

OBSERVATIONS ON THE ORIGIN OF THE PAIRED LIMBS OF VERTEBRATES.

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WITH 5 PLATES.

Perhaps in no field of Vertebrate zoölogy have two diametrically opposite views been more steadily and skillfully maintained than in that which forms the subject of the present paper. Disregarding the earlier speculations in regard to the origin of the paired limbs, we may date the real work in this field from the appearance of Gegenbaur's first paper on the subject in 1865. This prolific student adopted the earlier suggestion of Owen that the limb girdles correspond to misplaced gill-arches and proceeded to defend this view with such vigor and resource that it was for many years the accepted hypothesis. At the same time the unpaired fin skeleton was held to be a derivative of the axial skeleton. These views were steadily maintained by Gegenbaur through thirty years of investigation, indeed, up to the appearance of his last paper on the subject in 1895. His students have also contributed much to the support of the hypothesis.

Opposed to the gill-arch theory (Gegenbaur theory, archipterygium theory) is that known as the fin-fold, or lateral-fold theory, which postulates a similar origin for the paired and unpaired fins as local outgrowths from the body-wall, independent of gills, axial skeleton, or any other structures. This view was first developed in the researches of Thacher, 77, Balfour, 78, and Mivart, 79, all working independently, and has become pretty generally accepted by zoölogists, other than those of the Gegenbaur school. Very much has been added to the support of the theory since it was first propounded, but, in spite of the exploitation of anatomical, palæontological, and embryological fields there have always remained numerous ambiguous points, the interpretation of which depended on the attitude with which they were approached. That the problem was not fully settled by the older investigators witness at least

a dozen papers dealing more or less directly with its various phases appearing since 1900.

The work of the gill-arch theorists has been confined chiefly to drawing comparisons between the skeleton of the paired limbs and that of the gills, to studying the possibilities of migration in the paired fins, and to searching for connecting stages between the branchial and pectoral regions. But the study of the unpaired fins they have almost ignored. The studies of the fin-fold theorists, on the other hand, have been particularly directed toward the similarities between the median and paired fins and have aimed to prove the local and metameric development of the paired limbs. To the fin-fold theory the chief obstacle has been the fact that the paired limbs possess girdles while the median ones do not, a difficulty which the adherents of the gill-arch theory have considered insurmountable. For the latter theory the most important stumbling-blocks have been: the lack of any intermediate stages between gill and fin, the absence of proof of migration sufficient to account for the position of the pelvic fins, and the difference in position between the gill-arch in the gut wall and the fin girdles in the body-wall.

The various fields of anatomy, palæontology, and embryology have all been gleaned by various investigators for evidence to bear upon the problem and all have proved fruitful, though lack of more complete knowledge has at times caused apparent conflicts. The anatomical side of the question has been most thoroughly worked and our knowledge of the facts may be said to be fairly complete. Unfortunately, however, anatomical evidence is not the most conclusive in the study of phylogenetic questions, and in the structures of the fins the adherents of both theories find what they consider good evidence in favor of their views.

Palæontological data would obviously be of inestimable value in deciding doubtful points, if not the entire problem, but the evidence from fossils may always remain fragmentary and even conflicting. The Cladodont sharks are without doubt the oldest fossil forms which give us any light on the structure of the limbs, and they agree in possessing a fin-fold type of fin. Cladoselache, from the Devonian, is particularly enlightening in this respect, but the gill-arch theorists have consigned Cladoselache to the limbo of an aberrant group (Braus, 04). On the other hand, the Permian Pleuracanthus, while regarded by the gill-arch theorists as convincing evidence on their side of the question, is rejected by the adherents of the fin-fold theory. There seems no absolute anatomical reason why the pectoral fin of the modern shark might not have been derived (by different methods, to be sure) from either the biserial

type of *Pleuracanthus* or the fin-fold type of *Cladoselache*, but the question is, from which did it evolve? In taking up this question we have to consider not only the type of fin but also the possibilities of the animal as an ancestor of modern sharks. While *Cladoselache* itself may not have been the progenitor of modern sharks, the group to which it belongs is of such a generalized type that, as Dean points out (95), almost any later group of fishes might have arisen from it. In fact, the *Cladoselachidae* approach more nearly to the ancestral condition of true fishes than any other group of which we have sufficient knowledge to form a judgment. This simplicity is coupled with an antiquity much greater than that of the *Pleuracanthidae*. In regard to the latter family it may be suggested that the nuchal spine, the condition of the dermal skeleton, the character of the two anal fins, and the diphyccercal caudal fin, remove it at once from our consideration as a possible ancestor of any known type of fish. Concerning the diphyccercal caudal it is worthy of remark that all the oldest fishes known (*Pleuropterygidae*, *Acanthodidae*, and *Diplacanthidae* among the sharks, the most ancient *Dipnoi* and *Ganoidei*, as well as the fish-like *Heterostraci*, *Anaspida*, *Antiarcha*, and *Arthrodira*, all older than the *Pleuracanthidae*), had the heterocercal condition developed, so that, as far as we are able to judge from palæontology, heterocercy seems to be the primitive condition in the gnathostomata. The diphyccercy of *Pleuracanthus* must then have been secondarily acquired, as it seems to have been in the *Dipnoi* (Dollo, 92, 93). Therefore, taking into consideration all the facts concerning these two ancient types of fishes, and bearing in mind that the *Acanthodidae*, *Diplacanthidae*, and *Pleuropterygidae* (all much older than the *Pleuracanthidae*), agree in having a fin-fold type of fin, we are led to believe that the evidence from palæontology is distinctly favorably to the fin-fold theory. It may be well to add here that even if the *Pleuracanthus* type of fin were proved to be primitive the branchial origin of the fins would still be unproved, for the fins of *Pleuracanthus* are no more gill-like than those of modern sharks. It would not at all preclude the possibility of the local origin of the fin structures, which is after all the most important contention of the fin-fold theorists.

In regard to the embryological evidence it may be remarked broadly that the recent investigations tend to show that in early development there is scarcely a point in which the paired and unpaired fins are not in perfect agreement. The only important exceptions, the girdles and the trapezius muscle, have, I believe, a satisfactory explanation as secondary rather than primary characters. It was the original intention of the

writer in taking up the present studies, to discuss thoroughly the embryological work on the origin of limbs, but the recent able papers of Professor Braus, though taking an opposite view of the question, have dealt so thoroughly with the literature as to make such a discussion no longer necessary. In May, 1906, the writer paralleled the arguments of the fin-fold and gill-arch theorists as a preliminary to the present paper. In the month following there appeared the admirable paper of Professor Goodrich, 06, in which he arrives at conclusions very similar to my own, based chiefly upon a study of *Scyllium*. The present writer has examined especially *Cestracion* and *Chlamydoselachus*. However, under the belief that embryological evidence from the last two forms mentioned should have special consideration on account of their primitive position among the genera of *Selachii*, and for the reason that certain heretofore unpublished facts have been brought to light during the pursuit of my studies, the publication of my results seems desirable.

I may state at once that as far as my own studies overlap those of Goodrich they are entirely corroborative of his work, and where they do not cover the same ground they are quite confirmatory of the fin-fold point of view. It should be said that our work was carried on in parallel lines and without any knowledge of the other's research. This, in itself, must add weight to our results. As will be seen, the evidence indicates strongly that the unpaired fins have originated as external structures entirely independent of the axial skeleton, and the remarkable similarity of the paired to the unpaired fins in mode of development can only be explained on the ground of similarity of origin. The failure of Braus, 04a, to find in *Spinax* any marked similarity between these fins is explicable only under the supposition that he did not make a careful comparison of the earlier stages in the development of the various component structures of these organs, or that he did not possess the proper material for such comparison. As a matter of fact, the unpaired fins of *Spinax* are very much concentrated (the anal is entirely wanting) and the early stages of development seem to be passed through much more rapidly than in *Cestracion*, though the dorsal fins of the latter species seem, in the adult, to show nearly as much concentration as those of *Spinax*.

Zoölogists generally agree in holding that the sharks approach more nearly than any other group the original condition of the gnathostome vertebrates, and it is to this group that we naturally look for embryological evidence bearing on the origin of the paired limbs. Naturally, also, we look for the best embryological evidence as to the origin of fins among those sharks which on anatomical and palæontological grounds

are to be regarded as most primitive. In this respect the writer has been most fortunate in having at his disposal a very complete series of embryos of the cestraciont shark *Heterodontus japonicus* Duméril,¹ and a number of embryos of the Notidanid shark *Chlamydoselachus anguineus* Garman, 85-86. Together with this material I have had for comparison many stages of *Spinax*, *Mustelus*, and *Torpedo*. Professor Bashford Dean has very generously placed this valuable material at my disposal, and I am indebted to him also for many kind suggestions and criticisms.

Certain observations have been made by various students of the fins and corroborated to such an extent that they may be considered as points definitely settled in selachian embryology, especially since they are not disputed by the followers of either the gill-arch or the fin-fold theory. Such are:

I. Each fin at its inception consists of a longitudinal fold of the epidermis. This has been observed by all students of shark embryology from Balfour, 78, down to the present. It may be added that the same observation holds almost universally among fishes, the few exceptions being among Teleosts whose limb structures we have reason to believe are highly specialized.

II. This fold of the epidermis is soon invaded by mesenchyme cells which establish a dense plate or mass of cells (mesenchyme plate or mesenchyme thickening) lying partly within the epidermal fold and partly within the body-wall. (Balfour, 78, 81; Dohrn, 84; P. Mayer, 86; Mollier, 93; Rabl, 97, 01; Braus, 04b, and others.) So much at least is beyond question. The exact origin and fate of the mesenchyme plate will be discussed later.

III. The fin-fold with its mesenchyme plate is next provided with segmentally arranged muscle-buds from the dorsal and ventral ends of the neighboring myotomes. This ingrowth in the paired fins is similar to that in the median fins. (Balfour, 78, 81; Dohrn, 84; P. Mayer, 86; Mollier, 93; Rabl, 97, 01; Braus, 98, 04a; Goodrich, 06, and others.)

IV. In the embryonic fin, whether paired or unpaired, there are abortive muscle-buds which degenerate without entering the fin. These are found in the posterior as well as in the anterior margin of the fin. In the paired fins these rudiments have been traced by Dohrn, 84; Mollier, 93; Braus, 98; Rabl, 01, and Goodrich, 06, and in the median fins by Dohrn, 84; Paul Mayer, 86, and Goodrich, 06.

V. The most anterior and most posterior muscle-buds which enter the

¹Throughout this paper *Heterodontus* is referred to as Cestracion, the older name by which the genus is usually known among morphologists.

fins, paired and unpaired alike, are compelled to reach out of a direct position (*i. e.*, out of the transverse plane of their myotomes) in order to get into the fin-fold. That is to say, the fin base is shorter at this period than the combined length of the myotomes concerned in supplying muscle-buds to the fins. This condition has been carefully discussed by Mollier, 93; Braus, 98, and Goodrich, 06, in the paired fins, and by Paul Mayer, 86, and Goodrich, 06, in the case of the unpaired fins. The writer has also observed it to be true for *Cestracion* and *Spinax* in both paired and median fins, 06b.

VI. The nerves which supply the paired and unpaired fins arise segmentally in the same manner as external rami of the dorsal and ventral branches of the spinal nerves. (Balfour, 78, 81; P. Mayer, 86; Mollier, 93; Braus, 98, 01; Osburn, 06b; Goodrich, 06.)

VII. The blood-vessels which supply the various fins all arise in a similar manner. They are all branches of body-wall blood-vessels which take their origin on the dorsal side of the dorsal aorta.

VIII. The procartilaginous anlage of the fin skeleton arises in the same way in all fins, differentiating out of the mesenchyme plate; and, when basals are present, as in the paired fins of all sharks and the dorsal and anal fins of many, the rays and basals (and the girdle in the paired fins) form one continuous structure. (Balfour, 78; Mollier, 93; Ruge, 02; Braus, 04a; Osburn, 06b; Goodrich, 06.)

IX. As the continuous procartilaginous anlage of the fin skeleton becomes differentiated into cartilage, the formation of joints takes place (Ruge, 02), with the result that the elements of the adult fin are defined. The process is identical in all the fins, but the amount of separation varies greatly according to the species, depending probably upon adaptation, *i. e.*, as to the special way in which the fin comes to be used.

X. The sequence of development of the various structures entering into the formation of the fin is the same in all cases, viz.:

- (a) The epidermal fold is raised.
- (b) The mesenchyme pushes its way into the fold and forms the mesenchyme thickening.
- (c) The muscle-buds migrate into the fins accompanied by their respective branches of the spinal nerves.
- (d) The continuous procartilaginous anlage of the fin skeleton becomes differentiated *in situ* out of the thickened mesenchyme (this includes also the girdles of the paired fins).
- (e) The chondrification of the skeleton takes place, with the formation of joints and the consequent separation into skeletal elements.

XI. Collector nerves and plexuses are known to occur commonly in both paired and unpaired fins, and, though usually more marked in the anterior margin of the fin, they are of frequent occurrence in the posterior as well. (For the paired fins, Davidoff, **79**; Mollier, **93**; Punnett, **00**, **01**; Braus, **98**, **04a**; for the unpaired fins, P. Mayer, **86**; Goodrich, **06**.)

XII. The bases of the paired fins and of the dorsal and anal fins become concentrated during development. (Mayer, **86**; Mollier, **93**; Goodrich, **06**.) This is least marked in the case of the caudal fin and most marked in the pectoral fins, and between these extremes there exist all intergradations in anal, dorsals, and pelvics. Measurements show that the base of the pelvic fin of *Chlamydoselachus* is comparatively longer than that of the dorsal fins of *Cestracion* or *Spinax*.

XIII. All types of fins may migrate or be displaced during development. Such migration is always of slight degree, though often measurable, and may be in either direction (Dean, **02**; Punnett, **04**).

XIV. Ceratotrichia, or horny rays of the fins, develop in both paired and unpaired limbs and occur in no other part of the body. They are equally ancient in either type of fin (Goodrich, **03**; Osburn, **06b**), and appear at about the same time in ontogeny (Goodrich, **03**).

The foregoing points may be considered as already decided. Upon the points which are still under consideration, the writer desires to present the following data and discussion:

FUSION OF MUSCLE-BUDS.

Muscle-buds may fuse during their early development in the unpaired as well as in the paired fins. Such fusion or blending was first described and figured in the pectoral of *Torpedo* by Mollier, **93**. Later, Fürbringer, **02**, and Braus, **04a**, used this fact, in opposition to the fin-fold theory, as evidence against the metamerism of the adult muscles of the paired fins, and so, also, of the corresponding skeletal rays. My own work on *Cestracion*, however, shows that fusion of muscle-buds is not confined to the paired fins, but, on the contrary, may occur in any of the unpaired fins. Hence, as I have already indicated, **06b**, any argument against the fin-fold theory based on such ground is altogether futile. In *Cestracion* fusions were found in all of the unpaired fins,—even in the caudal, though more sparingly here,—and the nature of the blending is exactly similar to that in the paired fins. Fig. 17 shows such a fusion in the anal fin of a 35 mm. *Cestracion* embryo. A comparison with Mollier's figure (**93**, Taf. III, Fig. 15) of this condition in

the pectoral of *Torpedo* will indicate the similar nature of the fusions even in such distantly related forms.

As to the later fate of these blended muscle-buds there remains yet some uncertainty. Fürbringer, **02**, and Braus, **04a**, have maintained that from the time of fusion of the buds the muscles are dysmetameric and their innervation polyneurous. This supposition as to the secondary polyneury of the paired fins is by no means borne out by the recent experiments of Goodrich, **06**. The latter investigator has tested physiologically the exact distribution of the branches of the spinal nerves which enter the fins, and he finds that in *Raja* each motor nerve is distributed to one and only one radial muscle, and that under stimulation there is no spreading of the impulse such as would be the case if polyneury existed. The confused plexus at the base of the fin must then, as Goodrich observes, embrace only the sensory nerves, while the motor nerves pass through the plexus without losing their individuality. The muscles after fusion must, therefore, again separate without losing their haplo-neurous condition, at least as far as the motor nerves are concerned.

Goodrich has even ventured the suggestion (**06**) that this fusion is not a fusion of muscle-buds involving embryonic muscle-tissue at all, but that what has been supposed to be such a blending is merely the anlage of the sensory nervous system which, arising in this region, gives the appearance of the fusion of muscle-buds. We cannot subscribe to this opinion, however, for, by actual observation, the muscle-buds at an early stage may be seen to be in contact and that with such clearness as to leave no doubt as to the interpretation. Such fusions are of frequent, but very irregular, occurrence in *Cestracion*, and there is no apparent order in their arrangement. They are most abundant in the anal fin in which the adult muscles are blended into a confused mass, and rarest in the caudal where the muscles of the adult are very regularly arranged. Moreover, blended muscles certainly do occur in the older embryo (Fig. 18, of the condition in the second dorsal fin of a 58 mm. embryo of *Cestracion*), and remain blended in the adult. In this case the bases of the muscle-bands no doubt remain fused because of the great amount of concentration at the base of the fin. The condition in the anal is similar, only carried much farther in concentration.

How are these fusions to be explained? Not, as Braus, **04a**, concludes, for the purpose of accomplishing the polyneury of the fin muscles, since Goodrich's experiments show that the muscles are not so innervated; and not, as Goodrich, **06**, suggests, that the apparent fusions are rudiments of the developing sensory nerve plexus, for blending actually

occurs and remains in the adult. Rather they seem to the present writer to represent accidental points of contact of neighboring muscle-buds which in their embryonic condition fuse merely because of the juxtaposition of similar cells, and which may later become separated by the growth of intervening connective tissues forcing the muscles farther apart, and by the development of the embryonic muscle-cells into fibers.² As we have seen, they sometimes remain in contact. That these fusions are merely accidents of development is indicated by the fact of their sporadic and variable occurrence. They do not occur between the distal ends of the muscle-bands where they are farther separated, they are most abundant where muscle-buds are crowded together (*e. g.*, anal of *Cestracion*), and least abundant where there is least crowding (*e. g.*, inferior caudal of *Cestracion*). In the paired fins they are most abundant near the ends of the series of muscles and they are sometimes entirely wanting between the buds at the middle of the fins. Moreover, there is no uniformity in the extent of the fused portions.

DISCREPANCIES BETWEEN MUSCLES AND CARTILAGINOUS FIN RAYS.

Discrepancies between the muscles and cartilaginous fin-rays with regard to arrangement may be present in unpaired as well as paired fins. Braus, 04a, first carefully worked out the discrepancy as it exists in the pelvic fin of *Spinax*, and he at once interpreted it as an argument against the origin of the paired fins as metameric structures. That such discrepancy may exist in the paired fins is probably beyond question. This condition, however, it now appears, is not confined to the paired fins and therefore the fact does not bear against the fin-fold theory, since the median fins, which show an equal amount of discrepancy, are by the gill-arch theory assumed to be strictly metameric in origin. Fig. 15 shows this discrepancy in the second dorsal fin of a 53 mm. embryo of *Cestracion*. It is in all respects similar to that which Braus figures in the pelvic of *Spinax* (04a, Taf. XIV), and is of even greater extent.

If we inquire into the cause of such discrepancy as above indicated I am convinced that sufficient reason can be found in the adaptation of the fin to meet the greatest mechanical needs. This explanation is given weight by the variation shown by different fins in the degree of concordance they exhibit. In some cases which I have examined,—*e. g.*, the pectoral of *Raja* and *Cestracion*, the anal and pelvic of *Chlamydoselachus*,

² A somewhat analogous process is found in the reopening of a portion of the Amphibian blastopore in the formation of the anus.

and the inferior caudal of most sharks,—there is a very close correspondence or concordance throughout the fin. In certain cases,—*e. g.*, the pelvic of *Spinax* (Braus) and the dorsals of *Cestracion*,—there is a concordance over a large portion of the fin and discrepancy over the remainder, while in the anal fin of *Cestracion* it would be a difficult matter to trace any exact concordance between the cartilage plates of the fin skeleton and the broad sheet of muscle derived from the intimate fusion of the muscle-buds. Thus, instead of weighing against the fin-fold theory, the facts of discrepancy only point more certainly to the close relationship between the paired and median fins.

MODE OF ORIGIN OF THE FIN SKELETON.

The origin of the mesenchyme cells which first occupy regions of the body in which the fins are later to be developed is already well known, thanks to the researches of Balfour, 78, 81; Boyer, 92; Rabl, 91, 97, and Mollier, 93. The concentration or thickening of this mesenchyme which gives rise to the fin skeleton begins in all fins just beneath the ectoderm at about the same time as the uplifting of the ectoderm to form the fin-fold. Figs. 1, 3, 4, and 5, show it in various fins. From this position the concentration extends outward with the growing fin-fold and inward until it covers all the region which the fin skeleton later occupies. The skeleton is derived from this concentrated mesenchyme,—not only the more externally situated fin-rays but also the basalia of the median and paired fins and the girdles of the latter as well. The change takes place by the direct differentiation of the mesenchyme tissue into the continuous procartilaginous anlage of the skeleton, and this later, by chondrification, becomes the definitive skeleton. In this process there are no topographic changes, the formation of joints taking place *in situ*. The concentration of the mesenchyme is from the first easily distinguishable from that which develops into the ordinary connective tissue. Figs. 1 to 6, inclusive, illustrate the difference in the appearance of the two kinds of cells. There can be no doubt that, ontogenetically, the earliest support of the fins in all cases is this concentrated mesenchyme which makes its appearance in and beneath the fin-fold long before the muscle-buds and nerves enter, and which becomes directly differentiated into the cartilaginous skeleton of the adult fin. There seems, therefore, no good reason for thinking that the evolution of the fin has followed any other course than this during its phylogeny.

THE INFERIOR CAUDAL FIN.

It is important to observe that the inferior caudal fin of *Cestracion* in its earlier stages agrees exactly with the other unpaired fins. This particular fin has always been a point of contention among students of the limb problem, since in the development of the definitive skeleton the rays in most cases arise in direct connection with the hæmal spines of the axial skeleton, while in no other fin of any fish are the rays known to arise in this connection (with the one exception of the superior or epichordal portion of the diphyccercal caudal fin of *Lepidosiren* (Braus, **04a**, **04b**), the most highly specialized of the Dipnoi). There can be but three views in regard to this difference: 1st, The inferior caudal may be considered to have had an entirely different mode of origin from the other fins; 2d, it may be looked upon as the type of all the unpaired fins under the supposition that the others have lost their connection with the axial skeleton; or, 3d, that the connection of the rays of this fin with the axial skeleton has come about secondarily. Balfour and Parker, pioneers in vertebrate embryology adopted the first view, but no one since their time has suggested it. The second view has been adopted by the adherents of the gill-arch theory, following Gegenbaur's assertion that the cartilages of the dorsals are only modified spinous processes, "losgelöste und selbständiger gewordene Dornfortsätze." Professor Braus attempts (**04a**) to support this hypothesis by the observation on the superior caudal fin of *Lepidosiren* already alluded to, making this dorsal connection an intermediate step between the inferior caudal and the dorsals. This sort of argument seems to us hardly warranted when the high specialization of *Lepidosiren* and the wide phylogenetic gap separating the modern Dipnoi from the Selachii are considered. The third view, viz., that the unpaired fins have all had a similar, external origin, and that the inferior caudal has become secondarily attached to the axial skeleton for mechanical reasons, is the one adopted by the fin-fold theorists. This view was advanced by Dohrn, **84**, and strongly supported by Paul Mayer, **86**, who found in the anterior part of the inferior caudal fin the evidence of a separate origin of the rays of this fin,—“ferner wäre vom Knorpel noch zu bemerken, dass er wie bei allen anderen Flossen erst secundär mit der Wirbelsäule in Verbindung tritt.” Now, *Cestracion*, at an early stage in the development of the inferior caudal, offers a very striking confirmation of the view that this fin has arisen in an external manner similar to the other unpaired fins. Fig. 3 shows a section through the fin at a time when the mesenchyme plate from which the fin rays develop is entirely separated

from the region of the axial skeleton. The latter, moreover, has not at this stage become noticeable in the region of the hæmal spines. The mesenchymè of the fin continues to develop toward the axial region while that of the latter becomes more concentrated and at last the two regions are united. When the rays become evident by the differentiation of the mesenchyme they arise *in situ* and do not grow out³ of the hæmal spines. The same statement holds good for the development of the rays and basals of all fins, paired and unpaired,—all arise by differentiation in their proper position from the mesenchyme plate.

The other unpaired fins not only resemble the inferior caudal in having an external origin for the mesenchyme plate, but they never originate in contact, much less in continuity, with the axial skeleton. In case spines are present, as in *Spinax*, *Cestracion*, etc., the spine secondarily comes into contact with the vertebral column for support. That this attachment is secondary is admitted even by the gill-arch theorists. Species, among the lower sharks, which do not possess fin spines usually have the fin skeleton widely separated from the axial skeleton (*Notidanus*, *Chlamydoselachus*, *Mustelus*, *Scyllium*, *Lamna*, etc.). Figs. 19 and 16 are camera drawings from Van Wijhe preparations of the dorsal and anal fins of *Chlamydoselachus* showing the relation to the vertebral column in an embryo of 225 mm. In *Cestracion* the large basale of the anal fin comes nearly or quite into contact with the ends of the hæmal spines. A study of the development of this form, however, shows plainly that the basale in question arises earlier than, and entirely independent of, the hæmal spines. Figs. 12 and 13 are camera drawings of vertical sections through the anal fin of a 40 mm. embryo, illustrating the independent origin of the fin skeleton.

PAIRED FINS CONTRASTED WITH GILLS.

The followers of Gegenbaur have always asserted the similarity of the paired fins to the gills, and recently K. Fürbringer, 03, and Braus, 04a, have renewed the attempt to compare these structures, the former ana-

³ As I have elsewhere (06b) pointed out, the terms "grow out," "auswachsen," etc., are entirely misleading when applied to the development of the fin skeleton. The muscle-buds may be rightly said to grow out into the fin, since by internal development the tip of the bud is moved forward. Its progress is marked by the disarrangement of the connective tissue and cells of the mesenchyme plate as the bud forces its way by such growth into its position in the fin. Figs. 5 and 6 illustrate this disarrangement and show how the cells are pushed out of the way. There is nothing comparable to this in the development of the fin skeleton since the rays elongate by the continued differentiation of mesenchyme cells at their ends.

tomically, the latter embryologically. The latter author, in particular, insists that as good a comparison can be drawn with the gills as with the unpaired fins and in the same points, viz.:

- " 1. Isolierte Radien.
- " 2. Basalia als ontogenetisch einheitliche Anlagen.
- " 3. Ausbildung uniserial angeordneter Radien: Monostichopterygium.
- " 4. Ausbildung biserial angeordneter Radien: Distichopterygium."

It may be true that such arrangements of skeletal parts are to be found in the gills as well as in the fins, but even in the skeleton the weight of evidence is against such comparison and when we attempt to carry it to the other structures all similarity ceases. The following points will serve to indicate on what a slender basis rests the comparison of gill with fin:

1. The concentration of mesenchyme cells which gives rise to the gill skeleton originates internally in contact with the pharyngeal endoderm and spreads outward, while that from which the fin skeleton arises originates externally in contact with the ectoderm and develops inward. Figs. 1 and 2 show this for the fins.

2. The paired and unpaired fins arise external to the blood system, *i. e.*, to the main blood-vessels, while the gill-arches lie internal to these (Fig. 7).

3. The paired and unpaired fins are external to the coelom, the gill-arches internal.

4. It is worthy of note that the structures in the branchial series which resemble the fin (the arch excepted) are confined to the hyoid whose function as a gill is somewhat degenerated, and the structures are unquestionably the result of concentration and reduction. But the hyoid arch with its appended structures is most certainly not becoming a fin, so of what avail is the comparison?

5. As shown elsewhere, the pectoral girdle, though somewhat similar in shape and position to the gill-arches, is not in series with them.

6. The radial structures of the gill are always arranged in a vertical series (this is equally true of those of the hyoid arch above mentioned), while those of both paired and median fins are always in longitudinal series.

7. The fin-fold, which is the earliest indication of the fin, in all cases extends longitudinally, *i. e.*, parallel with the axis of the body. The gill membranes arise in a vertical position, at right angles or nearly so to the body axis.

8. The muscles of the median and paired fins are in all respects similar in origin while those of the gills are entirely different.

9. The nerves which supply the paired and unpaired fins are of the same sort, all branches of the spinal nerves (that of the trapezius muscle excepted) while the gills are innervated entirely by visceral nerves.

10. The blood-supply of all the fins is the same in character, *i. e.*, all are supplied by those vessels which go to the body-wall of that particular region. In the pectoral fin at the earliest stage there is not the slightest indication of any other blood connection than that of the brachial artery. Fig. 14 shows the origin of this vessel in the manner characteristic of all arteries supplying the outer wall of the trunk region, in a young embryo of *Cestracion*, in contrast with the termination of the last efferent branchial artery.

11. *Ceratotrichia*, or horny fin-rays, are always present in both paired and unpaired fins of all sharks, even the most ancient (Dean, 94; Goodrich, 03; Osburn, 06b), and are unknown in gills.

FIN GIRDLES AND GILL-ARCHES.

The gill-arch theorists still maintain (Fürbringer, 02; Braus, 04a, 04b), as a necessary foundation stone of their theory, that the limb girdles are serially homologous with, and in every respect the counterpart of, the gill-arches. Let us examine this so-called serial homology. It is true that the pectoral girdle does originate close behind the gill region, and that in form it is similar, as any structure situated in the body-wall as the pectoral girdle is, must of necessity be arciform. But here the evidence in favor of the serial homology ceases. Examining the evidence on the negative side of the question, we find in the first place that the pectoral girdle makes its appearance quite ventral to the gill region. Braus's own figures of *Spinax* show that the anlage of the girdle is situated almost its whole length below the gill region (Braus, 04a, Fig. 1, Taf. XIII), and the accuracy of this illustration I can attest from my own studies on a 20 mm. embryo of *Spinax*, as well as from my *Cestracion* studies. Fig. 7 shows a camera drawing to the same scale, of a section through the fourth gill-arch and one through the pectoral girdle at an early stage of the latter before the dorsal portion makes its appearance. The dotted lines connect similar points. The contrast is obvious.

In the second place the more external position of the pectoral girdle prevents any homology with the gills. Fig. 7 illustrates this contrast. The gill-arch is in contact with the pharyngeal endoderm and is internal to the blood system while the pectoral arch comes into contact with the

ectoderm and lies not only external to the body cavity but also to the larger blood-vessels. This condition is continued into the adult where a portion of the last gill-arch is overlaid by the pectoral girdle.

MIGRATION OF THE PECTORAL ARCH.

The question of the migration of the paired limbs is a vital one for the gill-arch theory since the origin of the limb girdles from gill-arches involves their translation from the branchial region. That a certain amount of shifting of position may occur during the development of the paired fins no one will deny, but that the same sort of shifting may also occur in the growth of the unpaired fins is equally true. Such migration is always comparatively slight, and it may take place either forward or backward. Moreover, the shifting of the paired fins is correlated with that of the unpaired fins (Dean, 02; Punnett, 04) and with that of the center of gravity of the body of the developing embryo (Dean, 02). With regard to the supposed early backward migration of the pelvic described by Braus, 98, the writer has already (06b) suggested a different interpretation, and Goodrich, 06, has stated, as a result of careful observations on *Scyllium*, that the facts of development will not bear the interpretation given by Professor Braus. The abortive muscle-buds anterior to the pelvic fin cannot, then, represent the path over which the pelvic fin migrated to its present position, but, like those in front of and behind the unpaired fins and even behind the pelvic itself, they represent muscles which once functioned before the base of the fin became as constricted as in recent adult sharks. The attempt to explain the abortive muscle-buds behind the pelvic fin as due to a secondary forward migration of that member (Punnett, 00) is a *reductio ad absurdum* of the migration hypothesis. In their earlier appearance the anterior abortive muscle-buds merely follow the law of all such serial structures of the body, in that the most anterior are the first to arise.

The presence of a collector nerve in the anterior part of the pelvic fin cannot be considered as evidence of migration of the fin since such structures are now known to occur in the posterior part of the same fin and in the unpaired fins, both posteriorly and anteriorly. (Cf. Mayer, 86; Punnett, 00; Braus, 04; Osburn, 06b; Goodrich, 06.)

Forward migration of the pectoral fin.—By the biometric study of a very complete series of embryos of *Cestracion*, Dean in 02 showed that the pectoral fin as a whole shifts forward during development, instead of backward as the gill-arch theory would require. The present writer has investigated the internal structures of the pectoral fin in this form and

finds the shifting concerns not only the distal portion but that even so deep-seated a structure as the pectoral girdle is involved in the forward migration. Fig. 8 shows the relation of the pectoral girdle to the last two gill-arches at the time of the first differentiation of the dorsal part of the girdle from the mesenchyme into procartilage. Figs. 9 and 10 show later conditions in embryos of 35 mm. and 53 mm., respectively. A comparison of these figures shows that at its earliest appearance the girdle is removed from the gill region by a space much greater than that which separates consecutive gill-arches, and that as development proceeds the space is gradually lessened. In the adult *Cestracion* the girdle and last gill-arch have shifted past each other to the extent that a portion of the gill-arch lies internal to the girdle. Could any further evidence be desired to disprove at once the hypotheses of the serial homology of these structures and of the origin of the paired fins by migration? One more point, however, demands our attention.

The trapezius muscle.—This muscle, which is derived from the visceral musculature and is supplied by visceromotor nerves, is attached to the anterior surface of the scapular portion of the pectoral arch. With this sole exception, all the muscles of the fins, paired and unpaired, are derived from myotomes and innervated by spinal nerves. This one exception, however, has been the occasion of much controversy, for it is considered by the adherents of the gill-arch theory to be a relic ("Die alten Relikte des einstmaligen Kopfmuskelversorgung," Fürbringer, 02) of the former visceral muscle supply of the pectoral arch when it was a gill-arch and before it was abstracted from the branchial region (according to the hypothesis) by the action of the spinal muscles (Fürbringer, 02; Braus, 04a). From the contrast which we have already drawn between the gills and fins it is evident that such an explanation of the trapezial connection is not the correct one. But, aside from such inference, I think we can prove the case on its own merits. The studies of E. Ruge, 02, and Braus, 04a, showed that in *Spinax* the first anlage of the pectoral girdle consists of the ventral portion only, from the region of the fin downward, and that the dorsal or scapular portion appears later. This I have been able to confirm in *Spinax* and to determine also for *Cestracion* (Fig. 7). Now, it is important to note that the trapezius muscle is attached to the dorsal or scapular part of the girdle while the ventral portion lies entirely within the region of somatic muscles. Furthermore, at the time when the scapular part of the girdle appears the trapezius has not yet grown backward from the branchial region to its point of attachment with the girdle, but a little later grows down and

comes into contact with it. In short, the first anlage of the pectoral girdle is wholly situated within the domain of somatic muscles and the trapezial connection is accomplished later by the dorsal growth of the girdle and the postero-ventral growth of the muscle. If the time element is at all trustworthy here (and we must believe so until it is proved otherwise) the above facts can only be interpreted to mean that the ventral portion of the girdle is more primitive than the dorsal, and, if this is true as the development indicates, then at one time the pectoral girdle consisted only of a ventral portion and was in somewhat the same condition as the pelvic girdle in most fishes to-day.

The discovery of this early condition of the pectoral girdle, I conclude, shows its complete distinctness from a gill-arch and places it in the same category with the pelvic fin. The gill-arch theorists have generally considered the pelvic fin as simplified from a condition still retained in the pectoral, or, in other words, as the more modified of the two,—a deduction necessarily following their assumption as to its mode of origin. But the facts indicate clearly that the pelvic fin represents the more primitive type, and that the pectoral fin passes through a similar stage of development and then progresses beyond this to the condition seen in all recent sharks.

The connecting links between the pelvic and unpaired fin skeletons have been so clearly presented (Thacher, 77, 78; Mivart, 79; Wiedersheim, 92; Regan, 04) as to need no particular comment here. I wish to bring up the case of *Chlamydoselachus* in this connection, however, because it has also a bearing on another point. The adherents of the Gegenbaur theory have tried to find some dorsal projection of the pelvic girdle to homologize with the scapular portion of the pectoral girdle, but the "*pars iliaca*" of Davidoff, 79, 80, cannot be considered, and the "*processus iliacus*" of Braus, 04a, must also be thrown out of comparison since it does not bear the same relation to the nerve foramen as the scapula does in the shoulder girdle. In *Chlamydoselachus* the pelvic girdle is a broad flat plate (see Fig. 20 from a camera drawing of a Van Wijhe preparation of a 225 mm. embryo) which serves also as a basale for about half of the rays of the fin. It is pierced by eight spinal nerves instead of a single collector. It has not the slightest indication, even in a 120 mm. stage, of any dorsal prominence whatever. Such a condition is impossible of explanation under the gill-arch theory, for the pelvic of *Chlamydoselachus* cannot by the greatest stretch of the imagination be made to homologize with a gill. In fact it resembles nothing so much as it does the flat, plate-like basalia of certain unpaired fins.

THE ORIGIN OF THE GIRDLES.

While upon this point it must be admitted that the evidence is not as complete as we would desire it to be, and while in a few respects it is even conflicting, yet, reviewing the whole matter carefully, the origin of the girdle may, I believe, be traced to the supporting elements of the fin.

The *raison d'être* of the girdle is, naturally, the necessity for a solid base in the soft body-wall, against which the remainder of the fin skeleton may brace itself. The rays of the unpaired fins may, when necessary, find support against the axial skeleton, but as the paired fins are situated support is impossible unless developed for that special purpose. Is such a development impossible of conception or unparalleled in morphology? For answer we will cite the extradigital cartilages which support the swimming membranes of the seal, the extension of the cartilage area, and the development of accessory digits in Cetacea and Ichthyosauria for the same purpose (Kükenthal, 90; Osburn, 06a) the calcar of the bat's wing, auricular and nasal cartilages, etc., etc., not to mention the visceral skeleton which must at some time have arisen *in situ* for the support of the gills.

Is there anything similar to this process in the unpaired fins? Undoubtedly, for in those forms in which, in the adult condition, the fin skeleton rests against the axial skeleton for support (Spinax, Cestracion, Acanthias, etc.), the embryonic fin skeleton is at first developed separately from the spinal column and by later growth comes into contact with it. In fact, in the unpaired fins of nearly all sharks there is more or less development of the proximal portion of the radials into basalia. The pelvic plate or girdle of *Chlamydoselachus* is certainly most similar to such basalia of the median fins. It serves as a direct support for half of the rays of the fin (without the intervention of any other cartilages), and the two girdles meet at the mid-ventral line for mutual support (Fig. 20), just as the basalia of certain median fins grow into contact with the axial skeleton for the same reason. The pelvic basalia or girdles are not in contact when they first appear but meet as development proceeds. The pelvic skeleton is not very unlike that of the anal if we suppose a similar amount of "fusion" to take place in the latter.

Is it a mere matter of coincidence that this simple condition of the pelvic fin should appear in a species which gives so many other evidences of great antiquity? We think not, especially when we take into consideration the evidence from *Cladoselache* (the oldest fossil shark in which the pelvic structures are known (see Dean, 94, Pl. VII, Fig. 2,

for figure of this fin), in which the pelvic fin skeleton is in a condition similar to the anal of *Chlamydoselachus* at present). Regan's important observations (04) on *Psephurus* are corroborative, as are also the earlier researches of Thacher, 77, 78; Mivart, 79, and Wiedersheim, 92.

An intermediate condition between the pelvis of *Chlamydoselachus* and that of ordinary sharks (such as *Scyllium*, *Spinax*, *Mustelus*, etc.) is seen in the other *Notidani* (*Hexanchus*, *Heptanchus*).

The pectoral girdle is of one type with very little variation through the whole group of sharks. In *Spinax* and *Cestracion*, and probably in all sharks, it consists, at the time when it first becomes evident in the mesenchyme, of a short bar lying next to the ectoderm. Its upper end is continuous with the primary basal of the fin and there is at this time no dorsal (scapular) portion. In this condition the pectoral girdle corresponds very closely to the pelvic girdle at the same stage of development. With later growth the dorsal part appears and the ventral end extends downward toward the mid-ventral line. The similarity of the two girdles is thus lost by the pectoral passing into a more specialized condition while the pelvic remains in a more primitive state.

Professor Braus has recently (04a) tried to show that the pelvic girdle is a degenerate structure in the adult, through the loss of a dorsal process which he homologizes with the scapular portion of the pectoral girdle, and therefore, of course, with the gill-arch. While we cannot doubt the accuracy of Professor Braus's observation as to the occurrence of such a dorsal process in *Spinax*, we cannot agree to the interpretation he places upon it. The writer has elsewhere, (06b) stated his objections to this view, which are, in brief: That the prominence in question is posterior to the nerve foramen, while the "scapula" is anterior in all sharks; that the lowest recent sharks known, the *Notidanidæ*, have no indication of such a prominence either in the adult or the young embryo; that the most ancient fossil shark of which the pelvic fin skeleton is known (*Cladoselache*) gives no indication of such a dorsal prominence. Whatever the aforementioned process in *Spinax* may represent, it certainly cannot be the vestigial homolog of the "scapula" unless the nerve foramen has shifted from the posterior to the anterior side of the process, and even then we should have the paradox of the most degenerate condition known in the shark limb occurring at once in the oldest fossil, and in the most primitive recent, sharks.

Concerning the discovery by Ruge, 02, and Braus, 04a,—and the writer has verified this discovery,—that in *Spinax* the first part of the procartilaginous anlage of the pectoral fin skeleton to appear is the girdle, it

must be urged that at a still earlier stage the mesenchyme thickening from which the fin skeleton arises has its origin next to the ectoderm within the developing fin-fold. In Cestracion, according to the writer's observations, the first part to appear as procartilage is distal to the girdle and includes a portion of the primary basal and the proximal ends of the fin-rays in the forward half of the fin. From this point the process of differentiation spreads in all directions and soon the ventral half of the girdle makes its appearance. This is after the fashion which has been described by the older embryologists. Fürbringer, 02, and Braus, 04a, have used Molliers' figures (1893, Pl. III, Fig. 13, and Pl. IV, Fig. 16) to prove that in *Torpedo* a portion of the girdle is included in the first part of the skeleton which becomes evident. In this they are probably correct, but had they observed a little more closely they would have noticed that this portion of the anlage of the skeleton is not at all girdle-like in form but is merely an inward extension of the primary basal, while the real girdle or arch appears later growing out ventrally and dorsally from this region.

The apparent contradiction in the development of the pectoral fin girdle earlier or later than the more distal part of the fin skeleton is entirely cleared up when we go back to the previous stage in the formation of the skeleton. Here, as we have already seen, the concentration of skeletogenous mesenchyme progresses uniformly, as in all fins, from the ectoderm inward and forms the most primitive support of the fin-fold. Finally, after the muscles and nerves are all in position (the trapezius excepted), the fin skeleton appears in procartilage by differentiation of the mesenchyme in the position which it holds in the adult. The whole development of the pectoral and pelvic fins is just what we should expect for structures arising as local organs of the body-wall, and, except for the trapezial connection already explained, involve no other structures but the muscles, nerves, blood-vessels, and skeletogenous tissues of the immediate region in which they arise.

CONCLUSION.

It will be seen, in conclusion, that all of the important objections of the gill-arch theorists have now been met and answered. Nearly every condition observed in the paired fins has been shown to exist also in the median fins. The facts used by recent writers in defense of the gill-arch theory, viz., abortive muscle-buds, fusion of muscle-buds, migration of fins during development, collector nerves, origin of the skeleton as a continuous procartilagenous anlage, discrepancy of rays and muscles, and post-axial rays, are thus shown to have absolutely no weight in such

argument but merely indicate still more clearly the exceedingly close relationship which exists between the paired and median fins. The serial homology of limb girdles with gill-arches is shown to be impossible, and the trapezial connection can only be secondary. The branching cartilages observed in the hyoid region are to be regarded only as parallelisms,—produced probably by similar causes to those which have been operative in producing the fusion of rays to form basalia in the fins. Concentration or abbreviation of the region at base of the radii would seem sufficient to cause this in either fin or gill.

On the other hand, the manner of development of the pectoral girdle proves it to have been derived through a type similar to the pelvic, showing the latter to be the more primitive in form, while proof is not wanting to show the connection between basalia (girdles included) of paired and unpaired fins. The study of the earliest conditions in the formation of the inferior caudal places this fin on the same basis as the others and indicates the similar external origin of all. When we consider, in addition to the foregoing points, the exactly similar origin and development of the muscles, nerves, blood-vessels, and ceratotrichia in both kinds of fins, the case becomes so strong as to appear a certainty. I think we may safely conclude that the external or fin-fold origin of the paired limbs is clearly demonstrated, at least as fully as is possible until palæontology shall reveal the whole story by supplying the absolute serial stages in the evolution of these organs.

COLUMBIA UNIVERSITY,
March 9, 1907.

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DESCRIPTION OF PLATES.

PLATE I.

FIGS. 1 to 6. Cross-sections through various fins of *Cestracion* to show origin of concentrated mesenchyme (later giving rise to skeleton) within the fin-fold in every case. The difference in appearance between the concentrated mesenchyme in the fin-fold and the ordinary mesenchyme in the body-wall is clearly indicated. All the figures are from camera drawings.

FIG. 1. Through anterior end of pectoral fin-fold shows muscle-buds (*m*) descending into the fin. From the collection of cells below it and the partially free space above it, the bud seems to be pushing the mesenchyme cells out of its way.

FIG. 2. Through middle of same fin as Fig. 1.

FIG. 3. Through inferior caudal fin-fold. The axial skeleton is not yet evident and the mesenchyme thickening is confined to the fin-fold at this stage as it is in the other fins.

FIG. 4. Through superior caudal fin-fold.

FIG. 5. Through anterior end of first dorsal fin-fold.

FIG. 6. Through middle of the same fin shown in Fig. 5.

PLATE II.

FIG. 7. Cross-sections through pectoral girdle (*p*) and fourth gill-arch (*g*). The dotted lines connect similar points. The girdle (*p*) is in its first stage, prior to the development of the dorsal (scapular) portion, and it is still continuous with the procartilage (*b*) within the fin-fold. Note that the girdle

(*p*) is situated quite ventral to the gill-arch (*g*) and that it is also situated outside of the blood-vessels next to the ectoderm, while the gill-arch is internal to the blood-vessels and next to the enteron.

In the region indicated at "*x*" the mesenchyme cells are just beginning to take the first step in concentration toward the formation of the scapular part of the girdle.

PLATE III.

EMBRYONIC STRUCTURES OF CESTRACION.

FIGS. 8, 9, 10. A series showing the gradual approach of the pectoral girdle to the gill-arches. The fourth gill-arch is included in the drawing to show the distance between the gill-arches as compared with that between the girdle and the fifth arch. Fig. 8 shows the girdle at an early stage after the formation of its dorsal (scapular) part. Fig. 9 is a somewhat later stage (length 35 mm.). Fig. 10 is a still later stage (53 mm.). Somewhat later than this the fifth gill-arch passes partially under the girdle.

FIG. 11. The skeleton of the anal fin is differentiating out of the mesenchyme plate as a continuous anlage (*n*, neural cord; *nc*, notochord; *ca*, caudal artery, and *cv*, caudal vein).

FIGS. 12, 13. Cross-sections through the anal fin of an embryo of 40 mm. to illustrate that the fin skeleton arises independently of the axial skeleton. Fig. 12 is through the anterior end, Fig. 13 through the middle of the basale (*b*) of the fin skeleton.

FIG. 14. Cross-section showing origin of brachial artery (*b*) from dorsal aorta, and the junction of the last pair of efferent branchial arteries (*e*) with the dorsal aorta.

PLATE IV.

FIG. 15. Reconstruction of second dorsal fin of Cestracion (53 mm.) to show discrepancy of muscles (outlined in black) and skeleton (shaded) (*s*, fin spine).

FIG. 16. Camera drawing of a Van Wijhe preparation showing skeleton of anal fin of a 225 mm. embryo of Chlamydoselachus. The separation from the axial skeleton is very marked (*hs*, hæmal spines).

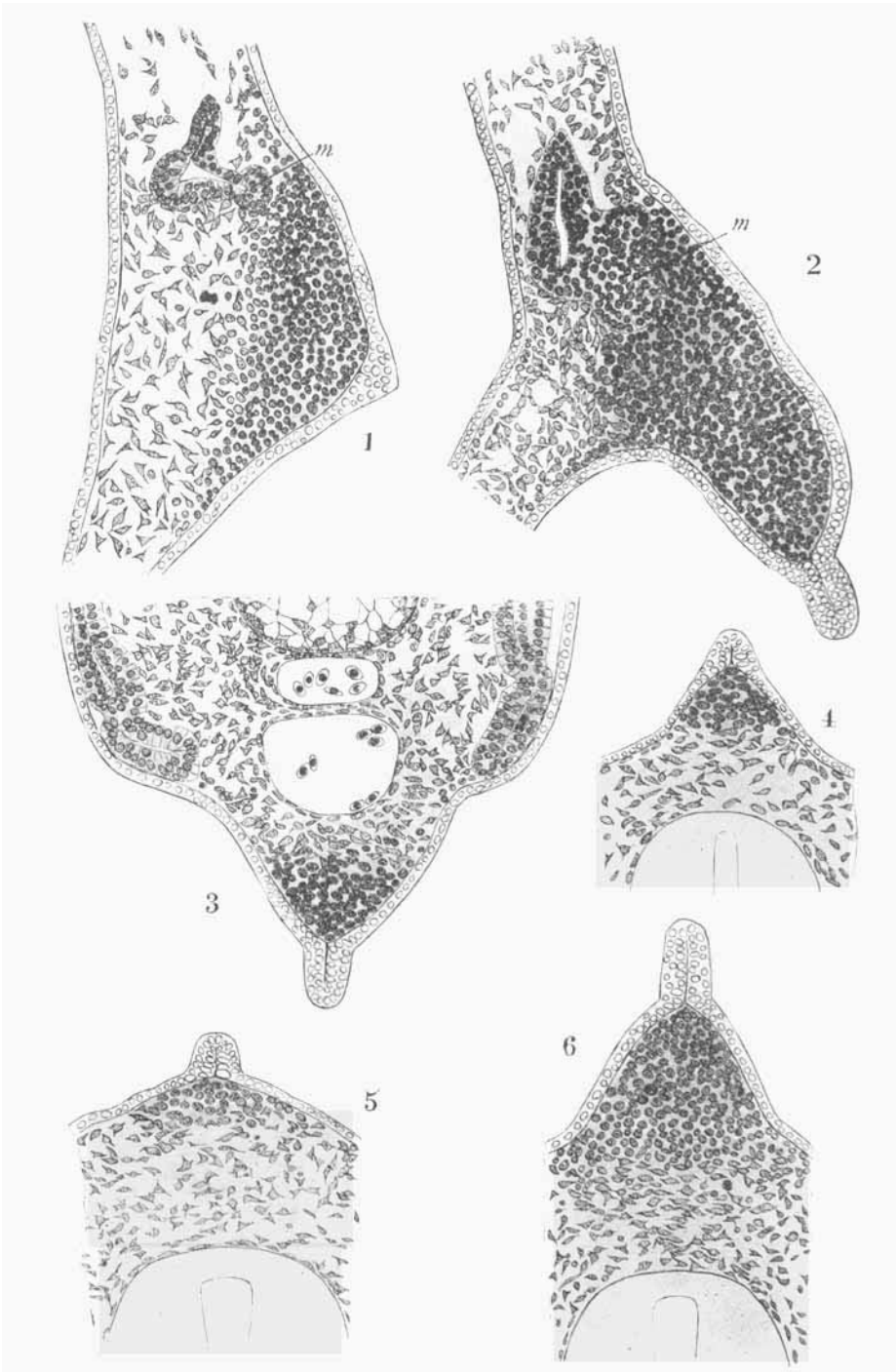
FIG. 17. Fusion of muscle-buds (*m*) in the anal fin of a 35 mm. embryo of Cestracion. Drawn with camera.

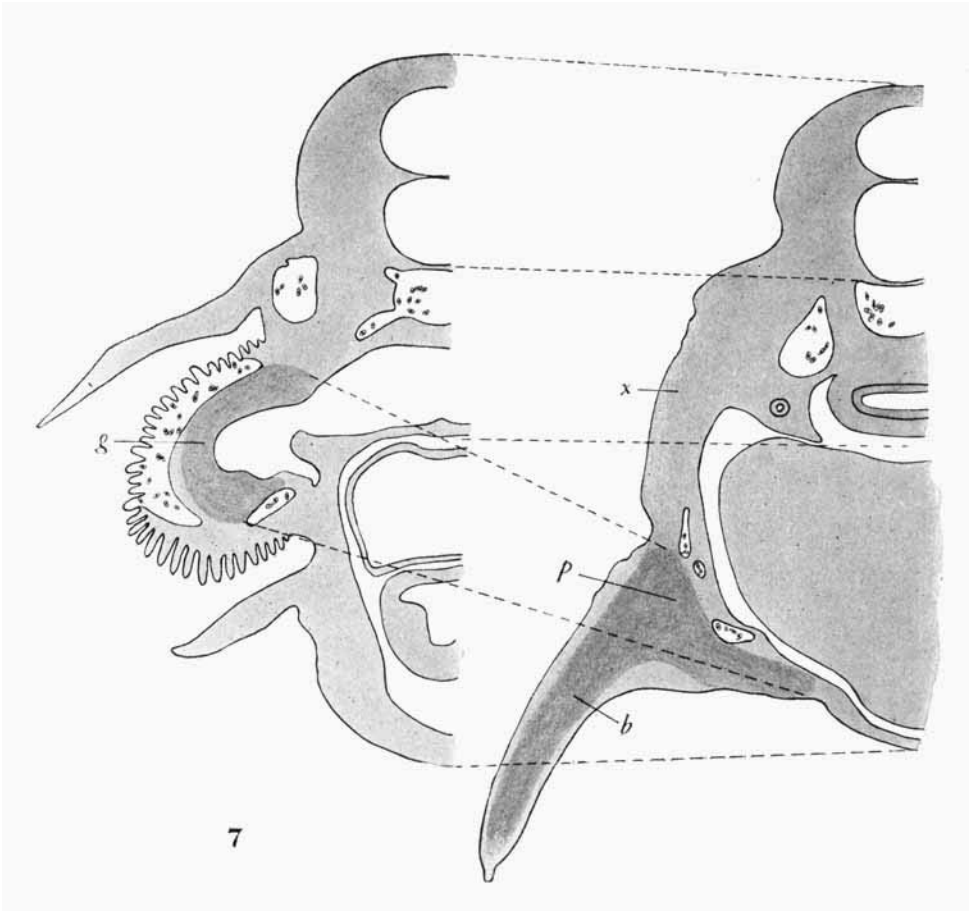
FIG. 18. Second dorsal fin of Cestracion, 58 mm., showing fusion of muscles. Camera drawing from an actual section.

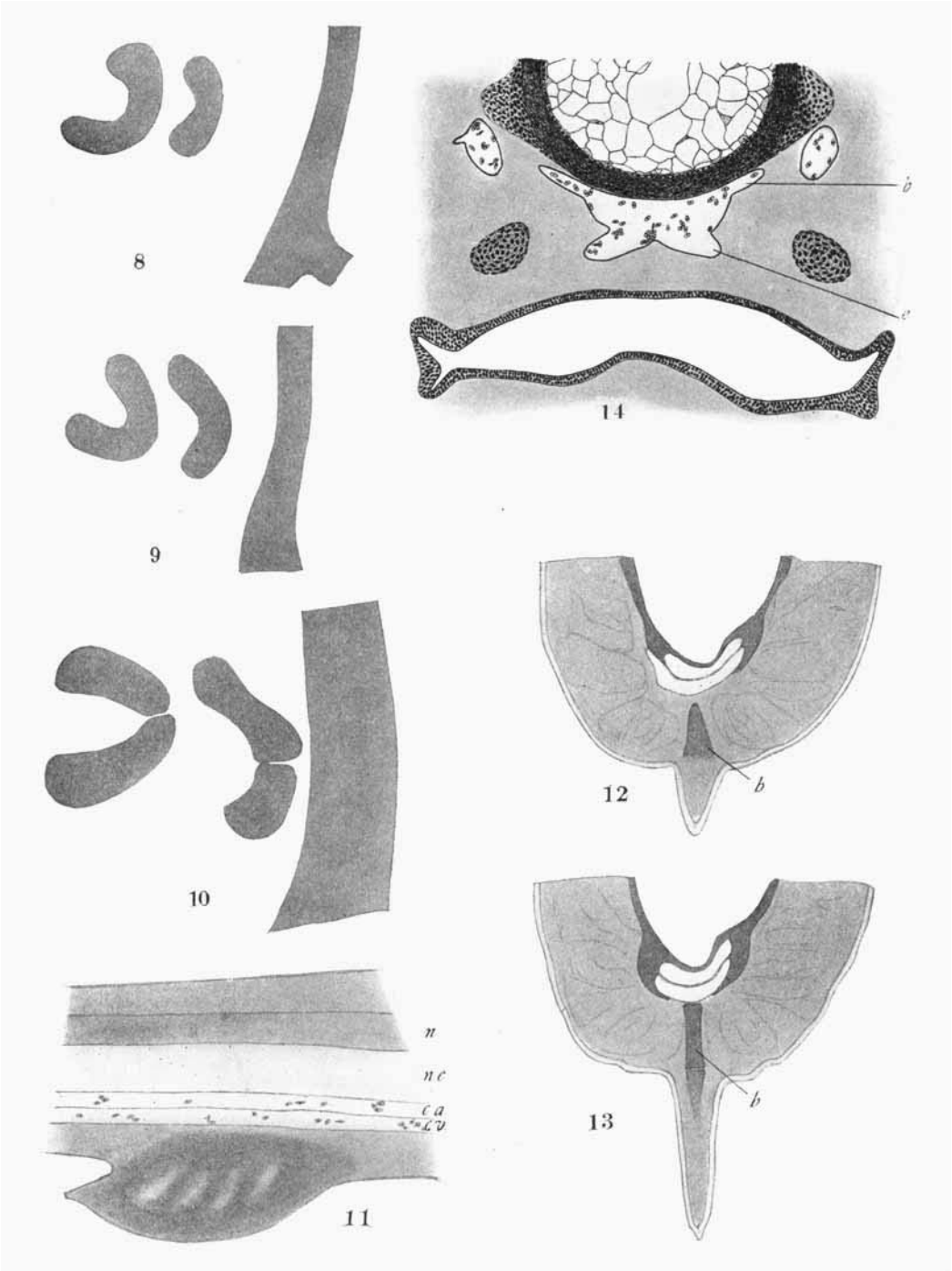
PLATE V.

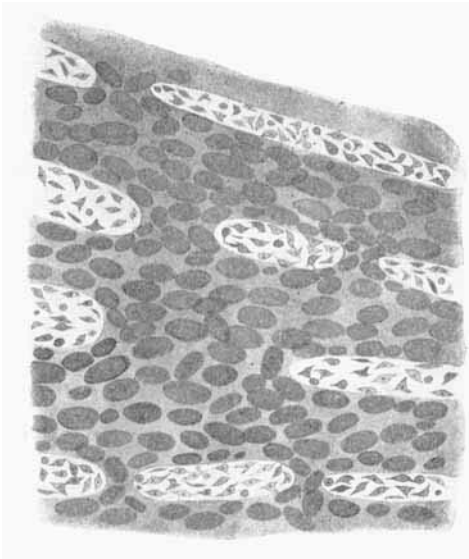
FIG. 19. Dorsal fin of Chlamydoselachus, 225 mm. Camera drawing of a Van Wijhe preparation. Note the wide separation from the axial skeleton (*sp*, spinous processes).

FIG. 20. Pelvic fin skeleton of Chlamydoselachus, 225 mm. Camera drawing of a Van Wijhe preparation. Note the flat girdle (*b*) pierced by eight nerve foramina, and serving as a basale for about half of the radials of the fin. The two girdles fuse at the midline in the mesenchyme stage and the separation at the anterior end is not yet complete. There is no indication as yet of the antero-median wedge-shaped element figured by Garman, 85-86, as lying between the girdles at their anterior ends in the adult.





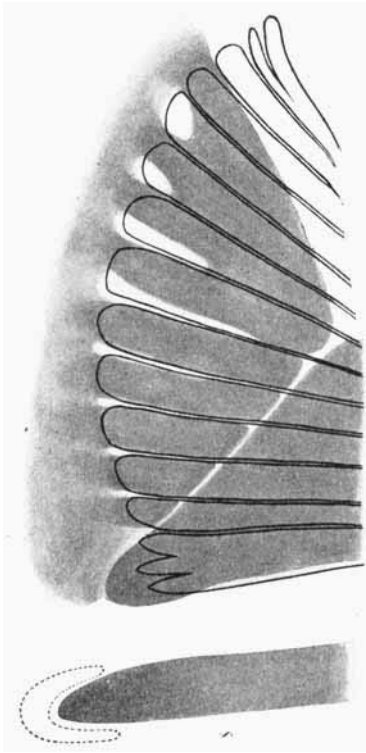




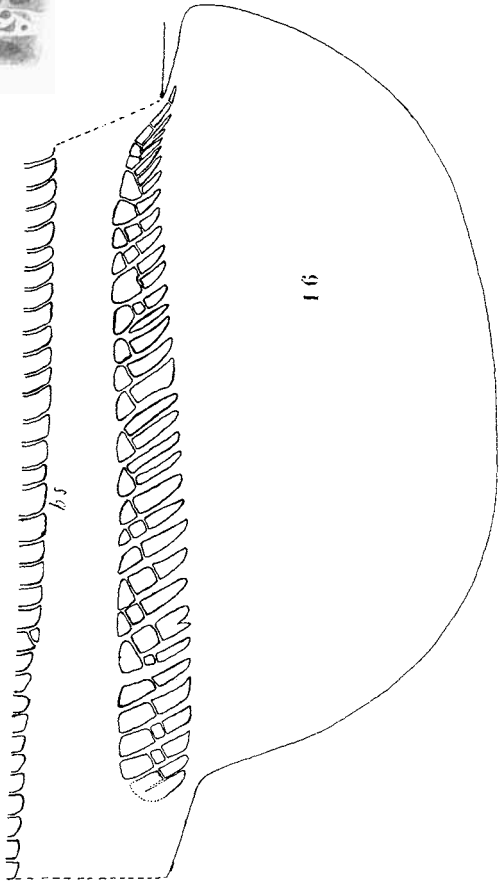
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