in an effort of the will of a higher animal as ordinarily understood, has evoked a secondary set of phenomena which had their origin in an automatic set of organic elements, and which have at their command the vaso-motor and vaso-accelerator systems in such higher forms. When such an adjustment and distribution of functional effort become approximately stable, the species itself becomes approximately so. Let any new demand of the environment arise, however, and a recoördination of the functions must take place, which leads to a redistribution of organic matter and organic motion, which must continue until such a recoördination is completed.

The method of recoördination seems to be contemporaneously increscent and decrescent in different parts of an organism by small degrees, and these two processes are apt to affect each other reciprocally; that is, while one part is growing and becoming able to assume its function, some other structure which previously had the same or a similar function is degenerating, just as we saw that the permanent caudal replaces by such a process of substitution the lophocercal tail of larval fishes. Other instances occur where the atrophy is complete, and no structure functionally comparable is developed, as in the case of the larvæ of Anurous Batrachians, in which total atrophy of the larval tail takes place, in consequence of a process of physiological disintegration of this part, which occurs relatively late, and in the course of which the material so torn down is reintegrated into new structures near by, having a totally different function, as in the case of the hind limbs of these animals, which violate the general rule which obtains amongst the embryos of *Vertebrata* by budding out as paired rudiments before any traces of front limbs have shown themselves externally, they being concealed under the opercular membrane. The tendency of all other vertebrate embryos is to develop the anterior limbs first; and even in the case of the Kangaroo, among mammals which have the hind limbs so disproportionally enlarged in the adult, their rudiments in the very immature embryo taken from the uterus of the parent are, according to Chap-man, disproportionally small, as compared with the rudimentary front limbs, and present only as a pair of minute papillæ.

The rapid and accelerated outgrowth of the hind limbs of the embryos of *Anura* becomes partially explicable on the ground that the disintegration or rapid metabolism, involving the tail, which occurs during their larval metamorphoses, happens very near the point where the hind limbs are to grow out, and thus places in close proximity a supply of available protoplasm, ready to be used in thus precociously accelerating the outgrowth of these appendages, which probably represent, in part at least, the reintegrated substance of the tail, which had developed so far as to have a chordal and a nervous axis, together with a long series of myotomes on either side before its singular retrogressive metamorphosis began.*

The part played in this metamorphic process by certain cells, denominated *phagocytes* by M. Metschnikoff, is very significant, and his conclusions, as given in a short extract below, as bearing upon pathological phenomena involving muscle and nervous tissue, in such cases as were long before described by Rayer (Mém. de la Soc. Biol. de France), are of the highest interest. Not less interesting to the writer are the conclusions of Metschnikoff as illustrating the possible origin of the vaso-motor system in the way in which it has been discussed above, since he speaks of "a struggle between phagocytes and septic material." This struggle implies that the phagocyte includes a sensitive center or reflex sensorium lodged somewhere in its substance, in virtue of which it practically manifests reflex actions like an organism of the Protozoan grade. In the metamorphosis of the Batrachian tail, which is literally eaten up phagocytically, so to speak, by internal wandering cells, we have an instance of the normal exhibition of phagocytic action.

"The tail of the Batrachia, during the early stages of its absorption, contains a number of cells, which, when left undisturbed, throw out fine radiating pseudopodia; these contained remnants of nerve-fibers and muscle-cells. Phagocytes, then, play as important a part in the metamorphosis of Batrachians as of Echinoderms; and pathologists have afforded evidence of their agency in the so-called active degeneration of muscles and nerves.

"The author has tested in a *Triton* the theory he holds as to the phenomena of inflammation in Invertebrates being primitively nothing more than a collection of phagocytes assembled to devour the exciting object. He touched the point of the tail of a *Triton* with a small piece of nitrate

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*To what extent I may have restated in the two preceding paragraphs, in another form, what E. Ray Lankester has said before me in his book on Degeneration, or what Dohrn has stated in his essay entitled *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels*, I do not know; but I have ventured to give the preceding examples in order to illustrate the reciprocal relation existing between degenerative processes involving transient organs and the formation of permanent ones, without having previously read either of these authorities, or knowing what their general conclusions were.

of silver and then washed it with salt solution. Branched connective tissue-cells collect around the inflamed spot and eat up blood corpuscles, carmine granules, and particles of pigment. * * * When a fully-gorged phagocyte dies it is immediately devoured by another. Inflammation then is not, as is ordinarily supposed, due primarily to a morbid condition of the walls of the blood-vessels; it is a struggle between phagocyte and septic material, and it is in Vertebrates alone that the vascular system, owing to the insufficient number of extra-vascular phagocytes, takes part in the struggle."*

The exaltation of metabolism shown in phagocytic phenomena accounts for the rise in temperature when they are manifested in the higher forms. It is not singular that the storage of proteids in cells should occur in certain cases, especially where these are destined to become greatly exaggerated in amount in order to afford the pabulum from below to the growing blastoderm and embryo, which is superimposed upon a supply of proteinaceous matter known as the *yelk*, which in turn is literally consumed by cells of hypoblastic origin (megasphæra) or by a plasmic layer standing in a similar relation to the embryo, as fast as the yelk material is needed for the growth of the latter.† The primitive egg-cell of the ovary may, therefore, in one sense, be looked upon as a phagocyte of a special kind in such forms as develop a yelk.

Just beneath the hypoblast of the yelk of the Rays there exists a stratum of singular amœbiform cells, which are much branched and irregular in form. They are not in contact with each other except by their pseudopodal prolongations. They contain coarse granules in the central parts, which are doubtless disintegrated vitelline tablets which have been taken in from the true yelk below and converted into their own more mobile protoplasmic substance. These bodies are quite outside of and below the hypoblast and vascular mesoblast. The apparatus for the absorption of the yelk of the Elasmobranch vitellus is therefore quite different from that which is found in the Teleosts, as may be learned upon consulting the papers by the writer last cited, where he has described the homogeneous converting layer in the eggs of the latter group, calling it the *yelk hypoblast* for reasons which appear valid, because its function is a temporary one, the structure disappearing with the necessity for its existence.

The quasi-phagocytic action of primitive ovicells,‡ in consequence of which the germinative vesicle or nucleus suffers displacement, just as the cells of the notochord and adipose tissues have their nuclei displaced

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*E. Metschnikoff. Quar. Journ. Mic. Sci., XXIV, p. 112-117.

†Development of the Silver Gar (*Belone longirostris*), with observations on the genesis of the blood in embryo fishes, and a comparison of fish ova with those of other vertebrates. Bull. U. S. Fish Comm., I, pp. 283-301, 1881.

Observations on the mode of absorption of the yelk of the Embryo Shad. Bull. U. S. Fish Comm., II, pp. 179-187, 1882.

‡The law of nuclear displacement, and its significance in embryology. Science, I, 1883, pp. 273-277.

by the absorption of water, or the formation of oil, or by the incorporation of large amounts of plasmic matter is remarkable; yet there are phenomena met with which are apparently the very reverse of anything comparable to phagocytic; these are such as show minute granular bodies developed outside of the vitellus and between it and the egg membrane, as occurs in the case of *Amiurus albidus*,* in which the granules are quite free. In the young Spanish mackerel somewhat similar granular bodies lie beneath the skin and represent a homogeneous stratum found largely developed in the fin-folds of the embryos of certain forms, as in *Alosa*, for example. C. Emery first called attention to the existence of this homogeneous substance in the fin-folds of the lophocercal stages of young Teleosts in a memoir† published about a year since. He regards this substance as a secretion; that is, it is *mesenchymal*, and may be derived from the mesoblast, the epiblast also taking a share in its formation, and may possibly be comparable to the body of the gelatinous substance found in the umbrella of Medusæ.

This homogenous stratum precedes the cellular mesoblast in its advent into the fin-folds of fishes, but it may be doubted if it has any influence in determining heterocercy further than that it may supply the material which is eventually converted into cellular mesoblast. In thus tracing the causes and phenomena which are directly concerned in inducing heterocercy, or which collaterally throw some light upon it, it becomes very evident that it is a very complex problem, but this is no reason why its elucidation should not be attempted.

XV.—ON THE MOVEMENTS OF PARTS OF LIVING BODIES CONSIDERED AS THE CAUSES OF MORPHOLOGICAL DIFFERENTIATION.

It is noteworthy that the *Lyrifera* is the only group of Vertebrates in which the termination of the axis of the body is commonly and fixedly upturned, and this, together with the usual development of mesial basalia for the support of the true fin-rays, which basalia extend outward usually to the level of the integument covering the body of the adult, and in contact or not in contact proximally with apophyses of the vertebræ, constitute two of their most frequent, though not absolutely constant, characters. The dorso-ventral symmetry of the terminal caudal skeleton is thus more or less impaired because of this departure from the usually almost rectilinear form of the vertebral axis of the *Ichthyopsida* and the Lacertilian phylum of the *Sauropsida*.

The other groups of *Vertebrata* present differentiations of their vertebral axis, which may be regarded merely as other departures from the nearly rectilinear series of vertebral segments of the lowest Vertebrates.

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* Preliminary notice of the development and breeding habits of the Potomac Catfish. Bull. U. S. Fish Comm., III, 1883, pp. 225–230. Such granules are also found floating inside the egg-membrane and around the embryo of *Thymallus*.

† Sulla esistenza del cosidetto tessuto di secrezione nei vertebrati. Atti della R. Ac. delle Sci. di Torino, XVIII, 1883.

These higher groups seem to fall into six arbitrary categories, habitual movement in particular ways having brought about the special modifications.

Professor Marsh* in speculating upon the origin of the forms of the vertebræ of the different groups of Vertebrates reaches the following conclusions:

"(1) *Biconcave vertebræ* (Fishes and Amphibians): the primitive type; a weak articulation, admitting free but limited motion. From this form have been directly derived the other varieties, namely:

"(2) *Plane vertebræ* (Mammals): affording a stronger joint, with motion still restricted.

"(3) *Cup and ball vertebræ* (Reptiles): a strong and flexible joint, well fitted for general motion, and evidently produced by it. The vertebræ are procœlian when lateral motion is dominant (serpents); opisthocœlian with varied motion (Dinosaur cervicals).

"(4) *Saddle vertebræ* (Birds): the highest type; a very strong and free articulation, especially adapted to motion in a vertical plane, and mainly due originally to its predominance. (Is predominant in the cervical series.)"

Professor Cope has found a fifth type of vertebral column in a reptilian type from the Permian formation of Texas, in which there are lateral and inferior intercentral pieces wedged in between the true centra of sucessive vertebræ. The vertebral column of this type, which represents a very important group, which he calls *Theromorpha*, thought by him to be ancestrally related to the oviparous Monotremes, he thinks was developed by the peculiar lateral flexures to which the vertebral axis was subjected. Further studies may throw some additional light upon the mode in which the supplementary intercentra were formed in this group, as special or peculiar conditions have evidently determined this singular morphological differentiation.

A sixth type is found in armor-bearing forms, as in the extinct Armadillos and the recent and fossil emydoid *Testudinata*, which has been developed in consequence of a loss of mobility of the axial column due to the existence of an inflexible outer carapace, as pointed out by Spencer and myself.† In what way this degeneration of the centra has been developed in the fossil Armadillos has been discussed by me in the paper cited, as follows: "The carapace was supported for nearly half its length upon the haunch bones (ilia and ischia), as well as by the strong, longitudinal, median, bony crest rising from the lumbar and sacral vertebræ, consisting of their united neural or spinous processes. The carapace rested directly on these bones, and was joined to them by suture, as the roughened and expanded surfaces for such juncture show. The entire union of the lumbar and sacral vertebræ into a

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* Birds with teeth. Third Ann. Rep. U. S. Geol. Surv., 1881-'82, p. 82.

† The gigantic extinct Armadillos and their peculiarities, with a restoration. Pop. Science Monthly, XIII, pp. 139-145, 4 figs. in text.

hollow bony bar, and the union of this to the lateral elements of the pelvic arch, together with the union of both by suture with the carapace, rendered any lateral bending of the trunk impossible, so that an almost universal union of the trunk or body segments ensued, owing to this structurally enforced loss of mobility between the vertebral elements. As a consequence, the centra or bodies of the segments disappeared or were atrophied, leaving only their trough-like plates about one-fourth of an inch thick, formed of the degenerate united central bodies. This trough, with the united rib-bearing arches which arose from its edges, formed a tube for the lodgment and protection of the spinal or nervous cord. Unlike all other Vertebrates except Turtles, this tube, in that portion over the lungs, is perforated at intervals on each side, at points about midway of the length of each one of the united segments, to give egress to the spinal nerves.* The points of egress for the spinal nerves are usually between the spinous processes in other orders of Vertebrates.

"In living Armadillos the centra of the trunk vertebræ still remain as more or less depressed cylinders of bone, or, at least, they are distinguishable as centra, from which arise the rib-bearing arches, which do not completely unite, leaving lateral interspinous openings so as not to entirely close over the nervous cord, as happens in fossil forms. The reason why the vertebræ remained separated in recent species is undoubtedly because of the mechanical conditions to which these parts of their skeletons were subjected. Here the carapace was jointed and flexible, hence the need of flexibility in the spinal column. In the extinct species, as in Turtles, the degeneration of the centra into mere conduits for the nervous cord is one of the many contrivances the origin and teleological significance of which can only be explained by a mechanical theory. The vertebral column in both was similarly conditioned with respect to strains, mostly transverse—hence the similarity of structure, which it must be borne in mind is, however, no indication of zoological affinity.

"Beginning with the homogeneous notochord or rod-like axis of some such form as *Amphioxus*, Mr. Spencer points out how, as this axis became bony with the assumption of the characters of the higher fishes, the alternate pressure and tension incident to the flexures of this axis during locomotive acts would tend to differentiate the vertebral segments; for it is obvious that, in order to be flexible and at the same time bony, the vertebral axis must become segmented. The mechanical conditions under which vertebral axes are placed would indicate that the segmentation took place from within outwards, which is in accordance with observed facts. It is also obvious, in view of the premises, that, in the absence of flexures or bendings of the vertebral axis, we should have a return to the homogeneous structure [now replaced by a continuum

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* In birds, as, *e. g.*, the common fowl, the first segments of the sacrum, the centra of which are similarly atrophied, are perforated laterally in the same situation.

of bone], such as we actually find to result in the two cases under consideration, and as happens in a few of the posterior trunk-segments (sacral) of birds and mammals. Embryology and phylogeny both bear out these conclusions. Not only do the vertebral centra become more rudimentary as the young condition is departed from during the life-history of the individual tortoise, but the centra also become successively more rudimentary as we pass from the less completely armored genera *Sphargis* and *Trionyx*, to the more completely armored *Testudo* and *Cistudo*."

The data respecting the mode in which the primitive membrane of the rays of fishes is fractured and thus segmented evidently apply to the genesis of vertebral bodies the membranous basis of which invests the chorda as a continuum at first, its continuity remaining unbroken on the inferior face of the trabeculæ cranii, where it gives rise to the parasphenoid bone of fishes. The points of fracture of the osteogenetic membranes investing the chorda, which herald the subdivision of said membrane into the foundations of vertebral bodies, correspond homonomously in position with the intermuscular septa between the myotomes. These phenomena probably never occur till the embryo begins to make voluntary movements in the egg, egg-follicle, or temporary uterus in the lowest forms; such at least seems to be the case with the embryos of the *Ichthyopsida*.* Such interpretations of the genesis of structure bring the phenomena of development under the domination of natural law, and accept little or nothing in common with old-fashioned teleology, that inane creation of mystical metaphysicians, whose anthropomorphic preconceptions have hindered the progress of biological science for not less than two centuries.

Looking in an unprejudiced way upon a living body, we are forced to admit, after the strictest investigation, that its "vitality" is only one of many special modes in which matter may exhibit phenomena of motion or action. If life is a continuum in virtue of the fact of the production of germs, from which new and similar organisms may grow; if likewise the energy of an actively living, growing body is continuously exhibited, then that energy must be continuously expended, and food must be constantly appropriated, and as constantly must there be material waste in progress.

Newton's third law of motion states that "Action and reaction are equal." If, therefore, it is true that the body is continuously in action, it must be true that there is continuous reaction going on in the most ordinary voluntary physiological work done by the body. Further, we

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*It is of some interest to note in this connection that distinct diarthrodial articulations of the heads of the ribs with the vertebral bodies never occurred in the Vertebrates until the differentiation of the pneumatic respiratory apparatus. This articulation is changed to a sutural one in the Turtles, in consequence of the suppression of the thoracic respiratory movements of the ribs by the development of the rigid carapace to which the latter become fused.

can have no reason to doubt the fact that the energies of the universe are otherwise than continuously exhibited. The organism, like a planet, is bounded by a form; theoretically it is separated temporarily from the rest of the cosmos just as the former, but it is a parasite, crawling, walking, running, flying, or swimming, on or in the various media found on the surface of the planet. The organism is individualized like the planet, but the energies of both are reciprocally antagonistic. Action and reaction are equal and continuous in one sense. The energies of the planet and the cosmos, taken together, are, however, too great to be overcome by these superficial parasites, and in consequence of their small mass they must accommodate themselves, adjust themselves as the pull and push of the vast planet under them determine. They are modified in structure by their own actions and the reactions of the environment, or die if they fail to succeed in effecting this adjustment, a process in which their volition is of small effect in changing the result, because what will they may have must bend and adjust its demands to the demands of far stronger outward forces. The naturalist encounters upon every hand evidences of the effects of the struggle of the organism with its environment. This struggle is so real, so tangible, that it becomes palpable in every movement made by the body which calls for effort in its execution. It is the most continuously operative of all the forces of nature, effectual as modifiers of organization. There exists not a single bone known to the osteologist which does not bear the evidence of having been directly or indirectly modified in the course of the conflict between the organism and its environment, in consequence of the interaction between the forces of the latter and those exerted by nature. It will thus be seen that all the forces that are originative, except such advantageous actions as spring from acquired intelligence, are ultimately to be sought in the energies with which an organism has to contend during each and every moment of its existence. The beautiful adaptations which appeal so strongly to the teleologist are only the result of the action of natural forces which originally determined the deposition of inactive, active, sensitive, or contractile materials at definite places in a living body in sufficient proportional amounts to fit it to meet the demands made of it in relation to its environment.

This is the origin of "fitness," in precisely the same sense in which we may contemplate the origin of the equilibrium existing between the planets. A certain dynamically determined fitness, therefore, precedes the process of natural selection, from which the latter draws its material and upon which heredity fixes its stamp; but heredity, be it remembered, is not a whit more indebted to the action of natural selection than it is to the operation of those far more powerful interacting energies which primarily ordain adaptations.

The desire to get the most pleasure with the least exertion is probably a universal character of the habits of organisms, and those which, by stealth or by taking advantage of favorable environing conditions, can make use of such with but little effort doubtless often surpass the strong in the race for survival; but it must be borne in mind that this is only the practical expression of the doctrine of economy of effort or that of "least action," so that in a literal sense the degenerate loafers, blood-suckers, and parasites of the organic world are simply such types as have availed themselves of the favorable nidus which those higher free organisms which have been "heroes in the strife" afforded them. This takes into account the effect of intelligence in favoring the merely physical processes of evolution which lead to the morphological differentiation of organisms.

It may be objected that the views here put forth imply that the organism may be compared to a machine, and it may be well, once for all, to show why such an opinion is untenable. Two reasons show that such an hypothesis is untrue: first, unlike any machine, an organism repairs itself; and, secondly, unlike any machine, it first converts food into itself, then disintegrates part of itself in order that energy may be freed to conduct physiological or living actions. There is therefore no parallelism between the action of an engine of any sort and a living being. Further, no stimulus is capable of causing the liberation of energy from the component parts of an engine or mechanism, whereas the molecular instability of living matter is so great that a great number of stimuli may induce the liberation of some of its matter and energy and thus set the organism or some part of it a-moving.

The energy of live matter and that of the environment being in a constant state of interplay and antagonism, it follows that there is continual adjustment going on, as may be seen all round us in the attitudes we assume, as in the act of respiration, for example, which is a common and familiar instance of these incessant processes of adjustment, and it is so important that these should continually proceed that it is hard to realize at this late date that more of us should not be ready to accord a paramount influence to such causes in the determination of organic form. While the oxidation and decarbonization of living matter seem to be the processes that lie at the bottom of the incitement of the movements of animals, it is probably true that an organism once having reached a condition of stable adjustment retains its typical form, and is thus rendered more or less stable under uniform conditions as a species; yet all of us are aware to what extent a species may be variable.

The variations which we encounter in nature in the form of the bodies of animals and their structures are in all cases to be ultimately traced to the effect of the environment in calling forth adjustments. The forms of the fish, of the bird, of the mammal, &c., are familiar examples, and it is therefore manifestly vicious reasoning, as pointed out by Spencer, Darwin, and Parker, to look upon these types as a lineal series, as approximately expressed in the older classifications. On the contrary, they must necessarily be divergent, and by just so much as they have diverged are they thrown out of the direct line of descent, as in the cases of the Anurous Batrachians and Teleostean fishes, for example, each of which is an example of a high state of evolution, and mark extreme adaptations, which cannot therefore have any very close affiliations with other series. Besides all this, the record of the process is so blurred by adventitious adaptations, in consequence of the interaction of organs upon each other through substitution of function, inducing degeneration, or by special adaptive modifications, that real affinities are often much obscured and rendered difficult of determination.

Degeneration or abortion of certain structures, as well as the degeneration or degradation of a whole organism, not unfrequently results from such causes as involve the disuse of a certain set of structures and their atrophy, or extensive modification and changes in adjacent structures. This may be illustrated by the fact that vertebral segments are clearly indicated in the fore part of the chorda of the embryos of *Amiurus*, where five of them subsequently coalesce and a single compound segment is formed, due to a loss of mobility enforced by processes of the post-temporal bones coming into contact with the lateral processes of the anterior vertebræ. This also results in causing the abortion of about the same number of myomeres in this region and their confluence into a great muscular mass without any intermyomeral septa developed between them. This also reacts upon some of the ribs, which are also confluent or developed as a continuous osseous plate in the rib-forming layer of the embryo. The anteriorly bifurcate air-bladder encroaches as it becomes larger upon the lower end of the anterior myotomes, the pressure thus caused seeming to induce the abortion of the lower end of the latter at this point. The air-bladder, as it grows out from the fore-gut, finally has its parietes brought almost in contact with the integument just behind the pectoral arch, where it may act as a tympanic organ in connection with the internal ear, as already suggested by T. J. Parker in regard to a similar structure found in front of the pectoral arch of the Red Cod. In very young embryos of *Amiurus*, or those of the second day, the muscular segments are developed immediately behind the pectoral plate and fold in just the same way and as strongly as in the young Salmon of the same relative age, in the adult of which there is no such abortion of the muscular side walls of the anterior part of the visceral cavity. We have thus seen what a remarkable series of modifications result correlatively from a change in the mode of development of one or two adjacent parts.

As the results of direct pressure exerted rhythmically we have the superficial layers of cartilage cells overlying the articular ends of the bones of the limbs flattened, as Professor Leidy long ago suggested in explanation of this condition.

In the case of the dental armature of the Mammalia, I have sought to show that the crowns of the teeth, especially in the *Herbivora*, have been altered by use on the supposition that the enamel and dentine were more or less permanently flexible, in consequence of which the rhythmical pressure exerted in mastication and in a constant direction flattened and modified the primitive cusps of the teeth of the early Tertiary bunodonts, causing them to become gradually selenodont, as we actually observe to be the case when a series is examined the members of which come from successively later and later horizons.

The apparent correlation between the degree of complexity of the crowns of the teeth of the equine series and the degree of digital reduction can be regarded as such only so far as two distinct mechanical forces have operated continuously and contemporaneously. Many other instances of correlation may doubtless be similarly explained.

When we look about us and find that certain phenomena are caused by natural forces acting in certain well-defined uniform ways, we say that the phenomena and effects produced are natural ones. That they are determined in an approximately invariable manner we must infer from the fact that the effects are alike or similar. Coincidences of this kind occur in very great numbers in morphology, and there are few students who have not had them forced upon their attention during their investigations. Such series of similar effects imply the existence of similar causes, as, for example, the presence of selenodont teeth in Ungulates which move the mandible laterally, and bunodont teeth in those Ungulates which exhibit no lateral movements of the mandible. Such coincidences are too numerous to be regarded as accidental, and much as Dr. Tomes may desire to deny the real efficiency of a force generated by the muscles of an organism to produce changes of form in already developed hard structures, such as enamel and dentine, such a force nevertheless undeniably exists and produces its effects, as may be inferred without chance of error from the fact of the very existence of these very same numerous coincidences found in numerous recent and fossil forms. Facts communicated to me by dentists show that abnormal pressure may alter the form of a tooth during its growth and within a comparatively short period; yet Dr. Tomes has the hardihood to assert with great assurance the very contrary, without ever once having properly read my papers or having analyzed the data involved in the discussion.

Since natural selection cannot account for the origin of the reversal of position of the crescents in the crowns of the opposing series of teeth, for hundreds of other patterns would have answered just as well, or for the invariable coexistence of such a crown-pattern with lateral mandibular movements, in what manner are Dr. Tomes and those who agree with him to extricate themselves from the position in which their callow haste has placed them? It is very clear to me that the awkward position in which the English odontographer has placed himself will sooner or later dawn upon his consciousness.

The case of the teeth is a very strong one, and there can be no escape from the conclusion that here, as in the case of the evolution of the tails of fishes, natural selection is utterly incompetent to account for a too numerous series of coincidences which afford the most impregnable inductive basis for a theory of mechanical or dynamical evolution. The rule that similar acts govern or are associated with the production of definite morphological modifications is too clearly made out to be broken down by any *a priori* reasoning.*

I have sought to show, in a paper on the laws of digital reduction, how the expenditure of the energy dissipated in the act of locomotion, if exerted by way of the middle series of digits, those finally usurped the whole function of the original five, the lateral ones becoming rudimentary. How in like manner the difference in the number of digits in the fore and hind feet arose, assigning as a reason that whichever pair was subjected to the severest strains was most apt to have the digits reduced in number, as in the case of dogs, kangaroos, rabbits, &c., which habitually make more or less rapid and successive bounds in running.†

In now reverting to this subject, with a greater array of details in defense of my position, I must admit that the views expressed by me five years ago‡ were in accord with those expressed by Spencer in relation to the genesis of bilateral symmetry, since shown to be not altogether in harmony with the results of embryological research. The principle then stated, that the alternate bending of the soft rays of fishes from one side to the other led to their segmentation, I however still hold to be true, for the reason that the primitive embryonic rays are never segmented, but only after they have been blended and invested by membrane substance, to form the matrix of permanent rays, and when the muscles are already formed which move the latter, do the rays show any evidence of transverse segmentation. This is the nearest attainable approach to a demonstration that the alternate swinging movement from side to side of the rays of fishes by the muscles has to do with their transverse segmentation, since this segmentation is always developed secondarily and after the membranous basis of the

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* Professor Cope, Science, IV, No. 87, 339, in an abstract of a paper by him on the phylogeny of artiodactyle Mammalia, "considered the derivation of the selenodont dentition from the bunodont as established from a mechanical point of view."

The evidence in favor of dental specialization of Mammals as modified by the mechanical movements of the animals may be found in a series of papers by the writer, published during the years 1877 to 1879, and based on observations made on the living animals, as well as on the dentitions of living and extinct forms. See Am. Nat. 1877, 603. Nature, XVII, 1877, 128. On the mechanical genesis of tooth-forms, Proc. Acad. Nat. Sci. Philada., 1878, 45–80. The significance of the diameter of the incisors in rodents, Proc. A. N. S. Philada., 1877, 314–318. On the evolution and homologies of the incisors of the horse, Proc. A. N. S. Philada., 1877, 152–154. The mechanical genesis of tooth-forms (Abstract by C. N. Pierce), Dental Cosmos, XX, 1878, 465–472. Further notes on the mechanical genesis of tooth-forms, Proc. A. N. S. Philada., 1879, 47–51, and in a Review by E. D. Cope, Am. Nat., 1879, 446–449.

† On the laws of digital reduction. Am. Naturalist, Oct., 1877, pp. 603–607.

‡ On the origin of bilateral symmetry and the numerous segments of the soft rays of fishes. Am. Naturalist, XIII, 1879, pp. 41–43.

permanent rays is fully formed. It is also noteworthy that the most embryonic or solid type of rays, namely, those found in the *Dipnoi*, are not transversely segmented, apparently for the reason that they are not ossified, but retain very much the constitution of the embryonic horny fibres found in fish embryos. The Teleosts have the basal portions of the rays unsegmented, especially those proximal portions which are invested by muscles, as is the case with the caudal rays of many forms. The distal portions of the rays with their branches in Teleosts and Sturgeons are segmented and ossified. In young fishes the segments are relatively longer than in the adult, thus indicating that the number of segments of the rays increases with age, as I know from observations made on the development of the caudal rays of *Amiurus*, in which the segments are at least three times as numerous in very old specimens as in young ones, fifteen days old. This would indicate that the active movement of the fins, as the fish grew larger, caused the semitubular halves of the rays to fracture at more and more points so as to give rise to the increased number of segments. That such fracture does take place may be assumed upon the basis of the investigations of Lotz* and myself.

Lotz figures the point of fracture of a ray of the caudal of the young Salmon in which it is shown that the ends of the segments are jagged, as if broken (Fig. 3, Pl. III), and the membrane is thickened where they come together as if the ends had been bruised by pressing against each other while the whole ray was being bent. In *Amiurus*, in which I have studied this point, I do not find the broken, jagged ends of the semitubular radial membrane so much thickened, as shown by Lotz in the Salmon, but there is a distinctly defined interval between the membranous segments, which appear to be held together externally and internally by a thin membrane or sort of ligament, which is very thin and consists probably of fibrous connective tissue. These observations have been made upon longitudinal sections of caudal rays, so that there could be no chance of error in my interpretation of the essential facts. They show in the most conclusive manner that mechanical strains upon the membranes when the rays were in use as propelling organs had fractured them at the points described. Moreover, these points of fracture were found to very often coincide with those of adjacent rays, so that a slightly curved line drawn from the break in a central ray would cut through similar breaks in line with the first in the other rays lying on either side of the former.

Here we have an instance in which the breaks in a number of adjacent rays took place concurrently in time and coincidently in position, along a curved line with a generally transverse course across the fin. The probability is that whatever combination of conditions determined the first break in any ray along that line favored the formation of

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* Ueber den Bau der Schwanzwirbelsäule, &c.

breaks in those adjacent, for the reason that a break in one would weaken the support of the rays on either side.

The efficiency of physical forces as the causes of such phenomena no reasonable investigator can for an instant doubt, and to cry out against such a mechanical or kinetic process of evolution as here supposed, which has been assumed by critics not to convey any information, is to do no more than reject the truth; while to put natural selection in its place is not only illogical but absolutely absurd, because this mechanical method of developing the segments of the rays of Teleosts is repeated in every young fish the adult of which has segmented, well-ossified, branched rays. Survival of the fittest, or natural selection, has nothing to do with the process here under discussion, because whether the fish survives or not to become adult, the fracturing and segmenting of the rays has already happened by the time the rays are fairly formed, and when the animal is only fifteen days old, and is still very far from mature or in condition to transmit to its offspring the disposition to segment the fin-rays. It might be urged in objection that the disposition or the structural conditions favoring this mode of segmentation of the rays was inherited. Granting even that much, it does not dispose of the fact that the segmentation or fracturing is veritably caused by the mechanical resistance offered to the fins when the young animal, with developing permanent fin-rays, moves the latter. Moreover, it is undoubtedly true that the period when this segmentation occurs in the rays of the very young fish, the latter does not represent an older ancestral type, for the reason that the degree of rigidity caused by the extent to which ossific deposits are laid down during farther growth determines the number or frequency of the points of fracture, which increase in number with the advance in age.

XVI.—LAMARCK'S SHARE IN THE DEVELOPMENT OF THE PRINCIPLES OF DYNAMICAL EVOLUTION.

As Darwin and Haeckel have truly said, Lamarck is the real author of the doctrine of the evolution of organisms or the theory of the transmutation of species, as effected by the operation of natural causes controlled by natural law. Others before or shortly after him seem to have had some sort of dim conception of the same thing, but let us note how forcible and pregnant some of his ideas were which he put forth in the introduction to his great work entitled *Histoire naturelle des Animaux sans Vertèbres.**

On page 14 of that *Introduction* these fundamental principles find a place:

"First principle: Every fact or phenomenon of which observation makes us cognizant is essentially physical, and owes its existence or production to some body or to the relations between bodies."

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* Tome I, Bruxelles, 1837, 3d edition, revised by Deshayes and H. Milne-Edwards.

"Second principle: Every movement or change, every active force, and every effect whatsoever observed in a body depends necessarily upon mechanical causes, regulated by their laws."

"Third principle: Every fact or phenomenon observed in a living body is at once a physical fact or phenomenon, and a product of organization."

"Fourth principle: There is not in nature any matter which is possessed of the peculiar faculty of *living*. All bodies in which life manifests itself present in the organization which they possess, and in consequence of which movements are excited in their parts, the physical and organic phenomena which constitute life;* phenomena which are executed and maintained in the body as long as the conditions essential for their production subsist."

Now that protoplasm itself is beginning to be regarded as not utterly devoid of structure, and not a simple body, but a complex of many, how much more significant these utterances of Lamarck become. The progress of biological research also tends to show that growth and segmentation of simple cells is an exceedingly complex phenomenon, and that the very first steps of development are remarkably so, and that disturbances of the molecular energies of the germinative vesicle may lead to the production of double or triple monsters by mere multiple impregnation, as shown by Fol in the course of his investigations upon the development of the Star-fish. These and other investigations have cast doubt upon the hypothetical *Moncrula* stage of development, which is such an important part of a popular but now, probably in part, erroneous system of zoological philosophy.

Möbius,† recognizing the necessity of revising the older conception of protoplasmic bodies (monoplastids) as invariably constituting formless automatons, has suggested that since we find evidences of organization as in some *Protozoa*, their specialized parts might appropriately be called *organula*, the diminutive of the word *organ*, as conventionally applied to cellular aggregates having special functions in the organization of the *Metazoa.*

Lamarck's laws of metamorphosis are remarkable as showing how far he had advanced beyond the conceptions of his contemporaries as to the nature of the forces at work in effecting morphological changes. Quoting again from the Introduction to the *Animaux sans Vertèbres*, edition of Deshayes and Milne-Edwards, I, p. 57, the first of these laws is stated thus:

"Life, with its peculiar forces, tends to continually augment the volume of all bodies which possess it, and to extend the dimensions of their parts, up to the end of the term of life."

This approximates the doctrine of Nägeli (*Entsteh. un Begriff der*

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* Philosophie zoologique, I, 400.

† Das Sterben der einzelligen und vielzelligen Tiere. Biolog. Centralbl., IV, 1884, pp. 389-392.

naturhistorischen Art, München, 1865) who supposes that each organism has in itself a tendency to vary in a definite direction, to increase the morphological differentiation, or, as it is commonly expressed, to perfect itself. The tendency to vary in a definite or in an indefinite direction is, however, a purely transcendental statement of what are seemingly facts. *Tendency*, as we will soon find, is a word which may be made to cover a great deal of ignorance. Tendencies must have causes. If I say that an unsupported stone has a tendency to fall, I do not tell what it is that causes it to fall; it is certainly not the tendency which makes it do so, but a specific force, which acts in such a way as to pull the earth and the stone toward each other.

Huxley* states the grounds of the divergence of opinion amongst those who accept the doctrine of evolution in its main features. Three views may be taken of the causes of variations:

"*a*. In virtue of its molecular structure, the organism may tend to vary. This variability may either be indefinite or may be limited to certain directions by intrinsic conditions. In the former case the result of the struggle for existence would be the survival of the fittest amongst an indefinite number of varieties; in the latter case it would be the survival of the fittest among a certain set of varieties, the nature and number of which would be predetermined by the molecular structure of the organism.

"*b*. The organism may have no intrinsic tendency to vary, but variation may be brought about by the influence of conditions external to it. And in this case, also, the variability induced may be either indefinite or defined by intrinsic limitation.

"*c*. The two former cases may be combined, and variation may to some extent depend upon intrinsic, and to some extent upon extrinsic, conditions.

"At present it can hardly be said that such evidence as would justify the positive adoption of any one of these views exists."

These statements of the grounds of the hypothesis of evolution by one of the greatest biological thinkers of our time are, like everything else which he writes, logical and to the point; but let us see how Lamarck had already appreciated the interaction of the above-mentioned intrinsic and extrinsic forces in his second law (*An. sans. Vert.* I, 57):

"Second law: The production of a new organ in an animal body results from a new need which has arisen unexpectedly, and which continues to make itself felt, and which causes the new movements to be made to which this need gave origin and maintained."

Totally new organs, with new functions, are, as is well known, rarely developed; but the method of evolution seems to be to seize upon an organ already developed and modify it by adding or subtracting to or from its bulk, or so modifying it as to amount to a metamorphosis of

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*Anat. of Invertebrated Animals, pp. 41, 42.

the original structure. This is probably what Lamarck meant in speaking of new organs, since the doctrines of special and serial homologies were not developed in his time as they now are.

The causes or origin of variations are contemplated in this second law, as already urged, especially if we admit that the word *need* may be replaced by the term *stimulus*, as is fully justified by the closing phrases on the intrinsic or reflex actions evoked by a change in the environment.. The second law thus becomes very similar in its main features to Huxley's third and provisional statement of the first principles of the doctrine of evolution, as the final alternative, with which the greatest number of evolutionists would now probably be in accord.

While we must admit, with Mivart, that the formative forces controlling the growth of the embryo from an egg seem to be automatic or instinctive, we can assert with some confidence that, in many cases at least, there is positive evidence to the effect that growth force has a determinate direction along a certain axis, and that the first cleavage plane is coincident with the direction of the median long axis of the future animal.* The study of the promorphology of the ovum, as it has been called, thus indicates that the progress of development even during its very early stages exhibits polar phenomena, which are expressed not only as an external polarity, but also as an internal one, involving the most extraordinary rhythmical metamorphosis of the prmordial egg-nucleus and its descendants, which become the nuclei of the cells into which the original germinal mass subdivides. The successive events involved in the ordinary indirect process of segmentation seem to be principally the following: 1, the aggregation of the chromatin substance of the nucleus into looped fibers which are freed from the nuclear wall; 2, the radiated arrangement of the segments of chromatin fibers, with their loops directed towards the center of the nucleus and the free ends towards its periphery; 3, the longitudinal subdivision of the chromatin fibers into more slender ones, with the same arrangement as before; 4, systole, or aggregation of the more thickened chromatin fibers about the incipient plane of cleavage, with achromatin fibers forming the poles of the nuclear spindle; 5, diastole of the chromatin fibers, which subdivide again and retreat to the nuclear poles, leaving achromatin fibers intervening between the two polar wreaths which the chromatin fibers form; 6, completed diastole of the chromatin fibers, which now break up into bead-like masses which become applied to the walls of small nucleoplasmic vesicles which are gradually formed at the extreme ends of the polar wreaths of chromatin fibers; 7, coalescence of the small vesicles lined with chromatin at either end of the spindle to form two new nuclei,.which are the centers of the two new cells resulting from the division.†

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* On the development of some pelagic fish eggs: preliminary notice. A. Agassiz and C. O. Whitman. Proc. Am. Acad. Arts and Sciences, XX, 1884, pp. 74, 75.

† J. Bellonci: La Caryocinèse dans la segmentation de l'œuf de l'Axolotl. Arch. Italiennes de Biologie, VII, 1884, pp. 52–57, 1 pl.

The directions of the axes of the cleavage spindles change with each cleavage and stand at nearly right angles to each other. The directions of the spindles of alternate generations of cells are therefore for sometime nearly coincident in direction.

These phenomena, when contemplated in reference to the origin of variations, are very significant; extrinsic forces which are ever active even during the earliest stages of the nascent embryo, it must occur to every one, might very readily produce an impression upon a mechanism so delicate as the one just described, where the parts can be measured only in units of length of infinitesimally small dimensions, or in terms of thousandths of a millimeter. Variations in the action of intrinsic forces during early development need therefore be exceedingly slight in order to initiate and be productive of morphological changes which would cause the adult to vary within certain limits more or less from the parent in form, because these caryokinetic processes or nuclear metamorphoses preside over the genesis of the tissues, and the order of the manifestation of these nuclear changes seems predetermined, in consequence of which the germ of an organism may in the course of development give rise to something very nearly like the parent.

Variations in temperature affect the rate of these rhythmical metamorphoses of nuclei; low temperatures generally retard them, while higher temperatures accelerate them. This correlation between the temperature of the medium in which development goes on and the vital energy of the growing ovum exhibited during caryokinetic action is very remarkable, as shown in the course of experiments by the writer on the development of the eggs of fishes.*

We are thus brought face to face with some of the forces which must initiate variations even before there are organs present which can be exercised as in the adult, but when the germ is nevertheless complex enough, as the play of internal forces sufficiently shows through the activity which they exhibit. Matter and motion are the principal factors involved; but the matter may be said to be so compounded and in such relation to the cosmos as to be recognized as alive and capable of manifesting reflex actions. That last capacity is the thing needed by the doctrine of evolution as the justification of Lamarck's second law, which may be so extended as to involve the consideration of the primary causes leading to variation of a germ *in utero* or in the ovary; a seed in the form of the ovicell or in the ovary of the plant. In this way only does it seem conceivable that the origin of early or embryonic variations can be understood.

Lamarck's third law of metamorphosis is stated thus: "The development of the organs and their strength of action are constantly in proportion to the extent or degree to which they are used." This is now a recognized axiom of the doctrine of evolution.

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*Bull. U. S. Fish Commission, I, 1881, pp. 187-190 and 335-339, Pl. XVIII.

Fourth law: "All of that which has been acquired, outlined, or changed in the organization of individuals in the course of their lives is preserved and transmitted by the process of reproduction to the offspring which came from such parentage as had experienced such alterations." This law recognizes the influence of heredity.

The influence of the use or disuse of parts is stated in effect as follows by Lamarck in *Animaux sans Vertèbres*, I, p. 60, and also in his *Philosophie zoologique* (1809):

"Want of use of an organ, arising from acquired habits, gradually impoverishes an organ, and ends in causing it to disappear.

"The frequent use of an organ, arising constantly from such habits, augments its faculties or capabilities, causing it to acquire dimensions and a power of action which it does not have in animals exercising it less."

He also speaks of *penchants*, or impulses arising from the *sentiment intérieur* (*An. sans Vert.* I, 81), where he speaks of the efforts made by animals for their self-preservation, where the principle of the struggle for existence seems to be *dimly*, and perhaps tacitly, recognized. He alludes to the manifestation by animals of such impulses as these: "To fly from pain; to seek and seize their nourishment; to perform the sexual act when their organizations solicit them; to seek for pleasant places and prepare for themselves means favorable for their conservation; to withdraw from painful conditions and everything which constrains or incommodes them; to seek for pleasant, advantageous situations, shelter and the sun's heat during cold periods, shade and cool places during the hot season; to satisfy the need of nourishing themselves, sometimes with voracity, either from the pleasure they find therein or the unrest which arises from the want of food; to give themselves up to the enjoyment of the sexual act, or to ardently seek occasion for it when their needs provoke or solicit it; to take repose and sleep, when their other needs are satisfied."

Intelligent impulses he speaks of as impelling an animal "to chase its prey, to watch it with patience, to lay snares; to employ new and various means, according to circumstances, to satisfy each of its needs; to resort to poltroonery or cowardice when weak in consequence of an excessive fear of danger; to preserve itself from danger by means of various ruses."

Selfish impulses (*An. sans Vert.* I, p. 82) are spoken of as impelling an animal "to escape becoming the prey of others if the latter are stronger; to chase and combat other animals which approach its female, or such that covet her possession." In this last observation he recognizes the struggle for possession amongst rival males, but does not recognize the principle of sexual selection.

Finally, he says animals are impelled "to prefer above all else that which they can do to procure for themselves the enjoyment of some advantage."

It thus becomes evident that Lamarck never clearly recognized the principle of natural selection which it has been the great merit of Darwin and Wallace to discover and announce simultaneously, yet the father of the doctrine of transmutation of species seems to have had some sort of dim conception of the fact of the reality of a "struggle for existence," as implied in his remarks on rivalry amongst males, and when he implies that animals do things the purpose of which is to gain some advantage.

The frequently quoted instance of the long neck of the Giraffe, which Lamarck thought had been produced by the persistent efforts to feed upon the foliage of trees by successive generations of the animal, has made abundance of sport for superficial writers since his time. But let us look into this matter a little more closely, and see if natural selection is at all likely to have originated longer cervical vertebræ in this creature. Granting that the external conditions were such as to favor the survival of long-necked forms, the most that natural selection could do would have been to *preserve* the long-necked individuals to reproduce the species; it could *originate* no progressive morphological differentiation, but merely be the means of preventing the extinction of the acquired increments of that differentiation.

If Palæontology is of any value as throwing any light upon the history of the evolution of the Giraffe, we probably have in *Sivatherium*, *Bramatherium*, and *Helladotherium* forms which were antecedent in time. The latter, especially, had a pretty long neck, and seems to have been higher at the shoulders than at the rump, somewhat as in the Giraffe. Here we have a probable stage of evolution of *Camelopardalis*, or a survival of a form tending in that direction, but with a neck proportionally no longer than *Camelus*, which is also allied. Now let us soberly ask ourselves if it is likely that the effort to reach for herbage, if persisted in on grassless plains, where the only food was the foliage of trees, would not tend to cause the animal to lift its head and already long neck, strengthen the ligamentum nuchæ and cervical muscles, and in pulling or wrenching off this foliage stretch its neck more and more, generation after generation, each of which would thus gain an inherited advantage in obtaining food over the one which had preceded it in time. Manifestly there must have been causes for this variation in one direction which would lead to an increased growth in length of the centrum of each cervical vertebra. Variation would have had to constantly tend in the one direction through a great many generations, which is in the highest degree unlikely, if no adequate cause existed to determine that direction. Darwin himself never lost sight of this difficulty, but his followers have frequently expressed themselves as if variation itself and natural selection were forces irrelative to the intrinsic forces exhibited by living bodies; for neither natural selection nor variation could produce any effects whatsoever if the environment were constantly the same about a living individualized entity without rivals, any more than we would look for a moving body to ever swerve from traversing space in a right line if it were forever exempt from all disturbing resistances and attractions along its path. Dr. Tomes, in his work on Dental Anatomy, second edition, finds it inconceivable that intrinsic forces are capable of modifying the forms of the crowns of the teeth of Ungulates, apparently unmindful of the fact cited by the writer that an inorganic crystalline body as brittle as marble could be permanently bent if subjected to a constant bending strain for many years. This, however, is only one instance among many where biological writers have ignored the logic of facts when dealing with the principles of the theory of evolution.

In recently glancing over the *Philosophie zoologique* the writer finds that Lamarck had in that work briefly recorded his views on digital reduction, assigning increased use in running as a cause, as asserted by Cope, Marsh, and the writer in later times. Some years since the writer attempted to discuss digital reduction, when it "was suggested that the fact of the number of toes being least wherever *mechanical strains* were greatest and *impacts* most frequent and severe, might be regarded as an effect of such increased intensity of strains." Cope afterwards showed that the grooving of the articular faces of the limb-bones of certain *Mammalia* was probably due in part to such a cause. The writer also called attention to the coexistence of accelerated digital reduction in the pes with jumping or bounding habits, in consequence of which the reduction began first in the hind limbs; pointing out, also, in this connection, that man, the highest and only strictly bipedal primate, is the only one in which a perceptible digital reduction has begun in the pes, so as to enlarge the inner toe.

The specialization of the limbs of the modern Sloths has also been discussed by Lamarck, who assigns their peculiar habits as the cause of certain modifications of the limbs and other portions of the skeleton. The writer, unaware at that time of Lamarck's published views, had prepared an essay upon the same subject, in which he has given expression to certain views which were already expressed by the earlier author; but inasmuch as the writer had also discussed the digital and dental reduction which occurs in this group, including the fossil species, it has been decided to hand the manuscript to a palæontological friend competent to revise and bring it up to date for publication at an early date.

It has been thought proper to make these acknowledgments to one of the most far-sighted intellects that has ever honored the pursuit of biological investigation, for the reason that many of the students of to-day seem forgetful of the man to whom indirectly they owe so much. The writer also would acknowledge his indebtedness to this pioneer evolutionist, and would frankly admit that Lamarck was the first to perceive that morphological changes were traceable to the action of forces, the effects of which we have been seeking to follow in this study of the evolution or morphological differentiation of the fin-systems of the *Lyrifera*.

XVII.—A STATEMENT OF SOME OBJECTIONS AND CONCLUDING REMARKS.

I am aware that it may be objected that the development of an opisthure in *Chimæra monstrosa*, while it is absent in *C. plumbea*, would seem to militate a good deal against the hypothesis here set forth, since it might be asked why the same forces should not produce the same effects in both these forms otherwise so nearly allied. Nor is this the only objection which might be raised, for why is it, it may be inquired, that certain physostomous forms, as *Alosa* for example (which is evidently lower in respect to the development of the air-bladder than the *Physoclisti*), should exhibit a specialization of caudal development not found to occur in those forms which are evidently more advanced when their entire organizations are considered in this comparison? But none of these or the numerous kindred objections which might be raised need dismay us in our inquiry for the reason for the present morphological composition of the caudal fins of fishes, in which we have been at least measurably successful in demonstrating something akin to order in the elucidation of the most important of all the questions relating thereto, namely, that the skeletal parts are, beyond any doubt whatever, serially homologous. When once this fact is appreciated, and it is at the same time understood that the skeletogenous layers are also homologous throughout the different groups of fishes, it will be evident to any reasonable person that the causes which would lead to the production of very different morphological effects would need but little modification to make them effective. This is all the more evident when it is remembered that the habits of the different groups vary very greatly, and that the special modification of some part through the exercise of some special habit must affect other parts correlatively, so that it becomes impossible to predict what the effect will be upon the many parts taken singly in such a complex aggregate. It is now at least self-evident that the possibility of *chance variations* having anything to do with determining the mode of evolution of the tail of fishes is in the highest degree improbable. Extreme reduction and degeneration in certain directions have also been clearly shown to occur, the evidence on this point being too palpable and conclusive to admit of dispute.

Not less weighty than the objection urged in the case of the *Holocephali* is that which might be urged in the case of *Caturus* and *Leptolepis*, Liassic and Oolitic forms, almost as outwardly homocercal and structurally almost as heterocercal as the most differentiated existing Teleosts. Why is it, it might be inquired, that these forms have reached heterocercal and outwardly homocercal specialization so soon? Or why should the archaic or primitive diphycercal type be preserved in the existing *Dipnoi* if these and their kindred have been subject to the same outward mechanical forces as the line which ended in the production of the extreme heterocercy of the Teleosts? Have the *Dipnoi*, however, developed such an inequality in the relative width of the unpaired epural and hypural fin system as could lead to the production of heterocercy? We see that such inequality has not arisen and that perfect diphycercy has been maintained in the *Dipnoi*, from which it follows that it is safe to assert that there must have been some difference between the forces which acted upon the ancestry of the latter and that of the existing *Teleostei*. In this way only can we conceive archaic characters to have been preserved and handed down to the present.

Huxley's statement,* that "in all Teleostean fishes the extremity of the spinal column bends up, and a far greater number of the caudal fin-rays lie below than above it," must now be qualified so far as to admit that in some Teleosts there is no such upbending of the end of the axial skeleton, as in *Mola*, *Fierasfer*, and *Gastrostomus*, for example; nor is it invariably true that a greater number of fin-rays lie below than above the termination of the axial skeleton. The result of these investigations has accordingly been to modify somewhat the accepted views of the evolution of the caudal fin from a prototype which was essentially *orthaxial* posteriorly, or one in which the posterior terminus of the axial skeleton was straight and in line with the thoracic portion.

The parallelism existing between the tails of the orthaxial lophocercal larvæ of existing fishes and the orthaxial caudal of *Cœlacanthus*, *Coccosteus*, *Glyptolæmus*, and *Gyroptychius* is not exact, because these extinct forms had more or less clearly marked rays or apophyses developed. *Coccosteus* seems to have had no caudal fin, but had apophyses developed above and below its notochordal axis posteriorly, thus attaining a specialization almost as marked in this respect as that observed in the existing genus *Hippocampus*. These are facts which must not be lost sight of, for we may assume that the development of a form recapitulates the development of the phylum to which it belongs, when in fact it does so very inexactly, as the examples above citêd show. Another illustration may be cited, viz, that of the protopterygian stage of the Salmon embryo when its embryonic rays, cartilaginous apophyses, and notochord recall the permanent condition found in the *Dipnoi*. But in the Salmon embryo we find has no perichondrial ossifications developed at this time about the epaxial and hypaxial apophyses of its axial skeleton, as in the *Dipnoi*, nor is the end of the chorda any longer orthaxial at its termination, as in the latter.

These accelerated departures from the primitive type are evidently dependent for their manifestation upon heredity, since structures characteristic of classes, orders, families, genera, and species seem to appear in most embryos in about the order of rank in which they stand above, though in many cases so pronounced is the direct influence of heredity that a family or, at most, an ordinal, character will appear at the end of the first day, as in the case of the development of the barbels of *Amiurus*.

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* Anat. of Vertebrated Animals, p. 131.

These data might be used as objections to the conclusions reached in this paper, were it not that we have the most conclusive grounds for believing that the morphological differentiations or metamorphoses, so rapidly passed over during the embryonic stages of many vertebrated organisms, are the transitory expression of characters acquired during the adult life of ancestral series, extending back into long ages past. The embryo has obviously not had time during its brief career of development to acquire the differentiations which we note in the adult. Many embryonic traits are also the necessary complements of a mode of development which is characteristic of all Vertebrates, namely, their evolution from a spherical, more or less meroblastic egg. We may therefore, I think it probable, look upon almost every character above classical value as acquired by a type during the post-larval history of the individuals constituting its ancestral series; and inasmuch as natural selection cannot be looked upon as an originative force, but only as a conservative law or principle, we are forced to conclude that advantageous variations must have arisen as the direct results of the interaction and retroaction constantly going on between an organism and its environment.