E ORIGIN OF VERTEBRATE LIMBS.

RECENT EVIDENCE UPON THIS PROBLEM FROM STUDIES ON PRIMITIVE SHARKS.

BY

RAYMOND C. OSBURN.

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For nearly thirty years the Fin-fold Theory has been commonly accepted to explain the origin of the limbs of the Vertebrata. This theory has as its main thesis that all fins, both paired and unpaired, have arisen *in situ* and in the same manner, as local developments from the body wall. Thus conceived, they are primarily external structures which have as their primitive form a longitudinal fold of skin supplied with muscles, nerves, and blood-vessels derived in a segmental way from the adjoining body wall, and with supporting structures which have had their origin within the fins. This theory first took form in the work of Thacher ('77), Mivart ('79), and Balfour ('78), all of whom arrived at the same conclusion independently, the first two on anatomical grounds, the last from the embryological standpoint. The theory has been ably supported by Dohrn ('83 and '02), Paul Mayer ('86), Wiedersheim ('92), Mollier ('93), Rabl ('01), Dean ('02), Regan ('04), and others.

Opposed to this view is the older "Archipterygium" or Gill-arch Theory, first definitely stated by Gegenbaur ('65 and '70) and maintained by him through all his later work ('95). Ranged on this side of the question are Bunge ('74), von Davidoff ('79 and '80), Fürbringer ('96 and '02), Braus ('98 and '04), and others of the Gegenbaur school. As far as the origin of the unpaired fins is concerned, the gill-arch theorists admit that they arose as local outgrowths, and go farther than their opponents in assuming a rigid metamerism of all the structures of the unpaired fin, deriving the median fin skeleton from processes (dorsal and

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hæmal spines) of the axial skeleton, while according to the
fin-fold theory the skeleton is supposed to have been developed
independently of the vertebral column. But it is in the origin
of the paired fins that differences of opinion are most in evidence,
for while the fin-fold theorists consider that the paired fins have
had in a general way a similar origin to the unpaired, the gill-
arch theorists hold that they have been modified from gills
and that the girdles and rays of the fins are directly homologous
with the supporting structures (arches and rays) of the gills.

During all the years in which these theories have been under
discussion unsettled points have not been lacking, and within
recent time a number of objections have been urged against the
fin-fold theory. With the hope of deciding some of these vexed
questions and with a view to testing the validity of the objec-
tions raised, the writer has been led to investigate the develop-
ment of the paired and unpaired fins of a cestraciont shark
(*Heterodontus japonicus*, Duméril), a form belonging by direct
lineage to a group of very ancient sharks,—much older, as far
at least as can be judged by palæontological data, than any
selachian that has hitherto been investigated.[1] For comparison
the writer has had various stages of Spinax, Mustelus, and
Torpedo, and has been especially fortunate in having access to
a number of embryonic stages of *Chlamydoselachus anguineus*
Garman, a form generally recognized as being one of the most
primitive of modern Selachii. The series of Cestracion (Hetero-
dontus) embryos at my command is very complete. For the use
of all of this valuable material my thanks are due to Professor
Bashford Dean, to whom I am also grateful for much encourage-
ment and many helpful suggestions in pursuit of the work.

The present paper embodies only the main results of my
studies and will be followed by another more extended in scope,
in which will be given the evidence upon which these results
are based and in which the literature of the subject will be treated.

It may be briefly stated that the results of my work indicate
that many of the objections raised against the fin-fold origin
of the paired fins apply equally well to the unpaired fins, which

[1] All references to Cestracion, Chlamydoselachus, and Spinax in the
following pages are from my own observations, unless otherwise accredited.

are held, even by those who have raised the objections, to be of strictly metameric and local origin. Other objections can be shown to be based upon faulty evidence, or upon facts which bear a different and more probable interpretation.

The principal objections to the fin-fold theory are, briefly stated, as follows:

A. Relating to the comparison of the paired fin girdles with gill arches the followers of Gegenbaur contend that:

I. The pectoral girdle arises in serial order with the gill arches.

II. The pectoral girdle makes its appearance earlier than the basalia and rays.

III. The basalia grow out of the girdles and the rays out of the basalia.

IV. The dorsal end of the pectoral arch comes into relation with the visceral muscles.

V. The pelvic girdle is the homolog of the pectoral in every respect and so corresponds to a gill arch.

B. Relating to the supposed migration of the paired fins from the gill region:

I. The pelvic fins have been shown to undergo slight migration or shifting during ontogeny.

II. As a proof of migration there appears a strong collector nerve in the anterior part of the pelvic fins.

III. Also, in the early development of the pelvic fin the most anterior muscle-buds degenerate without entering the fin, while those just posterior to these are compelled to reach backward to enter the fin.

C. Relating to the contrast of paired with unpaired fins:

I. The skeleton of the unpaired fins consists of modified vertebral (spinous and hæmal) processes.

II. The girdles of the paired fins have nothing to represent them in the unpaired fins.

III. The presence of post-axial rays in the pectoral fin proves the primitive biseriality of the paired fins.

IV. The fin-rays of the paired fins do not arise separately and later become fused to form basalia as the fin-fold theory would lead us to expect.

V. The fusion of the muscle-buds in the paired fins before

the appearance of the skeleton precludes the possibility of the metameric origin of the latter.

VI. The early discrepancy between muscles and rays in the pelvic fin proves the primitive dysmetamery and independent origin of the paired fin skeleton.

Let us now examine the foregoing objections point by point and determine whether they are well founded.

A.

I. The pectoral girdle cannot be considered serially homologous with the gill arches for the following reasons:

(1) The first anlage of the pectoral girdle lies almost its whole length below the gill arches, as shown by Braus's reconstructions ('04) of Spinax, and by my own observations on Cestracion.

(2) It arises near the external wall of the body, while the gill arches arise near the pharyngeal wall, according to my studies on Cestracion.

(3) The thickening of mesenchyme from which the girdle is differentiated takes its origin next to the ectoderm and spreads in an inward direction till it occupies all the region in which the pectoral fin skeleton arises, which latter is therefore of external origin, since it arises out of this mesenchyme thickening. The gill arches, on the other hand, arise next to the enteron.

(4) The study of Cestracion shows that the first anlage of the pectoral fin lies wholly within the region of spinal muscles.

(5) In Cestracion at least, the pectoral girdle is relatively much farther from the last gill arch at its first appearance than it is during later growth. That is, it grows toward the gill-arch region.

(6) The first four points apply with even more force to the pelvic girdle which in a general way must be considered the homolog of the pectoral.

II. The observations of E. Ruge ('02) and Braus ('04) that the pectoral girdle of *Spinax niger* is the first part of the fin skeleton to make its appearance, are probably not to be questioned, but since Spinax is the only form so far examined in which the time relations are thus, and as in Cestracion, which is unquestionably a much older type of fish, the first anlage

of the skeleton undoubtedly makes its appearance in the region of the base of the rays and the neighboring part of the primary basal, we must conclude that this objection is at least not final. On the contrary, it seems plain from the evidence at hand that Spinax is the exception to the rule.

III. Against this objection we must weigh the following facts:

(1) The writer finds that in Cestracion the rays and basalia begin to appear before the girdle. Other investigators since the time of Balfour ('78) have found the same to be true in various species (Spinax excepted).

(2) The basalia and rays do not "grow" out of any pre-existing structure, but are differentiated, both in the same manner, out of the same band or layer of mesenchyme. This layer gives rise also to the rudiment of the girdle. The above distinction is an important one since upon it depends the interpretation that all of these skeletal structures of the fins are developed *in situ* by differentiation instead of "growing out." The latter term implies internal development and change of location during the process, a condition contrary at least to the present observations. [1]

IV. The fact that the dorsal end of the pectoral girdle has relations with the visceral musculature (trapezius group, innervated by viscero-motor nerves), has been interpreted by the gill-arch theorists to show a primitive connection,—"die alten Relikte der einstmaligen kopfmuskelversorgung des Schultergürtels" (Fürbringer '02). The connection is beyond question, but that the above conclusion is not final is evident from the fact that in Cestracion the first anlage of the pectoral girdle arises entirely ventral to the anlage of the trapezius, quite separated from it, and comes into relation with the visceral muscles only by its later dorsal growth. This is true also of Spinax, as shown by my preparations of a 20 mm. embryo.

V. The pelvic girdle cannot be strictly homologized with the pectoral, point for point, for the following reasons:

(1) In the oldest fossil sharks in which the pelvic is sufficiently

[1] By way of comparison, it is worthy of notice that the muscle-buds do grow into the fins. They disarrange the mesenchyme cells and push them out of the way during their progress. Nothing of this nature takes place in connection with the development of the fin skeleton.

known (Pleuropterygidæ) there is no pelvic girdle developed
beyond the condition of basalia. If the gill-arch theory were
true, the pelvic girdle should be best developed in the oldest
forms.

(2) In the lowest modern sharks (Notidanidæ) there is in
the adult no evidence of a dorsal prominence in the pelvic to
correspond with the scapular portion of the pectoral. It is
difficult to see how the pelvic girdle of Chlamydoselachus, a
long, flat plate pierced with eight nerve foramina, could be
made to homologize with the pectoral girdle of any shark.

(3) In none of the stages of Chlamydoselachus in my pos-
session in which the pelvic is sufficiently developed (from 110
mm. upward) is there any indication of a dorsal prominence.
The pelvic girdle develops as a flat basale-like plate.

(4) The argument for the anterior prominence which is
present in some sharks and which was originally homologized
with the scapula by von Davidoff has already been given up by
the gill-arch theorists. The small dorsal prominence recently
described (Braus '04) in the pelvic of Spinax and homologized
with the scapula can scarcely be considered homologous, for
the reason that it is situated posterior to the nerve foramen,
while the scapular portion of the pectoral girdle is always, so
far as my observations have extended, anterior to the foramen.

The various parts of the pelvic girdle cannot, therefore, be
homologized with all parts of the pectoral, and certainly the
pelvic girdle is much farther removed from comparison with
the gill arch.

B. It becomes evident that no migration yet shown is quan-
titatively sufficient to account for the distance between the
pelvic fin and the gill region, for:

I. The slight measurable migration which the pelvic may
undergo in its ontogeny cannot be accepted as evidence in favor
of migration from the branchial region.

(1) The pelvic fin in some cases migrates forward during
ontogeny.

(2) The supposed demonstration of migration in the pelvic
fin at an early period is better explained as due to the concen-
tration of the fin from a longer basis, as I will show under another
heading.

(3) The migration of the pelvic, as well as of other fins, has been shown biometrically to occur in accord with the shifting of the center of gravity during development (in Cestracion by Dean '02). By the same method it has been proved that the pelvic shifts its position in correlation with the dorsals (in Spinax by Punnett '04). Hence the observed migration becomes merely an adaptive process without any special meaning in phylogeny.

(4) While we have no direct evidence that any fin has ever migrated backward to any extent, we have abundant proof of the migration of the pelvic fins forward in many Teleosts, in extreme cases to a position in front of the pectorals. This, also, can be due only to adaptation.

(5) No satisfactory reason has ever been offered why a fin, when once in the most important place in the body, viz. the pectoral position, should ever have migrated out of it into a region of such minor importance as the pelvic fin occupies in sharks and other primitive fishes.

II. The argument based upon the collector nerve is negatived at once by the following facts:

(1) Collector nerves appear also in the unpaired fins, both in the anterior and posterior parts of the fins, as Paul Mayer ('86) showed in Acanthias, Heptanchus, and Centrophorus, and as my own observations show in the first and second dorsals of Cestracion. Yet it is contrary to the Gegenbaurian conception of the unpaired fins that they have migrated at all in their phylogeny.

(2) A small posterior collector is known in the pelvic fins of certain species. This is assumed by the gill-arch theorists to be due to a secondary migration of the fin in a forward direction. However, the results of Punnett's studies ('00) on Mustelus indicate that in this species the pelvic fin of the female migrates farther forward than that of the male and yet has no posterior collector, while that of the male which indicates less migration none the less possesses it.

(3) In those Teleosts which show a migration of the pelvic to a thoracic position, the nerves of the fin are carried forward during the process, while no nerves are picked up on the way and no new collector is formed as a result of the migration.

The hypothesis of migration is therefore very far from meet-
ing all the conditions.   The only adequate explanation (Mollier
'93) is that all the fins have shortened up at the base and have
formed the collectors by bringing together nerves which once
entered separately to innervate the longer fin.   In favor of this
view we have direct evidence that the fins of modern sharks
do shorten up at the base during ontogeny, and we know also
that the fins of the oldest fossil sharks (Pleuropterygidæ,
Acanthodidæ, and Diplacanthidæ) were of the fin-fold charac-
ter, broadest at the base and without any posterior indentation
or notch such as modern selachian fins possess.

III. The facts of the degeneration of the most anterior
muscle-buds, and of the backward extension of those buds
immediately posterior to these to enter the fin, can not be
accepted as proof of the migration of the fin, as has been so
strongly urged by the gill-arch theorists (Braus '98), for:

(1) The same process occurs at the posterior border of the
same fin. The observations of Braus ('98) demonstrate that
in Spinax the last pelvic muscle-bud degenerates without enter-
ing the fin, while the buds immediately in front of it are com-
pelled to reach forward to enter. My preparations of Spinax
show that four such buds extend forward to attain their posi-
tions in the fin, and the same condition is observed in
Cestracion.

(2) But, most significant, the same process, I find, occurs
in the unpaired fins. In the dorsal fins of Cestracion the most
anterior buds extend backward while the most posterior reach
forward to enter the fin. Again, in Paul Mayer's work ('86),
published more than twenty years before this objection to the
fin-fold theory was raised, we learn from his description of
the unpaired fins of Scyllium and Pristiurus that there are
abortive muscle-buds both before and behind the dorsal fins,
and we may observe from his plates that the most posterior
and most anterior buds which enter the fins have to reach out
of position to accomplish it.

(3) The fact that in the pelvic fin these most anterior muscle-
buds are the earliest to appear is not to be taken as a proof
that they are phylogenetically older than those which appear
later, as the gill-arch theorists assume (Braus '98), but rather,

they appear first because they are most anterior, for it is in the
nature of all such serial structures to develop from anterior to
posterior (*e. g.*, gills, somites, pronephric tubules, etc.) This
condition is observed in the unpaired fins as well as in the
paired, for in the dorsals of Cestracion the most anterior buds
are the first to develop. The same principle, according to my
observations, holds also among the various fins, the pectoral
preceding the pelvic, the first dorsal preceding the second, in
time of development, etc., yet this cannot be considered a proof
that the first dorsal is phylogenetically older than the second
nor the pectoral older than the pelvic. (According to the gill-
arch theory the pelvic should be the older, yet it develops
later than the pectoral.)

These facts are readily interpreted on the hypothesis that
the bases of the fins once extended over a larger number of body
segments than at present. In the pelvic it is evident that the
shortening has been much greater at the anterior than at the
posterior edge of the fin. As a result the present fin is now
situated in advance of what was once its posterior limit, though
the anterior edge of the present fin is much farther back than
formerly. Certainly this is not migration, but a concentration
of the fin basis in a manner similar to that occurring in the
unpaired fins.

C. If the six objections given under this heading can be
answered, the paired fins should be compared rather than con-
trasted with the unpaired fins.

I. If it were true, as the opponents of the fin-fold theory
maintain, that the skeleton of the unpaired fins consists of
modified spinous and hæmal processes, then evidently the skele-
ton of the paired fins could not have a similar origin to that
of the unpaired. Opposed to such a view, however, are the
following facts:

(1) In the first and second dorsals, the anal, and the superior
caudal fins there is not the least indication of such a close
relation of the rays to the vertebral processes as we should
expect from the above view of their origin. In the lowest
sharks, especially in such forms as do not possess fin spines,
the rays of the dorsal and anal fins are usually widely separated
from the axial skeleton, according to the present studies on

many species. In the ancient fossil shark Cladoselache, also, the rays of the dorsal fin are widely separated from the vertebral column.

(2) In ontogeny the skeleton of the unpaired fin is plainly developed from a plate of thickened mesenchyme which first appears next to the ectoderm.

(3) During early development the unpaired fin skeleton is never in contact with the axial skeleton, as shown by my studies of Cestracion, Chlamydoselachus, Spinax, Mustelus, and others.

(4) The only exception to the last statement, and the only case where corresponding rays are known to come into contact with vertebral processes, are found in the inferior caudal fin, and even here there are frequent discrepancies. This fin is then an exception to the rule, and if all the unpaired fins have had a similar origin, as seems probable, we must explain the condition in this fin as due to secondary fusion of the rays with hæmal spines to secure better support. On account of their mechanical relation to the ventral lobe of the caudal fin, which is the chief organ of propulsion, these rays stand in need of just such support. (This is the part of the fin which becomes the functional caudal in Teleosts.) Examples of parallel cases are the dorsal spines of sharks (undoubted secondary structures), which, in order to secure firmer support, have become secondarily attached to the axial skeleton, and the superior rays of the secondarily diphycercal tail of Dipnoi.

II. With regard to the comparison of the girdles of the paired fins with the basalia of the unpaired fins a number of facts present themselves.

(1) The girdles exhibit so much variation in form that they show themselves to be adaptive structures such as the basalia of unpaired fins are admitted to be.

(2) In the fossil Cladoselache we have the evidence that the pelvic girdle was formed in the same way as the basalia of unpaired fins,—indeed it is in the same condition as many of the unpaired fins of modern sharks.

(3) In the Notidanidæ, which are without doubt the lowest and most primitive of recent sharks, the pelvic girdle is merely a flat plate, not more complicated in form than the basalia of many unpaired fins and in Chlamydoselachus twelve of the

twenty-five rays of the pelvic fin attach directly to the girdle, thus indicating its primitive position in the category of basalia.

(4) In the more primitive Ganoids the skeleton of the paired fins has a close resemblance to that of the unpaired, as Thacher and Mivart demonstrated long ago. Regan ('04) has recently brought forward a remarkably clear case in *Psephurus gladius*, in which the series formed by the anal, pelvic, and pectoral is most convincing. The pelvic resembles the anal even more than it does the pectoral.

III. The presence of post-axial rays in the pectoral fins of the fossil Pleuracanthus, and to a limited extent in modern selachians, is held by the gill-arch theorists to prove the "primitive biseriality" of the paired fin skeleton. Opposed to this conclusion we have the facts:

(1) The fossil Pleuropterygidæ, Acanthodidæ, and Diplacanthidæ, all of which occur in older strata than does Pleuracanthus, have the fins all decidedly of the fin-fold type, with not even any opportunity for the presence of post-axial rays.

(2) Post-axial rays are entirely absent from the pelvic fins of all sharks, modern and ancient (unless we are to accept the questionable cartilages in the mixipterygium of Pleuracanthus, the homology of which with post-axial fin-rays is at least doubtful).

(3) The occurrence of post-axial rays in the pectoral fins of recent sharks is so sporadic and variable, and they are wanting entirely in so many species, that they are better considered as adaptive structures without peculiar phylogenetic significance.

(4) There are known cases of post-axial rays in the unpaired fins (dorsal of Raja, anal of Heptanchus; also the dorsal of the Devonian Ganoid, Cœlacanthus), where they have all the appearance of those in the pectoral. This again shows their adaptive nature.

(5) In higher vertebrates which have taken up aquatic life we have well-known examples of extra or supernumerary digits formed adaptively on the post-axial side of the limb. This in the whales is proved to have taken place by a longitudinal division of the fifth digit (Kükenthal '88 and Symington '06). A migration of the fifth digit into a well-marked post-axial position for adaptive purposes is also well illustrated in certain

aquatic reptiles and mammals, as I have elsewhere indicated (Osburn '06)

IV. Kerr ('99) pointed out that the real stumbling-block for those who have found themselves unable to accept the fin-fold theory lies in the fact that the fin-rays do not arise separately and later become fused to form the basalia. However, when we examine the mode of formation of the fin skeletal this difficulty disappears. It must be noted that the skeletal structures of the fin are the last of all to develop, and that the fin already has approximately its permanent shape when the skeleton begins to take form. It consequently makes its appearance as an adapted structure, suited to the mechanical needs of the fin at the time it develops. In the unpaired fins, which the gill-arch theorists consider primitively metameric, the process is precisely similar to that in the paired fins. Wherever, in the unpaired fins, the rays have become joined to form basalia, these basalia are present from the first, according to the writer's studies, just as they are in the paired fins, and they are not formed by the fusion of separate rays. There is, then, no more difficulty in accepting the origin of the paired fin basalia from rays than there is in accepting such an origin for the unpaired fins, since both proceed exactly alike. In neither case is there any fusion of once discrete rays to form basalia, but in both the basalia are adaptively formed as such from the first, due to the failure of the mesenchyme to differentiate into smaller elements.

V. The opponents of the fin-fold theory have lately insisted (Fürbringer '02, Braus '04) that the fusion of the muscle-buds described by Mollier ('93) in the paired fins proves the original dysmetamery of the paired fin skeleton, since the fusion to form the "musculi radiales" takes place before the appearance of the rays.

The writer's investigations on Cestracion show conclusively that such an argument cannot be considered valid, for the reason that fusion occurs also in all the unpaired fins, which are held by the gill-arch theorists to be strictly metameric. I have carefully traced the process from its inception and compared it with the same process in the paired fins and there is no observable difference. On the other hand, it only shows more clearly the close relation of the paired and unpaired fins.

VI. The discordance or discrepancy between muscles and rays which has also been strongly urged as proof of the primitive dysmetamery and independent origin of these structures in the paired fins (Braus '04) has likewise no place in argument against the fin-fold theory, for again the same condition is found to occur in the unpaired fins. My reconstructions of the first and second dorsal fins of Cestracion show the same sort of discrepancy that has been proved to exist in the paired fins.

In the foregoing pages the objections to the fin-fold theory have been considered; we may now mention the following objections to the gill-arch theory:

I. The indications are that the primitive fin possessed a far greater number of rays than the primitive gill.

II. There has never been discovered any indication of an intermediate stage representing a transition from the gill to the fin.

III. My observations indicate that the paired fin girdles have not been abstracted from the branchial region by the spinal muscles in the manner assumed by the gill-arch theorists.

IV. The gill-arch theory violates important time and place relations.

To further explain these statements:

I. The gill-arch theorists have tried to show that the gill rays have degenerated, and they reason that at one time the gill might have had rays enough to equal those of the primitive fin. The only evidence of degeneration thus far produced has been in the hyoid arch, the rays of which are reduced somewhat in number, but that is no indication that the number of rays in the true gills has been diminished by more than one-half. Certainly in Cestracion there is no evidence of any reduction in the number of rays in the true gills.

II. It would seem that, if the paired limb had been derived in the way the gill-arch theorists maintain, there should remain in ontogeny some indication of the intermediate steps through which the gill passed while becoming a fin. That no such steps are known to occur in embryology, palæontology, or comparative anatomy is a very forcible argument against such an origin of the fins.

Fusions of gill rays resembling somewhat by their branching structure the basalia and rays of a fin have been described in sharks (Braus '04). However, the only cases of this kind thus far made known have occurred in the hyoid arch, and even the most sanguine adherent of the gill-arch theory would scarcely maintain that the hyoid is progressing in the direction of becoming a fin.

III. Because both the spinal and the visceral (trapezius) muscles attach to the dorsal end of the pectoral arch, we are hardly justified in supposing that the one is abstracting it from the other. Yet on this basis the gill-arch theorists assume that the anterior spinal muscles not only deprived the branchial region of the pelvic arch but passed it over to their neighbors and proceeded to abstract another. Why this kleptomania should have been satiated with two arches, while half a dozen yet remained, does not appear.

If the above assumption were true, it might indeed make a strong argument for the gill-arch origin of the paired limbs, but that it is without foundation appears in the light of the following facts in selachian embryology:

(1) As we have shown, the pectoral girdle is differentiated from a thickening of mesenchyme cells which grows inward from the region of the epidermis.

(2) According to my observations on Cestracion and Spinax, the first anlage of the pectoral fin is situated entirely ventral to the place of origin of the trapezius muscle, and it is by the later growth of both these structures that they finally come into contact. The connection must, therefore, be interpreted as secondary.

(3) The pectoral girdle of Cestracion as it develops moves toward the gill region. When it first appears, the scapular portion of the girdle is separated from the last gill arch by a considerable space, but as development proceeds the girdle and the arch approach each other until the intervening space is eliminated. At first this space is fully twice as great as that between the gill arches; at 35 mm. it is half passed over, and at 60 mm. the arch and girdle are practically in contact. In the adult they overlap slightly.

There is, moreover, no evidence that gill arches may be

crowded or pushed out of the branchial region. It has, on the other hand, been proved that the sixth gill of Cestracion degenerated *in situ*, if the structures which Mrs. Hawkes ('05) describes are to be interpreted as the vestiges of a gill arch.

IV. First, as to time relations, it is important to note that all the other structures of the fin make their appearance in advance of the skeleton, and before the gill arches are differentiated. On the assumption that the fin has been formed out of a displaced gill, we should expect to find the skeleton developing in an outward direction and carrying with it the other structures which form the fin. But instead of this, the fin fold, with its muscle-buds, nerves, and blood-vessels, as well as the primitive support of the fin (the mesenchyme thickening), is well developed before the skeleton becomes evident. Moreover, the fin skeleton does not grow into the fin fold, for there is no disarrangement or shifting of parts as the skeleton appears, but the skeleton forms *in situ* by differentiation of the original mesenchyme support. This is just as it should be on the fin-fold theory, but exactly opposite to what would be expected on the gill-arch theory, if time relations stand for anything. The order of appearance, furthermore, is precisely as it is in the unpaired fins.

Second, with regard to place relations, we have already shown that the first rudiment of the pectoral arch is more ventral than that of the gill arch, that it is more external, and that in Cestracion at least it grows toward the gill region as it develops.

A number of arguments in favor of the fin-fold theory yet remain, and may be summarized as follows:

I. All fins of sharks arise as longitudinal folds of the epidermis.

II. The muscle-buds which give rise to the muscles of the fins originate exactly alike in both kinds of fins.

III. The nerves which supply the paired fins take their origin in the same way as those of the unpaired.

IV. The origin of the blood supply is alike in both kinds of fins.

V. The earliest support of the fins, a plate of thickened mesenchyme, is of the same character in paired and unpaired fins and arises in the same manner in both.

VI. The time, place, and manner of differentiation of the fin skeleton is similar in all the fins.

VII. The later growth of the fin fold and the constriction of the fin at its base are similar in paired and unpaired fins.

VIII. Fusions of rays, basalia, etc., occur sporadically as well as regularly in the fins of both categories.

IX. Fin spines are known in both kinds of fins.

X. Ceratotrichia or horny dermal rays are present in all the fins of sharks.

Examining the above arguments in the order given:

I. Whether or not the longitudinal folds which give rise to the fins have once been entirely continuous is a matter of no great consequence,—though it seems entirely possible from the evidence at hand that the fins may have been connected in their early history. Be that as it may there is no disputing the fact that all the fins of sharks, and indeed of practically all fishes (the only known exceptions are very rare and embrace forms of highly specialized development, *e. g.*, Lepidosiren, Gambusia), originate as folds of skin. It must be noted that these folds are always longitudinal. The gill membrane, which may be considered the homolog of the fin according to the gill-arch theory (since it contains the rays of the gill), is, on the other hand, vertical in origin. If time and place relations have any meaning in embryology we cannot avoid the conclusion that the most primitive ancestral fin was a fin fold. Add to this the evidence from the oldest fossil sharks (Pleuropterygidæ, Acanthodidæ, and Diplacanthidæ) and we have a clear case.

II. The muscle-buds supplying the fins on the dorsal side of the body arise from the dorsal ends of the myotomes, while those supplying the fins on the ventral side, paired and unpaired alike, arise in exactly the same manner from the ventral ends of the myotomes. There is nothing in this process to indicate otherwise than that the fins have arisen *in situ* as outgrowths from the body wall.

III. The fins on the dorsal side of the body are supplied by branches of the dorsal rami of the spinal nerves, the same in character as those which supply the adjoining parts of the body, while on the ventral side, paired and unpaired fins alike, are similarly supplied with branches of the ventral rami.

IV. In the embryology of Cestracion I have carefully followed the development of the blood supply in both kinds of fins. In every case the blood-vessels are those which also supply the adjoining body wall, and which take their origin as dorsal branches of the dorsal aorta, or, in other words, are typical body-wall blood-vessels.

V. The earliest support of the fins, paired and median alike, is, as we have already stated, a dense or thickened mesenchyme. The thickening in all cases begins next to the ectoderm and becomes noticeable immediately after the fin fold makes its appearance. As growth progresses this denser mesenchyme extends inward until it occupies all of the region in which, later on, the fin skeleton is formed. The procartilage is differentiated right in place out of the mesenchyme support, and later becomes chondrified to form the cartilaginous skeleton. This sequence in development is just what the fin-fold theory would lead us to expect, and it seems altogether probable that such has been the phylogenetic history of the supporting structures of the fins.

VI. In Cestracion the first indication of the formation of the skeleton is seen in the region near the middle of the fin, and the bases of the rays and the adjoining portions of basalia appear at the same time and are the first structures to be observed. The differentiation spreads in all directions, and the girdles, in the case of the paired fins, appear very rapidly. In the unpaired fins the process is identical, except for the girdles. We must insist upon the fact that the rays do not "grow out" of the basalia but that both structures are differentiated in the same way out of the same mesenchyme plate. Similarly the girdles do not grow out of the basalia, nor *vice versa*.

VII. As we have seen, the fin fold originates in precisely the same way in paired and unpaired fins. The process of further development is also similar in both. The base of the fin grows relatively slowly, while the body is elongating and the external part of the fin fold is pushing out very rapidly. This results in a concentration of the fin base, in the manner described by Mollier ('93) for the paired fins. The median fins pursue a similar course, though usually the process is not carried to such a degree. The shape taken by the fins during development

depends upon what Mollier has termed their "direction of growth." The amount of constriction at the base of the fin is presumably measured by the amount of mobility required of the fin.

VIII. The so-called "fusions" of rays and basalia, which, in reality, are merely failures to differentiate separately out of the mesenchyme and are not due to the growing together of parts, may occur at any part of the fin skeleton, but according to my observations made on many preparations as well as on data provided by the plates of various authors, they occur much more commonly at or near the ends of the series of rays. It would seem that mechanical conditions would naturally be most effective in producing them here. The mode of formation of these "fusions" and the manner of their occurrence, both of which are similar in all fins, lead us to conclude that they are of one kind with the larger basalia and that all such sporadic as well as regular cases are produced in adaptation, i. e. to meet the mechanical needs of the particular fin in which such structures occur.

IX. While spines are not found in the paired fins of modern sharks, they are to be found in those of some of the oldest fossil forms (Diplacanthidæ and Acanthodidæ, also Gyracanthus, Haplacanthus, and Heteracanthus). This shows the very similar nature and potentiality of the two kinds of fins at a very remote period,—Upper Silurian and Devonian.

X. Horny fin-rays or ceratotrichia are very characteristic structures of the fins of sharks and occur nowhere else in the body. The importance of these structures in phylogeny has recently been discussed by Goodrich ('04) who finds them to be very ancient and very conservative. They occur alike in the paired and unpaired fins of all sharks, even the most ancient. (Goodrich's failure to find the ceratotrichia in the paired fins of Cladoselache can be attributed only to insufficient material, for an examination of the many specimens in the American Museum of Natural History proves their presence beyond a doubt.) As these structures occur equally in every respect in all the fins, and develop in the same way and at the same relative time, they may be taken to indicate a community of origin for all of the fins.

When we consider the facts derived from embryology, anatomy, and palæontology which are arrayed in the preceding pages, the conclusion is borne in upon us that the paired and unpaired fins are primarily similar structures, and the evidence from the present investigations is overwhelmingly in favor of the origin of all fins as local outgrowths from the body wall.

Columbia University, New York City,
March 28, 1906.

LITERATURE REFERRED TO.

Balfour, F. M.

'78. *Monograph on the Development of Elasmobranch Fishes.* London, 1878.

Braus, H.

'98. Ueber die Extremitäten der Selachier *Verh. Anat. Gesellschaft.* Apr., 1898.

'04. Tatsächliches aus der Entwickelung des Extremitätenskelettes bei den niedersten Formen. *Häckelfestschrift (Jenaischer Denkschriften XI)*, Jena, 1904.

Bunge, A.

'74. Ueber die Nachweisbarkeit eines biserialen Archipterygium bei Selachiern und Dipnoern. *Jena. Zeitschr. für Naturwissenschaft*, Bd. VIII, Jena, 1874.

Davidoff, M. von

'79. Beiträge zur vergleichenden Anatomie der hinteren Gliedmassen der Fische. *Morph. Jahrb.*, V, 1879.

'80. Ueber das Skelet der hinteren Gliedmassen der Fische. *Morph. Jahrb.*, VI, 1880.

Dean, B.

'02. Biometric Evidence on the Problem of the Paired Limbs of the Vertebrates. *Am. Naturalist*, Vol. XXXVI, 1902.

Dohrn, A.

'83. Studien zur Urgeschichte des Wirbelthierkörpers, VI. *Mitt. Zool. Stat. Neapel*, V.

'02. Studien zur Urgeschichte des Wirbelthierkörpers, XXII. *Mitt. Zool. Stat. Neapel*, Bd. XV, 1902.

Fürbringer, M.

'96. Extremitäten Theorie. *Festschrift für Gegenbaur, III.*, Leipzig, 1896.

'02. Morphologische Streitfragen. *Morph. Jahrb.,* XXX, 1902.

Gegenbaur, C.

'65. Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. 1. Schultergürtel der Wirbelthiere. 2. Brustflosser der Fische. Leipzig, 1865.

'70. Ueber das Skelet der Gliedmassen der Wirbelthiere in allgemeinen und der hintergliedmassen der Selachier insbesondere. *Jena. Zeitschr.,* V, 1870.

'95. Das Flossenskelet der Crossopterygier und das Archipterygium der Fische. *Morph. Jahrb.,* Bd. XXII, 1895.

Goodrich, E. S.

'04. On the Dermal Fin-rays of Fishes, Living and Extinct. *Quart. Journ. Microscop. Sci.,* March, 1904.

Hawkes, O. A. M.

'05. The Presence of a Vestigial Sixth Branchial Arch in the Heterodontidæ. *Journ. Anat. and Physiol.,* Vol. XL, 1905.

Kerr, J. G.

'99. Hypotheses as to the Origin of Paired Limbs of Vertebrates. *Proc. Cambridge Philos. Soc.,* X, Pt. IV, 1899.

Kükenthal, W.

'88. Ueber die Hand der Cetaceen. *Anat. Anzeiger,* 1888.

Mayer, P.

'86. Die unpaaren Flossen der Selachier. *Mitt. Zool. Stat. Neapel,* VI, 1886.

Mivart, St. Geo.

'79. Notes on the Fins of Elasmobranchs, with Considerations on the Nature and Homologies of Vertebrate Limbs. *Tr. Zoöl. Soc.,* London, X, 1879.

Mollier, S.

'93. Die paarigen Extremitäten der Wirbelthiere. *Anat. Hefte*, 1893.

Osburn, R. C.

'06. Adaptive Modifications of the Limb Skeleton in Aquatic Reptiles and Mammals. *Annals, N. Y. Acad. Sci.*, Vol. XVI, Pt. 3, March, 1906.

Punnett, R. C.

'00. On the Formation of the Pelvic Plexus, with Especial Reference to the Nervus Collector in the Genus Mustelus. *Phil. Trans. Royal Soc. of London*, Vol. 192, 1900.

'04. Merism and Sex in *Spinax niger*. *Biometrika* Vol. III, No. 4, 1904.

Rabl, C.

'01. Gedanken und Studien. *Zeitschr. Wiss. Zool.*, Bd. 70,1901.

Regan, C. Tate

'04. The Phylogeny of the Teleostomi. *Annals and Magazine Nat. Hist.*, 1904.

Ruge, E.

'02. Die Entwickelungsgeschichte des Skeletts der vorderen Extremität von *Spinax niger*. *Morph. Jahrb.*, Bd. XXX, 1902.

Symington, J.

'06. Observations on the Cetacean Flipper, with Special Reference to Hyperphalangism and Polydactylism. *Journ. Anat. and Physiol.*, Vol. XL, Pt. 2, 1906.

Thacher, J.

'77. Median and Paired Fins. A Contribution to the History of Vertebrate Limbs. *Tr. Connecticut Acad. Sci. and Arts*, III, 1877.

Wiedersheim, R.

'92. Das Gliedmassenskelett der Wirbelthiere mit besonderer Berichtsichtigung des Schulter- und Beckengürtels bei Fischen, Amphibien und Reptilien. Jena, 1892.