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THE EVOLUTION OF THE SKULL AND THE CEPHALIC MUSCLES: A COMPARATIVE STUDY OF THEIR DEVELOPMENT AND ADULT MORPHOLOGY.*

By H. Leighton Kesteven, D.Sc., M.D.

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Preface.

This work is the result of half a lifetime devoted to the study of the small portion of comparative anatomy and embryology it deals with. For the most part it records actual personal observation. The deductions relative to homologies and the evolution of the vertebrata which the work contains are those which, from my own observations, appear to me to be the most acceptable. These conclusions are in several important instances at variance with those commonly accepted.

Nowhere are the conclusions in the fields of speculative morphology, homologies and evolution, presented as proven. In no single instance have I felt entitled to write Q.E.D. at the end of any section.

An attempt has been made to describe the cephalic musculature of a representative range of each group of the vertebrates. Only such references to the nervous structures have been made as appeared necessary to a proper understanding of the musculature. It is regretted that it has not been possible to include references to the main arterial and venous trunks in their relation to the muscles. It was very early found that it was impossible to dissect, with any degree of success, the blood-vascular system in specimens which had not been injected. Following on this discovery, it was found impossible to obtain specimens already injected, or sufficiently fresh to inject, in sufficient number to make the study even approximately complete. Whilst one must admit that a knowledge of the relation of the muscles to the main blood vessels is desirable, it is believed, looking back over the work done and the observations made, that the conclusions relative to the homologies and phylogenies of the muscles are based on sufficient evidence to justify them, and that a knowledge of the relation to the pertinent blood vessels would, in all probability, add further evidence in support of these conclusions.

Very naturally the embryological work has been largely confined to the later stages of development, during which the muscles are assuming their adult forms. My observations are largely based on actual dissections or serial sections.

In the sections dealing with the cranial structures, descriptions and illustrations of representative forms are given and then the serial homologies of certain of the bones are discussed. It may be accepted that throughout the work all those bones which have been named alike and not been discussed are believed to be homologous, wherever found. These are, of course, those bones about whose homology there is at present complete agreement. Discussions only centre around certain of those about whose homology there is a diversity of opinion.

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* The complete Memoir, of which this is the first part, contains the following sections: I. The Fishes; II. The Amphibia; III. The Sauria; IV. The Theria.

The work was begun in almost complete ignorance of myology and without any preconceptions, either definite or indefinite, as to what I was going to learn. I had been interested in the cephalic muscles of *Callorhynchus antarcticus* (Kesteven, 1933) and was rather dissatisfied with my description thereof. Although a few bony fishes had been dissected in an attempt to understand the musculature of that fish, it was felt that the attempt had been a failure. This caused me to dissect a number of Selachians, and in the course of this work I conceived the idea that since the mandibular and hyoid arches were probably modified branchial arches, their musculature must be modified branchial musculature. At this stage the work took its first form: the objective was to test this theory.

In this part of the work it was believed that success in the interpretation of the muscles could be expected only if due weight were given to the probable mechanical factors operative during the change in form and function of the arches. These mechanical factors were deemed to have been, in all probability, more potent than mere spatial relations. The most important result of this investigation, in its bearing on the outlook over the subsequent fields of investigation, was the conclusion that the muscles of the mandibular and hyoid segments could only be interpreted in terms of the branchial on the assumption that not all the branchial muscles had been retained, some had been aborted.[1]

The reasons for this conclusion will be found in the text, but, apart from the circumstantial evidence specifically applicable to each case, there is collateral evidence of a quite general kind in support. The wide variation observable in the muscles of the vertebrates justifies the belief that " muscles ", wherever they are found, may be regarded as contractile tissue fashioned to fit the mechanical needs and spatial relations of the structures they are called upon to move. Therefore every muscle must be regarded as a particular exemplar of this generality; in point of general significance none is unique. Therefore the mere existence of those instances of adaptation to peculiarities which are to be found in small groups and single species only, illustrates the fact that muscles are only developed in association with a mechanical need, and this implies and accepts the converse as equally true—muscles are not developed in the absence of the mechanical need. One outstanding and unchallengeable illustration of the concept alone will be quoted. The branchial constrictors of the Selachii have completely gone from the higher Vertebrata with the loss of the interbranchial septa.

The importance of this concept is that it has constantly determined the mental approach to the problems arising throughout the whole of the work subsequent to that on the Selachii. The Selachii were regarded as the most primitive vertebrates, and it was anticipated that all the muscles of the higher vertebrates would prove to have been derived from some of those of these primitive fishes, but it was not anticipated that all the muscles of the fishes would prove to have been retained throughout the series.

Lightoller has claimed, for the adoption of a belief that " all the groups of muscles found in the Selachian hyoid and mandibular regions are represented in each of the higher orders of Vertebrates ", that " it corrals imaginative theory, and is less open to objection than the inconsequent dropping of an inconvenient muscle sheet ". (Lightoller, 1939, p. 350.)

Dr. Lightoller and the writer have worked alongside of one another almost, and have discussed the work as it progressed. This is one of the questions on which we have agreed to differ.

My colleague's position seems untenable for the following reasons. It is demonstrable that single muscles and whole sheets are aborted. Quite apart from the phylogenetic example quoted above, the absorption of single muscles and groups of muscles may actually be observed during the metamorphosis of the amphibians. If it is demonstrable that muscle sheets, groups and/or individuals have been aborted in certain segments, then it seems that one is not justified in denying the possibility of abortion in all segments.

Undoubtedly my decision of the last paragraph has been influenced by the personal factor, and that factor appears even more strongly in the following. Lightoller dismisses the branchial interarcual and adductor muscles with the remarks (p. 355) " These, embryologically (Edgeworth),

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[1] I plead guilty to a belief which appears to be old fashioned and to be becoming discredited. I am unable to believe that the growing organism does not respond to its environment by adaptation thereto, nor can I think that this response is without effect upon the germ cells. I know of no evidence, experimental or otherwise, which should destroy a belief that the germ cell will react to changes in its environment. The environment of the germ cell is the body fluid in which it grows. The content of this fluid will surely vary with the size and degree of activity of every part of the body. Here is not the place to elaborate this belief further, but this short statement of the thought processes behind the attitude adopted in the above paragraph seemed called for.

are derived from the constrictor sheet, and are no longer recognisable in the hyoid arch. It is thought that their fate must be that of the parent constrictor, so no special description of them has been given." It is quite impossible to keep the personal factor out of inquiries of this kind. In the absence of mathematical methods of testing the accuracy of one's conclusions there is left only the expression of one's opinion, and to deny the existence of the personal factor, even tacitly by ignoring its presence, would be to adopt a quite unjustifiable dogmatic attitude. In this case it appears that Lightoller has, at the outset, departed from his intention to find representatives of all the groups by discarding a quite important group before he begins. To the writer the branchial adductors stand as the first stage in the evolution of the muscles of mastication.

Finally, it appears to the writer unwise to " postulate conditions " into which the facts are to be fitted. That this was done by Lightoller seems evident from his statement relative to his third clause, quoted above, that it had made his " task more difficult and, at times, its wisdom seems questionable ".

The writer's view may be stated as follows : The myotome alone is unquestionably persistent, and only those derivatives of it which investigation seems to demonstrate so may be regarded as having persisted throughout the groups and orders of the vertebrata.

The weight given to the influence of mechanical factors in the evolution of the muscles has been such that always it has been assumed that these factors have persisted with the muscle, or that there has been a gradual change in them which has permitted or brought about the changed relations of the persistent muscles.

During these ten years of study of comparative myology of the head and neck, the ease with which it has been possible to recognize so many of the muscles of the last class in the next which fell for study has been recurrently surprising. Infinitely more difficulty in recognizing homologous muscles was anticipated, and the rarity of difficult and insoluble puzzles was very unexpected.

It is realized that this absence of difficulty may have been more apparent than real, that puzzles have not presented difficulties because wrong solutions have been accepted. It is believed that this will prove to have been the case in very few instances and that in the main the conclusions arrived at are correct.

One outstanding generality seems to emerge from this simplicity of the problem, namely, that the association of nerve and muscle in the neuromuscular unit must have been very firmly established very early in the process of differentiation of the vertebrate stock, because this constancy of neuromuscular association has been so successfully used throughout the work as the initial guide to the identification of the muscles.

It is a fact that, with very few exceptions, muscles of any given segment are, without doubt, innervated by the nerve of the same segment. The exceptions to this rule are for the most part questionable. The statements that they *are* exceptions are based upon dissections, and are inadequately or not at all supported by experimental evidence and/or embryological proof. In almost every instance, moreover, such statements conflict with those of other investigators. The rarity of these cases is itself a reason for doubting the verity of the exceptional association said to be present.

The statement that a muscle is innervated by a nerve other than that of the segment to which the myotome belonged, e.g., that a muscle derived from the mandibular myotome is innervated by the seventh nerve, implies a great deal more than the mere anatomical association. It is a statement which implies the breakdown of the definite forces, whatever they may be, which direct the progress of ordered ontogenetic growth and development.

We are faced, it appears to me, with two, and only two, possibilities in this connection ; we must assume that there are physico-chemical forces directing the processes of growth, or else we must assume that there are no directors whatever. The facts of ordered growth are, in themselves, the complete refutation of the second.

The first assumption, however, at once forces upon us the recognition that the governance of ordered growth is under the direction of both stimulating and inhibiting forces.*

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* It would not add to the exactness of this discussion to attempt to employ any of the recognized designations. We might, for instance, refer to the responses as tropisms, or positive and negative morphogenetic substances or centres, or as excitors or inhibitors or evocators. Until we know a great deal more about these things they are little more than useful terms defining the method of approach to the general problem, and implying a belief in the existence of a directing force.

Since the muscles come to assume certain constant and definite relations, in each species, to contiguous structures, we must assume that something has directed development to this end, and further, that something has prevented them from acquiring other relations. Similarly, both positive and negative forces must have been effective in determining the association of nerve and muscle, and this will have been so whether the theory of His be correct, or that of Hensen; whether the nerves have grown peripherally or centripetally.

The experimental work of Lehmann, Detwiler (Detwiler, 1936, pp. 147–150) and others has provided the proof of the existence of the positive force determining the direction of nerve growth, and (accepting the His theory) that it resides in the mesoderm of the segment for the segmental nerve, and in the limb bud for the brachial plexus. It has been further shown that, if the mesoderm be completely excised, the development of the segmental ganglion and of the peripheral fibres is more or less completely inhibited.

The negative controlling force has not as yet been located. It is here suggested that this may reside in the growing nerves themselves and be exercised upon contiguous nerves, so that they exercise a mutual repulsion upon one another. This would explain why segmental nerves are confined to girdle areas of the body and only overlap to a small extent. This idea may be given better definition by suggesting that a morphogenetic hormone is formed in the neighbourhood of the growing nerve, which, diffusing into the surrounding tissues, inhibits the growth of other nerves in the regions of its greatest concentration.

This suggestion might be tested by the early excision of half of the neural crest in a single segment. If the suggestion be the correct explanation, then one would expect the segmental nerves on both sides of the gap to supply at least sensory nerves to the area deprived of its own nerve.

However, whatever be the correct explanation, it seems certain that the orderly growth of nerves must be under the direction of positive and negative forces. Therefore heterogeneous innervation* can only have resulted from the breakdown of these forces.

If the reality of those forces be admitted, it becomes worth while considering just what their " breakdown " must imply. The experimental work previously referred to demonstrated that nerve-muscle attractions were not specific, that mesoderm, or more specifically muscle plate, from any segment was capable of receiving nerve tissue from any other segment into which it was transplanted in place of the muscle plate thereof, and that the limb bud was capable of exciting the development of the nerves from other segments than the normal, if transplanted, so that its plexus was derived from segments other than the normal.

Therefore, it might seem that any muscle might exercise an attracting influence on any nerve. Whilst the muscle is in the normal situation, however, it will be supplied by its own proper nerve. Before we can admit the occurrence of heterogeneous innervation we must postulate the failure of the proper nerve to grow, although, since it attracts another nerve, *ex hypothesi*, the muscle was possessed of the power to have attracted its own proper nerve.

If we assume that the change over was gradual and not effected at a single step, then we assume something for which there is no evidence in support from experimental work : we assume that the invading nerve had grown away from its own proper stimulating directive force and against the inhibitory force which seems to reside in any area supplied by its own proper nerve.

Finally, although experimental work appears to have demonstrated that the stimulating directive force is not specific, we are called upon to postulate its failure to stimulate one nerve whilst retaining the power to stimulate another to growth, that is to say, we have to postulate specificity in one small isolated phenomenon, as well as postulating the failure of an inhibiting force which also is probably not specific.

Whilst it is recognized that these thoughts relative to the control of the development of the nerve-muscle units are very largely pure speculation, it is claimed that they do present the probabilities, and the conclusion they force upon one is that all claims for heterogeneous innervation must be regarded with grave suspicion.

The evidence for and against the specific examples of apparently heterogeneous innervation will be found in its appropriate place in the text.

Scattered throughout the work will be found specific acknowledgments and thanks for assistance from colleagues and friends, too numerous to detail here, but I should like in this

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* This term is used to indicate the innervation of structures derived from one segment by a nerve from another segment.

place to express my thanks and acknowledge my debt to Dr. C. Anderson, formerly Director of the Australian Museum, Professor A. N. Burkitt of Sydney University, and Dr. Lightoller.

Throughout the progress of the work Dr. Anderson placed the resources of the Museum at my disposal, and to his kindly interest in this way I owe a multitude of interesting specimens.

To Professor Burkitt's active interest in my work, I owe inspiration and direction in many ways. I am also indebted to him for assistance which I have constantly had from the Department of Anatomy, which he directs.

Dr. Lightoller's assistance has taken the form of keen criticism, which his own work in muscle homologies and consequent understanding of the problems has always justified. The fact that we have not always been able to agree has been, in those instances, a spur, for the resultant discussions have indicated wherein my case was weak, leading, in some instances, to modification of my views and, in others, to the strengthening of my argument by further investigation.

Finally I should like to acknowledge my indebtedness to the Executive of the Commonwealth Council for Scientific and Industrial Research for grants which have purchased material and instruments for my use.

Post Scriptum.—After this first part of my work was completed, Edgeworth's exceedingly fine book on the Cranial Muscles of the Vertebrates (1935) reached me. Brief comment on certain points of agreement and of difference between us appears desirable.

Edgeworth states (p. 25) : " Ichthyopsida and Amphibia can be divided into two groups with reference to the developmental phenomena in the masticatory muscle plate . . . The first comprises Dipnoi, Holocephali and Amphibian larvae ", and presumably adult Amphibia. The second group comprises Plagiostomi and Teleostomi. The former are said to exhibit a " primary " mode of development of the masticatory muscle plate, the latter group a " secondary " mode. He comes to the conclusion that on account of this difference in the mode of their development the Mm. adductores mandibulae of the former are not homologous with those of the latter group, and therefore designates the adductors in the first group " levatores mandibulae ". Edgeworth further stresses the fact that the secondary mode of development, that of the Plagiostomes and Bony fishes, is found in the Sauropsida, whilst the primary mode is present in the Mammals. This complete discontinuity he explains by assuming that the secondary condition has been separately acquired.

Edgeworth appears to be of the opinion that early embryonic conditions must represent and be derived directly from ancestral features ; or is it that his conviction that the Dipnoi are the most primitive of living forms leads him to adopt the above view ?

There is so much clear and conclusive evidence that no embryo may be accepted as representing an adult ancestor that the first position appears to the writer as untenable. The second position, if that be the correct interpretation of his attitude, will have been the result of the personal factor in the equation, and must be recognized as entirely justifiable.

Obtruding that same personal factor, I have always regarded the appeal to coincidences and fortuitous happenings as a weakness in attempts to explain phenomena of development and adult anatomy.

It appears to me that the most we are entitled to assert is that the mesodermal segments and their derived neuro-muscular units *as a whole* are homologous. Beyond that we enter the realm of speculation. This is not to be interpreted as meaning that we are not justified in attempting to derive this muscle from that or the other, and to that extent regarding them as homologous. I would derive the M. depressor mandibulae of the Amphibia from portion of the primitive hyoid constrictor sheet of muscle fasciculi of the Elasmobranchs, but with quite different origin and insertion it hardly seems reasonable to claim complete homology for the two muscles.

With so wide a variation in the adult structures, and so much evidence of the variability of the earliest embryonic features—an outstanding example is the varied development of the premandibular somite—it does not appear that one is on safe ground when basing argument for, or against, homology on the early condition of the muscle plate.

In the present instance we do not know, and are likely to remain unable to know, whether the missing dorsal muscle is incorporated into the Mm. " levatores mandibulae ", or whether the mother cells of these muscles have simply dropped from the ontogeny altogether.

Whilst it were very largely in accord with my own interpretation of the modification of an originally continuous primitive constrictor sheet, to regard the continuous, uninterrupted craniomeckelian maxillary muscle plate as the more primitive condition, I am unable, in view of the evidence, as I see it, to adopt this view. To my mind the simpler explanation and the one that avoids the appeal to coincidence is that the muscles derived from the dorsal part of the sheet, the constrictor dorsalis portion, have been so completely lost or incorporated in the lower muscles by the members of the first group, and by the Mammalia, that there is no division of the embryonic sheet.

In support of this view, I would point out that the Holocephali so closely resemble the Plagiostomes in the great majority of their cephalic characters, that one is obliged to regard them all as Elasmobranchs. The greater geological antiquity of the Plagiostomes leads me to expect them to present the most primitive conditions. I have regarded the subdivision of the mandibular muscle sheet into dorsal constrictor-levator, middle adductor and ventral constrictor components as being the modifications of a branchial sheet, brought about by the modifications of the related mandibular arch. The absence of the dorsal component, observed in the Dipnoi etc., I would regard as the suppression of these muscles, which might be expected to follow naturally upon the firm fixation of the maxillary half arch.

The same line of thought leads me to regard the selachian evidence relative to the ocular muscles, as indicating that they were originally derived from the premandibular, mandibular and hyoid muscle plates, and to regard the VIth nerve as part of the VIIth and the IVth as part of the Vth. To me, the varied mode of origin of these six muscles and of the premandibular somite appears as the result of the pressure or other influence of the varying juxtaposed structures.

It is pleasing, however, to note that Edgeworth regards the Dipnoi and the Amphibia as being derived from a primitive Dipnoan stock. I arranged the evidence in support of this view some years ago (1931), and was closely followed by Kerr (1932) in the same vein. It is also pleasing to me to find that the similarities to one another, presented by certain of the cranial features in development and adult anatomy of the Holocephali, Dipnoans and Amphibians, have appealed to Edgeworth as being fundamental.

After carefully studying Edgeworth's book I still feel that my diagram II, schematically portraying the phylogenetic relationships of the Anamniota, most nearly represents the correct interpretation of the facts at present available.

THE MUSCLES OF THE ELASMOBRANCHS.

INTRODUCTION.

Profound modifications of both the skeletal structures and their activating muscular mechanisms are to be observed in the heads of recent fishes. Muscle entities seem to develop, disappear, and reappear in bewildering variety with each change in underlying skeletal frame, or overlying dermal condition.

The head develops a rostrum and at once levator and depressor rostri appear; let the dermis be rigid and there are no facial muscles, but if the dermis be soft then, as in the Holocephali, a complete set of superficial facial muscles is at once developed; given a modification of the attachment of the superior labial bones, as in *Drepane* or *Epibulus*, so that the upper lip becomes protrusible, the requisite modification of the muscles of mastication surely follows. Clearly the homologue of the levator rostri should not be sought in a fish which has no rostrum, nor that of the protractor labii superioris in a fish which has rigidly attached labial bones.

These last two instances exemplify extreme limits of the problem of the evolution of the cephalic musculature of the vertebrata. They are special developments in harmony with special skeletal developments, and are not to be found in the absence of those skeletal modifications. But whence came they? Not from nothingness: they are to be regarded as derivatives of some portion of that early muscle plate which gives rise to the other more normal muscle entities present.

It appears as though modification of the muscular system and its evolution are essentially dependent on, or conditioned by, modification and changes in the skeletal system. There is, moreover, a marked difference of attitude to be maintained in the study of cranial evolution on the one hand and of phylogenetic myogeny on the other. In the former case experience points to the expectation of reduction in the number of the component elements, either by more or less complete fusion or deletion of the elements, and an absence of the introduction of new elements. In the latter case one must be prepared, not only for fusions and deletions, but also, and increasingly in the higher forms, for the introduction of completely new entities.

Thus a study of the evolution of the musculature of the vertebrate head may prove an attempt to understand the origin and modification of the various muscles rather than a search for homologies.

As an introduction to such a study, this first section is devoted to an attempt to understand the metameric serial homologies of the muscles of the heads of the various fishes. It would seem that, omitting the epibranchial and the hypobranchial spinal muscles, the muscles of the fish's head are modified forms of the original metameric repetition of similar muscles related to the visceral arches. If these original elements can be identified in their modified forms, such identification should assist us in understanding the further modifications in the higher vertebrata.

It is probable that the primitive vertebrate was provided with a terminal, or subterminal, mouth, behind which ranged seven visceral arches. It is further probable that a myotome, or muscle sheet, was present in front of each arch and behind the branchial cleft, that is to say, in the anterior portion of the thickness of each interbranchial wall, and in front of the first arch around the mouth opening. The muscles related to these arches were probably constrictors only, in the most primitive condition, the resilience of the unjointed arches being relied upon to effect a return after constriction (Fig. 1, A).

The accumulated evidence on the form of the visceral arches indicates that each was very early segmented into four pieces on each side, united below by a median piece. There may have been five pieces in each side and the ventral pieces became fused in pairs.

Clearly unless the joints of the arch bent in opposite directions, constriction would have been productive of dorsi-ventral or lateral flattening, or would have displaced the apex of the compressed arch forwards or backwards. The mechanical disability in the way of compact constriction of the throat and mouth could only be overcome by development of these flexions observed in the arches available for study. It is therefore reasonable to believe that the "⩾" shape of these arches is a very ancient feature. As generic terms for the four segments will prove convenient, pharyngo-, epi-, cerato- and hypo-"arcual" are suggested.

There was no "face", and, of course, there were no facial muscles in the primitive prognathostomatous vertebrate.

It appears that early modification of the musculature resulted in the attachment of deeper parts of the circular sheet to the jointed arch, and there resulted those muscles which we designate levatores arcuum branchialium, obliqui dorsales, adductores arcuum branchialium and obliqui ventrales (Fig. 1, B).

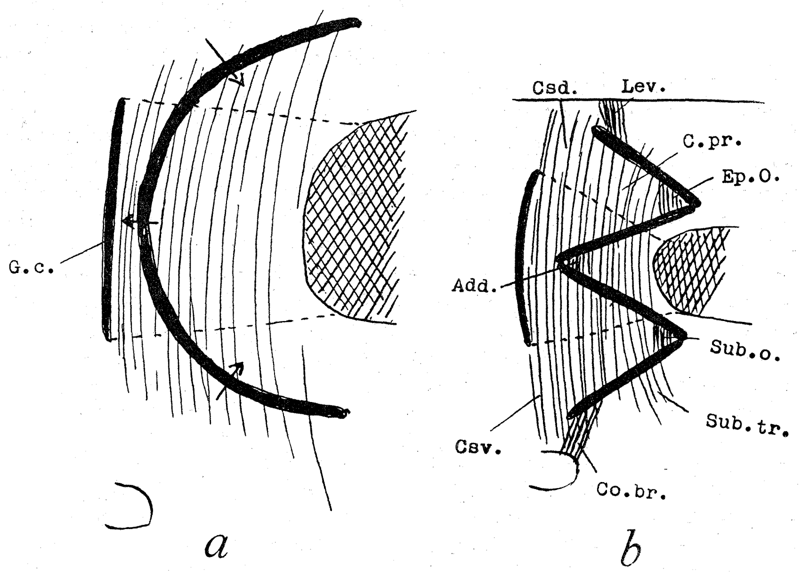


Fig. 1.—A. An hypothetical branchial arch, with its continuous constrictor sheet of muscle and unjointed cartilaginous arch.

B. Scheme of the jointed arch and modified muscles derived from Figure 1A. In both drawings the atrio-pharynx has been indicated by cross-hatching. Add., adductor arcuum. C.pr., deep constrictor. Co.br., coraco-branchialis. Csd., superficial dorsal constrictor. Ep.o., oblique epi-arcual. G.c., gill cleft. Lev., levator arcuum. Sub.o., subarcual oblique. Sub.tr., transverse subarcual.

The effect of this more perfect musculature was to approximate the bisected dorsal and ventral halves of the arches more efficiently, bringing about the actual contact of their fore ends. These fore ends of the folded arches, it will be remembered, are the upper and lower ends respectively of the middle segments. The contact of the fore ends of the front arch would have surely been early availed of as a means to prehension of food. I have elsewhere designated this hypothetical stage in the evolution of the maxillo-mandibular arch, " neognathostomatous ". The first arch was assumed to have functioned as a jaw, but was not deemed to have been modified to any degree and was assumed to be slung to the cranium and to its fellows much as the other arches are now.

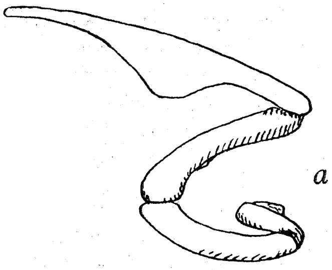
Further modification is regarded as having resulted in the fixation of the first " epiarcual " and it became the palatoquadrate. The first cerato-arcual increased in size and became Meckel's cartilage. The joint between these two became more perfect and stronger. The first pharyngo- and hypo-arcuals became reduced and perhaps persisted as the labial cartilages. Finally, there was increased complexity and efficiency of the muscles related to this first arch and there resulted the perfected jaws.

Along with these changes, and perhaps conditioned by size and backward growth of the upper and lower jaws, there was a modification of the hyoid arch, whose upper element was either impressed as a suspensorium for the first, as in the generality of fishes, or much reduced in size, as in Holocephali, Dipnoi and higher vertebrates generally.

A primitive branchial arch is depicted in Figures 2 and 3, seen from the side and from in front. These drawings also represent conditions present in almost any Elasmobranch. They serve to illustrate the fact that the cerato-branchial cartilages are very closely approximated to one another in the midline, whilst the epibranchial cartilages are nearly as closely related superiorly. There is here nothing to indicate the impossibility of the two most anterior pairs of elements becoming united at the midline above, to form the palatoquadrate arch, just as Meckel's cartilages and the other arches are joined together below.

The remarkable uniformity in the general plan and arrangement of the branchial arches throughout the fishes justifies the conclusion that they are but little modified from the primitive jointed type from which all are evolved. If this be so, one may also assume that their musculature will have undergone relatively little modification.

Since, however, there is variation in the number and arrangement of the branchial muscles in the various fishes, no one of them may be justly accepted as typical of the primitive condition. On the other hand, one may, with tolerable confidence, reconstruct that typical arrangement by making a " composite " picture which shall include all those muscles which commonly occur in all or in the majority of the known forms in each class, omitting muscles which are present only exceptionally and in single classes only. Such a composite picture is presented alongside a schematic presentation of the primitive unjointed arch and its simple muscle sheet, in Figure 1, B.



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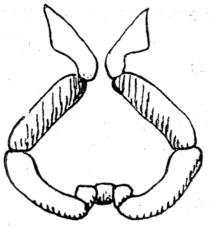

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Fig. 2.—The jointed branchial arch viewed from the side. A., anterior end.
Fig. 3.—The same, viewed from in front.

In this composite arch the following muscles may be recognized :

Superficial constrictors	dorsal (csd.) ventral (csv.)
Deep constrictor	constrictor profundus (C.pr.)
Levator	levatores arcuum branchialium (lev.)
Epibranchial spinal	passing from one branchial arch to another (d.i.) (not shown)
Adductors	dorsal (epiarcualia obliqui· (ep.o.) middle (adductores arcuum branchialium) (add.) ventral (subarculia obliqui) (sub.o.)
Ventral interarcual	subarcuales recti, passing from one arch to the other (v.i.) (not shown)
Depressor	coraco-branchiales (co.br.)

The nomenclature of Marion, Vetter and Tiesing has been in part adopted. The departures are in the partial acceptance of Edgeworth's nomenclature for the specialized ventral muscles and its extension to the similar dorsal muscles. Edgeworth recognizes subarcualia transversi, obliqui and recti. Of these the first two might be described as *intraarcualia* since they extend from one segment of an arch to another segment of the same arch or to its fellow of the opposite side. This is not entirely true, for the obliqui do in some cases gain attachments to two different arches, but even in these cases the muscle acts essentially as a flexor of the joint it crosses. The recti, on the other hand, are essentially *interarcualia*, for they extend from one arch to another and act to bring these arches together. I would therefore classify these as " interarcual " muscles whilst retaining Edgeworth's specific designation " sub-arcualia recti ".

On the other hand, I have applied a modification of his terminology to the essentially similar dorsal intraarcual muscles which, in the past, have been designated " lateral series of dorsal interarcual muscles ". These I designate epiarcualia obliqui, but classify them functionally as dorsal adductors.

The dorsal interarcual muscles (" median series of dorsal interarcual muscles ") I designate " epibranchial spinal " muscles to convey their origin from spinal myomeres.

It is, of course, always regrettable to add to synonymy, but it appeared essential to obtain a set of designations that was completely free from ambiguity, and in which each term was sufficiently self-explanatory to give rise at once to a mental concept of the situation of the muscle named.

The table which appears above is not only a list, it is also a classification, and it is well worthy of note that all of these muscles, excepting only the levators and depressors, are constrictors of the atriopharynx. In the absence of the levators in such a form as *Heterodontus*, it is found that there is dorsally a deep portion of the interbranchial muscle which is capable of acting as a levator and, further, that in many of the fishes there is a very similar portion of the interbranchial muscle ventrally which is capable of depressing the lower half of the arch and acting as a dilator of the arch and pharynx. That a portion of the deep constrictor should thus easily be modified to act as a dilator is significantly interesting.

We may also here draw attention to the fact that, according to the view adopted in this work, the superficial constrictors and the deep constrictors are to be regarded as but slightly modified primitive muscles, whilst the adductors are specialized developments from the deepest layers of the primitive sheet.

It has been demonstrated by a number of observers, but particularly and with especial clarity by Edgeworth, that the muscles related to the maxillo-mandibular arch are developed from a single " mandibular myotome " and are innervated by the fifth nerve, that the muscles of the hyoid arch are developed from a single " hyoid myotome " and are innervated by the seventh nerve, and that the muscles of each branchial arch are developed from the corresponding " branchial " muscle plate and innervated by a corresponding segmental branch of the ninth and tenth nerves.

A slight discordance is produced by the innervation of the coraco-branchiales muscles in the Plagiostomi, which are innervated by the spino-occipital plexus; there is also further discordance in the innervation of branchial levators and superficial dorsal constrictors by spinal nerves. The epibranchial spinal muscles are innervated by the spinal nerves of the myomeres from which they are developed.

Since the coraco-branchialis muscles are developed from the fused ventral ends of all the branchial muscle plates (Edgeworth, 1926) it was to have been expected that they would be innervated by branches from the proper branchial nerves. Apparently their innervation is a secondary modification. The trapezius, or, preferably, cucullaris, developed from the upper ends of all five branchial muscle plates in *Scyllium*, is innervated by the vagus nerve only.

I have deduced from purely morphological evidence that the primitive musculature was a simple constrictor sheet. It is worthy of note that there is embryological evidence in support of this conclusion.

If this is the fact, and in each branchial wall there has been developed from a simple constrictor muscle sheet the series of muscles illustrated diagrammatically above, we have a fundamental illustration of the truth of an earlier contention—that in the study of the evolution of the cephalic musculature we search for derivatives rather than serial homologues.

The whole of the complicated musculature of the Elasmobranch branchial wall is the homologue of a primitive constrictor sheet and we are irresistibly led to the same conclusion in the case of the muscles of the maxillo-mandibular and hyoid arches; but further than that, if those have evolved from arches similar to the branchial and have passed through similar stages of evolution, it should be possible to recognize in their musculature some trace of that evolution. In short, if in the past the musculature of all the seven arches was the same, it should be possible still to recognize the serial homologues in the modified arches.

There is little doubt that the Elasmobranchs are the most primitive vertebrata available for study, and one naturally turns to the more primitive first in such a problem as the present.

Accepted classification of the Elasmobranchs recognizes two orders, the Plagiostomi and the Holocephali, with two sub-orders of the former, the Selachii, containing the sharks, and the Batoidei, containing the rays.

To these I would add, with ordinal value, three families of the Chondrostei, namely the Chondrostidae, Polyodontidae, and Acipenseridae. The remaining families of the Chondrostei (Bridge, 1904) I would assign to the Osteolepida. A study of their visceral musculature confirms a previous opinion that the above acipenserid fishes are more closely related to the cartilaginous than they are to the bony fishes (Kesteven, 1931).

It has also been found that, whilst there are very definite features in the musculature of the sharks and rays in support of the sub-ordinal division of the Plagiostomi, there are just as definite characteristics in the musculature of *Heterodontus* to justify it being placed in a third sub-order. It appears probable that the Notidanidae and the Cochliodontidae should be placed with the Heterodontidae in this sub-order.

There are therefore five types of elasmobranch cephalic musculature to be described: Selachian, Heterodont, Batoid, Holocephalan and Acipenserid.

1. The Selachii.

In the study of the selachian cephalic musculature I have been enabled to dissect the following material. *Mustelus antarcticus* Günther (ten specimens), *Brachaelurus modestus* Günther (three specimens), and one specimen each of *Orectolobus maculatus* Bonaterre, *Squalus* (*Acanthias*) *megalops* Macleay, *Sphyrna Blochii* Cuv., *Pristiophorus cirratus* Müller and Henle, *Chiloscyllium punctatum* Müller and Henle. This last was obtained prior to the specimens of *Brachaelurus*; their dissection proved the two to be so completely similar that the dissection notes on *Chiloscyllium* have been used, in fact they were found to describe the *Brachaelurus*.

In addition to these, Dr. Lightoller has kindly demonstrated to me his dissections of *Mustelus, Orectolobus* and *Carcharhinus*, and I have gratefully to acknowledge his kindness.

For the School Sharks, *Mustelus*, the Wobbegong, *Orectolobus*, and the little Rock Shark, *Brachaelurus*, I have to thank various of my fishing friends. These specimens reached me in the fresh state. For the rest of the specimens I have to thank the Trustees of the Australian Museum and Mr. G. P. Whitley.

Only in the hyoid and mandibular segments was it found desirable to present detailed descriptions of the various muscles in each species. The branchial musculature proved so essentially similar throughout the series that it has been described in general terms.

THE SELACHII.

——		Branchial Segments.	Hyoid Segments.	Mandibular Segment.
Superficial Constrictors.	Dorsal ..	Csd.3–6	Csd.2	Absent
	Ventral ..	Csv.3–6	Csv.2	Csv.1
Deep Constrictors.	Dorsal ..	Cp.3–6	Cp.2	Cd.1
	Ventral ..	Absent	Interhyoideus	Absent
Levators		Lev.3–6	Lev.2	Lev.max.sup.
Epibranchial Spinal muscles		Ep.br.3–6	Absent	Absent
Adductor Muscles.	Dorsal ..	Ep.3–6	Absent	Pterygoideus Lev.lab.sup. (Marion) Add. (Vetter)
	Middle ..	Add.arc.br.	Absent	Quadrato-mandibularis
	Ventral ..	Absent	Absent	Absent
Depressors		Coraco-branchialis	Co.hyoideus	Absent

Hypobranchial spinal muscles. Coraco-mandibularis and coraco-branchialis communis.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

THE SUPERFICIAL CONSTRICTORS.

A. Dorsal. Each of the dorsal constrictors presents two portions which, following Lightoller,* I will designate partes inscriptionalis and arcuata. It should be clearly grasped at the outset that each of the constrictor sheets, both superficial and deep, is placed behind its

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* Lightoller (p. 352) regards the deep constrictor as portion of the superficial, and designates it " pars branchialis ". I have followed earlier workers in designating this part of the perfectly continuous branchial sheet the " deep constrictor ", because in the hyoid segment throughout the whole of the vertebrata this part of the sheet is deep to the rest; even in the branchial segments the designation is justified by the fact that this part of the sheet is deeply placed, and the other two parts superficially placed.

respective gill pouch, but in front of the cartilaginous support of the septum of which it forms the muscular component. This fact is likely to be overlooked by reason of the caudad growth superficially of the septa, causing the posterior portion of each septum to act as the lateral wall of the pouch behind, and, in this portion, not limiting the pouch in front of it. This is liable to lead one to regard the constrictor sheets as being placed in front of their respective pouches.

That portion of the dorsal superficial constrictor which lies superficially, and lateral to the pouch behind, constitutes the pars arcuata; the portion more deeply placed is the pars inscriptionalis. These dorsal constrictors take origin from the aponeurotic investment of the trunk muscles, fascia dorsalis. Each pars arcuata has an origin in common with the pars inscriptionalis of the muscle behind it. From their origin the direction of the fasciculi is ventrad with a convexity laterad. At the superior fornix of the gill pouch the pars arcuata of the one passes superficially, whilst the pars inscriptionalis of the other passes more deeply. At the line of the divergence of these fibres there is either the dorsal extrabranchial cartilage or simply a tendinous interruption.

These dorsal superficial constrictors may pass uninterruptedly ventrad into the corresponding ventral constrictors, or the continuity of the fasciculi may be interrupted by the insertion of more or fewer of their number into a prominent mid-lateral gill-ray, and/or a mid-lateral tendinous interruption which may or may not be confined to the pars inscriptionalis.

B. Ventral.—The four ventral superficial branchial constrictors present partes arcuata and inscriptionalis which correspond to the portions of the respective dorsal constrictors, and in most cases are simply ventral continuations thereof. The insertion of these is: (1) superficially, into the ventral deep fascia on either side of the hypobranchial spinal muscles, and (2) into deeper structures which may be (*a*) the ventral extrabranchial cartilages, which in turn are bound to the ventral surface of the gill arch by fibrous membranes, or (*b*) simply such fibrous membranes without the cartilage. It is, of course, the pars arcuata which is inserted superficially and the pars inscriptionalis which is inserted the more deeply.

THE DEEP CONSTRICTORS.

A. Dorsal.—There are four interbranchial muscles. These are essentially similar to the partes inscriptionalis of the superficial sheet. Not only is this so but, in many examples, it is quite impossible to decide definitely where the one begins and the other ends. The deep portion of the superficial constrictor lies anterior to and in contact with the outer ends of the gill rays, the deep constrictor lies against the inner ends of the same rays. These interbranchial muscles take origin above from the extrabranchial cartilage which at its deep, inner, end is firmly bound to the aponeurosis of the trunk muscles, or they take origin from the fascia dorsalis direct. They are inserted below either into the ventral extrabranchial cartilage or, without its intervention, into the ventral end of the arch. These deep constrictor sheets may or may not be interrupted by the insertion of more or fewer of the fasciculi into one or more of the gill rays. In none of the examples dissected was there found any portion of the interbranchial muscle passing direct to either the epibranchial cartilage from above or the cerato-branchial from below as was found in *Heterodontus*.

B. Ventral.—No complete subarcualia transversi were observed in any of the selachians dissected. On the other hand, I have been able to confirm Marion's observation that some of the fibres both of the pars inscriptionalis and of the deep constrictor in *Squalus* (*Acanthias*), as also in *Mustelus*, find an insertion into the deep fascia of the coraco-mandibularis muscle.

THE BRANCHIAL LEVATOR MUSCLES.

The branchial levator sheet was first described by Lightoller. I have been able to confirm his observations upon *Mustelus* and *Orectolobus*, and have found the same sheet in *Brachaelurus*, *Sphyrna*, *Pristiophorus* and *Chiloscyllium*. In *Squalus* (*Acanthias*) also, the levator sheet is present but so very fine are the several muscles that, had one not been searching for them, it is doubtful whether they would have been observed. *Orectolobus* and *Brachaelurus* are closely related to *Scyllium*, a form which has been studied by several writers. Although none of them has described the branchial levators, it is probable that they will be found when carefully sought for.

When the dorsal superficial constrictors are carefully freed from the fascia dorsalis, a dorsal venous sinus is exposed. This is of variable size and is particularly large in *Mustelus.* When it is opened along the length of the dorsal limit of the branchial basket and its glistening lateral wall dissected off the wall of the atriopharynx, the branchial levator sheet is exposed. This consists of five muscles; each is a thin quadrilateral muscle which takes origin above from the deep surface of the tendinous origin of the corresponding superficial dorsal constrictor, and is inserted into the fibrous strands and membranes which bind the pharyngo- and epibranchial cartilages together, but, as the ventral margin of each muscle lies above the epibranchial cartilage not far from the centre of its length, the insertion is, in the main, into that cartilage. These muscles lie one behind the other in the median wall of the gill pouches above the level of the pharynx, and in an antero-posterior vertical plane.

Innervation.—Innervation is certainly by the anterior spinal nerves, but there is, possibly, also a motor supply from the post-trematic rami of the IXth and Xth nerves.

THE EPIBRANCHIAL SPINAL MUSCLES.

The epibranchial spinal muscles are constantly present in all the selachians heretofore examined. The most anterior, which, following Vetter, will be designated the subspinalis, takes origin from the ventrum of the cranium, the underside of the trunk muscles and the lateral vertebral spinous processes close thereto, and passes ventrad, caudad, and slightly laterad, to be inserted into the dorsum of the first pharyngobranchial near its posterior end. Each of the remaining three muscles takes origin from the posterior edge of the first, second or third pharyngobranchial cartilage near the joint with the epibranchial, and is inserted onto the anterior edge and dorsal surface of the pharyngobranchial behind.

These, like the branchial levator muscles, are innervated by spinal nerves.

THE BRANCHIAL ADDUCTOR MUSCLES.

A. Dorsal.—The oblique epiarcual muscles are four in number. Each takes origin from the lateral edge of a pharyngobranchial cartilage and passes across the joint to an insertion on the posterior edge of the epibranchial cartilage of the same arch. In some species the muscles also gain attachment at the upper end to the pharyngobranchial cartilage of the arch behind, but this is always a secondary origin. The muscles lie in the angle formed between the two cartilages. The lateral edge of the pharyngobranchial is also the posterior, so that the muscles lie behind the arches.

B. Middle.—The adductores arcuum branchialium are four in number. Each is a relatively small muscle which spans the angle between the cerato- and epibranchial cartilages, each lying in front of and medial to its arch. The muscles lie close against the capsule of the joint and may be said to take origin from the epibranchial and to be inserted into the ceratobranchial.

C. Ventral.—There are no oblique subarcual muscles developed in connection with the branchial arches of any of the selachian examples examined.

Ventral interarcual muscles are not developed either in any selachian as yet examined.

BRANCHIAL DEPRESSOR MUSCLES.

The coraco-branchialis is a composite muscle presenting five very similar component portions. They arise together from the lateral portion of the coracoid arch or from a very strong investment of the hypobranchial spinal muscles which is attached to that arch. From this origin they diverge as they pass dorsad and cephalad on the lateral wall of the pericardium to be inserted onto the ventral surface of the first to the fourth hypobranchial cartilages. The most anterior slip of the muscle may obtain an insertion into the hypohyal, and the last commonly extends back to be inserted also into the fifth basibranchial as well as the fourth.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The hypobranchial spinal muscles are so essentially similar to those of *Heterodontus,* which is described in detail later, that it is quite unnecessary to describe them here.

The following table of synonymy of the hyoid and mandibular muscles is printed for purposes of check-reference.

Synonymy of the Hyoid Muscles in the Selachii.

Kesteven.	Lightoller.	Marion.	Vetter	
Csd.2a pars arcuata	Csd.2c	Csd.2	Csd.2	Dorsal
Csd.2b pars inscriptionalis	Csd.2b	Csd.2	Csd.2	
Cd.2pr. interbranchialis	Csd.2a	Csd.2	Csd.2	
Csv.2a pars arcuata	Csv.2c	Csv.2	Csv.2	Ventral
Csv.2b pars inscriptionalis	Csv.2b	Csv.2	Csv.2	
Interhyoideus	Csv.2a	anterior part of interhyoideus	Csv.2	
Levator hyoidei	L.2	Levator hyoidei		
Coracohyoideus	Not mentioned	Coracohyoideus		

Synonymy of the Mandibular Muscles.

Cd.1	Csd.1b″ Csd.1c	Csd.1	Csd.1
Csv.1a pars intermandib.	Csv.1a″	Csv.1	Csv.1
Csv.1b^2 pars extramandib.	Csv.1b″	Csv.1	Csv.1
Lev.max.sup.	L.1	levator maxillae superioris	
Pterygoideus	Csd.1a	Lev.lab.sup.	Add. B
Quadrato-mandibularis	Csd.1a + Csd.1b′ Csv.1a + Csv.1b′	Adductor mandibulae	

THE MUSCLES OF THE HYOID SEGMENT.

It will save repetition to state at the outset that these muscles are all innervated by the hyo-mandibular branch of the VIIth nerve.

The Superficial Constrictors.

The most detailed description of the dorsal superficial constrictor muscles in the selachians is that of Lightoller. He has described those of *Mustelus, Galeus* and *Orectolobus.* Whilst my own dissections enable me to confirm his descriptions, I find myself unable to accept the whole of his interpretation of the muscles.

LIST OF ABBREVIATIONS USED ON THE ILLUSTRATIONS TO PART I, SECTION 1.

Add.br., Mm.adductores arcuum branchialium ; Add.hy., M.adductor hyoidei ; B.br., Basibranchial cartilage ; Cd.1, Mandibular dorsal constrictor muscle ; Cd.2.pr., Hyoid deep constrictor, interbranchial, muscle ; Cer.br.c., Ceratobranchial cartilage ; C-g., M.coracomandibularis ; C-h., M.coracohyoideus ; C.n., Capiti-nuchal muscles ; Cor., Coracoid arch ; Cr.gl., M.cranioglossus ; Csd.2b, Pars inscriptionalis of the dorsal superficial hyoid constrictor muscle ; Csd.3-6 a & b, Partes arcuata and inscriptionalis of the dorsal superficial branchial constrictor muscles ; Csd.3.pr., The first deep branchial constrictor, interbranchial, muscle ; Csv.1a., Pars intermandibularis of the ventral mandibular superficial constrictor muscle ; Csv.1b^2., Pars extramandibularis of the ventral mandibular superficial constrictor muscle ; Csv.2b, Pars inscriptionalis of the ventral hyoid superficial constrictor muscle ; Csv.3-6 a & b, Partes arcuata and inscriptionalis of the ventral superficial branchial constrictor muscles ; Ct., The thick perichondrium of the symphysis ; Cu., M. cucullaris ; D.a-o.p., Dorsal antorbital process ; E.c., Ethmoid cartilage ; E.m., External branch of the hyomandibular ramus of the VIIth nerve ; Ep.br.c., Epibranchial cartilage ; Epi.o., M. epiarcualis obliquus ; Epi.sp., M. epibranchialis spinalis ; Ex.br.c., d & v., Dorsal and ventral extrabranchial cartilages ; F.1 & 2, The line of the floor of the first and second gill pouches ; G.c.1 & 2, The position of the first and second gill clefts ; H-h., M. interhyoideus ; Hy.c., Hyomandibular cartilage ; Hy.br., Hypobranchial cartilage ; Hy.br.c., Hyobranchial cartilage ; Hy.gl., M. hyoglossus ; Hy.m., Hyomandibular cartilage ; I.h. & I.hy., M. interhyoideus ; Lb.c., Labial cartilage ; L.hy., M. levator hyoidei ; L.l.i., M. levator labii inferioris ; L.l.r., The lateral ligament of the rostrum ; L.l.s., M. levator labii superioris ; L.mx.s., M. levator maxillae superioris ; Lev.hy-mn., M. levator hyomandibulae ; Lev.pal., M. levator palatini ; L.r., M. levator rostri ; L.r.r., Ligamentum radicis rostri ; Mck. & Mn., Meckel's cartilage ; Md.l., M. mandibulo-labialis ; Mn.V., The mandibular ramus of the Vth nerve ; Mx.l., M. maxillo-labialis ; Op., Opercular flap ; Op.r., Opercular rays seen through the flap ; P.l.s., M. protractor labii superioris ; P.s.l.i., M. protractor superior labii inferioris ; Pt., M. pterygoideus ; Pty.a. & p., Partes anterior and posterior of the M. pterygoideus ; Qm., M. quadratomandibularis ; Qm.a., p. & v., Partes anterior, posterior and ventralis of the M. quadratomandibularis ; R., Superficial raphe ; Sp., The spiracle.

The roman numerals indicate the appropriate cranial nerve or its foramen, V^1, V^2 & V^3, the three rami of the Vth nerve.

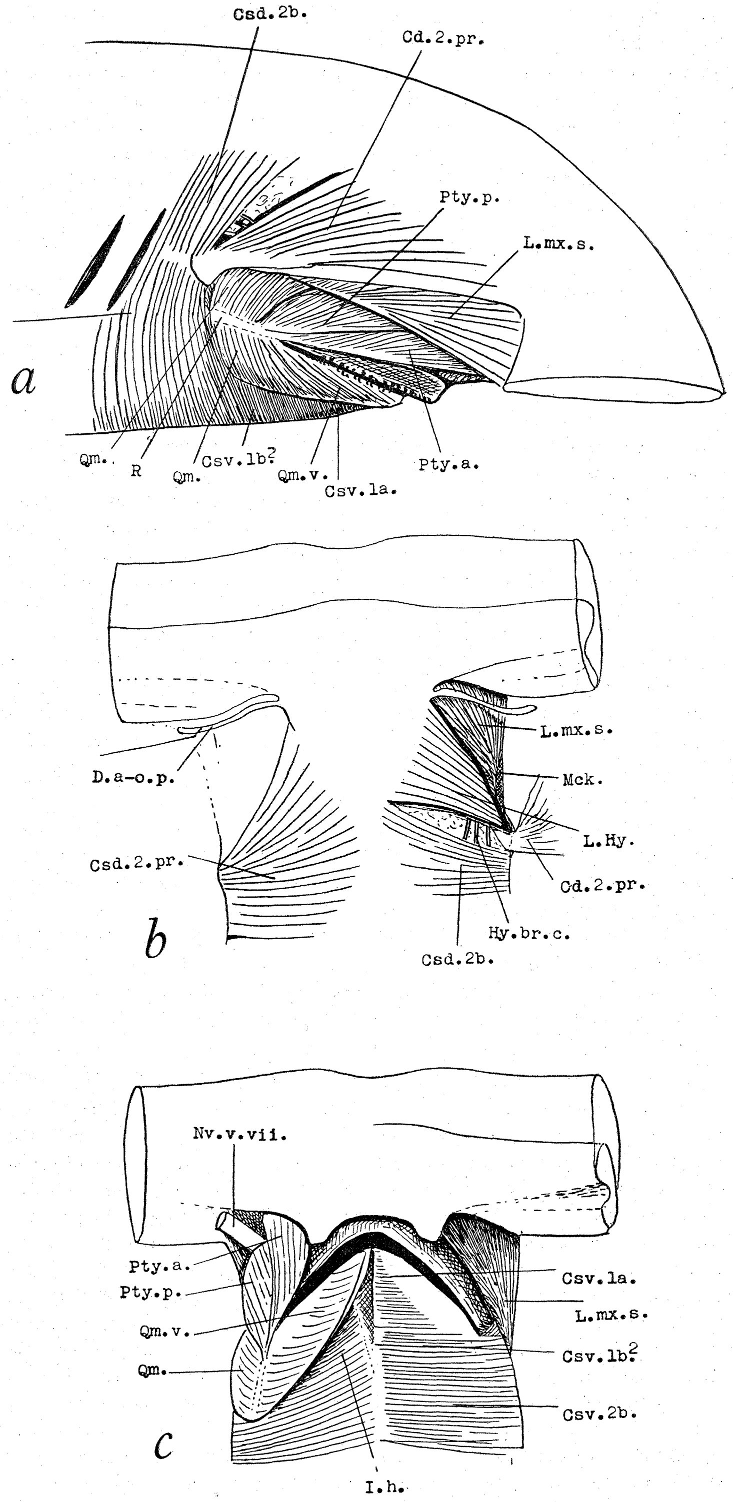

Fig. 4.—The hyoid and mandibular muscles of *Sphyrna*. A, lateral; B, dorsal; and C, ventral views. The right side more deeply dissected than the left.

A. Dorsal.—The superficial dorsal hyoid constrictor is essentially similar to the branchial muscles. There is, however, no similar muscle anterior to it, so that whilst there is the community of origin between the pars arcuata of this and the pars inscriptionalis of the muscle behind—the first dorsal superficial branchial constrictor—there is no similar common origin of two muscles dorsal to the spiracular cleft. The origin of the two portions of the muscle is from the fascia dorsalis posterior to the spiracle, and separated therefrom by the deep constrictor, which has acquired a superficial position. Ventrally the muscle is, in conformity with the superficial constrictors behind it, either continued more or less uninterruptedly over into the ventral constrictor or interrupted by the insertion of more or fewer of its fasciculi into a prominent middle gill-ray.

B. Ventral.—The ventral hyoid superficial constrictor also is essentially similar to the branchial constrictors behind it, and its origin medially is either from a median ventral raphe, and this is the commonest condition, or from the aponeurotic investment of the hypobranchial spinal muscles.

THE DEEP HYOID CONSTRICTORS.

A. Dorsal.—This is represented by that anterior portion of the superficial dorsal constrictor which lies against the inner ends of the pseudo-hyoidean gill rays. A careful analysis of the musculature of the interbranchial muscles and their related partes inscriptionales will demonstrate that the latter cannot be regarded as extending deeper on the septum than the outer ends of the gill rugae. At this depth, if not more superficially, it is commonly found that there is a change in the texture of the fasciculi, the deeper being the finer, and in most forms there is, in addition, above and below, a very readily demonstrable difference of direction, and/or origin and insertion. Now in the hyoid dorsal superficial constrictor in the selachians one finds that, in every instance, the portion of the muscle which Lightoller designates pars inscriptionalis extends forward and deeply, quite uninterruptedly, till it comes to lie in contact with the deep ends of the pseudo-hyoidean gill rays, with the gill rugae on the other side of those rays. That is to say, its most anterior portion occupies a position relative to the gill rays and filaments which, in the branchial segments, is occupied by the deep constrictors.

The origin of the muscle is from the fascia dorsalis, its insertion being into the loose fibrous tissue which separates the posterior margin of this muscle from the pars extramandibularis of the first ventral superficial constrictor. Posteriorly the muscle is, as already stated, quite inseparable from the pars inscriptionalis of the superficial constrictor. Anteriorly above it blends, without limiting margin, with the hyoid levator; below it is limited by its own loose perimysium, by which it is separated from the insertion of the hyoid levator and from the insertion of the pars extramandibularis, Csv.1b^2.

Briefly the contention here is, that the muscle which previous workers, except Lightoller, have designated the superficial dorsal constrictor of the hyoid segment, is *that* muscle plus the interbranchial muscle or deep dorsal constrictor of the segment.

The truth of this contention is most strikingly proven by the muscle in *Chiloscyllium.*

Commencing at the posterior margin of the muscle there is first a typical pars arcuata, which arises in common with the pars inscriptionalis of the first dorsal superficial branchial constrictor. In front of this, and perfectly continuous with it, is a typical pars inscriptionalis. The pars arcuata is covered on the deep surface as well as on the superficial by the skin. The pars inscriptionalis is covered superficially by skin, but has the outer free ends of the hyoidean gill rays against its deep surface, with the outer ends of the gill rugae on the other side of these rays. The anterior margin of the pars inscriptionalis is a slightly curved line which commences, at the common level of the dorsal superficial constrictors, above and a little forward of the first gill slit. From this point it passes ventrad and cephalad to the posterior margin of the outer end of the hyo-mandibular cartilage. There is along this line a narrow ribbon of fascial tissue from which the fibres of the pars inscriptionalis appear to take origin, and which also separates the anterior margin of the pars inscriptionalis from the hyoid levator in front of it. When, however, the fibres of the pars inscriptionalis which appear to arise from the narrow ribbon are carefully dissected free from it, they are found, every one of them, to turn mediad and pass deeply between the posterior surface of the hyoid levator in front and the deep, attached ends of the hyoidean gill rays behind them. These fibres are beyond doubt completely homologous with the fibres of the deep branchial dorsal constrictors. Like them, they provide a muscular layer for the anterior wall of the branchial pouch in its depth, and arise from structures along the dorsal fornix of the depth of the pouch.

They also reproduce very faithfully the conditions found in the anterior wall of the first gill pouch in the rays.

In *Sphyrna* (Figs. 4, A, B and C) the pseudo-hyoid and the hyo-branchial rays are very superficially placed throughout their length. The Cd.2.pr. arises from the fascia dorsalis, reaching almost to the mid-dorsal line and so far forward as to lie almost above the anterior margin of the lower jaw. The fibres are directed caudad and ventrad and are inserted into the subdermal tissues attached to the outer end of the hyo-mandibular. The first branchial pouch is continued far forward above the mouth, almost so far as the anterior margin of this Cd.2.pr. These fibres, however, are not in contact deeply with the hyoid gill rays, except just a few of them along the posterior margin of the muscle. Whilst the hyoid levator appears to have retained its normal origin from the skull, at the posterior margin of the orbital region, the absence of spiracle and of the orbital structures has permitted the first branchial pouch to grow forward beneath it, capturing the spiracular space. The Cd.2.pr. has grown forward, but superficially to the levator. It is significant, however, that none of the fibres are superficial to the levator muscle at their insertion.

The Cd.2.pr. grows forward over the levator hyoidei in *Carcharhinus* also. In this form the two muscles are fused along their anterior margins but are readily separable posteriorly. It is worthy of note that this peculiar forward growth of the Cd.2.pr. superficial to the hyoid levator was found only in these two genera which are both devoid of a spiracle. Lightoller has described the muscle in *Carcharhinus* under the designation pars epihyoidea (Csd.2a) of the second superficial dorsal constrictor.

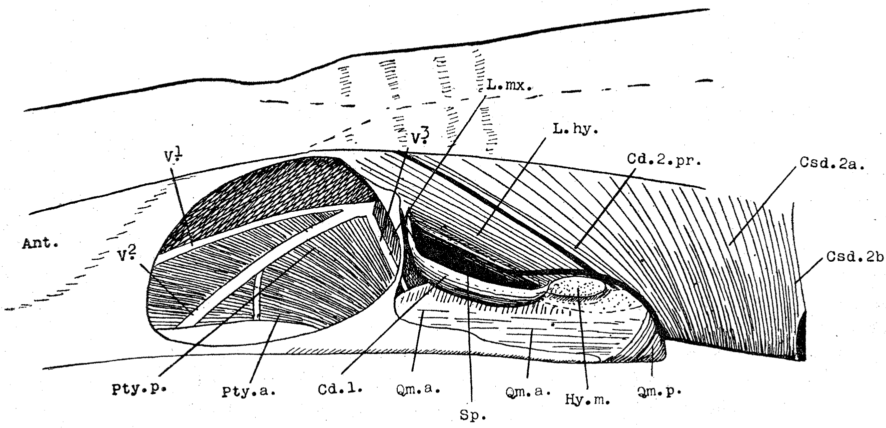

Fig. 5.—Some of the hyoid and mandibular muscles of *Pristiophorus*. Lateral view.

Pristiophorus (Fig. 5).—The superficial dorsal constrictors arise from the fascia dorsalis along a line which is level with the upper margin of the orbit in front and slopes ventrad as it extends backwards. This is the line of origin, not only of all the superficial dorsal constrictors, but also of the hyoid levator in front of them, and the swelling of the muscles immediately below their origins causes a longitudinal sulcus along the line of origin which is quite obvious before the skin is removed. The anterior limit of Cd.2 is over the middle of the spiracle, the posterior limit directly dorsal to the first gill slit. The most anterior fasciculi of the Cd.2.pr., some half dozen or so, slope ventrad and caudad to be inserted into the subcutaneous tissue over the outer end of the hyo-mandibular. Behind these a narrow band of fasciculi is inserted into the quadrate itself just below the joint with the hyo-mandibular cartilage. The most posterior fibres, also quite a few fasciculi, are inserted behind these last into the hyo-branchial rays. Fibres immediately behind these belong to the pars inscriptionalis.

The anterior margin is in contact with the posterior margin of the levator hyoidei, but there is no fusion of the two muscles ; they may be cleanly and readily separated from origin to insertion.

In *Acanthias* and *Mustelus* the muscles fit the general description given above.

The Cd.2.pr. in *Mustelus* is somewhat peculiar in that it blends indefinitely with the hyoid levator in front of it. Lightoller finds a cleavage plane parallel to the surface which divides the levator into superficial and deep portions. The superficial portion he regards as the anterior "pars epihyoides" of the Csd.2. The deep portion alone he identifies as the levator. The cleavage plane which he describes is undoubtedly present, but I am not able to satisfy myself that it is not fictitious. With a view to determining this point I have dissected four individuals. In the eight muscles thus dissected I have found a single clean cleavage in four, two such in one, and three such in three. In each case the anterior limit of the muscle was determined on each side and the head was then cut right through in the transverse vertical plane immediately in front of the muscle, then cut through in the same plane at the first gill slit. It was next divided down the mid-sagittal plane. The muscle was then cleaned both on its superficial and deep surfaces, and cleavage planes sought for. None was accepted as a cleavage plane unless no fasciculi were severed in the separation of the two portions of the muscle.

Both Vetter and Marion state that in *Acanthias* a large portion of the anterior fibres of the Csd.2 are inserted into the dorsal and posterior edge of the quadrate end of the palate quadrate. Vetter and Marion described *Acanthias vulgaris*; I have worked on the allied species *A. megalops* Macleay. In this form I find that only two fasciculi on each side are inserted into the back of the palate quadrate, and that the remainder pass deeply under the fibrous tissues, into which they appear to be inserted, behind the jaw, and are either inserted into the bases of two or three of the hyoidean gill rays or are continued ventrad into the pars profunda of the ventral constrictor of the hyoid segment.

The apparent difference arises from the fact that both these authors regard the hyoid levator as the anterior portion of the hyoid constrictor.

The Pars Epihyoidea.—This term was introduced by Lightoller to designate the anterior portion of the dorsal constrictor sheet in the hyoid segment. As already stated, he regarded this as the anterior portion of the superficial constrictor, whilst I have just been describing it in detail as the pars profunda of the sheet, or the deep constrictor.

It is a fact that in a majority of the examples studied more or fewer of the fibres of the muscle are inserted into either the outer end of the hyomandibular or the posterior edge of the quadrate portion of the palatoquadrate or into both. The number of fibres so inserted is, however, very variable and in some instances none of the fibres are so inserted. This variability, taken in conjunction with the fact that throughout the whole of the batoid plagiostomes none of the fibres of the pars profunda of the dorsal hyoid constrictor have an insertion onto either of these two cartilages, leads me to regard the insertion as of entirely secondary importance.

In other words it is not regarded as an inherited feature, but rather as an individually acquired feature resulting from the mechanical or spatial conditions imposed by the variations in the skeletal structures.

B. Ventral.—The interhyoideus is a narrow strap-like muscle which takes origin from a relatively extensive length of the ventral median raphe under cover of and in contact with the first ventral superficial constrictor. From this origin the muscle tapers to a short rounded tendon which is inserted into the contiguous ends of the hyomandibular and ceratohyal cartilages. The proportion of fibres inserted into each is variable, but the greater number in all the examples studied are inserted into the lateral end of the ceratohyal.

The anterior margin of this muscle is always clearly defined and the separation of the muscle from the overlying Csv.1 is quite easy and definite, but posteriorly it becomes gradually fused with the superficial layer. In some forms this fusion implicates the pars extramandibularis of the first ventral constrictor, but in the majority of the examples it was possible to separate the muscle completely therefrom. On the other hand, in no case was it possible to define the posterior margin of this hyoid deep ventral constrictor from the anterior margin of the pars inscriptionalis of the superficial ventral hyoid constrictor. This fact has led to the muscle being treated, by previous observers, as the anterior portion of the superficial constrictor of the hyoid segment.

Undoubtedly it is part of the primitive constrictor sheet, but it is the deeper part, completely comparable with the dorsal deep constrictors of the branchial segments, each of which lies in continuity with the more superficial portion of its own sheet behind it.

THE HYOID LEVATOR.

Sphyrna (Fig. 4, B).—The hyoid levator in *Sphyrna* is an unique flat triangular muscle, with a thin posterior and thicker anterior margin. It arises in common with the pars profunda of the Cd.2, though not extending quite so far back as that muscle. It has also an origin from the vestigial antorbital process and from the perichondrium of the skull in front of this last. Its fibres pass ventrad and caudad, but at an angle with those of the pars profunda, to be inserted along the posterior half of the dorsal edge of the lateral surface of the hyomandibular cartilage.

The relation between this muscle and the deep constrictor, superficial to it, at their origin is of some interest. Actually they have preserved the relation of the branchial levator and deep constrictor.

It will be remembered that the superficial dorsal constrictors arise from the fascia dorsalis, but that the pars inscriptionalis of each is interrupted by a tendinous intersection which is attached to the dorsal extrabranchial cartilage. Now, the levator passes down on the medial wall of the branchial pouch taking origin above from the tendinous origin of the superficial constrictor. It, therefore, passes, and is bound to, the medial edge of the deep end of the extrabranchial cartilage. The interbranchial muscle takes its origin from the inferior edge of this same cartilage.

In the branchial segments the presence of the pharyngo-branchial cartilage limits the dorsal extent of the gill pouch. In the hyoid segment of *Sphyrna* there is no cartilage to stay the dorsal extension of the pouch which has therefore been able to rise internal to the levator as well as the constrictor.

Pristiophorus (Fig. 5).—The hyoid levator in *Pristiophorus* lies anterior to and parallel with Cd.2.pr. Superficially it is in series with the constrictors, but extends more deeply. It takes origin in front of Cd.2.pr. from the tendon of insertion of the trunk muscles into the skull, and from the post-orbital process and the side of the auditory capsule, extending deeply, almost to the ventrum of the skull behind the orbit. It is inserted onto the dorsal edge of the outer two-thirds of the length of the hyomandibular cartilage. This is a thick fleshy muscle which provides the full depth of the posterior wall of the spiracle lying between that cleft and the anterior wall of the first gill pouch.

Innervation.—This is by two or three twigs which leave the hyomandibular ramus of the VIIth nerve as it winds laterad, caudad and superficiad across its anterior surface under cover of the skin, on the posterior wall of the spiracle.

Chiloscyllium (Fig. 6).—In *Chiloscyllium* the muscle is placed in front of the pars profunda of the constrictor, which, as already described, turns deeply in contact with its posterior surface. The levator is a compact thick muscle which arises from the side wall of the auditory capsule and passes cephalad, laterad and ventrad to the outer end of the hyomandibular cartilage. Its relation to the spiracle and its nerve supply are as in *Pristiophorus.* In fact so constant is this relation that it will not be repeated in the descriptions which follow.

Acanthias is essentially similar to *Chiloscyllium.*

Mustelus.—In *Mustelus* the levator is not definable from the pars profunda of the constrictor sheet behind it. For the purposes of description it is assumed that the fibres inserted into the outer end of the hyomandibular alone are levator fibres. If this assumption be granted, then we may briefly describe the levator of *Mustelus* as differing from that of *Pristiophorus* only in that the peculiar backward extension of the tensor palpebrae muscles lies between the levator and the skull, and occupies some of the space on the skull side wall that, in *Pristiophorus,* the levator arises from.

THE HYOID DEPRESSOR MUSCLE (Innervated by spinal nerves).

The coracohyoideus muscle is in series with the components of the coracobranchialis. The origin is from the coracoid lateral to the origin of the coracomandibularis and from the aponeurosis on the lateral and deep surface of this muscle. In some examples the origin from the coracoid is only indirect through the aponeurosis. The muscle is one of the largest of the hypobranchial spinal muscles, and its insertion is on to the hyoid copula just behind the lower jaw.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

THE CONSTRICTORS.

The excessive development of the middle adductor of this segment, to form the muscles of mastication, has, apparently, been responsible for the complete suppression of the middle fibres of both dorsal and ventral constrictors, so that they do not meet in the midline anywhere. Further, the dorsal constrictor has been crowded against the levator so that the two muscles are, at times, fused together.

A. Dorsal.—As might have been anticipated, this muscle is least modified in those forms with the largest spiracular apertures, such as *Pristiophorus.* In this genus the dorsal constrictor, Cd.1, takes the form of a well developed constrictor spiraculi (Fig. 5, Cd.1). It is a thin sheet of fasciculi which supplies the greater part of the thickness of the anterior and lateral wall of the widely open spiracle. An arcuate ridge around the anterior and lateral edge of the spiracle, formed by this muscle, is quite obvious before the skin is removed.

The muscle arises from the antero-lateral edge of the auditory capsule below the post-orbital process and in front of the origin of the M. levator hyomandibularis. From this origin the muscle trends horizontally, first laterad, then caudad, and finally mediad round the outer margin of the spiracle, to be inserted into the hyomandibular just above and medially to the hyomandibulo-palatoquadrate joint.

In *Acanthias, Orectolobus* and *Brachaelurus* the Cd.1 is essentially as in *Pristiophorus,* but in these other genera the spiracle is much smaller.

In *Mustelus* the muscle presents division into a more superficial and a deeper portion. The former is again divided into a superficial and a deep part. The last takes origin from the fibrous tissue about the upper end of the hyomandibular cartilage, above and behind the spiracle and, running forward, terminates in a fine tendon which is inserted into the upper eyelid at the outer posterior canthus. The superficial portion is a much larger component, which takes origin from the ventro-lateral portion of the occipital part of the skull deep to the origin of the second levator. This also runs forward and its terminal tendon is inserted into the lower eyelid, also at the outer canthus.

The deeper portion of this muscle is closely adpressed to the levator maxillae superioris and appears fused with it. Careful dissection reveals that superficially to the levator there is a muscle which may always be cleanly separated from it. The bulk of this muscle lies posteriorly to the levator ; it arises from the posterior edge of the post-orbital process and is separately inserted onto the outer margin of the upper surface of the palatoquadrate.

Mustelus is, in respect to its Cd.1, intermediate between the species with large spiracles and those devoid of the spiracle. In these last, *Sphyrna* and *Carcharhinus,* the whole of the muscle is modified to act upon the eyelid ; in *Mustelus* only portion is so modified.

Lightoller* (1939, p. 348) designates this the pars cranio-maxillaris of the muscle and failed to find the more normal part in *Mustelus* ; he failed to separate it from the levator (*l.c.*, Pl. II, fig. 6).

In *Chiloscyllium* the Cd.1 is very similar to that which we have just discussed in *Mustelus.* It is a small thin sheet of muscle which takes origin from the outer edge of the auditory capsule at the back of the orbit, and passes cephalad, laterad, and slightly ventrad, to be inserted into the superior margin of the quadrate portion of the palatoquadrate. Immediately in front of, and deep to, it is the small first levator, separated by a short but quite definite interval.

Innervation.—Norris and Hughes (1920, p. 337) state that in *Squalus acanthias,* " From the dorsal border of the main trunk of the ramus mandibularis (V) shortly after leaving the ganglion there are given off a few (three or four) small branches, which break up into numerous small twigs, motor elements supplying the levator palatoquadrati and spiracular muscles ". This levator palatoquadrati can be none other than the levator maxillae superioris which, as Marion has stated (1905), is confluent with the " Csd.1 ". I have found a similar innervation for the two muscles in *Pristiophorus, Chiloscyllium* and *Brachaelurus,* and I find the large levator maxillae superioris of *Sphyrna* to be similarly innervated.

My own dissection notes on *Pristiophorus* read as follows : The innervation (of the levator maxillae superioris) is from the mandibular ramus of the Vth nerve by a relatively large twig which leaves the ramus, just after that leaves the other rami, and plunges into the anterior surface of the muscle. A fine twig of this nerve was followed right through the muscle and found to terminate in a twig that had been observed passing from the posterior surface into the Cd.1. This confirms the findings of Vetter (1874).

For reasons which are stated later, this Cd.1 is regarded as being homologous with the deep constrictors of the branchial segments, the interbranchial muscles.

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* The pars nucho-maxillaris of Lightoller is the muscle which has been identified in this work as the M. adductor hyoidei in *Heterodontus.* It is innervated by the facial nerve. This muscle has not been found in any Selachian, but it is believed that its homologue is very generally present in the Batoids, where also it is innervated by the facial nerve.

B. Ventral.—The intermandibularis muscle of the selachians takes origin on each side from the inferior and posterior edge of the lower jaw and is inserted into a median ventral raphe. In most instances it is possible to recognize anterior, intermandibularis, and posterior, extramandibularis, portions of the muscle, Csv.1a and Csv.1b^2. The former takes origin entirely from the edge of the jaw, whilst the latter extends laterad and dorsad over the cartilage of the jaw to take origin in the aponeurosis of the quadrato-mandibularis. It should be understood, however, that in most examples this distinction is more or less arbitrary and that no definite line of cleavage between the two parts can be demonstrated.

More or fewer of the anterior fasciculi may be quite continuous from one side to the other. I find this condition in *Squalus* and *Brachaelurus*, and Lightoller finds a relatively araphic portion of the muscle in *Mustelus* and *Orectolobus.* The araphic portion is not present in *Carcharhinus, Sphyrna* or *Pristiophorus.* The presence of an araphic " M. submentalis " developed from the fifth muscle plate in the great majority of the vertebrata above the Elasmobranchs gives to these araphic fasciculi in some of the Sharks an added importance and significance.

Innervation.—The anterior and posterior portions of the muscle are both innervated from the terminal twigs of the mandibular ramus of the Vth nerve. There is also some motor (?) supply to the posterior portion from the ventral terminal twigs of the hyoid branch of the ramus hyomandibularis of the VIIth nerve.

THE LEVATOR.

As in the segments behind, the levator arises in close association with the deep constrictor, and in most instances the two muscles are inseparable at their origin. Actually the levator takes its origin deep to and in front of Cd.1, from the side wall of the auditory capsule in the majority of examples studied, but in some genera departs widely from this apparently more normal condition.

In six of the eight selachians dissected the levator maxillae superioris is a relatively small rounded, oval or flat muscle which arises from the side of the auditory capsule either just in front of the lateral angle so as to be within the orbit or just behind the orbit. From this origin it passes ventrad commonly with an inclination laterad and caudad to be inserted on the dorsal surface of the palatoquadrate.

In *Sphyrna* (Fig. 4) and in *Carcharhinus,* one of the forms dissected by Lightoller, the muscle is much more extensively developed.

Sphyrna (Figs. 4, 6 ; L.mx.s.).—The levator maxillae superioris is a massive flat triangular muscle which takes origin from the posterior edge of the proximal portion of the inferior antorbital process and from the side wall of the skull from that process back to the hyomandibular articulation. This latter area, along the side of the skull, is along the whole of the length where, normally, the structures of the orbit are situated. The origin is placed above the exit of the optic nerve and the origin of the extremely tenuous tendons of the oculomotor muscles. The lateral edge of the muscle is quite thin at the origin and these lateral fibres run almost directly caudad to their insertion. The posterior, medial margin of the muscle is thick and these fibres run nearly directly laterad to their insertion. The whole of the fibres converge to an insertion onto the capsule of the hyomandibulo-maxillary joint and onto the quadrate in front of the joint.

Innervation.—This, in my experience, is always by twigs from the mandibular ramus of the Vth nerve. This nerve always lies in front of the muscle altogether, or, as in such forms as *Sphyrna* in which the muscle is more extensive than usual, it lies beneath the muscle. The maxillary ramus of the Vth nerve in these forms runs to its destination between the levator maxillae superioris, placed superficially or dorsally to it, and the pterygoideus, situated medially or ventrally to it.

THE ADDUCTOR MUSCLES.

Two of the primitive adductors are recognizable in the mandibular segment, namely, the epiarcual oblique and the middle adductor. It is believed that the former is completely homologous with the pterygoideus muscle of higher forms, and it will be described under that designation. The middle adductor will be designated the quadrato-mandibularis, a name adopted from Lightoller. It is believed that it presents the fore-runners of more than one of the adductor muscles of the mandible of higher forms and, since the term adductor mandibularis of Vetter, Marion and other previous workers includes that which I designate the pterygoid, it seemed desirable to make use of another name and one that had not been applied to any of the muscles present in the higher forms. Lightoller included the "pterygoideus" under his designation, but, as it has not been generally adopted, its use is not so liable to convey a misconception as would the use of any designation already generally adopted.

THE PTERYGOIDEUS* (EPIARCUAL OBLIQUE) MUSCLE.

This is the muscle which Vetter designated Add. β and to which Marion applied the name levator labii superioris, adopting a suggestion by Vetter that the muscle were more correctly included among the superficial constrictor muscles. Lightoller describes the muscle with the quadrato-mandibularis and regards it as being an undifferentiated portion of the first dorsal superficial constrictor. He designates it Csd.1a.

Typically, that is to say, in the majority of the examples studied, the pterygoid muscle arises from the ventrum of the skull in front of the mouth, usually from the nasal capsule or from some process thereof. The origin is relatively extensive and the fibres converge to a tendon which is inserted into the mandibular cartilage immediately behind the gape. This insertion may extend down across the outer face of the cartilage to its median inferior edge. Always on the outer, superficial, surface of the mandible, the insertion may be confined to the upper edge or may be in part into that edge and in part into the tendinous raphe which is commonly found strongly developed on the surface of the quadrato-mandibularis muscle or at close to the angle of the gape of the jaws.

The muscle always presents two component parts, which may be more or less completely blended along their contiguous surfaces or may be readily and quite cleanly separated along those surfaces. At and close to their insertions the two portions are always blended.

In the majority of those examples in which the superior labial cartilages are well developed this pterygoideus muscle is intimately bound to the upper of the two.

In *Acanthias megalops* (Fig. 7) I find the pterygoideus muscle to be essentially similar to that of *Acanthias vulgaris* as described by Marion. It takes origin from the inferior surface of the skull to one side of the midline a little distance behind the nasal capsule. It is a rounded muscle and proceeds laterad with a slight curve caudad till it reaches the angle of the gape; here it crosses the palatoquadrate and terminates in a fine strong tendon which penetrates the quadrato-mandibularis, and becomes lost as it breaks up among those fasciculi of that muscle, which are inserted into the tissues of the side of the mouth. Near its origin, the ventral surface of the muscle is intimately bound to the upper labial cartilage, whilst its concave posterior surface lies against the front of the palatoquadrate.

The superior maxillary division of the fifth nerve crosses the muscle just behind its origin. The mandibular division crosses the palatoquadrate some distance further back and divides into two branches, one of which passes ventrad in front of the quadrato-mandibularis and, crossing the tendon of the pterygoid muscle, ends in the deep fascia beneath the skin behind the jaw and innervates the Csv. (Norris and Hughes). The other branch burrows beneath the adductor and will be described later.

Careful dissection reveals that the muscle is composed of two parts: (1) A pars anterior which arises as just described and which is inserted onto the anterior tip of the labial cartilage. This portion is very short. (2) A pars posterior arising from the upper surface of the labial cartilage and inserted as just described.

In *Mustelus* (Fig. 8) the origin of the pterygoideus muscle is much more extensive: (i) from the greater part of the posterior wall of the nasal capsule; (ii) from the inferior surface of the floor of the same capsule along a line, immediately in front of the attachment of the palatoquadrate thereto, which extends from the lateral edge almost to the midline; (iii) from the lateral edge of the ethmoid process on the dorsum of the palatoquadrate behind the nasal capsule. The superficial fibres of the muscle are inserted into the anterior end of the median superficial raphe of the quadrato-mandibularis; the deeper fibres are gathered into a fine strong cord-like tendon which burrows beneath the superficial fibres and is inserted into the tissues of the side of the mouth. When the muscle is released from its origin, it is found that the portion which arises from the posterior wall of the nasal capsule provides practically all the deep fibres and that this portion is incompletely separable from the rest, and further, that when that separation has been effected, the appearance is that one has thus separated a muscle which completely corresponds

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* See discussion on this designation on p. 60.

with the pars anterior of *Acanthias*, and that the remainder of the muscle is the pars posterior. The superficial fibres take origin, not only from the other situations but also from a band of tendinous fibre which connects them and arches over the deeper portion without being bound thereto. Fusion of the superficial and deep portions commences a short distance behind this band and becomes more definite as the quadrato-mandibularis is approached.

The maxillary division of the fifth nerve crosses the surface of this muscle in front of the band uniting the origins of its superficial portion. The mandibular division of the nerve plunges out of sight between this muscle and the quadrato-mandibularis under cover of a strong band of fibrous tissue which unites the muscle superficially along their line of cleavage. On separating the muscles, the nerve is found proceeding backward and medially parallel to the cleavage plane, imbedded in the anterior face of the quadrato-mandibularis, and here it gives off the motor branches to the muscle. At the angle of the mouth it crosses the tendon of the pterygoid muscle and breaks up into its terminal branches to the tissues on the ventrum of the mouth and to Csv.1.

Sphryna (Fig. 4, Pty.a., Pty.p.).—The pterygoideus in this form is very nearly completely divided into its two components. The pars anterior (Pty.a.) is a relatively thick short muscle which arises from a pocket formed, at the anterior end of the orbital region of the skull, by the cranium itself medially, the lateral " hammer-head " process ventrally, and the inferior antorbital process in front. The muscle tapers rapidly as it passes caudad with a slight inclination laterad. It is clothed on its median surface by the tendon into which its fasciculi are inserted. The tendon continues caudad, crosses the upper jaw in the fold of the upper lip just in front of the angle of the mouth. At the angle of the mouth it breaks up into a brush of fine tendrils which attach it to the fascial structures of the quadrato-mandibularis, and of these especially to the transverse raphe which crosses it from the gape to the Q-M. joint.

The pars posterior (Pty.p.) arises from the lateral and inferior surface of the palatoquadrate for about the centre one-third of its length. It is a blunt-ended spindle-shaped muscle similar to the pars anterior and, like it, is clothed on the median and inferior surface by a tendon into which its fasciculi are inserted and which serves very efficiently to separate it from the pars anterior for the greater part of their contactual surfaces. The tendon is inserted into the superficial raphe of the quadrato-mandibularis in common with that of the pars anterior. Most of its fasciculi are inserted into its own tendon, but those arising from the palatoquadrate close to the posterior end of the area of origin are inserted into the tendon of the pars anterior, which lies ventral to it at this point. The dorsal surfaces of both parts of the muscle are in contact with the ventral surface of the levator maxillae superioris.

Innervation.—This is by a branch of the mandibular ramus of the fifth nerve which leaves the main ramus just after that separates from the maxillary ramus.

Pristiophorus (Fig. 5).—Here, too, the pterygoideus is very completely divided into its two components.

The pars anterior (Pty.a.) is quite a small group of fibres which arise by a fine tendon from the apex of a spur which projects posteriorly from the middle of the inferior and posterior edge of the nasal capsule. The tendon is continued down the lateral edge of the muscle as well as investing its tenuous apex. The fasciculi are inserted onto the lateral edge of the tendinous investment of the posterior end of the pars posterior.

The pars posterior (Pty.p.) is a very massive muscle. It arises from the inner edge of the spur from which the pars anterior arises, and from the lateral half of the inferior surface of the nasal capsule and skull back to the articulation of the ethmoid tubercle of the palatoquadrate with the skull. From this extensive origin the fibres pass caudad and laterad, converging to be inserted into a broad tendinous sheath which invests the medial and inferior surface of the posterior one-half of the length of the muscle. This tendon lies against the inferior edge of the lateral surface of the palatoquadrate, and anteriorly and medially the thick, rounded posterior edge of the muscle lies in a broad sulcus on the anterior surface of the palatoquadrate. The tendon passes behind the angle of the gape and is inserted onto the outer surface of the mandible medial to the insertion of the quadrato-mandibularis.

Innervation.—This is from the mandibular ramus of the fifth nerve by a branch which leaves the main ramus and crosses forward and ventrad onto the upper surface of the pars medialis.

The main ramus runs caudad and mediad along the posterior edge of the pars medialis and then dips under the anterior edge of the pars anterior of the quadrato-mandibularis along the fissure between the two muscles. Behind the angle of the gape the muscles become intimately blended and here the nerve burrows under the tendon of the pterygoideus and turns forward and superficiad. The motor twigs to the quadrato-mandibularis are given off by the nerve whilst it lies in the fissure.

Chiloscyllium (Fig. 6).—This is one of the most interesting and instructive forms that have been dissected. In this genus we find the pterygoid passing up onto the dorsum of the cranium just as it does in *Chimaera* and as in *Neoceratodus* and the Tetrapoda generally. Particular attention is drawn to these several forms because it is believed that there is no room for doubt that the pterygoideus muscle of *Chiloscyllium* is completely homologous with the other pterygoideus muscles just described; it is also believed that the study of *Chimaera* and *Neoceratodus* leads us naturally to the identification of the same muscle in the Axolot and finally in the amphibians and tetrapods generally.

The pars anterior is here much the larger of the two parts (Fig. 6, Pty.a.). It arises from (i) the dorsum of the skull medially to the orbit and as far forward as the nasal capsule, (ii) from the front of the antorbital process, (iii) from the posterior wall of the nasal capsule, and (iv) from the side of the skull between these last two. This remarkable massive muscle is clothed along its postero-medial (deep posterior) edge by a strong tendinous sheath into which its fasciculi are inserted. The tendon crosses the palatoquadrate behind the angle of the mouth, then crosses Meckel's cartilage between the partes ventralis and posterior of the quadrato-mandibularis muscle and is inserted into the inferior, postero-medial, edge of the cartilage.

The pars posterior (Fig. 6, Pty.p.) is a quite small muscle which arises from the lateral and inferior corner of the antorbital process. The fibres of this muscle are inserted close together onto the posterior edge of the tendon of the pars anterior as that tendon crosses the palatoquadrate.

Innervation.—This is by a branch of the ramus mandibularis of the Vth nerve which leaves the main trunk just as that nerve reaches the upper margin of the palatoquadrate at the anterior and inferior margin of the orbit. The main nerve then continues on its way against the anterior surface of the quadrato-mandibularis and beneath the tendon of the pterygoideus and fibres of its pars posterior. It burrows beneath the tendon of the pterygoideus and turns mediad and superficiad.

THE QUADRATO-MANDIBULARIS (MANDIBULAR ADDUCTOR) MUSCLE

In general terms this muscle may be described as a complexly arranged mass of muscle fasciculi which arises from the quadrate portion of the palatoquadrate and are inserted into Meckel's cartilage, and, indeed, it is essentially in this manner that previous workers have described it.

The careful comparative study of many forms, however, leads one to the discovery that there is, underlying the apparently orderless arrangement of the fibres, one fundamental plan.

Each of four component "parts" is quite definitely recognizable in more or fewer of the types that have been studied. On the other hand, in no one of these are all four of those parts completely separable one from the other, neither is there any one of them in which all the four parts are not recognizable and definable to some degree at least.

In general terms the parts may be described as follows: (1) Pars posterior. This arises from the posterior portion of the quadrate end of the palatoquadrate, and its fibres pass directly across the axis of the Q-M. joint to be inserted on the posterior end of Meckel's cartilage.

(2) Pars medialis. The fibres arise from the deep surface of an aponeurotic sheet on the surface of the muscle, which may or may not be attached to the cranium dorsally, and they may be inserted onto Meckel's cartilage along its posterior edge or they may blend absolutely inseparably with the fasciculi of the partes posterior and anterior which lie behind and in front of them. When the part retains its individuality it may be quite superficial and be inserted only along the edge of Meckel's cartilage, or it may burrow deeply between the other two parts to an insertion on the outer surface of the cartilage.

(3) The pars anterior takes origin from the quadrate in front of the pars posterior. Its fibres, in the majority of instances, have an inclination to the plane of the palatoquadrate arcade as they pass ventrad, to be inserted into Meckel's cartilage in front of the pars posterior.

(4) The pars ventralis (Add. μ of Vetter). This portion is best developed in those forms in which the long axis of the jaws from joint to symphysis approaches most closely the long axis of the body. The fasciculi arise from a fibro-tendinous strand which is attached behind to a superficial raphe which crosses the other three parts from the gape to the Q-M. joint, and, passing forward subdermally parallel with the outer edge of the teeth, is attached to Meckel's cartilage

at the symphysis. From this origin the fibres pass, with an inclination towards the symphysis, to the distant edge of the cartilage. In short, this muscle lies in contact with the outer surface of Meckel's cartilage in front of the angle of the mouth.

All these four parts are, in the majority of instances, fused more or less intimately along their contactual surfaces. They are all posterior to the mandibular ramus of the Vth nerve.

This quadripartite condition of the quadrato-mandibularis muscle is found not alone in the selachians, but also in the batoid elasmobranchs and in the heterodontids.

The significance of these parts will be discussed in the review and summary of the Elasmobranchs as a whole. I proceed to describe the quadrato-mandibularis as it was found in the forms dissected.

Chiloscyllium (Fig. 6).—Pars anterior (Qm.a.). This has a fibro-tendinous origin from the anterior edge of the quadrate portion of the palatoquadrate. The fibres curve cephalad and ventrad, and then ventrad, mediad and caudad to an insertion along the anterior one-half of the ventral edge of the expanded part of Meckel's cartilage.

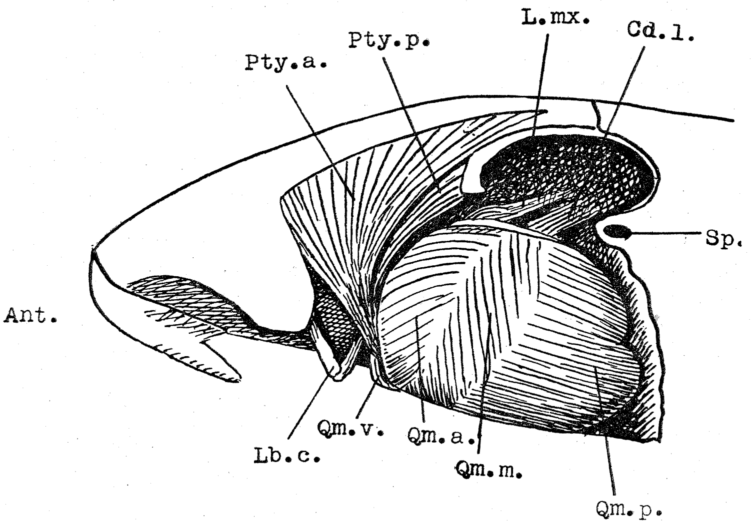

Fig. 6.—Mandibular muscles of *Chiloscyllium*.

The pars medialis (Qm.m.) is represented by a vertically disposed group of fasciculi whose surface appears as a narrow band of muscle behind the pars anterior, and whose fibres have a general direction ventrad and caudad, taking origin from a superficial fascia and passing deeply under the pars posterior behind. The upper fibres are inserted into the anterior surface of the muscular ridge along the posterior border of Meckel's cartilage. Those arising lower down are either blended with the pars posterior or inserted into the expanded portion of Meckel's cartilage in front of the muscular ridge.

The pars posterior (Qm.p.) arises from the greater part of the lateral surface of the expanded quadrate. The whole of the superficial fibres have a direction nearly horizontally caudad across the outer surface of the muscle, the lower portions of these horizontal fibres arise from the pars medialis. At the posterior border of the muscle these fibres all turn mediad and ventrad, and are inserted onto the posterior surface of the muscular ridge at the posterior end of Meckel's cartilage. The great bulk of the fibres, arising more deeply, pass ventrad and slightly caudad to be inserted onto the outer surface of the expanded portion of Meckel's cartilage between the ridge and the pars anterior.

The pars ventralis (Qm.v.) is quite small. It arises by a short tendon from the lower edge of the palatoquadrate and the subdermal tissues at the angle of the mouth, just in front of the tendon of the pterygoideus, and passing ventrad, mediad, and caudad, it crosses the mandible and the pterygoideus tendon, to be inserted on the mandible just behind the insertion of the tendon.

Pristiophorus (Fig. 5).—The pars medialis (Qm.m.) arises from the inner surface of the backwardly-projecting antorbital process and from a strong superficial aponeurosis which is attached to the upper margin of that process behind the orbit. The fibres pass cephalad, mediad, and ventrad, to mingle indistinguishably with those of the underlying pars anterior.

The pars anterior (Qm.a.) arises from the lateral surface of the palatoquadrate as far forward as the subocular muscular process. In this origin it covers the whole of the lateral surface of the palatoquadrate below the spiracle, except the narrow inferior strip against which the tendon of the pterygoideus lies. The insertion of these fibres is onto the lateral surface of Meckel's cartilage behind the angle of the gape.

The pars posterior (Qm.p.) is not defined from the posterior portion of the pars anterior; it arises from the quadrate portion of the palatoquadrate. Its fibres have a direction caudad and ventrad, to be inserted onto the lateral surface and posterior edge of Meckel's cartilage. The fibres having the latter insertion may be traced from their origin, which is along the dorsal edge of the quadrate.

These three portions are so intimately blended that it was only the directional differences of their fibres that enabled one to determine that the compact mass presented the usual divisions.

The pars ventralis is represented by a few fasciculi which arise from the anterior edge of the tendon of the pterygoideus below the angle of the mouth, and pass to be inserted on the inferior edge of Meckel's cartilage just in front of the insertion of the tendon.

In *Sphyrna* (Fig. 4) and in *Mustelus* (Fig. 8) the obvious division is into partes anterior and ventralis. When, however, the compact mass, which is apparently divided into upper and lower portions by the superficial raphe (R), is detached and studied from the deeper surface, directional differences corresponding to the four usual divisions become apparent. In both of these forms it is the pars medialis which is least definable.

Acanthias (Fig. 7).—This form was described by Marion and by him compared, not only with those described by Vetter, but also with *Raja*. If *Acanthias vulgaris* is similar to the species I have dissected, it would appear that Marion failed to dissect and study the adductor muscles from their deep surface, for his description is at variance with the conditions as I find them in certain particulars.

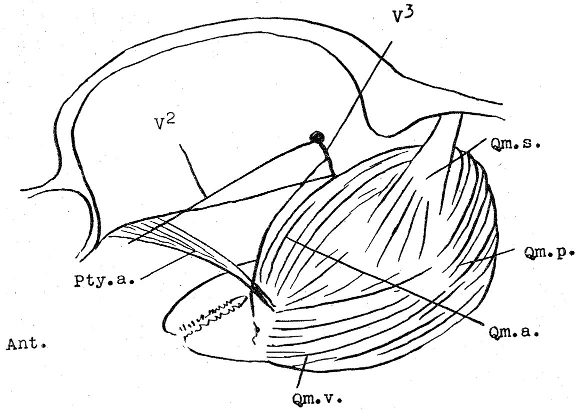

Fig. 7.—Mandibular muscles of *Acanthias*.

Pars medialis (Qm.m.) is a relatively small portion of the muscle which takes its origin from the very strong aponeurosis which covers the surface of the muscle in its upper portion. The aponeurosis itself is bound to the inferior margin of the spiracle and to the postorbital process. The direction of the upper and more superficial fibres is caudad and ventrad to an insertion on the posterior, and superficial, edge of the lower jaw below the Q-M. joint. The lower and more anterior fibres pass more directly ventrad and deeply, to blend with the partes anterior and posterior and to be inserted in the lateral surface of Meckel's cartilage.

Pars posterior (Qm.p.) takes origin from the lateral surface of the quadrate and from the posterior surface of its muscular process. The fibres take a curved course around the upper and under the ventral, superficial, portion of the pars medialis. Their direction is first ventrad and caudad, then ventrad, and finally cephalad. This direction is taken more by the fibres which arise from the posterior surface of the muscular process and from the upper area of the lateral surface of the quadrate, the deeper fibres passing more directly to the insertion. All the fibres are inserted on the lateral surface of Meckel's cartilage in front of the posterior insertion of the pars medialis.

The pars anterior (Qm.a.) arises from the anterior surface of the muscular process of the palatoquadrate. The fibres curve in the opposite direction to the superficial fibres of the pars posterior and the two have the mass of the pars medialis between them. Deeply the muscle blends with the partes medialis and ventralis, so that its insertion is inseparable from them.

The pars ventralis (Qm.v.) arises in part from the tendon of the pterygoid and in part from the strong fibrous tissues at and near the angle of the gape ; also it may be said to arise from or become the deep, insertional, continuation of the partes anterior and medialis. Omitting the fibres thus blended with those parts, the insertion of those having independent origin is onto the outer surface of Meckel's cartilage. Their direction is from origin mediad and cephalad.

The forward bulging of the anterior edge of the pars anterior and the blending thereof with the upper surface of this pars ventralis has resulted in the complete submergence of the tendon of the pterygoideus. In fresh specimens with quite soft muscles it was found, however, that almost the whole length of the tendon could be brought into view without actually detaching any muscle fibres from origin or insertion.

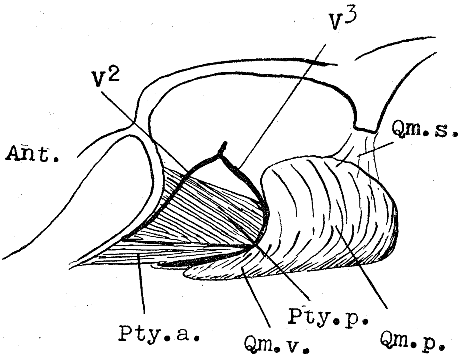

Fig. 8.—Mandibular muscles of *Mustelus*.

The motor nerve to the quadrato-mandibularis separates from the rest of the mandibular ramus of the Vth soon after that issues from the cranium. The main nerve then crosses the floor of the orbit and reaches the median border of the pars anterior of the quadrato-mandibularis and runs forward and laterad under the " overhang " of that muscle. At the angle of the mouth it crosses the tendon of the pterygoideus and turns mediad, caudad, and superficiad. The nerve to the quadrato-mandibularis crosses the orbit behind the main ramus, and disappears under the pars anterior at the base of the muscular process. It extends some distance into the muscle before breaking up into its numerous branches. There is a definite line of cleavage between the pars anterior and the muscle behind it which is occupied by the undivided motor nerve before it breaks up.

Marion's description mentions the origin of the pars medialis and the " broad thin sheet of fibres " related to it. He indicates the pars ventralis with the letter " x ", but fails to describe its relations to the other portions correctly or fully. Vetter's description (1874) is more precise. He correctly describes and figures the pars medialis and figures the superficial portion of it (Add. γ).

Heptanchus was described by Vetter (1874) and one may recognize in his description and figures that all four parts of the quadrato-mandibularis are present in that form. His Figure 1 quite clearly shows partes medialis (Add. γ) and ventralis, and the blended partes anterior and posterior.

2. **Heterodontus** (Figs. 9–14).

I have had for dissection five large specimens of *H. portus-jacksoni*, for which my thanks are due to the Director of New South Wales Fisheries Department.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Constrictors. (Figs. 9, 10.)

A. Dorsal.—These are completely similar to the partes inscriptionalis and arcuata of the dorsal superficial hyoid constrictor, which will be described later.

B. Ventral.—Each of these may be regarded as taking origin at the mid-lateral line, where it is uninterruptedly continuous with the corresponding dorsal constrictor. The fibres pass ventrad and mediad. Those of the pars arcuata become bound to the outer end of the ventral extrabranchial cartilage as they cross ventral to it ; they then turn caudad slightly and become inserted onto the perichondrium of the coracoid between the insertion of the coracohyoideus and pectoral muscles. The fibres of the pars inscriptionalis also turn caudad and mediad ventral to the floor of the gill pouch. These are inserted into the aponeurosis of the coracomandibularis near its insertion onto the coracoid. These fibres of Csv.3 fuse with fibres of the pars arcuata of Csv.2. Fibres in front of these, that is, deeper into the gill pouch, which turn forward and are inserted into the extrabranchial cartilage are portion of the interbranchial muscle, for, if they be followed up into the vault of the pouch, it will be found that they are attached to the dorsal extrabranchial deep to the decussion with the Csv.2. Csv.4, 5 and 6 differ from Csv.3 only in that the ventral insertion is entirely into the coracoid.

HETERODONTUS.

——		Branchial Segment.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors.	Dorsal ..	Csd.3–6	Csd.2a and Csd.2b	Absent.
	Ventral	Csv.3–6	Csv.2a and Csv.2b	Csv.1a and Csv.1b
Deep Constrictors.	Dorsal ..	Cpr.3–6	Csd.2 pars profunda (C.pr.2)	Levator maxillae
	Ventral ..	Absent	Interhyoideus	Absent
Levators		Absent	Lev.2	Absent
Epibranchial Spinal Muscles		3–6	Absent	Absent
Adductors.	Dorsal ..	Ep.Ob.3–6	Absent	Pterygoideus
	Middle ..	Add.arc.br.3–6	Retractor mandibulae (add.hy.)	Quadrato-mandibularis
	Ventral ..	Absent	Absent	Absent
Depressors		Co.br.3–6	Coraco-hyoideus	Absent
Hypobranchial Spinal Muscles				

The Deep Constrictors. (Fig. 10.)

A. Dorsal.—The first interbranchial muscle, Cd.3.pr., third deep constrictor, takes origin above from the first dorsal extrabranchial cartilage. It is a thin sheet of fibres which lies against the anterior surface of the deep ends of the gill rays. The fibres run an arcuate course from origin to insertion onto the inferior extrabranchial cartilage. For the most part the fibres run parallel with the contiguous margin of Cs.3. Both above and below there is a small quadrate area of the muscle whose fibres are attached to the epibranchial and ceratobranchial cartilages respectively. These are parallel with those of the rest of the muscle, so that the effect produced is as though the acute angle these two cartilages make, one with the other, had invaded the interbranchial muscle and interrupted the continuity of the deep portion.

The remaining interbranchial muscles are essentially similar. The last two present similar relations but with absence of the extrabranchial cartilages.

There are no ventral deep constrictors in any of the branchial segments.

THE LEVATORS.

Whilst there are no levators, the arrangement of the deepest part of the deep constrictor is such that it is capable of acting as a levator. The superficial dorsal constrictors take their origin from very strong fine strands of fibrous tissue which in turn take origin from the septum between dorsal and ventral trunk muscles. The dorsal trunk muscles are considerably more massive than the ventral; the origin of the superficial dorsal constrictors is from the ventro-lateral aspect of the trunk muscle mass, close above the vaults of the gill pouches. The inner ends of the dorsal extrabranchial cartilages, from which, in other elasmobranchs, the levator muscles largely take origin, are bound to the ventral surface of the tendinous origins of the dorsal constrictors, and thus each is brought quite close to the dorsum of its respective arch. Just distal to the inner end of each extrabranchial cartilage we find a small quadrate piece of the deep constrictor which, taking origin from the extrabranchial, is inserted onto the epibranchial cartilage (Fig. 10).

Whether this piece of the deep constrictor is capable of acting independently cannot be stated, but it is fairly obvious that under such circumstances it would act as a levator, and we may, therefore, regard it as demonstrating a stage in the evolution of the levator muscles from the deeper portion of the deep constrictor sheet.

EPIBRANCHIAL SPINAL MUSCLES.

Each of these four muscles takes its origin from the outer, dorsal, surface of a pharyngobranchial cartilage near its postero-lateral margin. From this origin the fibres pass cephalad, covering the greater part of the surface of the cartilage of origin, and converge somewhat to be inserted onto the deep surface of the pharyngobranchial cartilage in front (Fig. 11).

THE ADDUCTOR MUSCLES.

A. Dorsal.—There are four oblique epiarcual muscles, which lie in the angles between the pharyngo- and epibranchial cartilages. Each takes origin from the proximal end of the pharyngobranchial and is inserted along nearly the full length of the posterior edge of the epibranchial cartilage of the same arch (Fig. 11).

B. Middle.—Each of the four adductores arcuum branchialium takes origin from a short length of the epibranchial cartilage close to the middle joint of the arch, and is inserted in a similar length of the ceratobranchial cartilage (Fig. 11).

There are no ventral adductors nor are there are ventral interarcual muscles in any of the branchial segments.

THE DEPRESSOR MUSCLES.

The coracobranchialis muscle is described in connection with the hypobranchial spinal muscles (Figs. 12, 13).

THE HYPOBRANCHIAL SPINAL MUSCLES.

When the ventral superficial constrictors and the deep hyoid constrictors are removed, the only muscle which is brought into view is the coraco-mandibularis. This is a relatively thick muscle which rises from a crescentic area on each side of the ventral surface of the coracoid and, narrowing as it extends forward, is inserted into the angle between the lower jaws (C-g., Figs. 12, 13). If this be detached in front, and on one side behind, and thrown back and to one side, practically the whole of the muscles rising from the coracoid will be brought into view.

The anterior coraco-branchialis rises from the deep aponeurosis of the coraco-mandibularis on either side of the midline immediately in front of the coracoid. The muscle is inserted alongside of its fellow of the other side, onto the junction of the hypohyal and first hypobranchial cartilage. There is no attachment to the floor of the pericardium, the insertion being well forward of the anterior limit of that cavity.

This muscle may be the "coraco arcualis communis" of Marion's descriptions; it is, however, absolutely in series with the other coraco-branchial muscles lying between the two coraco-hyoideus muscles and beneath the coraco-mandibularis. Were it not for the fact that it is completely separated from the rest of the muscles, doubt as to its complete serial homology would not arise.

The coraco-hyoideus muscle (C-h.) arises from the coracoid beneath the outer half of the area of origin of the coraco-mandibularis on each side; just anterior to its origin the muscle passes in contact with the lower end of the first extrabranchial cartilage and is firmly bound thereto, and receives fibres from the first interbranchial muscle which also is inserted onto that cartilage. The muscle extends mediad, cephalad, and dorsad, beneath the edge of the coraco-mandibularis, with the anterior coraco-branchial muscles lying medial to it for about half its length, and its fellow of the opposite side in front of them. It is inserted onto the ventral face of the medial end of the cerato-hyal cartilage.

The coraco-branchial muscles rise from the antero-ventral edge of the coracoid along the boundary of the pericardium. The inseparable posterior components are inserted onto the ventral surface of the cardio-branchial along the lateral and antero-lateral border. The remaining members of the set are inserted onto the ventral surface of the first three hypobranchials.

THE MUSCLES OF THE HYOID SEGMENTS.

The Superficial Constrictors.

A. Dorsal (Fig. 9).—There is an intimate fusion between the successive superficial constrictors of the branchial region, especially so dorsally.

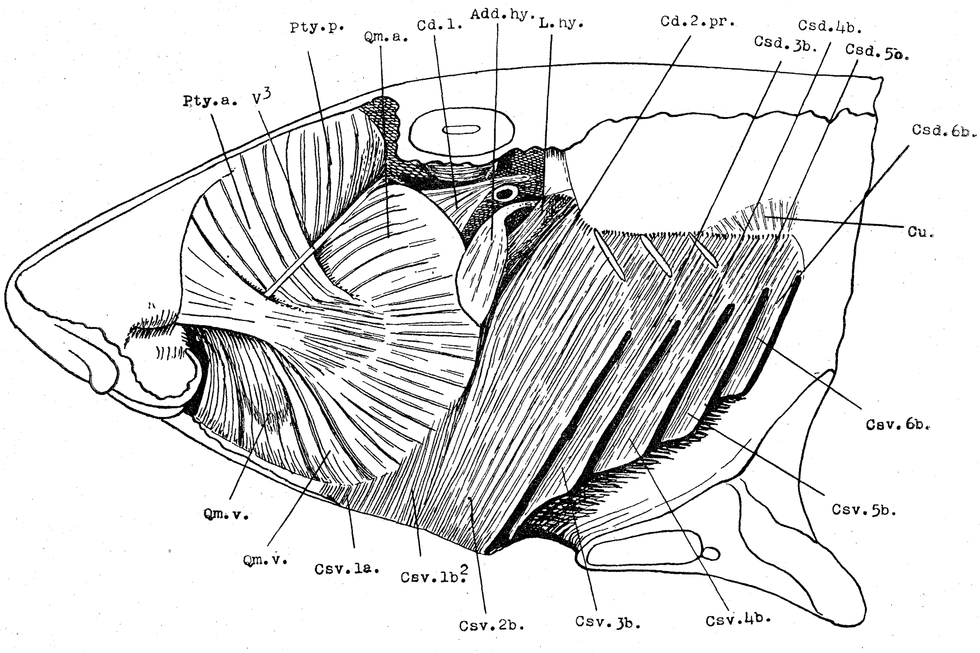

Fig. 9.—*Heterodontus portusjacksoni*. Lateral view of a superficial dissection.

The first of these is the hyoid (Csd.2). This takes origin from the hyoid levator and from the aponeurosis of the lateral trunk muscles. The most anterior fibres, those arising from the levator hyoidei, are deeply placed and lie against the pseudo hyoid cartilage from which the hyoid gill rays spring. Those immediately behind these lie more superficially against, anterior to, the deep portions of those gill rays. These fibres arise from the fascia dorsalis and are uninterrupted throughout their length. The fibres behind these, lying against the outer ends of the gill rays, are interrupted at the first dorsal extrabranchial cartilage. This lies oblique to the axis of the body above the first gill pouch at the confluence of the anterior (superficial) and posterior (deep) walls. The fibres of Csd.2 which we are dealing with take origin quite deeply from the aponeurosis of the trunk muscles above, behind and medially to the extrabranchial cartilage. Their direction from their origin is laterad and slightly cephalad and ventrad, and they are inserted into the perichondrium of the cartilage. From the other side of the cartilage two other sheets of muscle fasciculi take origin, a superficial and a deep sheet. The superficial sheet consists of the fibres of the Csd.2 which lie against the outer ends of the hyoid gill rays. The deep fibres are portion of the first interbranchial muscle, Cd.3.pr. The last and most posterior series of fibres of Csd.2 is completely mingled with Csd.3 fibres at their origin. They arise in part from the fascia dorsalis, aponeuroses of the trunk muscles, and in part from the lower edge of the second dorsal extrabranchial cartilage. They pass down in the anterior wall of the first gill pouch between the outer ends of the gill rays and the edge of the gill cleft. Unlike the last series of fibres these are not interrupted by the first dorsal extrabranchial cartilage. On the other hand, the continuation of the line of that cartilage corresponds to the dorsal fornix of the gill pouch and ends at the top of the cleft, and here there is a division into two sheets of fasciculi, a superficial and a deep, just as was found further forward. The superficial sheet is composed of the posterior series of Csd.2, the deep sheet of the anterior series of Csd.3 (the pars inscriptionalis); these lie in the posterior wall of the first pouch under cover of the anterior wall.

The first portion of Csd.2 is to be regarded as serially homologous with the interbranchial muscles and will be designated the second deep constrictor, Cd.2.pr. It lies against the arcuate pseudo-hyal cartilage and the deep ends of the gill rays, and its fibres are not interrupted by the extrabranchial cartilage. The second portion we will designate the pars inscriptionalis, Csd.2a, the third will be the pars arcuata, Csd.2b.

These last two designations are, of course, adopted from Lightoller, but if confusion is to be avoided it must be clearly realized that his Csd.2b and Csd.2c correspond to my Csd.2a and Csd2b, and Lightoller's "pars epiphyoidea, Csd.2a" to my Cd.2.pr.

Each of the remaining superficial dorsal constrictors presents portions which correspond absolutely to Csd.2a and Csd.2b, and may be described in all their relations to the successive dorsal extrabranchial cartilages and gill pouches by simply changing the numbers in each case. There are, however, no extrabranchial cartilages in the superior fornices of the last two pouches—slight tendinous interruptions take their places.

B. Ventral.—The superficial ventral hyoid constrictor presents features not found in any other elasmobranch. The muscle takes origin from the ventral median raphe. The pars arcuata arises superficially behind the extramandibularis portion of Csv.1, the pars inscriptionalis takes origin under cover of that same portion of Csv.1. The fibres of the pars arcuata are parallel with those of Csv.1 but those of the pars inscriptionalis incline forward, crossing the more superficial fasciculi at an acute angle. This difference of direction permits of the separation of the two muscles, but only by the most careful dissection, for they are very closely bound together. The fasciculi of the pars inscriptionalis are inserted into the posterior edge of the lower jaw under cover of the posterior fibres of the pars extramandibularis of Csv.1; this insertion is by a strand of fibrous tissue to which the muscle fasciculi converge. The pars arcuata is continued dorsally into the pars arcuata of Csd.2.

THE DEEP HYOID CONSTRICTORS.

A. Dorsal.—This muscle has been described in connection with the Csd.2.

B. Ventral.—The interhyoideus muscle takes origin from the ventral median raphe under cover of the intermandibularis portion of Csv.1; this origin extends from the anterior limit of the origin of Csv.2a almost to the symphysis. The muscle is fan-shaped, the fibres converging to be inserted onto the ventral edge of the ceratohyal not far from the joint with the epihyal and just medial to the median end of the pseudohyal cartilage. The posterior margin is, for most of its length, in contact with the anterior margin of Csv.2a.

The relations of the two portions of the hyoid superficial constrictor to one another and to the deep constrictor, and the relations of all three to the mandibular ventral constrictor in *Heterodontus* present quite accurately that primitive arrangement of the constrictor sheets which is observed throughout the elasmobranchs in the arrangement of the dorsal homologues in the branchial segments.

THE HYOID LEVATOR. (Fig. 9, Lev.hy.)*

The very primitive hyoid levator has its origin from the auditory capsule. This origin is, without any tendinous assistance, from the lateral ridge of the capsule above the attachment

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* Lightoller (1939) has designated this muscle pars nucho-maxillaris of the first (mandibular) dorsal constrictor; it is the Csd.1c of his description.

of the oto-hyoid ligament. The fibres pass ventrad, laterad, and cephalad, to be inserted directly into the hyomandibular cartilage behind and deep to the belly of the adductor hyoidei muscle.

THE HYOID ADDUCTOR. (Fig. 9, Add.hy.)

B. Middle.—The adductor hyoidei is that muscle which, in some other elasmobranchs, has been termed retractor mandibulae. In common with the branchial adductors it takes its origin from the anterior edge of the epiarcual element, hyomandibular. The origin extends onto the lateral surface of the cartilage. Some of its more superficial, and posterior, fibres take origin

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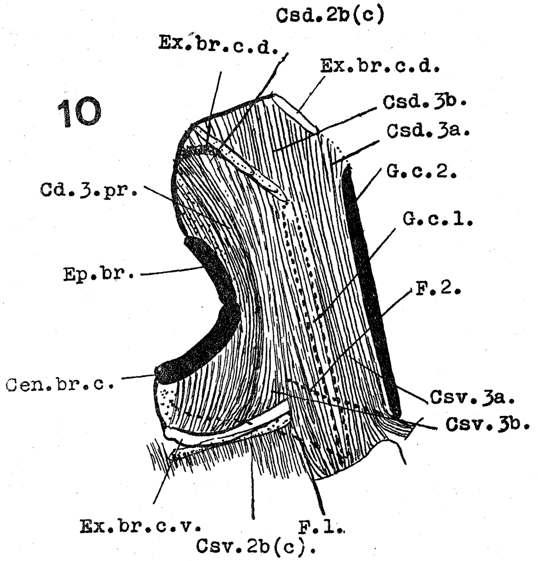

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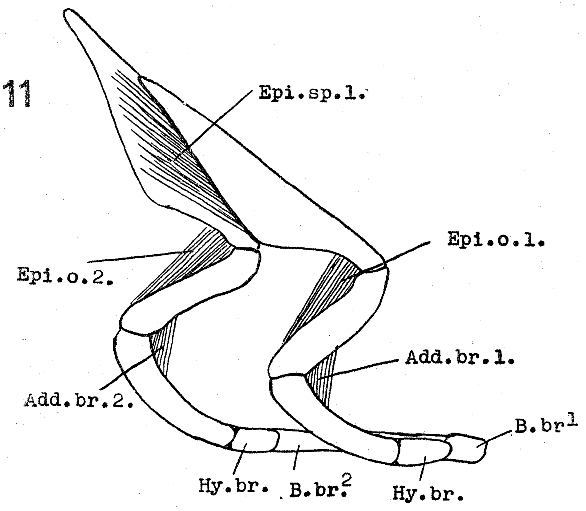

Fig. 10.—*Heterodontus.* The anterior view of the posterior wall of the first gill pouch. The hyoid constrictor sheet has been dissected off, and the muscles which lie in the floor of the gill pouch, and which turn mediad almost at right angles to the plane of the rest, have been represented as turned down into the same plane.

Fig. 11.—*Heterodontus.* Two branchial arches.

from the very strong oto-hyoid ligament, which, firmly attached to the hyomandibular above and behind the muscle, passes to the lateral ridge of the auditory capsule just above the incisura venae capitis lateralis. From this origin the fibres pass laterad, cephalad, and ventrad to a fleshy insertion onto the capsule of the Q-M. joint.

Innervation.—This is by a twig from the hyomandibular ramus of the VIIth nerve.

There is no ventral adductor and no ventral interarcual muscle in the hyoid segment, and the coraco-hyoideus has been described along with the hypobranchial spinal muscles.

THE MUSCLES OF THE MANDIBULAR SEGMENT. (Figs. 9, 14.)

The Superficial Constrictors.

A. Dorsal.—Immediately in front of the spiracle on removal of the skin, one displays the outer edge of a muscle whose anterior surface lies more deeply. This, which is regarded as representing the whole of the derivatives of the dorsal constrictor sheet of the mandibular segment, takes origin from a short line immediately above and internal to the oto-hyoid ligament. From this origin the muscle passes laterad, cephalad and ventrad to a much wider insertion onto the dorsal edge of the palatoquadrate. The superficial fibres pass most directly laterad, and the deepest have the greatest inclination cephalad.

The superficial portion of this muscle is, it is believed, unquestionably the primitive constrictor sheet. The deeper portion corresponds just as unquestionably to the mandibular levator of the selachians.

In all the segments behind, it has been observed that the deep constrictor (and its dorsal and deeper portion which is apparently capable of acting as a levator) form one continuous sheet.

Here again, then, it appears that *Heterodontus* presents the retention of primitive features. Whilst it is quite impossible to define the muscles, it is probable that this, which we designate Cd.1, truly represents also those other muscles.

B. Ventral.—The Csv.1 muscle presents, on either side of the median ventral raphe, no division into a and b but, on the other hand, the anterior portion is inserted into the ventral and median edge of the lower jaw, whilst approximately the posterior half is inserted into a strong fascia which is continued up and over the surface of the jaw. Partes inter- and extra-mandibularis are therefore recognizable, and definable by the insertion (Csv.1a, Csv.1b^2).

The Mandibular Adductors. (Figs. 9, 14.)

The adductor mass of *Heterodontus* is particularly complex and it was at first thought that the mass included both superficial and deep constrictor components. Later comparisons with the adductor masses of the various selachian and batoid forms which I have been enabled to dissect have convinced me that there are representatives of the dorsal and middle adductors only. Comparison is invited particularly with the adductor muscles of *Mustelus, Acanthias* and especially *Chiloscyllium,* which present two degrees of complexity, whilst *Heterodontus* is regarded as presenting a third, more complex than the last. In considering the interpretation to be placed upon the parts of this muscle, it is necessary to keep in mind the fact that the palatoquadrate has been brought into much closer union with the base of the skull than in any of the selachian or batoid elasmobranchs. This close approximation and union has permitted the transfer of muscular origins to skull areas which were not mechanically suitable in the other forms. Not only is this so, but the extraordinary increase in size of the palatoquadrate and its very close union with the skull below and in front of the orbit has covered those areas whereto muscles are attached in the selachians, and, as it were, necessitated new origins for these muscles.

The pars anterior of the pterygoideus (Pty.a.) (epiarcual oblique mandibular or dorsal adductor muscle) takes origin from the posterior subdermal edge of the nasal capsule and from the subdermal edge of the cranium for a short distance behind the capsule. Its fibres converge to a relatively broad flat tendon which does not burrow into the adductor mandibulae but becomes continuous with the superficial aponeurosis of the adductor. As in the selachians, this muscle is crossed by the superior maxillary branch of the fifth nerve between its origin and insertion.

The pars posterior (Pty.p.) arises more deeply, under cover of the pars anterior, from the side wall of the cranium, its origin extending back almost to the anterior margin of the orbit. Anteriorly it arises from the inner portion of the posterior wall of the nasal capsule. It has the superior labial cartilage imbedded in its deeper and anterior part, and some of its fasciculi take origin from the tough investment of the cartilage. Its deep surface is incompletely covered by a tough fibrous membrane which is loosely attached to the submucous tissues of the wall of the mouth between the jaws. Its fasciculi pass almost directly ventrad to be inserted into the upper edge of the lower jaw and the tissues of the side wall of the mouth just behind the angle of the gape. The posterior deep edge of the muscle is clothed by a strong tendon into which the bulk of its fibres are inserted, and it is this tendon particularly which is inserted onto Meckel's cartilage.

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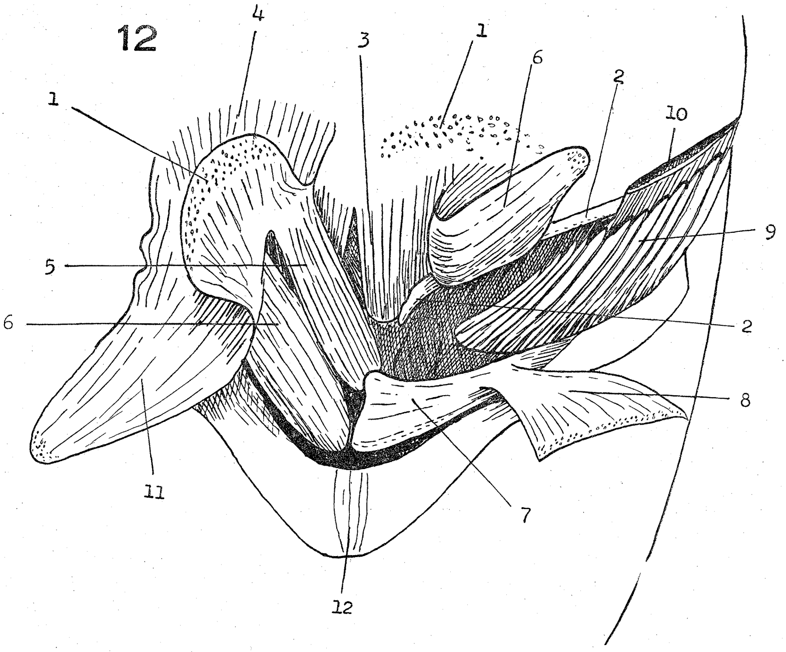

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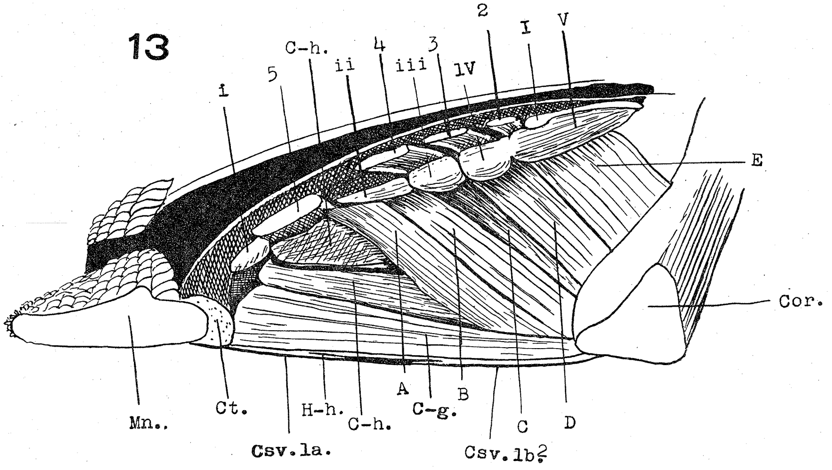

Fig. 12.—*Heterodontus.* A deep dissection of the floor of the mouth, seen from below. 1. Right head of the m. coraco-mandibularis, cut free and turned back. 2. First ventral interbranchial cartilage. 3. M. coraco-branchialis. 4. Left head of the m. coraco-mandibularis. 5. First slip of the m. coraco-branchialis. 6. M. coraco-hyoideus. 7. Ceratohyoid cartilage. 8. M. interhyoideus, cut free from the mid-line and folded back. 9. Hyoidean and pseudohyoidean gill rays. 10. First gill slit. 11. Body of the m. coraco-mandibularis cut free from the symphysis and pulled to one side. 12. Symphysis of the lower jaw.

Fig. 13.—*Heterodontus.* A dissection of the coraco-branchial and coraco-mandibular muscles seen from the mid-line. I-V, the basibranchial cartilages. A, B, C, D & E, the several slips of the m. coraco-branchialis.

Innervation.—This is by two branches from the mandibular ramus of the Vth nerve which leave the main nerve before it crosses the anterior inferior border of the orbit.

There is a little doubt as to whether it is the more superficial or the deeper part of this muscle which truly represents the pars anterior of the typical selachian muscle.

The mandibular ramus of the Vth nerve issues from the orbit along a deep fissure between the pars posterior of the pterygoideus and the pars anterior of the quadrato-mandibularis. After giving off the motor twigs to the quadrato-mandibularis, the nerve turns superficiad and crosses the tendon of the pars anterior of the pterygoideus.

As in the selachians, except just before their insertion onto Meckel's cartilage, there is no fusion between the contactual surfaces of the pterygoideus and the pars anterior of the quadrato-mandibularis.

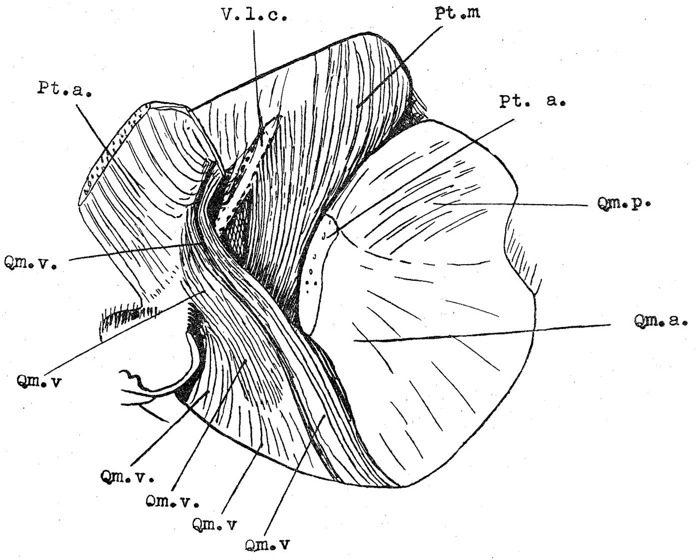

Fig. 14.—*Heterodontus.* A deep dissection of the mandibular muscles.

THE QUADRATO-MANDIBULARIS MUSCLE. (Figs. 9, 14.)

Pars medialis.—This portion of the muscle has largely lost its identity. The surface of the main mass is invested in a very strong superficial aponeurosis which, instead of being continued up onto the antorbital process, is firmly attached above to the superficial edge of the arch of the palatoquadrate below the posterior half of the orbit. This gives origin to a considerable proportion of the fasciculi of the muscle, and is to be regarded as representing the pars medialis.

Pars anterior (Qm.a.).—From the arch of the palatoquadrate below the anterior half of the orbit, a mass of thick fasciculi take origin and swing cephalad and ventrad, and then ventrad and caudad, to be inserted into Meckel's cartilage immediately behind the pars medialis of the pterygoideus. These clearly constitute the pars anterior of the muscle.

Pars posterior (Qm.p.).—The fibres arise from the palatoquadrate under cover of, and are immediately blended with, the medialis and pass ventrad to be inserted into the expanded posterior part of Meckel's cartilage.

The pars ventralis (Qm.v.) fibres arise from the deep tissues of the inner wall of the mouth around the gape and behind the fold of the lower lip. They are inserted onto the outer surface of Meckel's cartilage in front of the insertion of all the other portions. Some of the fibres of this part arise from the deep surface of the tendon of the pars anterior of the pterygoideus; they are the longest and most posterior fasciculi of the muscle, and their insertion is posterior and superficial to the tendinous insertion of the pars posterior of the pterygoideus.

The extent of fusion of the deep fibres of the pars anterior and the posterior fibres of the pars ventralis with the pterygoideus muscle is rather in excess of the normal as presented by the selachians generally, but not greatly in excess of the fusion in such a form as *Pristiophorus.*

3. The Batoidei.*

I have had for dissection one very large specimen of *Dasyatis brevicaudatus* Hutton, one specimen of *Raja australis* Macleay, three specimens of *Urolophus testaceus* Mull. & Henl., one specimen of *Hypnarce subnigra* Dumeril, and one of *Taeniura lymna.* For the specimens of *Raja* and *Taeniura* I have to thank the Trustees of the Australian Museum and the former Director, Dr. C. Anderson. For the others I have to thank various fishermen friends.

The *Dasyatis* was the first dissected and described, *Raja* being compared with it at each stage of the dissection. These two are, therefore, described at length. Such differences as called for note, observed in the dissection of the other forms, are recorded later.

I would at the outset draw attention to the discovery of two veritable glosso-pharyngeal muscles innervated by the facial nerve in *Dasyatis.* It is not proposed to anticipate a later section by discussing their bearing on the evolution of the cranio-glossal and hyo-glossal muscles

THE BATOIDEI.

Raja (R.) and *Dasyatis* (D.).

——		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors.	Dorsal ..	Csd.3–6. R.D.	Csd.2b. Levator rostri. R.D. Csd.2c. R.D.	Absent
	Ventral ..	Csv.3–6. R.D.	Csv.2b. depr. rostri. R.D. Csv.2c. R.D.	Csv.1a and Csv.1b
Deep Constrictors.	Dorsal ..	C.pr.3–6. R.D.	C.pr.2. R.D.	Lev. max. sup.
	Ventral ..	Sub.arc.tr.3–5. R.D.	Interhyoideus. R.D.	Lev. palati
Levators		Lev.3–6. R.D.	Lev.2. R.D.	Absent
Epibranchial Spinal .. Muscles.		3–6. R.D.	Absent	Absent
Adductors.	Dorsal ..	Ep.ob.3–6. R.D.	Ep.ob.2. Lev.hyomandib. R.D.	Pterygoideus
	Middle ..	Add.arc.br.3–6. R.D.	Cranio-glossus. D. Absent. R.	Quadrato-mandibularis
	Ventral ..	Absent. R.D.	Hyoglossus. R.D.	Absent
Depressors		Co.br.3–6. R.D.	Co-hy.	Absent
Not accounted for		Nil	Nil	Mandibulo-labialis Maxillo-labialis
Hypobranchial				

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* *Dasyatis* was the first of the large subjects that I stained prior to dissection. Some time previously, whilst at work on the development of the selachian muscles, it became necessary, in checking a dissection, to work on a specimen which had been stained with picrocarmine for sectioning purposes. It was found that the muscles and nerves had taken a macroscopic differential stain that made the dissection remarkably easy. This naturally led to the staining of all small specimens before dissection, and later to similar treatment of the larger subjects. The ease and confidence with which one can follow the finer nerve twigs after the staining needs to be experienced to be realized. The staining proceeds much more rapidly and satisfactorily after skinning, but if superficial nerves are to be studied the specimens should be stained for about a week before skinning. I use 50% alcohol saturated with picric acid and rendered alkaline with potash, and then add sufficient Grenacher's alcoholic borax carmine to give the solution a dark red colour. More carmine may need to be added as the specimen absorbs the colour. The use of the picric acid has the advantage of greatly deodorising the specimens, and the disadvantage of staining the fingers. But one early learns to put on one's gloves before handling the specimens. If the specimens have been long preserved and are darkened by age, the results are not so satisfactory. The carmine stain fails altogether, the picric acid alone is useful; it differentiates the nerves, but not nearly so well as in the fresh specimens. This staining is useful only if the muscles are white.

of higher vertebrae, but rather to invite a more critical examination of the interpretation of their serial homology with muscles of the branchial arches which is offered here.

In the Rays we find two muscles, undoubtedly hyoid, in front of the hyoid visceral cleft, the spiracle. In these fishes we have an undoubted division of the muscle sheet by the spiracle. It would seem, however, that the portion anterior to the spiracle has resulted from a secondary up-growth from the plate which, primitively, was situated behind the cleft after the closure of the ventral end thereof.

There is ample evidence of such a forward growth of the hyoid muscles in the history of the development of the Teleostomes, e.g. the adductor arcus palatins. We, therefore, explain these prespiracular hyoid muscles as much modified forms of the specialized deep muscles found in branchial arches.

As in the other subsections, I preface the description of the muscles by their tabulation.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Constrictor Muscles.

Dasyatis.—The dorsal and ventral constrictors are in series, one behind the other, presenting the appearance of a longitudinal muscle with a series of transverse tendinous intersections. The direction of the component fasciculi is antero-posterior with an inclination latero-caudad. On the dorsum the series is firmly attached medially to the fascia dorsalis, and is limited by that fascia. Inasmuch as the fasciculi strike that fascia with an inclination cephalad and mediad, the medial limiting fasciculi take origin from it. Laterally the dorsal constrictors appear to be limited by the fascia which binds the heads to the embracing propterygia. This, however, is not the fact. The dorsal perimysium, only, of each muscle is bound to that fascia, the muscle itself continuing uninterruptedly down the side of the head against the propterygium and its dorsal and ventral superficial tissues and muscles, until the ventral deep fascia is reached. Into this deep fascia the limiting fasciculi are inserted with a caudad and ventrad inclination. From the ventral and medial side of this limitation of the dorsal constrictors the fasciculi of the ventral constrictors take origin. There is a very definite, though narrow, tendinous interruption between the two sets of fibres along this line. But for this interruption the two muscles would be quite continuous, for their component fasciculi are absolutely parallel. Medially the ventral constrictors are inserted into the deep surface of the ventral deep fascia* beneath the depressor rostri in front and the tendon of the longitudinal muscles further back.

Each of the superficial constrictors* takes origin in front between its medial and lateral margins from a tendinous interruption in the interbranchial septum between it and the interbranchial muscle (deep constrictor) and is inserted into a similar interruption in the interbranchial muscle wall behind. It is the dip ventrad or dorsad to reach this interbranchial interruption which, superficially, presents the appearance of a tendinous interruption between the successive muscles.

The sixth dorsal superficial constrictor is inserted posteriorly into the fascia dorsalis and the deep tissues in front of the base of the propterygium.

The sixth ventral constrictor has a much more interesting insertion. The muscle disappears from superficial view beneath, i.e., dorsal to, the lateral edge of the coraco-arcualis communis. Under cover of this muscle it passes ventrally to the pars posterior of the coraco-branchialis, folds dorsad round the medial border thereof, and is inserted into the perimysium on its medial surface ; this insertion is one of the factors which gave rise to the view expressed in the last footnote. We have here a superficial muscle, which must in the primitive condition have been inserted into the superficial fascia, presenting an insertion deep to the invading spinal muscles. The superficial fascia has been split into superficial layers along its length or divided across its length. There is no submergence of primitively superficial insertions in front of the hyoid segment.

The insertion of the sixth superficial constrictor superficial to the pars posterior of the coraco-branchialis, thus separating that muscle from the longitudinal spinal muscles, is just as one would anticipate in view of the development of the former from the ventral ends of the

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* It is believed that the invasion of the cephalic region ventrally by the spino-occipital muscles was accompanied by a division of the deep fascia between the hyoid and branchial segments. The deep fascia being submerged behind the hyoid segment, but being superficial to the anterior attachments and prolongations of the spinal muscles at and in front of the hyoid segment.

branchial muscle plates. Their situation and their development prove them to be deep branchial muscles.

Raja.—Marion (1905, p. 11) says that in *Raja erinacea* there are seven superficial constrictors. I can find no evidence of this in *R. australis*, and in this form the superficial constrictors resemble so closely those of *Dasyatis* that they do not call for separate description. An examination of Marion's figures and description leads one to the discovery that his seventh constrictor is obtained by the division of the hyoid sheet. Since there be no deep muscles to correspond with the extra superficial constrictor, nor, indeed, any branchial arch to account for the seventh, one must conclude that he was in error in his treatment of the hyoid sheet. *R. australis* presents no indication of any division of the superficial hyoid sheet.

THE DEEP CONSTRICTOR MUSCLES.

Dasyatis.—The anterior wall of the first gill pouch is provided with a deep constrictor by the hyoid muscle sheet. Behind this are four branchial deep constrictors. These four interbranchial muscles are so very similar that a description of one serves as a description of all.

The outline of each interbranchial wall is that of a truncated wedge with the truncated end outwards and with a triangular gap cut nearly symmetrically out of the centre of the broad end of the wedge. This gap is occupied by the pharyngeal passage and bounded by epi- and cerato-branchial cartilages. The wall is clothed, antero-laterally to the gill rays, by the interbranchial muscle. This is divided into dorsal and ventral halves by a horizontal tendinous interruption, which extends from the pharyngeal angle to the outer margin of the wall and is due to the insertion of the adjacent ends of the dorsal and ventral fasciculi into the perichondrium of a dominant middle gill ray. The direction of the fasciculi is dorso-ventral, but with a slight inclination mediad from the horizontal midline both above and below.

Raja.—I find the interbranchial muscles of *R. australis* to be essentially similar. The fasciculi radiate at the outer end precisely as Marion indicates. For illustrations of these muscles Marion's work may be consulted.

THE SUBARCUALIA TRANSVERSI.

Marion (p. 17), writing of the branchial interbranchial muscles of *Raja*, says: " A few bundles of the most median fibres of the ventral portions are overdeveloped, and have extended so as to take their origin from the fascia covering the coraco-mandibularis muscle. A similar condition was noted above for *Acanthias*, but these fibres were not as prominent there as here. Tiesing, basing his opinion on the work of Vetter upon *Heptanchus*, has regarded these fibres as a deeper layer of the constrictor, but *Acanthias* shows this not to be tenable. There is the resemblance to a constrictor ", and yet on page 26 he writes : " It may be a question whether the interbranchiales, the interarcuales, and the adductors do not form a system of deep as opposed to the superficial constrictors ".

To these muscles, which Tiesing designated Csvp.3-5, I propose to apply the designation subarcualia transversi.

I have found them in all the rays I have dissected. They are, as it were, foreshadowed in *Heterodontus* and the Selachii by an always small and varying bundle of ventro-median fasciculi of the deep constrictor sheets, which swings across toward or to the midline with the deepest fibres of the pars interinscriptionalis.

These muscles do not conform to the definition of subarcualia transversi given elsewhere, for they do not cross the midline to meet their antimeres. On the other hand, they certainly appear to present, as it were, an incomplete attempt to form such a muscle, and to that extent they foreshadow a modification of the subarcual muscles found constantly in the bony fishes.

THE LEVATORS ARCUUM BRANCHIALIUM.

Dasyatis.—There are five branchial levators. Each consists of a dorsal and a ventral portion, separated by a relatively broad tendinous central area. These muscles lie in the medial wall of the gill pouches above the pharyngeal plane and against the capiti-nuchal muscles. Each takes origin from the fascia dorsalis beneath the median origin of the superficial dorsal constrictors. They lie in an antero-posterior vertical plane and the fasciculi have a dorso-ventral direction

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* It should be noted that there is in no one of these superficial constrictors any indication of divisibility into partes arcuata and inscriptionalis.

with a slight inclination caudad. The insertion is into the epibranchial cartilage lateral to the epiarcual obliqui muscles.

Raja.—The levators in this form would not be recognized as such had one not dissected the other form. They are found in the same situation in the two forms, but in *Raja* each muscle supplies a complete median wall to its pouch, and the fasciculi run in a cephalo-caudad direction with a slight inclination ventrad. They take origin from an interbranchial interruption in front, and from the fascia and the superficial constrictor above, and are inserted into the interbranchial interruption behind and the epibranchial cartilage.

Marion failed to describe these muscles in *R. erinacea.*

The Epibranchial Spinal Muscles.

Dasyatis.—These are essentially similar to those of *Heterodontus,* but are not as well developed; there are four, but there is no subspinalis.

Raja.—The muscles are, as Marion states, represented by fibrous bands, in which no muscle fibres can be detected.

The Adductor Muscles.

Dasyatis.—The epiarcualis obliqui and adductores arcuum branchialium are essentially similar to those of the Selachii.

Raja.—The muscles are essentially similar.

Ventral oblique muscles are developed in neither form.

The Depressores Arcuum Branchialium.

Dasyatis.—The coraco-branchialis muscle is divided into anterior and posterior portions which are not in contact with one another.

Pars anterior.—This consists of four small muscles which take origin together from the deep (dorsal) surface of the coraco-arcualis communis muscle well forward, close to the limit of its muscular portion.

From this origin these muscles pass dorsad, with an inclination cephalad, in front of the pericardium and in contact laterally with the expanded ends of the ventral extrabranchial cartilages. The muscles are quite inseparable either from one another or from the coraco-arcuales communes at their origin, but they taper to narrow tendinous insertions which are separated by the passage of the main branches of the ventral aorta. The insertions are onto the median ends of the cerato-branchial cartilages.

Pars posterior.—This massive muscle has an extensive origin from the lateral end and ascending portion of the coracoid arch lateral and dorsal to the lateral portion of the origin of the coraco-arcualis communis muscle. This area of origin extends dorsally on the anterior face of the pectoral girdle to the point of union of the fifth cerato-branchial cartilage with the arch, which is also the inferior limit of the insertion of the trapezius. From this origin the muscle passes cephalad and slightly mediad and dorsad along the posterior wall of the fifth branchial pouch, to be inserted along the length of the dorsal edge of the fifth cerato-branchial cartilage and the posterior edge of the fifth extrabranchial cartilage. Thick at its origin, the muscle is laterally flattened at its insertion.

Raja.—I find a very similar division of the muscle in *Raja.* Here, however, they might more descriptively be termed partes ventrales et dorsales. The anterior or ventral portion is continued back beneath the coraco-arcuales communes in contact with the posterior, or dorsal, part and terminates in a tendon which gives it origin from the coracoid arch beneath the lateral margin of, and independently of, the coraco-arcuales communes.

THE MUSCLES OF THE HYOID SEGMENT. (Figs. 15, 16.)

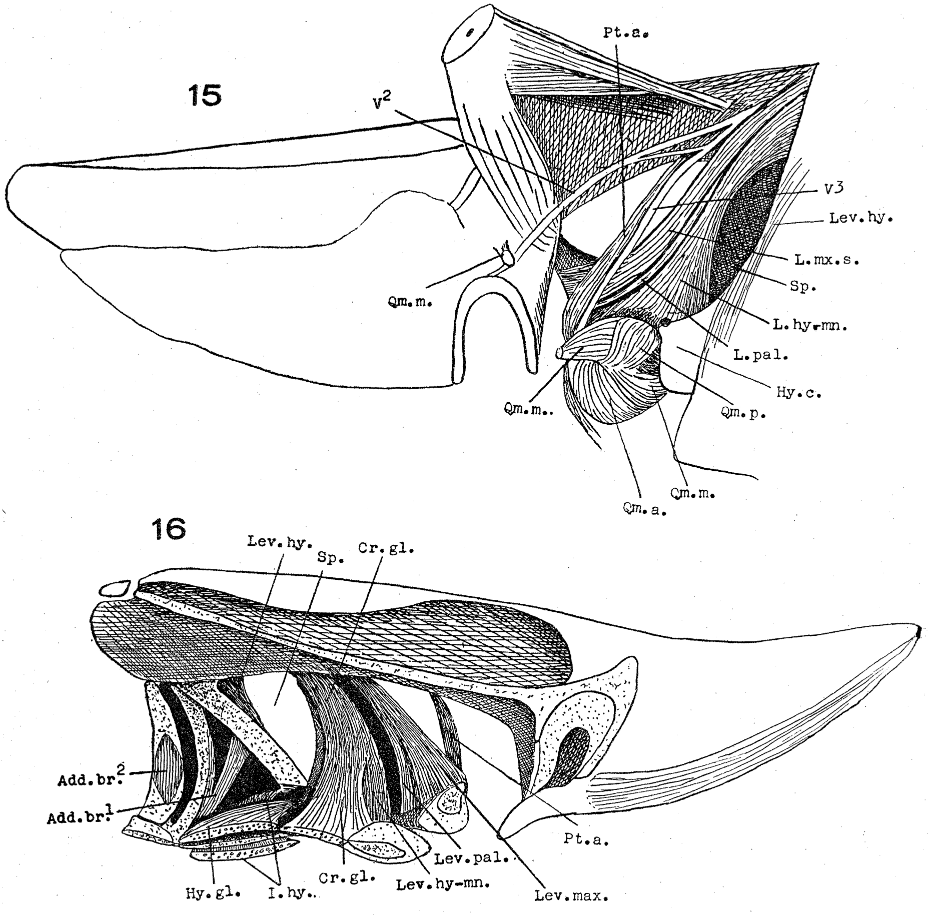
The Superficial Constrictor Muscles.

The form of the superficial and deep hyoid constrictors, and their relation to the gill pouch behind them, are, in their close resemblance to the homologous branchial muscles, particularly interesting and instructive.

Dasyatis.—The second superficial dorsal constrictor is not divisible in the Rays into partes arcuata et inscriptionalis. The fasciculi have a general direction from in front, caudad and laterad, parallel to those of the branchial constrictors behind them. The most anterior portion of the muscle is hidden from view, and here the fasciculi all take origin from a well-marked fascial band on the anterior wall of the first gill pouch. This band takes origin from the fascia dorsalis well towards the dorsal limit of the atrio-pharynx and passes horizontally laterad to be attached to the lateral gill-pouch wall. From this band the fasciculi first pass dorsad, and, becoming superficial, curve caudad and laterad as described, to be inserted into the first tendinous interruption, which latter is placed over the first interbranchial septum.

Raja.—The muscle in *R. australis* is almost entirely similar. As previously noted, Marion found here two superficial constrictors in *R. erinacea.*

The levator rostri, a muscle present in *Raja* but not in *Dasyatis,* is probably a specialized portion of the superficial hyoid constrictor. Marion's description of the muscle is correct in all particulars.



Figs. 15 & 16.—*Dasyatis.* Lateral and median view of some of the hyoid and mandibular muscles.

Dasyatis.—The superficial ventral hyoid constrictor is a sheet of muscle essentially similar to the branchial constrictors behind it. The more medial fibres are continuous with those of the first (hyoid) interbranchial muscle in front of and deep to it. The more lateral take origin in the connective tissues of the gill wall. The insertion of all is into the tendinous interruption beneath the first interbranchial septum.

The depressor rostri, which takes origin from the ventral deep fascia superficial to this last, is probably a specialized modification of this sheet.

Raja.—The muscles in *Raja* are essentially the same as in *Dasyatis.*

THE DEEP HYOID CONSTRICTOR MUSCLES.

Dasyatis.—The hyoid interbranchial muscle (Cd.2.pr.) in both *Dasyatis* and *Raja* are so completely similar to the branchial interbranchial muscles that they call for no further description.

The interhyoideus, which has been treated by previous writers as portion of the hyoid superficial constrictor, is essentially similar in the two forms. It is a fan-shaped muscle which takes origin in the ventral deep fascia superficial to the longitudinal ventral spinal muscles. From this relatively broad origin, the fasciculi converge to be inserted onto the posterior surface of the hyo-mandibular cartilage near the centre of its length by a short tendon which reaches nearly to the dorsal edge of the cartilage.

THE LEVATOR HYOIDEI.

Dasyatis and *Raja.*—This is a powerful muscle which has an extensive origin from the skull and fascia dorsalis, behind the auditory capsule and above the articulation of the hyo-mandibular cartilage to the skull. The muscle tapers rapidly and passes laterad, ventrad, and slightly cephalad, to be inserted onto the dorsal edge and anterior face of the hyo-mandibular cartilage extending a little more than half-way along the length on the dorsal edge.

THE ADDUCTOR MUSCLES. (Figs. 15, 16.)

In both *Dasyatis* and *Raja* and, in fact, in the other batoid forms dissected, the hyoid adductor is relatively a very extensively developed muscle. It is believed that there has been here a complete fusion of the adductor and the oblique epiarcual muscle, though it well may be that the whole muscle is the resultant of increase in function and, consequently, bulk of the adductor.

Dasyatis (Figs. 15, 16).—The adductor hyoidei in this form is a truly remarkable muscle, and for the purposes of a later section of this paper it will be described in two portions, an internal and an external, which will be designated " cranio-glossus " and " levator hyo-mandibularis " respectively.

Levator hyo-mandibularis (Lev.hy-mn.).—This is a very powerful muscle which takes origin behind the levator maxillae superioris and the levator palati from the side wall of the auditory capsule in front of the foramen facialis. The muscle is thick, and roughly cylindrical at its origin, but flattens out and becomes increasingly widened. Its posterior and superficial portions lie beneath the skin in the *anterior* wall of the spiracle. The direction of its fibres is generally ventrad, cephalad and laterad from their origin. The fibres which form the anterior wall of the spiracle are inserted into the distal end of the hyo-mandibular cartilage. The fibres arising most anteriorly are also the most median of the muscles ; they swing almost directly cephalad and ventrad to be inserted into the exceedingly strong fibrous binding between the palato-quadrate and the mandible just lateral to the joint. The fibres between these two sets descend almost to the same ventral level, but, instead of gaining attachment to the fibrous investment of the cartilages between the other two insertions, turn mediad and caudad and join the cranio-glossus muscle.

The cranio-glossus (Cr.gl.).—This muscle takes origin from the side wall of the auditory capsule deep to the levator hyo-mandibularis ; it passes down in the side wall of the mouth in front of the spiracle, forming the deeper portion of the anterior wall thereof. Arrived at the floor-level, the muscle turns mediad beneath the mucosa of the floor to the midline. The anterior fibres trend forward to be inserted into the posterior edge of the mandible not far from the symphysis. The posterior fibres are inserted into the anterior edge of the hypo-hyal and the lateral edge of the basi-hyal in front thereof. Between these two extremes the fibres are inserted into a median raphe. Those fibres which are inserted into the hypo- and basi-hyal pass ventral to the hyo-glossus to reach their insertion. The rest of the muscle is submucous, and dorsal to the visceral skeleton.

As viewed from the lateral aspect, the adductor hyoidei appears as a single entity with two insertions and a median portion whose fibres pass mediad out of sight without any insertion. As viewed from the medial aspect the pars cranio-glossus is distinctly definable from the rest of the muscle from about half-way down the descent from the origin. A little lower the two portions become completely separated.

The hyo-glossus (Fig. 16).—This we regard as the second oblique subarcual muscle, which has increased in size, lost its attachment to the postero-dorsal aspect of the basi-hyal and joined its fellow of the opposite side. The reduction, almost to extinction, of the cerato-hyal, as demonstrated by de Beer (1932), has been accompanied by the transfer of the origin of this muscle to the lower end of the hyo-mandibular.

Each half of the combined muscle is triangular, the broad end being at the midline where it meets its antimere ; from here it tapers to its origin, by a short strong tendon, from the antero-superior edge of the hyo-mandibular immediately behind the lateral insertion of the adductor hyoidei, that is, close to the lower end. The muscle is placed immediately beneath the mucosa and lies on the floor of the mouth between the two spiracles.

The relation of the spiracle to these muscles and to the hyo-mandibular cartilage now calls for attention (Figs. 15, 16).

The hyo-mandibular cartilage is articulated to the skull behind and below the auditory capsule. From this position it curves laterad, ventrad, and cephalad, round the posterior margin of the spiracle. Posteriorly it lies against, and is easily separated from, the anterior face of the first gill wall, which latter carries the pseudo-hyal cartilage, immediately behind the hyoid interbranchial muscle. The hyo-mandibular cartilage is covered dorsally for the first half of its length by the levator hyoidei, below that it is bedded against the propterygium and its muscles. Its anterior surface is covered for the greater part of its length by the skin of the posterior spiracular wall. Immediately in front of the origin of the levator hyoidei from the side wall of the cranium, and blending with it, is the origin of the adductor hyoidei ; this muscle curves round the anterior wall of the spiracle to gain its insertion into the distal end of the hyo-mandibular cartilage. The posterior spiracular wall gains thickness as it slopes caudad, the anterior has full depth, supplied by the two portions of the adductor hyoidei. Immediately within its outer boundary the lateral narrow end of the hyo-glossus muscle is found on the floor of the spiracle. The roof of the spiracle is supplied by the blended origins of the levator and adductor hyoid muscles, and by the side wall and base of the skull medial to them.

Raja.—The adductor hyoidei in this form is not divisible into two portions as in *Dasyatis*. Here we have only the portion which was described as the levator hyo-mandibularis. These fibres which in that form turn caudad to join the cranio-glossus are, in this, inserted into a fibrous band which connects the other two insertions. Marion described that portion of this muscle which bounds the spiracle the Csd.1 (p. 11), and the rest he regarded as a thin deep layer of the levator maxillae superioris. True, in *Raja* the insertion is carried round the lateral wall of the mouth and across the anterior, or superior, wall onto the maxilla for some distance. But in *R. australis* I find the muscle readily separable from the overlying levator maxillae superioris and, furthermore, the hyoid muscle is very definitely innervated from the hyo-mandibular branch of the facial, whilst the levator maxillae, a mandibular muscle, is just as definitely innervated from the mandibular division of the fifth nerve. There may be some overlapping of the nerves, but the obvious innervation is as stated.

The hyo-glossus.—This is the muscle which Marion designates (p. 33) the coraco-hyo-mandibularis. The muscle is relatively more extensive than in *Dasyatis* and extends further caudad, so that its lateral fibres have a direction caudad with an inclination mediad. The tendon of origin is longer.

It were quite misleading to adopt Marion's designation. de Beer has observed the muscle in *Torpedo* (1932, p. 312) and remarks that " it is not an ordinary coraco-hyoid muscle ". It is innervated from the hyo-mandibular division of the facial nerve, not by the spinal accessory. Its posterior limit is far short of the coracoid and none of its fibres are inserted into any fascia which is bound to the coracoid. It is entirely dorsal to the basal branchial elements.

THE HYOID DEPRESSOR.

Dasyatis.—The coraco-hyoideus is a stout, nearly cylindrical muscle which takes origin from the anterior edge of the first ventral extrabranchial cartilage and the deep surface of the coraco-arcuales fascia superficial to it. The direction of the fibres from origin to insertion is cephalad and dorsad. The insertion is onto the lateral edge of the hyoid copula.

Raja.—Marion's description of the muscle in *R. erinacea* correctly describes the condition in *R. australis.* Attention is drawn to the insertion onto the hypo-hyal cartilage in place of onto the basi-hyal.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Superficial Constrictors. (Figs. 15, 16.)

A. Dorsal.—There appears little doubt that in the selachians the more superficial portion of that muscle which, in its deeper portion, forms the levator maxillae superior, is the representative of the primitive dorsal constrictor sheet in the mandibular segment. In the batoid elasmobranchs there is developed as the anterior margin of the spiracle a muscle which, from its innervation entirely by a post-spiracular branch of the facial nerve, is identifiable as a pre-spiracular hyoid muscle, the adductor hyoidei. In front of this there is an elongated muscle which must undoubtedly be identified as the levator maxillae superioris.

Dasyatis.—The latter muscle arises from the anterior wall of the auditory capsule and the inner wall of the orbit behind the foramen quadringomini. It is a relatively long, strap-like muscle, and passes from its origin cephalad and ventrad and slightly mediad immediately beneath the oculo-motor muscles to an insertion on the superior margin of the upper jaw a little to one side of the symphysis.

The relation of the muscle to the maxillo-mandibular trunk of the fifth nerve calls for comment. The origin of the muscle is behind and lateral to the nerve foramen, and in its course to its insertion it passes beneath the nerve, lifting it away from the subjacent hyoid pre-spiracular muscle. The division of the nerve into maxillary and mandibular rami takes place on the dorsal surface of the muscle. The maxillary ramus is continued forward immediately beneath the floor of the orbit, the mandibular ramus passes ventrad across the muscle not far to one side of its insertion. The motor twig to this muscle is given off just after the separation of the two rami.

In *Raja* the muscle is essentially as in *Dasyatis*. It is that which Marion described as the dorsal part of the levator maxillae superioris.

B. Ventral.—In both *Dasyatis* and *Raja* the pars intermandibularis (Csv.1a) is a very thin and narrow band of fasciculi which, interrupted by a median tendinous raphe, extends between the two lower jaw rami. The pars extramandibularis (Csv.1b^2) is a stronger band of fasciculi. This also takes origin from the median ventral raphe and is inserted in *Dasyatis* by a fine tendon into the extreme lateral end of the mandible just lateral to the joint, but medial to the symplectic. In *Raja* the insertion is into the ventral edge of the mandible medial to the joint, and this insertion is as extensive as the muscle is broad.

The Deep Mandibular Constrictors.

It is believed that the levator is represented by a thin ribbon of muscle, the levator palatini (Fig. 15, L.pal.), which lies between the levator maxillae and the pre-spiracular hyoid muscle. This takes origin from the skull between the origins of those muscles and passes down beneath and in contact with, the levator maxillae to be inserted into the roof of the mouth behind the insertion of that muscle. It is innervated by the same twig of the mandibular ramus of the fifth nerve that innervates the levator maxillae superioris.

In *Raja* the muscle is not differentiated from the levator maxillae which must therefore be regarded as representing the constrictor and the levator.

The Mandibular Adductors. (Figs. 15, 16, 17.)

Although considerably modified by the separation of the maxillo-mandibular arcade from the skull, it is not difficult to recognize in the rays the same components of the adductor mass that were described in the selachians and in *Heterodontus*.

The Oblique Epiarcual Muscle.

In *Dasyatis* the oblique epiarcual, pterygoideus muscle (Pt.a., Fig. 15) is an elongated, flattened, relatively stout muscle which takes origin from the antero-ventral margin of the optic fenestra in the side wall of the cranium. This origin is by a very short tendon which invests the end of the muscle. From this origin the muscle passes cephalad and slightly laterad in contact with the floor of the sphenoidal cavity of the cranium. In front of this it is in contact with the under surface of the floor and posterior wall of the nasal capsule ; it next turns ventrad across the anterior surface of the upper jaw. Having passed the upper jaw it turns caudad and, after traversing the soft tissues in the side wall of the mouth lateral to the common insertion of the two labial muscles, ends in a relatively long and very strong tendon which burrows into the medial adductor mandibularis not far from its medial border and is inserted onto the postero-inferior edge of the *lower* jaw at about the junction of the outer and middle thirds of its length.

This muscle lies upon the levator maxillae (mx.s.) at its origin and is at that point medial thereto. As it passes forward and ventrad, it crosses the levator so that at the insertion of the latter it lies lateral to it. The division of the fifth nerve trunk into maxillary and mandibular rami takes place just after the nerve comes to lie against the lateral edge of this muscle dorsal to the levator. The mandibular division follows the lateral edge of the pterygoid muscle till its tendon disappears between the fasciculi of the quadrato-mandibularis. Motor branches to the pterygoideus, maxillo-labialis and partes posterior and medialis of the quadrato-mandibularis are given off before the tendon is crossed, those to the partes anterior and ventralis and to the mandibulo-labialis after it is crossed.

Taeniura (Fig. 17).—The pars anterior of the pterygoideus (Pty.a.) is almost precisely the same as in *Dasyatis*; in that form no pars medialis was recognizable. The pars posterior (Pty.p.) is a relatively small flattened muscle which arises from the palatoquadrate just in front of the lower end of the pars anterior and its tendon. It is inserted behind the tendon onto the outer surface of Meckel's cartilage.

Raja.—This muscle has been described by Marion (p. 22) as the first part of the levator labialis superioris, a most misleading designation, justified only by its homology with the similarly named muscle in the Selachii. It is relatively a smaller muscle than in *Dasyatis* and takes origin further forward, from the floor of the nasal capsule. Its insertion is, however, precisely similar, and the mandibular ramus of the fifth nerve lies to its outer side from origin to the dipping of the tendon just as in the other form.

THE MANDIBULAR ADDUCTOR, QUADRATO-MANDIBULARIS. (Figs. 15, 16, 17.)

Dasyatis.—(1) The pars medialis (Qm.m.) arises by a short investing tendon from the ethmoid region of the skull above the posterior wall of the nasal capsule and, swelling into a fairly stout flattened muscle, passes ventrad, cephalad and laterad. It penetrates between the massive partes anterior and posterior and, passing superficially to the dorsal edge of the pars anterior, is inserted onto the posterior edge of the lower jaw just below and lateral to the joint. (2) The pars posterior (Qm.p.) is particularly massive; it takes origin from a small area on the lateral surface of the palatoquadrate close to the joint. Increasing very rapidly in size, its lateral fibres curve round the pars medialis to be inserted almost alongside their origin, on the other side of the Q-M. joint, onto the posterior tip of the lower jaw cartilage; this tip lies behind and lateral to the joint. The symplectic cartilage is bound to Meckel's cartilage immediately behind and medial to its postero-lateral end and the fibrous strands of the capsule of this joint are continued across the lateral face of Meckel's cartilage to the capsule of the Q-M. joint. The band of fibres in question separates the insertion of the much-curved lateral fibres of the pars posterior from the insertion of the rest of the muscle, which is onto the posterior edge of Meckel's cartilage for a short distance medial to the band. (3) The pars anterior (Qm.a.) takes origin from a prominent tubercle on the outer surface of the palatoquadrate just in front of the joint, and from the surface of the cartilage between the tubercle and the attachment of the oral mucosa. The area extends from the posterior limit of the teeth to the capsule of the joint. The muscle increases in bulk as it crosses directly to be inserted onto the whole width of the outer surface of Meckel's cartilage for the posterior and lateral half of its length. The anterior limit of this portion of the muscle is very clearly determined by the tendon of the pterygoideus muscle. (4) The pars ventralis (Qm.v.) arises from the tissues in the side wall of the mouth in front of the pars anterior, from which it is separated by the tendon of the pterygoidal muscle, and is inserted in front of that tendon onto the outer surface of the lower jaw. This is quite a small muscle.

The terminal branch of the mandibular ramus of the fifth nerve, after giving off the motor twigs to the partes ventralis and anterior, passes along the anterior margin of the pars anterior, on its way to the ventrum of the jaw.

Comparison of these adductor muscles with those of *Acanthias* and *Heterodontus* discovers features of particular interest. The pars medialis arises from the skull as in *Acanthias*, but passes over the pars anterior to be inserted behind it as in *Acanthias*. The pars posterior is much more massive than in either of the other forms and its origin has extended over the insertion of the pars anterioris and reached the palatoquadrate superficially to it. The pars ventralis is much smaller than in the other forms. The origin of the pterygoideus muscle is peculiar, but its relation to the mandibular nerve and its insertion leave little room for doubt that it has been correctly identified.

Taeniura (Fig. 17).—The pars medialis (Qm.m.), as is usual, arises from the post-orbital angle of the skull. This origin is by a short rounded tendon and the muscle swells rapidly into a short thick rounded body which penetrates between the partes anterior and posterior, being almost completely enswathed by the latter. The muscle contracts rapidly and is inserted onto a spur at the lateral, posterior, end of Meckel's cartilage. This spur projects dorsal to the palatoquadrate, between it and the hyo-mandibular and is post-articular.

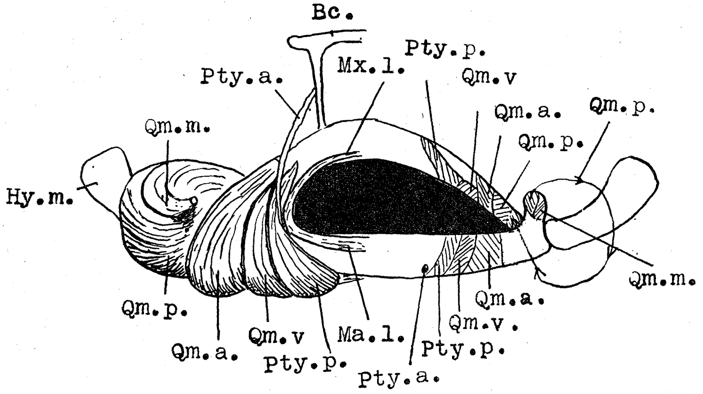


Fig. 17.—*Taeniura*. A slightly schematic drawing of the mandibular adductor muscles, seen from in front.

The pars posterior (Qm.p.) arises from the palatoquadrate just in front of the Q-M. joint, and swings right round the outer aspect of the pars medialis to be inserted onto the same spur of Meckel's cartilage.

The pars anterior (Qm.a.) arises from the palatoquadrate just in front of the origin of the pars posterior, and passes, with a curve ventrad and mediad, to be inserted onto the posterior end of Meckel's cartilage in front of the joint.

The pars ventralis (Qm.v.) arises from the palatoquadrate at the angle of the gape just behind the pars medialis of the pterygoideus muscle. The origin is confined to a very short length of the edge of the mandible, in line behind the teeth, and extends slightly onto the outer surface. The deeper fibres arise, not from the cartilage, but from the fibrous tissues of the side wall of the mouth behind the gape. The insertion is onto the inferior and posterior surface of Meckel's cartilage between the pars anterior of the quadrato-mandibularis and the pars medialis of the pterygoideus.

The relation of the mandibular ramus of the Vth nerve to these muscles is as in *Dasyatis*.

In *Raja* the muscles are essentially similar, but their interpretation by Marion is so different from that adopted above that it is advisable to review briefly the differences and to identify the parts of the muscle in *Dasyatis* with those of this standard batoid type.

Raja.—(1) The pars medialis is that muscle which Marion describes as the second division of the levator labialis superior. The muscle has the same origin as in *Dasyatis*, but loses its identity in the substance of the pars posterior. (2) The pars posterior is the superficial portion of the adductor mandibulae lateralis of Marion's description. The arrangement of the portion is essentially as described, but there is a very complete blending of this and the partes anterior and medialis. An added complication of the picture is caused by the fact that many of the fasciculi of all three parts take origin from, or are inserted into, a very strong superficial fascial sheath. (3) The pars anterior corresponds to the deep portion of the adductor mandibulae lateralis of Marion. There is here no noteworthy difference. (4) The pars ventralis is essentially the same in both forms ; it was not described by Marion.

The relation of the mandibular ramus of the fifth nerve is essentially similar in the two forms.

This comparison of the muscles in the two forms permits one to believe that, though those of *Dasyatis* are very intimately blended, they present the same fundamental arrangement as was observed in the selachians and in *Heterodontus*, and that the conditions presented in *Dasyatis*, wherein the muscles are not so intimately blended, provide us with an analysis of the muscles in the Rays generally.

In addition to the muscles already described, there are in *Dasyatis* two labial muscles. These I designate maxillo- and mandibulo-labialis respectively. Each takes origin from the subdermal edge of the upper or lower jaw to one side of the symphysis and passes laterad across the outer surface of the cartilage in the tissues of the lips at the angle of the gape. They are inserted in the tissues of the angle of the gape so closely together that it was at first thought that one had found an orbicularis oris which arose from one jaw and passed around in the lips to be inserted in the other. They are small cylindrical muscles.

In *Raja australis* there is only the mandibulo-labialis ; it was described by Marion as the adductor mandibularis medialis. His statement that in his species of *Raja* the origin of the muscle was from the anterior edge of the upper jaw suggests that both muscles are really present, but that he failed to discover the duality.

Doubtless these are specialized portions of the adductor complex, but I have been unable to find any muscles in any of the other elasmobranchs which are comparable with them.

THE TRAPEZIUS.

Dasyatis.—For some distance posterior to the skull the spinal segments are completely fused. The dorsal capiti-nuchal muscles are inserted by a cord-like very strong tendon into the dorso-posterior edge of the skull on each side of the foramen magnum. The branchial atrium extends a good distance posterior to this point. The capiti-nuchal muscles enlarge steadily as they pass backwards and are packed close against the crest formed by the fused dorsal spinal processes and enclosed in a very strong fibrous trough. At a distance behind the skull which is almost equal to the length of the cranial and sphenoidal cavities the scapula is attached to the fused lateral spinal processes. These latter, in front of this attachment, send a vertical flange dorsally, forming an outer wall to the trough of the capiti-nuchal muscles. The scapula is relatively very broad antero-posteriorly and extends forward of its attachment to the spinal column. There is thus formed a triangular space whose medial wall is the vertical flange formed from the fused lateral spinal processes ; this slopes from behind forward and mediad. The outer wall, the scapula, slopes from behind forward and laterad. The anterior wall is the convex posterior wall of the branchial antrum. The roof of this space is the deep superficial dorsal fascia ; its floor is in part the lateral portion of the roof of the pericardium, and lateral to that the dorsal surface of the pars posterior of the coraco-branchialis muscle.

This space is filled by the trapezius muscle, which takes origin from the inner wall and is inserted onto the outer.

Raja.—The muscle is essentially as above, but there is no cartilaginous outer wall to the sheath of the capiti-nuchal muscles. I can find no trace of the three divisions of the muscle described by Marion. The trapezius is innervated by spinal muscles.

THE VENTRAL LONGITUDINAL HYPOBRANCHIAL SPINAL MUSCLES.

These are, of course, the depressors of the mandibles, but, as they are not developed from cephalic myotomes, they have not been included in the table.

They are so essentially similar in both forms and follow so closely the conditions described by Marion that it were mere repetition to describe them.

The close similarity of the coraco-hyoideus to the separate portions of the coraco-branchialis justifies one in feeling doubtful as to whether the coraco-hyoideus of the Elasmobranchii is the same muscle as that of the bony fishes. In these latter there appears to be complete agreement that the muscle is developed from trunk myotomes, and it has a very definitely antero-posterior direction. On the other hand, there is not such complete agreement as to the derivation of the coraco-hyoideus of the Elasmobranchs. van Wijhe (1882) describes the muscle as being developed equally from the posterior head myotomes and anterior trunk myotomes, whilst Neal (97) and Edgeworth (1911) are in agreement in deriving the muscle entirely from trunk myotomes. In addition to the doubt this difference of interpretation gives grounds for, the muscle in the cartilaginous fishes commonly appears as though it were a separated portion of the coraco-branchialis.

4. Review.*

An appeal to embryology does not give the student of serial muscular homologies assistance of that definite kind which might have been expected. It has been demonstrated that the whole of the muscles related to any one branchial arch are developed from a single branchial muscle plate, that the muscles developed from the hyoid muscle plate are innervated by the facial nerve, and that those innervated by the fifth nerve are developed from the mandibular plate.

There are exceptions to the complete truth of the above statement, but the exceptions are for the most part taken cognizance of in the designations epibranchial and hypobranchial " spinal " muscles. The apices of the mandibular and hyoid muscle plates are broken off and divorced from the rest of the plate to give rise to two of the ocular muscles ; they will be discussed later, in Appendix A.

The evidence of the embryologist, however, is not against, but rather supports, our fundamental concepts of the course of the evolution of the segmentally arranged visceral muscles. The embryologist, except in isolated cases, is unable to offer any evidence of those more primitive conditions which it is believed the hyoid and mandibular musculature has passed through prior to the perfection of the profoundly modified muscular and skeletal mechanism which we find in these anterior two segments of even the most primitive of the forms available now for study.

Studies of the skeletal and muscular structure of the vertebrate head appear to justify the following beliefs :

The primitive vertebrate from which the whole of the recent forms and their fossil allies were evolved was possessed of a terminal or subterminal mouth, and had behind it seven gill slits on each side of the head. The mouth led into a respiratory antrum, into which the gill slits opened. Each of the slits carried branchiae on both walls. These walls were provided with unjointed cartilaginous supports, and each was also provided with a simple sheet of muscle fibres which was capable of acting as a constrictor and which was antagonized by the elasticity of the cartilaginous support. It was from these simple hoops that the branchial skeleton, as we now see it, was evolved. But further than that, it appears probable that all the seven hoops were modified in the same way originally. The mandibular and hyoid skeletons were precisely similar to the others. Their muscular equipment became modified and adapted to the later changes in the framework. Weak points were symmetrically developed in the hoops, at their centres and above and below those centres on each side ; these were replaced by joints and there resulted pharyngo-, epi-, cerato- and hypo-branchial segments on each side. Whether a ventral continuity of the hoops of the two sides was original or whether a basal element was added is immaterial to the present discussion. The deeper portion of the constrictor sheet of muscle fibres would have been bound to the cartilaginous hoop. When that hoop became segmented, the attached fibres were similarly segmented, and their binding to the hoop in the immediate vicinity of the joint was relaxed whilst their attachments immediately above and below became more perfect.

Thus, it would seem, the primitive muscle sheet became differentiated into a more superficial, almost unchanged, constrictor portion and a deeper portion divided into dorsal, middle and ventral flexors of the three joints of the arches.

With the disturbing growth of the brain there resulted marked changes. The resulting flexure of the head ventrad appears to have been accompanied by, and perhaps to have been responsible for, the coalescence of the anterior gill slit and the mouth. The primitive mouth was at once replaced by this newer one. All that now remains of the original oral musculature are the four primitive ocular muscles. The apices of the hyoid and mandibular muscle plates became captured by the (new) preoral segment to supply the two extra ocular muscles (*vide* Appendix A). Extra respiratory surface was obtained in the gill clefts without increasing the bulk of the branchial region by the oblique caudad growth of their walls so that they came to overlap.

More important changes, however, were those of the mandibular arch and its related muscles. There is evidence in almost every one of the fishes, that the dorsal and ventral ends respectively of all the epibranchial and ceratobranchial cartilages could be brought into close approximation

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* This review is confined to an examination of the serial homology of the muscles related to the seven visceral arches of the previously reviewed Elasmobranchii. Their homology with muscles in other vertebrates will be discussed after those other forms have been described.

by the action of the constrictor sheet and the two or three flexor muscles of the arches. In the case of the mandibular segment not only was this so, but when the gill slits and mouth coalesced or were opened into by the backward extension of the primitive mouth (de Beer, 1931), the ventral ends of the ceratobranchials of the two sides became joined in the symphysis of the lower jaw, whilst the dorsal ends of the two epibranchial cartilages were welded together in similar manner to form the symphysis of the upper jaw. The elements of this first arch above and below these were reduced, but perhaps persisted as the labial cartilages. The labial cartilages, may, however, be persistent branchial rays.

The opposed anterior ends of the mandibular cartilages now were brought into use as upper and lower jaw, and were increased in size and modified in other ways to carry out those functions more efficiently.

These cartilages and their activating muscles were increased very much in size, growing forward as the unfolding of the ventral cephalic flexure permitted, or indeed, perhaps, actually conditioning that unfolding. With their increase in bulk, these cartilages came nearer to the surface and, as it were, grew forward through the superficial constrictor sheet, which was attached above and below to superficial structures which were not carried forward with or by the forward growth of the mandibular skeleton. The deeper, specialized, muscles attached to the arch were, on the other hand, carried forward attached to the dorsal and ventral ends of the two middle elements and to the vanishing elements of the arch above and below them. Muscles evolved from these rests are recognizable, but profoundly modified.

Perhaps another result of the ventral flexure of the head was that there developed a biotactic stimulus between the anterior point of the ventral trunk myotomes and the ventral ends of the branchial arches. Whether this be the explanation or not, the anterior end of the trunk myotome grew forward, displaced to either side the ventral ends of the branchial constrictors, and, burrowing deep to the hyoid and mandibular ventral constrictor sheets, gained an attachment to the ventral, mandibular arcade.

This anterior hypobranchial spinal musculature immediately functioned as a depressor of the lower jaw, and later also assumed the functions of a general branchial depressor. To this end the branchial muscle plates also developed special slips of muscle (the coraco-branchialis) which acquired insertions either into the aponeurosis of the hypobranchial muscles or onto the ventral portion of the pectoral arch. It is also not improbable that the crowding effect of these hypobranchial muscles is reflected in the reduction of the cerato- and hypo-branchial elements, so commonly seen in the Elasmobranchs.

With the assumption of oral and prehensile functions the mandibular arch had need of firmer fixation of the middle joint. The remarkable growth of the two cartilages may be supposed to have already largely suppressed the gill cleft immediately behind it. This permitted the second arch to be brought into use to provide the needed fixed point, and hyostylic suspension resulted.

It is clear, on the evidence of the facts as we now see them, that the ventral elements of the hyoid arch grew forward between the increasing cerato-oral cartilages. Now, there was, ex hypothesi, no direct muscular and fibrous union between these two arches ventrally and the second had to be prevented from sagging below the first. This was effected by the retention and strengthening of the first two constrictor sheets ventrally.

The second arch had now also completely lost its respiratory function, its dorsal portion acting as a suspensorium of the first and its ventral elements, placed in the floor of the mouth, were called upon to function as assistants in the passage of food back towards the oesophagus, their musculature being modified accordingly. Not only was this so, but the closure of the gill slit, except for the small persistent spiracle dorsally, gave rise to an immobile area between the mouth in front and the respiratory antrum behind. This must not be left flaccid, and the need was met by increase in the bulk and strength of the dorsal and lateral portions of the second constrictor sheet and the levator.

Finally, it appears not too much to believe that we have here the explanation of that persistence of the second constrictor sheet, which we find throughout the whole vertebrate series.

The foregoing working hypothesis is based very largely on the development and adult anatomy of the branchial arches. Throughout the Plagiostomi there are certain constant features which must surely be regarded as inherited direct and almost unchanged from a common ancestor.

The skeletal framework is constantly composed of four segments joined to a median basal element. The muscles of each interbranchial septum are:

1, An entirely superficial constrictor sheet which, following Lightoller, we have designated the pars arcuata. This lies between two clefts immediately beneath the skin.

2, A constrictor sheet quite continuous with the last, placed in front of it; quite superficially above the level of the gill clefts, but passing under the pars arcuata of the septum in front of it and onto its own septum anterior to the gill rays thereof, and supplying that portion of the septum which lies between the edge of the cleft and the outermost ends of the branchial rugae. Ventral to the gill cleft it becomes superficial, again continuous with and in front of the lower portion of the pars arcuata. We have termed this the pars inscriptionalis, again accepting Lightoller's designation.

3, A third constrictor sheet which is related to the second precisely as the second is to the first. This we have termed the deep dorsal constrictor or interbranchial muscle. It does not become superficial in any part. Its position is antero-medial and deep to the second sheet, lying anterior to the gill rays and posterior to the branchial rugae. These three portions are absolutely constant in every interbranchial septum throughout these cartilaginous fishes and together they constitute an unchanged " rest " of the primitive constrictor sheet. Of the three parts the deep constrictor is the most primitive. Partes arcuata and inscriptionalis are later, caudad, growths. Even part of the deep constrictor is an added structure, for the primitive gill slits were shallow and led directly, without any obliquity, from the atrio-pharynx.

Though, in conformity with past practice, these three have been treated as separate muscles they undoubtedly constitute one continuous interbranchial sheet. It will avoid ambiguity and assist brevity in later discussion if we designate the sheet the *pars primitiva* of the branchial musculature.

4, A levator arcus branchialis. This, like the partes arcuata and inscriptionalis, takes its origin from the fascia dorsalis and/or from an extrabranchial cartilage which is bound to that fascia, and it is inserted onto the epibranchial cartilage. We know nothing of the development of this muscle in the Elasmobranchs. Unfortunately it is but poorly developed or differentiated in the forms whose development has been studied. On the other hand, the muscle is not always completely differentiated from the dorsal end of the deep dorsal constrictor, and we are able to say with a high degree of confidence that it is a specially modified portion of that muscle. Our evidence in this respect comes largely from the conditions described in *Heterodontus*.

5, A small muscle which lies in the angle between and behind the pharyngo- and epibranchial cartilages; this has been designated one of the " lateral series of dorsal interarcual muscles "; in the foregoing pages it has been described as the dorsal oblique (epiarcualis obliquis) and classified functionally as the dorsal branchial adductor muscle.

6, An adductor arcus branchialis, which has been classified as the middle branchial adductor in the previous pages. This lies in the angle in front of the joint between the cerato- and epibranchial cartilages. These two adductors are developed from the deep part of the primitive branchial muscle plate.

7, A depressor arcus branchialis. The several depressors are combined to form the coracobranchialis muscle; they are developed from the lower ends of the branchial muscle plates.

8, Incomplete subarcualia transversi are developed below the arches of certain Elasmobranchs. These are formed from the ventral ends of the partes inscriptionalis, which extend medially to gain insertions below the basibranchial elements.

9, In the great majority of the Elasmobranchs there are developed from trunk myotomes a series of muscles very similar to the dorsal branchial adductors but lying medial to them and extending always between segments of two arches. They have been designated epibranchial spinal muscles in the foregoing descriptions.

These are in many respects very similar to those ventral muscles which are present below the branchial skeleton of certain of the bony fishes, and there aptly designated subarcualia recti by Edgeworth. These latter, however, are derivatives of the branchial muscle plates and serve as a warning that muscles which seem similar may have completely different origins. This comment also applies to their similarity to the dorsal adductor muscles, with which they have, in the past, been classified. Marion designated these last the median series of dorsal interarcual muscles, following previous observers in so doing.

In closing this summary of the branchial musculature it may be finally stressed (1) that the components of the pars primitiva are absolutely continuous, each being placed in front of the other without interruption and the parts in front being each deeper than that behind, and (2) that the specialized muscles are developed from the deep part of the primitive branchial muscle plate.

In the hyoid segment there is nothing like the constancy of anatomical features which we find in the branchial segments. The variation in structure affects most strikingly the derivatives of the deep layer of the primitive plate. This we are able to state with a very high degree of confidence, because we find the pars primitiva almost unchanged and quite complete in all the typical Elasmobranchs, that is to say in the three suborders of the Plagiostomi. In the Holocephali and in the Chondrostei the first important modifications of this sheet are to be found, and the parts are not at once so clearly recognizable.

In the Plagiostomi, the pars primitiva is found in the typical situation relative to the gill cleft behind it. The pars arcuata is quite superficial and takes its origin above from the fascia dorsalis, exactly as does that part in the branchial segments. In front of it the pars inscriptionalis above the level of the gill slits has its origin just precisely as in the segments behind. There is here, however, no gill pouch in front for it to pass behind, and it is superficial throughout its length. The pars arcuata lies in the free edge of the gill slit and the pars inscriptionalis lies in contact with the outer ends of the hyoid gill rays. In front of this again is a similar sheet of fibres in contact with the inner ends of those rays, just as the deep constrictor lies against the inner ends of the branchial rays. Compare this with the interbranchial septum from another angle : If one examine the posterior face of a typical interbranchial septum one observes the mucosa covering the cartilaginous arch at its deep margin ; next to this one finds the branchial rugae, and outside these the smooth lining of the free edge in which lies the pars arcuata. Radiating laterad and caudad from the epi- and cerato-branchial cartilages are the gill rays. On the side of these, faced anteriorly and laterally, we find the deep constrictor close to the main cartilages, and the pars inscriptionalis between this and the pars arcuata. Covering these anteriorly are the branchial rugae deep within the pouch and the skin more superficially over the pars arcuata. In the anterior wall of the first pouch there is an arrangement of structures which differs only in that there is no gill anterior to the muscular layer ; this layer is the pars primitiva of the hyoid segment. It is not so much that the closure of the hyoid gill cleft has permitted the pars primitiva to reach the surface as that there has been no posterior growth of the pars primitiva of the segment in front to submerge it. There is no evidence of any backward growth of the primitive mandibular muscle plate in the development of the muscles of the mandibular segment. This we might have anticipated from a consideration of the adult anatomy.

Since we are able thus to recognize with confidence the pars primitiva of the hyoid segment and find it essentially as in the branchial segments, we may infer that the specialized muscles also were probably developed, but have now become modified in adaptation to the changed mechanical and skeletal conditions.

We have very clear evidence that superficial parts of the pars primitiva have been added behind the deeper muscles in this as in the branchial segments. We, therefore, look for the modified derivatives of those deeper muscles in front of the primitive sheet and probably deep to it—probably deep, but not necessarily so. It is obvious that, if, as it is believed, the mandibular arcades were deeply placed, they have now become actually subdermal in places. They have also apparently carried the attached hyo-mandibular cartilage towards the surface with them. Therefore, if we find muscles innervated by the facial nerve placed superficially in front of the pars primitiva of the hyoid segment, we are entitled to conclude that they are derivatives of the deep specialized muscles of that segment, carried to the surface in harmony with the changed skeletal structures to which they are or were attached. Further than this, the profound modification of the skeletal arch, its firm articulation, on the one hand with the skull and on the other with the mandibular arcades, and the disproportionate growth of some of its parts and more or less complete disappearance of others should prepare us to find the points of origin and insertion of those muscles quite different from their primitive positions.

In the branchial arches we find the levator to be dorsal and lateral to the dorsal adductor muscle, so that, were the pharyngobranchial cartilage lost and the epibranchial became articulated to the skull, whilst both these muscles were retained and were to retain their insertion onto the epibranchial cartilage, we should find the levator lateral, and that means superficial, to the other. Now, the skeletal changes just postulated are those which are believed to have taken place in the hyoid segment. In the Batoidei we find two muscles arising from the fascia dorsalis and the skull and inserted onto the epihyoid (hyo-mandibular); the more superficial may be regarded as derived from the levator and the deeper as from the dorsal adductor.

In addition to these there is also in *Heterodontus* a muscle which arises from the hyo-mandibular and is inserted into the posterior edge of the palatoquadrate and which is undoubtedly a hyoid muscle because it is innervated entirely by the hyo-mandibular branch of the facial nerve. This insertion of a muscle developed from the muscle plate of one segment onto a skeletal element of the segment in front is a secondary feature. It is not uncommon for ventral muscles to grow forward and/or backward to other than their segments of origin in the Teleosts. In the present case, however, the conditions are not exactly comparable, for the attachment of this hyoid muscle to a mandibular element has involved no growth anterior to its, presumed, primitive attachment. The muscle in question may be regarded as a derivative of the middle adductor of the hyoid arch. The joint of the hyo-mandibular cartilage with the posterior end of the mandibular arcade is placed close to the ventral end of the former, and therefore intervenes between the origin of the middle adductor and its primitive insertion onto the ceratohyoid. This then is to be regarded as the explanation of the insertion of the middle adductor onto the back of the palatoquadrate above the joint with the hyo-mandibular. The muscle we are describing is that which has been designated retractor mandibulae by previous observers. The origin of this muscle may be the primitive one from the hyo-mandibular, or, it appears, it may as a result of fusion with the dorsal adductor, gain an origin from the skull. In *Heterodontus* we find the more primitive condition; the muscle arises from the hyo-mandibular and is inserted onto the palatoquadrate cartilage. In the batoids the levator hyo-mandibulae and the cranioglossus appear to present more or less incompletely fused derivatives of the dorsal and middle adductor mucles, and these arise from the skull and are inserted onto the hyo-mandibular near its distal end and onto the palatoquadrate as well.

Although so similar to the component parts of the coracobranchialis, the coracohyoideus is one of the hypobranchial spinal muscles, and there is no true hyoid depressor.

Still limiting our observations to the Selachii we turn next to a review of the muscles of the mandibular segment.

In the consideration of the dorsal portion of the pars primitiva of this segment, there is one fundamental feature of adult anatomy and development which is apparently of prime importance. The spiracular cleft at no time presents any caudad superficial growth of its anterior wall. In the adult it differs from the other clefts in that its direction is almost at right angles to the long axis of the body. There has, then, been none of that backward growth which gave rise to the partes inscriptionalis and arcuata in the branchial segments.

It follows that we should find, of the pars primitiva, only the interbranchial muscle or deep constrictor. This is present but, because it lies against the outer edge of the spiracular cleft, in some forms appearing as a definite small hood, it has been designated by other writers the Csd.1 or the mandibular superficial dorsal constrictor. That which is conveyed by the separate tabular classifications of the muscles in each suborder, is now unequivocally stated, viz., this muscle is to be regarded as derived from the primitive constrictor sheet and believed to be actually serially homologous with the interbranchial muscles or deep constrictors of the hyoid and branchial segments.

The levator, so closely related to, and probably derived from, the deep constrictor, is commonly found in the mandibular segment to be intimately fused with, and in many cases inseparable from, the pars primitiva.

Of muscles derived from the specialized adductors there are, in the mandibular segment, apparently several. In the different plagiostome forms one finds muscles which at first sight are not comparable one with another. The study of many forms, however, leads to a better comprehension of those various muscles and it is realized that they are but modifications of one plan.

There is reason to believe that the quadrato-mandibularis or the adductor mass—composed as it is of relatively short fibres which pass without intermediate fibrous interruption from one ramus of the jaw to the other, from the cerato- to the hypo-arcual element—alone represents the primitive middle adductor of the mandibular arch. The complicated muscles anterior and superficial to this are to be regarded as having been derived from the dorsal adductor of the arch.

Unfortunately the evidence of embryology is not very helpful in the interpretation of the mandibular muscles. Edgeworth (1911, p. 179) says that in *Scyllium*, " On the formation of the palatoquadrate . . . the mandibular myotome lies outside of and across the palatine process, and then separates into an upper levator maxillae superioris and a lower adductor mandibulae ". Of the branchial muscles he says (p. 235) " Below the anlagen of the trapezius each branchial myotome forms a transversely broad plate in the branchial septum. The part internal to the branchial bar forms the adductor; the part external to the bar forms next the bar dorsally the arcualis dorsalis (our dorsal adductor), and below that the interbranchial, whilst the external edge forms the constrictor superficialis ". Here, in the branchial segments, the middle adductor is formed from that portion of the myotome which would lie ventral to the ceratobranchial cartilage if that cartilage were, like the cerato-oral (palatoquadrate), horizontal instead of vertical, whilst the dorsal adductor is developed from a portion which would lie above the bar. Edgeworth further states that the " upper edge of the adductor mandibulae (subsequently) gains an additional origin from the suborbital cartilage, and this anterior portion of the adductor separates . . . forming the levator labii superioris . . . " This origin of the anterior component of the adductor in *Scyllium* from the adductor anlage would appear to be in direct contradiction to my statement above that there is reason to believe that part only of the adductor mass is to be regarded as representing the primitive middle adductor of the mandibular segment.

On the other hand, it may be emphasized that the adductor alone is developed from that part of the branchial myotome which lies medial to the branchial arch, and that all the other muscles of the arch are developed from the rest of the myotome, whilst in the mandibular segment the ventral superficial constrictor also is developed from the portion which lies below the palatoquadrate. This portion below that bar is, therefore, not entirely homologous with that medial to the branchial bars. It contains the undifferentiated anlagen of more than one muscle.

The outstanding feature of the adult anatomy of the mandibular segment which would seem to indicate that the quadrato-mandibularis of the adductor muscle mass alone corresponds to the primitive middle adductor is the relation of the mandibular division of the fifth nerve to the muscles.

It becomes necessary here to refer to the mandibular adductors, not only of the Holocephali and Chondrostei, but also of the Teleosts and the Amphibians, including the Dipnoans. In all these one finds that there is a portion of the adductor musculature which takes its origin from the quadrate and is inserted onto the mandible. Both origin and insertion are close to the Q-M. joint and the muscle is separated from the rest of the adductor components by the mandibular and maxillary rami of nerve V. This is most strikingly seen in the Holocephali (Fig. 21) but is just as obvious in *Neoceratodus*. In *Psephurus* the two portions of the muscle are even more completely separated by the nerves. The separation of the pterygoid and other divisions of the adductor mandibularis by the same nerves is quite clearly seen in *Ichthyophis glutinosus* and in *Amblystoma tigrinum* and its immature Axolotl stage. In the adult Anura the relations, though somewhat obscured, are preserved unchanged, and are quite clear in the tadpoles.

These relations can also be demonstrated in the Teleostei.

It is neither necessary nor desirable to anticipate later sections of our work by entering on detailed descriptions of the features mentioned as being present in forms not yet reviewed. It is sufficient, having mentioned them, to draw the inference that a feature which is found constant in so large a range of vertebrate animals may be reasonably regarded as reflecting and resulting from a condition present in their common ancestor.

In short it must be regarded as an inherited character.

There is little doubt, then, that the portion of the adductor musculature which is found between the ramus mandibularis V and the joint is completely homologous in all the forms in which it is found, and it appears equally reasonable to assume that it is the persistent reappearance of the middle adductor of the primitive branchial musculature.

5. The Chondrostei.

PSEPHURUS.

In *Psephurus* there is observed a further stage in the reduction of the muscles in the branchial segments; the first stage is presented in the Holocephali.

I have had for dissection two very well preserved specimens which had a length over all of 30 cm. They were stained before dissection. I have also been able to dissect specimens of *Acipenser*, but as several species of that genus have already been fully described it is unnecessary to repeat the work (vide Vetter, 1878). The myology of *Polyodon* was described by Danforth (1913). His drawings so nearly represent the muscles of *Psephurus* that I have not thought it necessary to illustrate this description.

The innervation of the muscles in the acipenserids has been described by Norris (1925) and his work has saved me the necessity of tracing the motor nerves in my specimens.

PSEPHURUS.

		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors	Dorsal ..	Absent	Levator operculi	Absent
	Ventral ..	Absent	Csv.2	Csv.1
Deep Constrictors	Dorsal ..	Absent	Lev., hy.	Protr.hy. (?)
	Ventral ..	Trans.v.vent.	Interhyoideus	Absent
Levators		Lev.arc.br.	Levator hyomandibulae	Protr.hy.
Epibranchial Spinal Muscles		Absent	Absent	Absent
Adductors	Dorsal ..	Absent	Absent	Pterygoideus
	Middle ..	Add.arc.br.	M.hyo-mandibularis	Quadrato-mandibularis
	Ventral ..	Sub.arc.obl.	Absent	Absent
Depressors .. .. Hyobranchial spinal muscles		Co.br.	Absent	Absent

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The superficial constrictors are quite unrepresented.

Of the deep constrictors, a single delicate subarcualis transversus, which extends between the basibranchial cartilages of the third arch, is the only representative found in my specimens.

Three levatores arcuum branchialium are present. They arise close together, one behind the other, under cover of the dorsal superficial hyoid constrictor, from the side of the cranium. They are relatively slender muscles and pass caudad, laterad, and slightly ventrad, to their insertions. The first is inserted into the upper ends of the first and second epibranchial cartilages, which are bound together by the tissue into which the muscle is inserted. The second is inserted in similar manner into the second and third, and the third into the third and fourth epibranchial cartilages. It follows that the first is the shortest and the third the longest of these.

Typical small adductores arcuum branchialium, middle adductors, are present in each of the arches except the last.

Three subarcuales obliqui are present. The first of these takes origin from the basihyal and runs out along the ventral surface of the first basi- and cerato-branchial cartilages to be inserted on the latter close to its dorsal end. The other two, much smaller, arise from the basi- and are inserted onto the cerato-branchial cartilages of the second and third arches.

The coracobranchialis muscle is represented by three bands of muscle fasciculi which take origin from the clavicle and pass dorsad, laterad, and cephalad, to be inserted into the median ventral edge of the fifth cerato-branchial cartilage near its ventral end.

The hypobranchial spinal musculature is represented by the coracohyoideus muscle. This is an unpaired cylindrical muscle which arises from the deep surface of the clavicle and from a superficial tendinous interruption to the other side of which the rectus abdominis is attached. The muscle tapers as it extends forward to terminate in a cord-like tendon which divides anteriorly. Each half is inserted onto the posterior and median edge of the inner end of the basihyoid of its side. Two other very fine but remarkably strong branches of this tendon on each side are attached to the inner ends of the second and third basi-branchial cartilages.

THE MUSCLES OF THE HYOID SEGMENT.

The condition of the constrictor muscles in *Psephurus,* as in other acipenserid forms, is of particular interest. These peculiar transition forms between the typical elasmobranch and teleost musculature provide the key to the understanding of the latter.

The superficial and deep dorsal constrictors appear as one continuous muscle, which from its insertion may be treated in two parts. (*a*) The levator hyo-mandibulae takes origin from the cranium under the lateral edge of the parietal bone. There is a vacuity in the dorsal cranial covering bones between the parietal and the suturing ends of the post-temporal and the dermosphenotic. The line of origin of the levator hyo-mandibulae commences in front about one-third of the length of the vacuity from its anterior end and occupies about the middle third of that length. From this origin the muscle passes ventrad, caudad, and slightly laterad, to be inserted onto the dorsal edge of the lateral surface of the hyo-mandibular, which is here subdermal. (*b*) The levator operculi arises in the same line behind the levator hyo-mandibulae and passes parallel to it to be inserted into the dorsal margin of the operculum. The two portions are quite continuous and are only described separately because of their separate insertions, and because previous observers have divided the muscle in *Acipenser* and in *Polyodon.* The sheet of muscle fibres is subdermal throughout their length ; the dorsal cranial covering bones are but extensive dermal scutes. In their passage from origin to insertion they pass deep to the conjoined post-temporal and dermosphenotic. The muscle is innervated by twigs of the hyoid branch of the facial which passes deep to the hyo-mandibulo-cranial joint and winds superficiad, round the top of the hyo-mandibular cartilage. The twigs then course backward over the surface of the muscle.

The superficial ventral constrictors present the typical elasmobranch division into Csv.2 and interhyoideus.

The interhyoideus takes origin from the median ventral raphe behind, and partly under cover of, the Csv.1. The fibres pass laterad and slightly caudad to be inserted into the middle one-third of the length of the ceratohyoid along the median edge.

The Csv.2 is continuous with the posterior margin of the interhyoideus and it arises from the median ventral raphe behind it. From this origin the fibres pass laterad and caudad and then dorsad, behind the ceratohyoid, pseudohyoid* joint, along the free area of the opercular fold, to be inserted into the ventral edge of the splint-like suboperculum.

The muscle is innervated by twigs from the hyoid branch of the facial. This nerve, after becoming subdermal at the upper end of the hyo-mandibular, passes ventrad and caudad behind that cartilage under cover of the operculum, and then turns forward mediad to the ceratohyoid, crosses that cartilage superficially from behind and medially cephalad and laterad under cover of the suboperculum, and runs forward medially to the lower jaw. The motor twigs to the Csv.2 and interhyoideus are given off just before it crosses the ceratohyoid.

The middle adductor muscle of the hyoid arch is apparently represented by a small triangular sheet of fibres, the M. hyo-mandibularis, which arise from the deep edge of the anterior surface of the pseudohyal and are inserted into the posterior edge of the mandibular cartilage below the maxillo-mandibular joint. This little muscle may act as a depressor mandibulae or as protractor hyoidei.

The motor nerve for this muscle comes from the hyoid branch of the facial after it has crossed the ceratohyoid.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The intermandibularis (Csv.1) presents two portions. These, however, are not strictly comparable with the pars intermandibularis and pars extramandibularis of the typical Elasmobranch. Rather they foreshadow the pars submentalis and posterior of the Teleosts. A similar division of the Csv.1a has been described in *Mustelus* by Lightoller and in Acanthids by Marion. The pars submentalis is composed of short fibres which cross from one mandibular ramus to the other immediately behind the symphysis without any median interruption. The pars intermandibularis (Csv.1b) is a broader sheet of fibres which take origin from the mandibular ramus behind the first part and nearly as far back as the ramus extends. The fibres do not cross the

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* The hyoid arch of *Psephurus* possesses a remarkably large interhyal cartilage. This, in the light of de Beer's (1932) work on the development of the hyoid arch in the rays and Sharks, I have designated the pseudohyoid, though I have not been able to check the identification by determining the position of the artery.

mid-line but are inserted into a median ventral raphe. The posterior fibres incline caudad from the mid-line and overlap the insertion, but not the origin, of the interhyoideus muscle.

The levator maxillae superioris and deep dorsal constrictor of the mandibular segment in the typical Elasmobranchs are here represented by the remarkably developed protractor hyo-mandibulae. This muscle arises from the walls of a large sulcus in the side of the cranium. The sulcus extends forward above the orbit for some distance and backward behind the orbit to the cranio-hyo-mandibular joint. This is a massive spindle-shaped muscle whose thickest part lies between the orbit and the hyo-mandibular joint. The direction of the long axis of the muscle is from in front caudad, with an inclination ventrad and laterad. The muscle is inserted into the capsule of the hyo-mandibulo-symplectic joint.

The innervation is from the trunk of the fifth nerve immediately after it emerges from the trigeminal foramen. The innervation is somewhat peculiar in that the twig enters the deep ventral surface of the muscle immediately behind the orbit. It is unusual for the motor nerve to the muscles of the fishes to penetrate the muscle before breaking up.

The dorsal oblique adductor and the middle adductor muscles of the mandibular arch are both present.

The dorsal oblique (pterygoideus muscle) is the larger of the two parts of the adductor mandibularis of previous observers. It arises from the outer surface of the palatoquadrate cartilage right forward to the symphysis. Commencing as a quite thin muscle at the mid-line anteriorly, it increases in bulk as it extends back along the hollow of the expanding cartilage. Near the posterior end of the cartilage it turns sharply ventrad, passes through a check ligament and is inserted onto the outer and upper surface of Meckel's cartilage a short distance in front of the joint. The check ligament is a very strong band which arises behind from the fibrous capsule of the Q-M. joint, passes forward subcutaneously and then turns mediad beneath the buccal mucosa at the angle of the mouth and is inserted onto the deep surface of the same capsule.

The middle adductor (quadrato-mandibularis) is much the smaller component of the adductor musculature of the jaws. It takes origin from the outer surface of the expanded posterior and of the palatoquadrate cartilage. It tapers very rapidly and passes beneath the check ligament to be inserted onto Meckel's cartilage behind the pterygoideus and just in front of the joint.

These two muscles are not fused in any part. They are separated at their contiguous margins by a deep fissure in which is lodged the mandibular ramus of the fifth nerve. Both muscles are innervated by twigs from the mandibular V.

Psephurus, in its visceral musculature, is very similar, not only to the allied *Polyodon*, but also to *Acipenser*. I have tabulated below the muscles found in the latter by Vetter (1878) and in the former by Danforth (1913) along with those of *Psephurus*.

This table not only clarifies the synonymy of nomenclature, but presents also the agreements and differences in the three forms.

Acipenser (Vetter.)	*Polyodon.* (Danforth.)	*Psephurus.* (Kesteven.)
Cs.1	?	?
Cs.2 (and 6 ?)	Geniohyoideus	Csv.1
Cs.3 and 4	Not described	Csv.2
Cs.5	Not described	Interhyoideus
Add.mandibulae	Add.mandibulae	
	pars.ant.	Pterygoideus
	pars.post.	Quad.-mandib.
Protr.hyo.	Protr.hyo.	Protr.hyo.
Retr.hyom.	Retr.hyom.	Lev.hyom.
Mus.opercularis	Not described	Lev.operc.
Not described	Not described	Hyo-mandibularis
Lev.arc.br. (5)	Lev.arc.br. (4)	Lev.arc.br. (3)
Add.arc.br. (3)	Add.arc.br. (4)*	Add.arc.br. (4)
Interarc.vent. (5)	Interarc.vent. (4)	Subarc.obliqui (3)
Not described	Transv.dors.	Not found
Not described	Trans.vent.	Transv.vent.
Branch-mand.	Branch-mand.	Not found
Coraco-arc.post.	Coraco-arc.	Coraco-arc.
Coraco-arc.ant.	Pharyngo-clav.	Coraco-hyoideus
Interbranchiales	Not found	Not found

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* Norris (1925) reports a fifth add.arc.br. in *Polyodon.*

It is probable that further examination will discover the interhyoideus and the depressor mandibulae (hyo-mandibularis) in *Polyodon*, and also that the branchio-mandibularis is really present in *Psephurus* ; maybe, I failed to find it in my young specimens on account of its tenuity.

THE CHONDROSTEI AND PLAGIOSTOMI.

Comparison of the cephalic musculature of these two groups does not involve us in much that is controversial, most of the homologies being readily recognizable. The branchial musculature does not call for analysis here.

THE HYOID MUSCLES.

Of dorsal constrictors we have only the levatores hyo-mandibularis and operculi to consider. Vetter (1878) was of the opinion that these two muscles were comparable with the superficial and deep portions of the selachian Csd.2. It will be remembered that the Csd.2, as he viewed it, included the levator hyo-mandibularis. In our study of the dorsal constrictor sheet in the Selachians we found there was a variable tendency of the most anterior fibres of the sheet to become attached below to the hyo-mandibular and posterior end of the quadrate. Further than this an intimate association of the fibres in question and the levator hyo-mandibularis was observed in the majority of the examples. In *Heterodontus* we found the most internal and anterior fibres of the sheet acting as a levator, not only in the hyoid segment but also in the branchial. In view of all these circumstances it would seem that we should agree that Vetter's comparison is correct, and that these two muscles represent the whole of the dorsal constrictor sheet of the hyoid segment.

Hyo-mandibularis. The homology of this little muscle is very doubtful. Its innervation by the hyo-mandibular ramus of the VIIth nerve indicates that it is a hyoid muscle. Its relation to the middle joint of the arch suggests the identification given in the text and table.

Protractor Hyo-mandibularis.—There is no room for doubt that in identifying this muscle with the levator maxillae superioris of the Selachians Vetter was correct. Its innervation and position alone would lead to this decision, but when, in addition, one is able to compare the muscle with the levator maxillae superioris in such forms as *Sphyrna* and *Carcharhinus*, its remarkable forward extension ceases to be a peculiar feature. The transference of its insertion to the distant end of the hyo-mandibular is an interesting example of adaptation to the requirements of the altered skeletal structures.

The identification of the anterior part of the adductor of the jaws as the pterygoideus rests upon its relation to the mandibular and maxillary rami of the Vth nerve. That relationship, however, is so very constantly maintained in all the variations of the muscle among the Selachians that the identification is made with confidence.

6. **Holocephali.** (Figs. 18-21.)

Vetter described the musculature of the head of *Chimaera monstrosa* in 1878 and I described that of *Callorhynchus antarcticus* in 1933. The cranial nerves of *C. monstrosa* were described by Cole (1896) and those of *Callorhynchus* by myself.

For the purposes of the present work I have dissected *Chimaera ogilbyi* Waite.

I reproduce, with the lettering slightly altered, my drawings of the muscles of *Callorhynchus*, and describe the muscles briefly in order that their homology with those of the Plagiostomi may be discussed.

Nomenclature and synonymy :

	C. monstrosa (Vetter.)	*Callorhynchus* (Kesteven.)	*C. ogilbyi* (This work.)
Branchial Muscles.	Interbranchiales	Obliqui ventrales	Interbranchiales
	Protr.arc.br.	Lev.arc.br.ant.	Lev.arc.br.ant.
	Not described	Lev.arc.br.post.	Lev.arc.br.post.
	Not described	Med.dors.int.obl.	Epibr.spinal
	Not described	Lat.dors.int.obl.	Obliqui dors.
	Add.arc.br.	Exter.dors.obl.	Add.arc.br.
	Cor.br.	Cor.br.	Cor.br.

	C. monstrosa (Vetter.)	*Callorhynchus* (Kesteven.)	*C. ogilbyi* (This work.)
Hyoid Muscles.	Not described	Depr.rost.et vel.	Depr.veli
	Cs.2	Lev.operc.	Csd.2b (pars arcuata)
	Hyoideus sup.	Depr.mand.sup.	Depr.mand.sup.
	Hyoideus inf.	Genio hyoideus	Interhyoideus
	Not identified	Depr.mand.sup.	Depr.mand.sup.
	Cs.4	Not identified	Not identified
	Cs.3	Post. deep constr.	Csv.2b
Mandibular Muscles.	Labialis ant.	Prot.lab.sup.	Prot.lab.sup.
		Pr.sup.lab.inf.	Prot.sup.lab.inf.
	Labialis post.	Pr.inf.lab.inf.	Csv.1a
	Cs.5	Ant. deep constr.	Csv.1b^2
	Cs.1	Supf.vent.constr.	Csv.1b
	Not present	Lev.rost.	Not represented
	Lev.ang.oris 1	Lev.lab.sup.	Lev.lab.sup.
	Lev.ang.oris 2	Lev.lab.inf.	Lev.lab.inf.
	Add.mand.	Add.man.ant.hd.	Pterygoideus
		Add.man.post.hd.	Quadrato-mandibularis
	Coraco-mand.	Cor.mand.	Cor.mand.
	Cor.hyoideus	Cor.hy.	Cor.hy.
	Trapezius	Cucullaris	Cucullaris
	Not described	Sph.oes.	Sphincter oesophagi

The Muscles of the Branchial Segments.

Attention is particularly drawn to the reduced interbranchial muscles. Each is a small fan of fibres with a thicker median edge. The apex of the fan is at the insertion of the muscle onto the basibranchial cartilage. The expanded upper margin is placed in the septum above the middle joint of the arch. The thicker edge, alongside of the cartilages, extends upward to an origin from the epi-branchial cartilage close to the origin of the adductor of the arch.

These reduced interbranchial muscles will be met again in *Neoceratodus* and in immature stages of the other groups of amphibians. In these latter they have been described as musculi marginales (Edgeworth, 1911, p. 232).

Only two branchial levatores are developed in each of three holocephalans which have been studied. The anterior levator arises from the ventrum of the skull in the region of the orbit ; it is a narrow ribbon of muscle which passes ventrad, caudad, and laterad, to be inserted into the junction of the first and second epi- and cerato-branchial cartilages. It is innervated by the post-trematic ramus of the glossopharyngeal nerve.

The posterior branchial levator arises from the lateral edge and ventrum of the skull just behind the orbit. Its direction from origin to insertion is mediad and slightly caudad. Broader than the anterior levator, its insertion extends from the second well back across the fused third, fourth and fifth pharyngo-branchial cartilages.*

The adductores arcuum branchialium are quite typical muscles, so similar to those of the Plagiostomes that they do not call for description.

The coraco-branchialis also so closely resembles that of the Plagiostomes that it calls for no further comment.

MUSCLES OF THE HYOID SEGMENT. (Figs. 18 to 21.)

The depressor rostri et veli (Fig. 18, Csd.2) (in *Chimaera*, depressor veli only) is a very thin layer of muscle fibres which has an indefinite origin in the superficial fascia behind the jaws. Its fibres course forward and dorsad over the side of the face and have an indefinite insertion in the superficial tissues of the velum. In my account of the muscle in *Callorhynchus* I stated that it was innervated by the maxillary division of the Vth nerve. Observation of the depressor and levator rostri in batoid species leads me to think that I may have been in error in so stating. In the Batoidei the rostral muscles arise far back and, in some species, are certainly innervated by the facial nerve. In two of the species I dissected I found branches of the facial terminating by penetrating the muscle. In no species was I able to find any branch of the Vth reaching either of these muscles.

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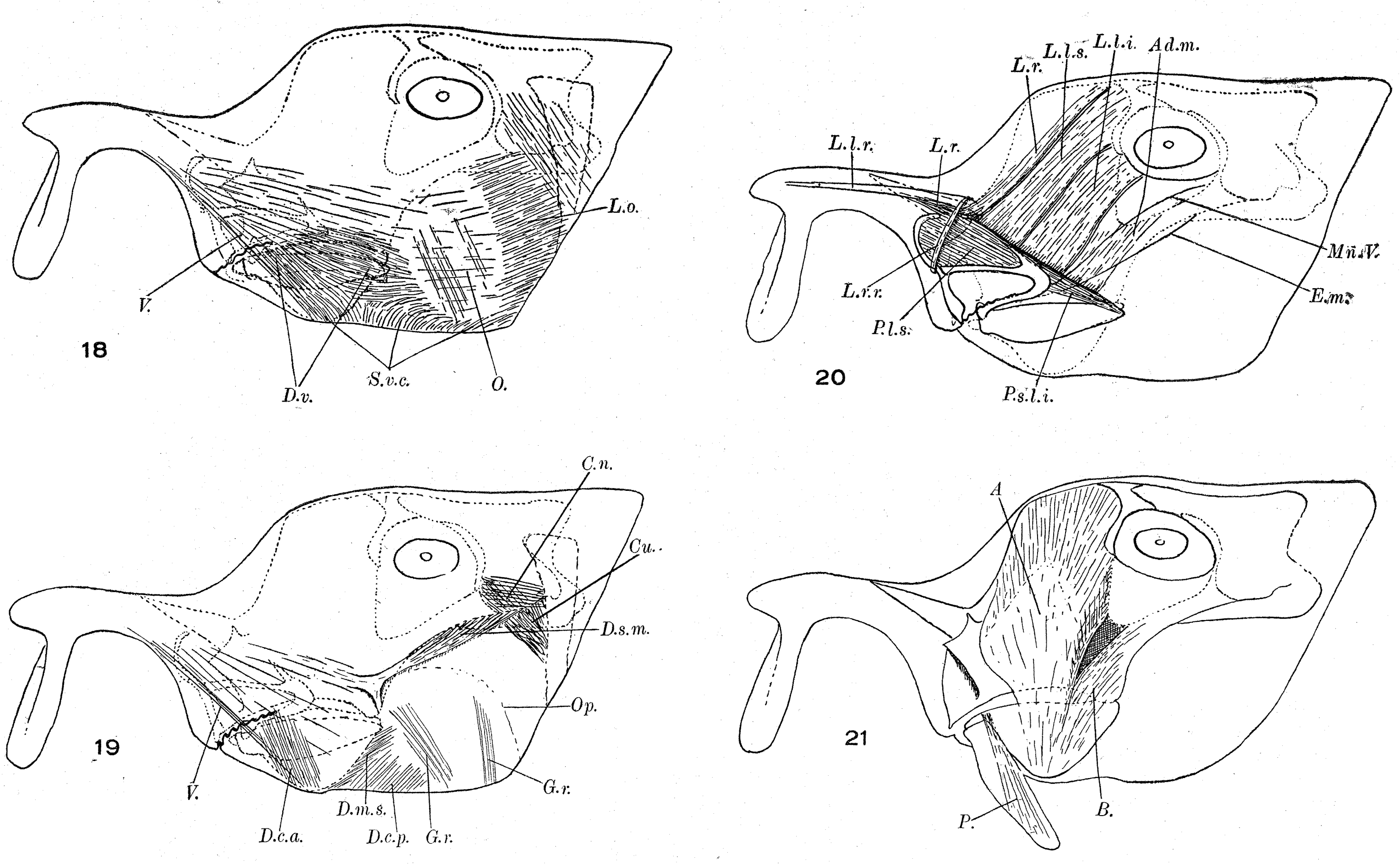
* It is worthy of notice that the composition of the branchial skeleton in its dorsal portion recalls strongly that of the Teleosts, especially so in the case of the fused pharyngo-branchials.



Figs. 18, 19, 20 & 21.—*Callorhynchus.* Lateral views of successively deeper dissections (from Kesteven, 1933).

In *Chimaera ogilbyi*, as in *Callorhynchus*, I find twigs of maxillary ramus of the Vth nerve penetrating the muscle from its deep side. These twigs are quite numerous and it was assumed that some of them supplied the motor nerve for the muscle. I find, however, in both of the species, that there are also a few twigs from the external mandibular branch of the hyo-mandibular ramus of the facial which course forward over the surface of the muscle. These I now regard as the motor supply to the muscle.

The levator operculi (Csd.2b, Fig. 18), a thin sheet of muscle fibres which arises above and behind from the fascia dorsalis and runs ventrad and cephalad over the opercular membrane, and which is innervated by the external mandibular branch of the hyo-mandibular of VII, can be none other than the posterior portion of the dorsal superficial constrictor of the hyoid segment, the Csd.2b.

The ventral superficial constrictors are not readily defined from those of the mandibular segment. It seems probable that the posterior part of the superficial ventral constrictor of my description of *Callorhynchus*, and the posterior deep constrictor beneath, under cover of it (Csv.2, Fig. 19) represent the superficial constrictor of the hyoid segment. These have an indefinite origin in the superficial fascial structures over the anterior and ventral part of the opercular fold and are inserted into a median ventral raphe. Twigs from both the mandibular ramus of V and hyo-mandibular of VII can be traced into the muscle.

The interhyoideus presents an interesting condition, apparently intermediate between the protractor hyoidei of the teleosts and the interhyoideus of the plagiostomes, but, as the interhyoideus is certainly innervated by the VIIth nerve, and the protractor hyoidei by the Vth as well, we cannot be quite certain that the condition is truly intermediate.

The muscle is inserted into the fibrous investment of the symphysis of the lower jaw beneath the mucosa of the mouth. Traced back to its origin the muscle passes laterad, caudad, and slightly ventrad, to arise onto the apex of the angular expansion of the posterior border of the ceratohyal about the centre of the length of the cartilage. The muscle is ribbon-like, tapering from its tendinous origin to the broader muscular insertion, and it is innervated by a twig from the superficial internal mandibular branch of the hyo-mandibular ramus of the VIIth nerve. There is also possible an innervation by the glosso-pharyngeal nerve, but it is believed that the branch of this latter nerve which was traced to the muscle is a sensory nerve.

The depressor mandibulae superioris (Cd.2.pr., Fig. 19) is particularly well developed in *Chimaera ogilbyi*. It arises by a strong fascia from the deep edge of the lateral border of the suspensorial lamina of the skull. This fascia is attached along the full length of the lamina and is continued back behind it, attached to the fascia dorsalis, deep to the origin of Csd.2b, to gain an attachment to the pectoral arch where that lies against the trunk muscles. The muscle itself commences at the posterior end of the cranial lamina and passes forward in contact with that lamina and then passes down behind the Q-M. joint and is inserted by a fibrous ribbon into the posterior edge of Meckel's cartilage below the joint, and by an extension of the ribbon, along the inner side of the cartilage, almost to the symphysis. The posterior and deeper fibres pass more deeply and transversely, also by fibrous extension, to gain an insertion onto the inferior surface of the hypohyal, passing under the coraco-mandibularis to reach this insertion. This is apparently the hyoideus superior of Vetter.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

There is no muscle in any of the three forms studied which may be identified as a representative of the dorsal constrictor.

Csv.1a.—In *Callorhynchus* this arises from the outer surface of Meckel's cartilage at the upper margin near the anterior end and is attached to the inner surface of the posterior end of the large lower labial cartilage. In *Chimaera* there is no such cartilage developed, and the muscle is inserted into the superficial tissues of the lip near the angle of the gape.

Csv.1b (Fig. 18).—This arises in the fascial structures of the deeper layers of the velum and side of the face behind and below the mouth. It is an indefinite sheet of fibres which pass ventrad and caudad to lose their identity in the deeper layer of the Csv.2 below the inferior angle of Meckel's cartilage. The muscle is certainly innervated by twigs from the mandibular ramus of the Vth nerve and also, apparently, by twigs from the external mandibular branch of the hyo-mandibular ramus of the VIIth.

Csv.lb^2 (Fig. 18).—In view of the fact that in *Callorhynchus* the posterior fibres of this muscle are continuous with the ventral fibres of the levator operculi and the anterior with ventral fibres of the depressor rostri, this muscle might be described as a typical extra mandibularis.

The protractor labii superioris (P.l.s., Fig. 20) and protractor superior labii inferioris (P.s.l.i., Fig. 20) form a flat muscle interrupted by the posterior superior labial cartilage. It arises from the anterior upper labial cartilage and is inserted into the tissues of the lip behind the gape or into the perichondrium of the large lower labial cartilage on its outer side near the posterior end.

The levator labii inferioris (L.l.i.), levator labii superioris (L.l.s.) (and the levator rostri (L.r., Fig. 20), present in *Callorhynchus* only) are three relatively thick strap-like muscles which arise in front of one another from the crest of the skull in front of the orbit. The first is inserted into the inner surface of the large lower labial cartilage and/or the tissues of the lower lip just behind the angle of the gape. To reach this insertion the muscle passes deep to the last muscle and the small lower labial cartilage. The levator labii superioris is inserted into the tissues of the upper lip at the edge of the upper jaw, having passed deep to the upper labial cartilages to reach its insertion. The levator rostri, parallel with these two and in front of the last, is inserted into the lateral ligament of the rostrum. To reach this insertion it turns sharply forward beneath a check ligament, the ligamentum radicis rostri.

These three muscles are not fused at their contactual edges, but may be cleanly and completely separated throughout their length. All three are innervated by twigs from the maxillary ramus of the Vth nerve.

The Pterygoideus (Fig. 21).—This is the massive adductor muscle of the lower jaw. It arises from the greater part of the lateral and dorsal surface of the skull between the orbit and the nasal capsule. From this very extensive origin the fibres converge to be inserted into the outer surface of Meckel's cartilage. Innervation is by twigs from both the maxillary and mandibular rami of the Vth nerve.

The relation to the nerves is important. I quote from my description of the nerves in *Callorhynchus*: "The maxillary and mandibular rami of the fifth nerve cross the floor of the orbit below all the ocular muscles, along with the buccal division of the seventh. The trigeminal branches lie medial to the buccal nerve. As the orbit is crossed the nerves broaden out and the buccal and maxillary nerves come towards the surface, the former overlying the latter. Their situation then is upon the ribbon-like levatores of the upper and lower lips and the rostrum, and beneath the velar muscles . . . The maxillary division of the trigeminal nerve runs forward under the main stream of the buccal branches, and its terminal fibres end on the surface of the muscles beneath it. Branches to the adductor mandibulae (pterygoideus) are given off within the orbit and reach the muscle deeply. The mandibular division of the fifth nerve leaves the orbit deeply between the two heads of the adductor mandibulae muscle. (That is between the pterygoideus and the quadrato-mandibularis muscles.) It gives off a number of twigs to that muscle, some three or four of which turn downwards to supply the small posterior head of the muscle. (The quadrato-mandibularis.) The nerve comes to lie upon the same ribbon-like muscles as does the maxillary division (but low down) at the anterior end of the valley . . . and (then) continues forward to the angle of the mouth."

The quadrato-mandibularis is reduced to quite a small muscle which arises from the quadrate part of the lateral expansion of the skull behind the origin of the pterygoideus and below the orbit. It passes down and forward to an insertion on the outer surface of Meckel's cartilage behind the pterygoideus muscle.

The hypobranchial spinal muscles, coraco-hyoideus and coraco-mandibularis are typical elasmobranch muscles and do not call for further comment here.

REVIEW.

The branchial muscles depart from elasmobranch standards in several interesting features, each of which may be regarded as foreshadowing either teleost or amphibian characters.

The levator sheet is reduced to two muscles only, omitting the trapezius. These resemble so closely the levatores of the teleosts that there appears little room for doubt that the muscles are completely homologous. Each of these muscles is innervated by two post-trematic nerves (Cole, 1896, pp. 665, 667, 668, 669), the anterior by post-trematic rami from the glosso-pharyngeal and the first branchial of the vagus, the posterior by those rami from the second and third branchial divisions of the vagus. This innervation may be accepted as evidence that each is a composite muscle, and that together they represent four branchial levator muscles. The levator muscles of the Teleosts also are innervated by the branchial divisions of the IXth and Xth nerves if Herrick's observations on *Menidia* hold true for the whole class (Herrick, 1899). This would seem to clinch the case in favour of the homology of the holocephalan and teleostean branchial levator muscles, but what of the question as between the former and the selachian levatores ? Here the decision is not so easily arrived at.

Lightoller asserts that the branchial levatores in the Selachians he studied are innervated by the first five spinal nerves, and these nerves, he states, also innervate the superficial dorsal constrictor muscles, these motor nerves coming from a dorso-lateral ramus of each nerve. He further states that the ventral rami of the first six spinal nerves combine to form a " large nerve trunk . . . (which) . . . proceeds caudally for a short distance to gain the space caudal to the gill basket . . . The terminal branches supply the ventral constrictors caudad to the second." Norris and Hughes (1920) omit to mention the innervation of the superficial dorsal constrictors and the levatores, but they state definitely (p. 369) that the ventral constrictors are innervated by the post-trematic rami of the branchial divisions of the Xth.

In *Pristiophorus* and in *Chiloscyllium* I found, in addition to the perforating twigs of the dorsal rami of the spinal nerves described by Lightoller, small twigs from the post-trematic rami of some of the vagal branches coursing over and ending on the medial surface of the levatores. I have been able to confirm Lightoller's observations in *Mustelus* and have not found any twigs from the post-trematic rami of the Xth related to these muscles.

In all the seven selachian types and in the five batoid types which I have dissected I have detected fine twigs from one or more of the eight post-trematic rami passing dorsad and laterad along the dorsal extrabranchial cartilage or, in its absence, the tendinous intersection which takes its place, and ending on the surface of the superficial dorsal constrictor. These I have regarded as the motor nerves to the muscles. Vetter describes the dorsal constrictor muscles as being innervated by the glosso-pharyngeal or vagus, in *Acanthias*, *Scymnus* and *Heptanchus*.

There is, then, a little doubt as to the innervation of the superficial dorsal constrictors and the branchial levatores in the Plagiostomi. If, however, we assume that the levatores are innervated by the spinal nerves and, on that account, look elsewhere for the homologues of the holocephalan and teleostean levatores we find that the only other epibranchial muscles present in the plagiostomes are the epiarcualia obliqui and the epibranchial spinal muscles, and these are both present in the Holocephali, and, moreover, the latter also are innervated by spinal nerves.

We are, therefore, compelled, per exclusionem, to conclude that the branchial levatores are homologous muscles in all three groups.

Having in mind the fact that the dorsal rami of the spinal nerves are entirely motor in character (vide Norris and Hughes), it seems certain that the twigs which Lightoller describes as reaching the levatores and dorsal constrictors must be motor nerves to these muscles. In view of the fact that the post-trematic rami are not pure motor nerves, it is not so certain that the twigs which I, and presumably Vetter, observed reaching these muscles are motor nerves. On the other hand, the innervation of the homologous levator muscles in the Holocephali and Teleostomi at least justifies the assumption that there is a double innervation of the levatores in the Plagiostomi, and that the spinal innervation has been lost by the muscles of the other groups.

The interbranchial muscles of the Holocephali are of interest, not only as foreshadowing those of the primitive and immature amphibians, but also as presenting a definite half-way stage between the fully developed muscles of the plagiostomes and their complete absence from the interbranchial septa of the teleostomes.

In the form of the epibranchial spinal, the epiarcualia obliqui and the coraco-branchialis muscles the Holocephali are typically elasmobranchian.

The peculiarly modified superficial muscles of the hyoid and mandibular segments are *sui generis*, and do not throw any light on the modifications of these muscles in the teleosts or higher vertebrates.

The interhyoideus is a particularly interesting muscle. It is quite certainly innervated by the facial nerve. Herrick (1899, pp. 157-160) discusses the genio-hyoideus and intermandibularis muscles of the bony fishes. He concludes that " the intermandibularis, geniohyoideus and hyo-hyoideus of ganoids and teleosts have unquestionably been derived from this ventral constrictor system of the selachians " innervated by the Vth and VIIth nerves. After discussing an ill-founded assumption by Rudge (1897) that the muscles are innervated by the VIIth nerve in all forms by anastomosis, peripheral or intracranial, he states : " In *Menidia*, at any rate, it is clear the exact reverse is true, the apparent innervation by the facial in reality being derived from the motor nucleus of the trigeminus, as there is no possible opportunity for a confusion at any point between the motor fibres of the V and VII nerves ". Vetter found the genio-hyoideus in *Esox* to be innervated by the facial, and Herrick confirmed this observation in *Gadus* (l.c., p. 157). In both these instances and in *Amia* (Allis, 1897) the innervation by the facial is by a branch which communicates with the trigeminus. From this Herrick infers that " in forms like *Esox*, in which the so-called genio-glossus (genio-hyoideus) is innervated from both V and VII nerves we may assume that the muscle represents both facial and trigeminal constrictor systems, comparable with those of *Ceratodus*, while in *Menidia* and most other teleosts the VII portion has been lost and the muscles 'genio-hyoideus', together with the intermandibularis, represent the ventral constrictor muscles of the 'trigeminus' segment, the facialis constrictor muscles being represented only by certain dorsal opercular muscles and by the branchiostegal muscles ".

The interhyoideus of the Holocephali differs from the similarly-named muscle in the Plagiostomi in arising from the fibrous investment of the symphysis of the lower jaw, deep to the insertion of the coraco-mandibularis instead of from the deep surface of the median ventral fascia superficial to that insertion.

Unless we are to regard it as an entirely new development, without any homologue among the muscles of the plagiostomes, we are forced, once again per exclusionem, to homologize the two muscles notwithstanding this difference. If we accept this identification we assume that the hypobranchial spinal muscles grow forward between the deep and superficial ventral constrictors instead of, as in the plagiostomes, deep to them both.

The assumption appears reasonable.

In 1910 Holmqvist described " many varieties of the interhyoideus and protractor hyoidei of the teleostei ". Unfortunately I have not been able to consult this work, but Edgeworth (1928, pp. 61-63) briefly reviews it and adds brief descriptions of the muscles in several bony fishes. He asserts that, " the Protractor hyoidei of many teleostei is a compound muscle, being an Intermandibularis posterior plus Interhyoideus ", and the assertion is based on sound embryological evidence.

It may finally be concluded that the interhyoideus muscle of the Plagiostomi and of the Holocephali are homologous muscles and that the protractor hyoidei of the Teleostomi is derived, in part, at least, from this muscle.

The return to a superficial position, which the muscle occupies in the bony fishes, is due to the fact that the hypobranchial spinal muscles do not extend forward to gain an insertion onto the mandible.

The depressor mandibulae superior. This muscle also is of particular interest. It is unquestionably derived from the anterior portion of the hyoid dorsal constrictor, the Csd.2.pr, and probably also the closely related hyoid levator of the plagiostomes. The particular interest attaching to the muscle is that it appears to confirm in part, at least, Lightoller's statement that the depressor mandibulae of the Axolotl " is a composite muscle and represents the second levator and the pars quadrate-hyoidea of the Elasmobranchei ". There is reason to believe that no IXth nerve components supply motor elements to the muscle in any of the Amphibians. Norris describes, in *Siren* (1913, p. 296) and Norris and Hughes (1918, p. 527) in the Caecillians, unmixed innervation by VII.

Any attempt to determine the homology of the muscle formed by the protractor labii superioris and the protractor superior labii inferioris, in the present state of our knowledge must be based on their innervation alone. Obviously they belong to the mandibular segment, for very definitely they are innervated by the Vth nerve.

The three levatores of the lips and of the rostrum are in much the same case. We observe, however, that the levator maxillae superioris, so constantly present in the plagiostomes, is apparently missing from the holocephalan head. As developed in such forms as *Mustelus Chiloscyllium* and *Heterodontus*, there is little in common between the lev.max.sup. and the muscles we are considering, but in *Sphyrna* and *Carcharhinus* we find the maxillary levator arising from an extensive area of the side wall of the skull between the orbit and the nasal capsule.

The resemblance in origins in these examples might suggest homology with the holocephalan muscles.

On the other hand, the levator maxillae superioris lies, always, caudad or superficial to the R. maxillaris V, whilst these holocephalan muscles lie rostrad and deep to that nerve. The development of the levator maxillae superioris from the upper portion of the mandibular muscle plate appears to render it quite impossible that the muscle should acquire a situation rostrad and deep to this nerve. For the present, the most that can be said is that these muscles are derived from the same part of the muscle plate as the pterygoideus.

The pterygoideus. That this is the homologue of the pterygoideus of the plagiostomes seems to be quite satisfactorily proven by its relation to the mandibular and maxillary rami of the Vth nerve, and by a comparison with the pterygoideus muscle in *Chiloscyllium.*

The quadrato-mandibularis muscle lying behind the pterygoideus, with the nerve between them, is very much reduced and would appear to represent the pars posterior only of the plagiostome muscle.

It will be noted that in these last two muscles the Holocephali again present resemblances rather to the Amphibia and Teleostomi than to the rest of the Elasmobranchii.

From the foregoing review it is apparent that in their epiarcualia obliqui, epibranchial spinal, coraco-branchialis and hypobranchial spinal muscles the Holocephali are essentially elasmobranchial in character. In the form of the branchial levatores, the levator operculi and the interhyoideus they resemble the teleosts. In the form of the interbranchial muscles, the adductors of the jaws and the depressor mandibulae they resemble the amphibians.

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CORRIGENDA.

Page 36, line 3. For *Taeniura lymna* read *Taeniura lymma*.
Page 82, line 10 from bottom. For Coccillans read Coecilians.
Page 187, lines 10 and 15. For Caecilians read Coecilians.
Page 100, line 15. For Bridge . . . (1879) read Bridge . . . 1878.
Page 200, line 26. For Bridge in 1893 read Bridge in 1898.
Page 253, line 4. For Lightoller (1935) read Lightoller (1939).
Page 267, line 18. For spheno-pterygoideus anterior read pterygoideus anterior.