Leighton Kesteven, H., 1945. The evolution of the skull and the cephalic muscles: a comparative study of their development and adult morphology. Part IV. The Theria, and index. *Australian Museum Memoir* 8(4): 294–310. [13 June 1945].

doi:10.3853/j.0067-1967.8.1945.514

ISSN 0067-1967

Published by the Australian Museum, Sydney

PART IV. THE THERIA.

The Superficial Facialis Musculature.
The Stylohyoideus Muscle.
The Posterior Digastric Muscle.
The Mandibular Muscles.
The Branchial and Hypobranchial Muscles.

In Part I of this work, dealing with the fishes, instead of describing the muscles of each species before proceeding to those of the next, each was described for the whole of each group. The object was to focus attention upon muscle groups and entities, rather than the musculature of the fishes themselves.

It appeared to the writer that the muscular systems of the vertebrata had been evolved, by adaptive modification, from some generalized fish type, and quite early it appeared that a deal of this adaptive modification might be observed in the conditions presented by the elasmobranchian cephalic musculature.

Therefore, the first portion of this work was devoted to establishing muscle groups and muscle entities, and at the same time, to an inquiry as to whether the varying complexity of the arrangement and modification of these, essentially similar, groups and entities in the process of functional adaptation in conformity with or response to skeletal changes within the fishes shed any light on their origin from a more generalized condition.

In that first part of the work the objective in view was deemed best attained by contrasting and comparing the muscles of the several segments, and it is believed that the comparisons made justified the belief that one could recognize, in the musculature of the mandibular and hyoid segments, certain of the muscles of the branchial segments, but more or less highly modified in adaptation to the changed form and/or function of the skeletal arches to which they are attached or otherwise related.

Passing to the Tetrapoda, it was decided that the study of the further modification of these muscles would be best carried out by observing their variation in relation to the whole of the muscles of each form studied. Having established the groups and entities, it became necessary to study their modification, and the range of their variations relative to other muscles and to the skeleton.

In this last section of the work there will be a return to the first method of study, firstly, because so many Therian types have already been fully described that it would be a work of supererogation to present the descriptions of a further series, and secondly because we have reached our goal. That goal has been to study the evolution of the musculature of the vertebrata with a view to determining the origin of those of the Theria, and especially that of the Mammalia. Clearly, then, it is not the function of this work to describe the wide variation of the Therian cephalic muscles, but simply to compare representative examples with those of the lower vertebrata.

Looking back, we recognize that in our passage from the fishes to the amphibians, it was the branchiate forms amongst the latter that presented us with the chain of beacons which assisted us in our passage along the stream of evolution. True, the chain was far from complete, many guiding lights appeared to be missing and others were hard to understand, but this chain of beacons made possible and profitable a passage which must have been much more difficult and much less satisfactory had we been called upon to pass directly from the fishes to the abranchiate amphibia.

Our further journey down the stream, from the amphibian territory to that of the Reptilia, was no more difficult than that from the fishes to the Amphibia. A surprising number of the guiding lights shone clearly, and with a good deal of confidence we have arrived at the farther confines of the Saurian territory, feeling that we have been able to chart the main current fairly correctly.

Briefly, it is believed that the evolution of the cephalic muscles, from the elasmobranchian type to the saurian, has been followed step by step and has been found to be relatively gradual and without markedly abrupt changes. It is now believed that the change from the saurian to the therian arrangement is really no more abrupt. The Mammalia have a remarkable and complex set of facial muscles which, at first sight, appear to be entirely new muscles, without anything to represent them in the lower forms.

It is, however, fairly satisfactorily demonstrable that this break in continuity of evolution is more apparent than real, and is due largely to failure to recognize the proper significance of the superficial facialis muscles of the Prototheria.

We find the same embryonic muscle plates in the Mammalia which we have become familiar with in the lower vertebrata, and related, of course, to the same segmental nerves. The similarity of the muscles developed from these muscle plates in all the forms already studied justifies the attitude adopted in this section. Broadly, this is that we have to seek detailed homologies amongst the individual muscles of groups whose homology, as groups, may be regarded as established.

It will be found that, in the Theria, the mandibular muscles are innervated by the branches of the fifth nerve, and, in their relation to one another, in a manner very similar to the divisions observed in the Reptilia and Aves, so that their interpretation in terms of the saurian musculature is not difficult. On the other hand, there the evidence bearing on the homology of certain of the muscles innervated by the seventh nerve is very indefinite.

In our approach to this question—the homologues in the Theria of the reptilian muscles innervated by the seventh nerve—it is necessary that we recognize at the outset that there has been a very marked change in the nature of the investment of the head, so that it is questionable as to how far one should press the inquiry. In what detail should one expect to be able to recognize homologies ?

In the introduction to this work it was stated that often we must expect to be able, at most, to indicate the derivation of muscles rather than their complete homologies. This appears to apply particularly to the muscles under discussion. In precisely the same way that it was contended that an homologue of the levator rostri could not be found in a fish without a rostrum, or a protractor labii superioris in a fish without a protractile upper lip, so the homologues of the facial muscles of the Theria, with their flexible skin and loose subcutaneous tissues, should not be expected in the Sauria, with their rigid head coverings.

This, however, does not debar us from speculating as to whether the muscles of the neck and throat in the Reptilia may not have provided the facial muscles of the Theria, and then seeking confirmation or correction of the idea by study of the distribution of the muscles derived from the hyoid muscle plate.

Although the cephalic musculature of a number of the Eutheria and of the Prototheria has been well described by previous workers, the writer's approach to the Therian musculature has been by actual dissections and serial sections of the embryonic material. This laborious course was decided upon for two reasons : firstly, actual familiarity with the structures was known, from experience, to be indispensable to their proper understanding, and, secondly, it was desired to preserve a point of view which had been steadily and deliberately built up by and during the compilation of the work as far as it had gone at this point.

Until I had almost completed my survey of the cephalic muscles of the lower vertebrata I refrained from study of the therian muscles. It was desired to approach these with as complete a knowledge as possible of those of the lower forms, so that they, the therian muscles, should appeal to me as modifications of those of the lower vertebrata. The desire was to avoid, as far as possible, interpreting the lower in terms of the higher.

This study of the therian muscles was carried to the stage of deciding their probable homologies or derivation before the work of previous investigators was consulted. This must not be taken as implying an expectation of errors of interpretation in the work of others ; it was simply carrying to its logical conclusion the policy, dictated by my desire to avoid the risk of interpreting the lower in terms of the higher, which had caused me to become familiar with the musculature of each group in turn, before studying that of the next higher group.

The development of the premandibular, mandibular, hyoid and branchial muscles differs in well known, important respects from that of other muscles. It has been generally agreed to regard these differences as being of fundamental importance and to regard these as "visceral" muscles, developed from visceral muscle plates, in contradistinction to the limb and body muscles, developed from " myotomes ".

There is reason to believe that it would probably be more correct to regard the " muscle plates " as the myotomes of their respective segments and to use the term visceral, when applied to these muscles, as a morphological term, having no particular genetic significance.

The Vertebrata did not spring " full formed " into existence ; they have, undoubtedly, been evolved from some invertebrate form.

There is little reason to doubt that the mouth of the Gnathostomata and the branchial apparatus of the whole of the Vertebrata are completely new structures, developed in the course of the evolution from the invertebrate form. Further, it is highly probable that a number of body segments were impressed into the formation of these new structures. There can be no reasonable doubt that these segments were equipped with muscles developed from segmental myotomes, as in the rest of the segments.

We must, therefore, decide which of two alternatives is likely to be the more probable explanation of the origin of the musculature of the " visceral " arches. Either the original myotomes and their muscle were aborted, or their musculature was adapted to the new formation. To assume that muscular tissue already available was aborted and replaced by newly formed tissue of the same kind seems an altogether unnecessary exercise of the imagination. It is to be concluded that there is every probability that the so-called visceral muscle of these segments developed from modified myotomes. There is, therefore, no fundamental difference between these and the rest of the striped musculature of the body. Actually the modification is no greater than that of the muscles related to the ribs and sternum, and less than that of those related to the limb skeletons.

Edgeworth and others have recorded the fact that striped muscle, e.g. the constrictor pharyngis, may develop directly from the mesenchyme in the visceral wall or in the mesenchyme independently of any particular structures, e.g. the superficial facialis muscles of the Theria. These contributions constitute a definite demonstration that the muscles in question have developed by differentiation of the mesenchyme at a distance from myotome or muscle plate.

These, however, are not the only muscles to be so developed. It is not uncommon for muscular tissue of the limbs to make its appearance at a distance from the main body of the muscle buds of the limb. Not only is this so, but portions of the visceral muscle plates, in some instances, make their first appearance divorced from the rest of the plate, and make this appearance after the plate has been more or less well differentiated from the surrounding mesenchyme. Again, no muscle plate or myotome develops in the whole of its extent at the same time, always the plate increases in extent after the first portion has been differentiated.

There will, of course, be complete agreement that the plate which develops as a continuum is a single genetic entity, but if we are to regard as a new formation portions which are not continuous with the muscle plate or myotome, we must either make this distinction absolute, or we must make some purely arbitrary distinction as to what degree of separation shall be regarded as constituting the portion in question a new formation.

We may view the matter from a different angle : Earlier or later every myotome and muscle plate divides into its component muscles ; this separation into parts does not take place at the same stage of differentiation in every species, nor, as a rule, does the plate divide into its component parts at the one time. First one and then another muscle anlage is split off from the main differentiating mass. It would appear that in some instances, e.g. limb buds in numerous lower Tetrapoda, this splitting takes place before there is sufficient differentiation to make the myoblasts recognizable from the surrounding mesenchyme. Stated generally, this is to say that there is reason to believe that groups of myoblasts may migrate from the original site of formation whilst still in morphologically undifferentiated condition. If this be not the explanation of the very early divisions of muscle plates which have been recorded, and which may be seen in examples of all the lower Tetrapoda, the only other interpretation is to regard perfectly normal muscles developed from these separate portions of the plates as " new formations " in the particular species in which they are found.

Such an explanation is, of course, completely untenable.

It follows that we remain within the bounds of complete reasonableness and, indeed, of probability when we suggest that those apparently new formations, the constrictores pharyngei and the Therian superficial facialis musculature, have been developed from their appropriate myotomes or muscle plates, but that their myoblasts had migrated far from the rest of the plate before differentiating. This interpretation has the advantage that it permits us to seek the origin of every muscle found in each group of Therians in that other group which may be regarded as presenting an approach to the ancestral form of the group under study.

To one who has observed the remarkable plasticity and adaptability of muscle tissue in a very large variety of species and genera of all the groups of vertebrates, it is difficult to believe that there has ever, in the evolution of the vertebrate musculature, been the need of new muscle tissue to supplement that already existing. With so many and such wide extensions and adaptations in mind, one is quite unable to believe that isolated muscles and/or groups of muscles must be regarded as entirely new formations whilst all the rest are demonstrably varying arrangements of the same muscles and muscle derivatives.

THE SUPERFICIAL FACIALIS MUSCULATURE.

The superficial facialis musculature is discussed first for the single reason that it is the most superficial of the cephalic muscles in the Theria.

Huber (1930) says of the facialis, hyoid, musculature of the Monotremes (Figs. 188–189) that they " developed along their own line, on a ground plan which is distinctly different from the common marsupio-placentalian ground plan ". Whilst this is correct, it fails to impress the really significant feature of the Monotreme facialis musculature, which is that it has *no* ground plan.

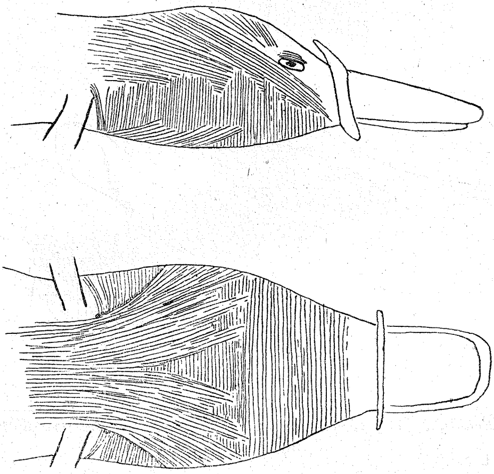


Fig. 188.—*Platypus.* The superficial facial muscles and the panniculus carnosus.

In several species amongst the lower Vertebrata we have observed a tendency of the superficial facialis musculature to extend dorsally. Compare, in this respect, *Varanus, Sphenodon, Chelodina* and *Ichthyophis* with other Reptiles and Amphibians. The observable extension of the superficial hyoid muscle sheet is in each of these instances associated with increased mobility of the skin and subintegumentary tissues. Whether the increased mobility, or, in other words, the extension of the muscle sheet, was a cause or a result it is not possible to decide, but there is in each of these instances a further factor which, probably, was causally contributive to the changed condition—the elongation and increased flexibility of the cervical region. It seems, at least, not improbable that this increased flexibility demanded and possibly caused increased mobility of the skin. If this be so then it may well have been that extension of the superficial muscle sheet was permitted by the increased freedom of the skin from the underlying fascia, and perhaps further conditioned by the need of control of the folding of the skin. This is the view which appeals to the writer as offering the most probable explanation of the observed facts.

It will be remembered that in the Holocephali we observed a somewhat similar modification of superficial muscles in association with increased mobility of superficial structures. In that instance it was the more superficial components of the trigeminal musculature which had been modified.

The ability of muscles to change and alter in conformity with altering related structures is strikingly illustrated by a number of isolated examples of peculiar muscles in individual species and genera in every group we have studied, as well as by the changes which are believed to have taken place and which have been regarded as fundamental to our understanding of the hyoid and mandibular musculature in terms of the branchial.

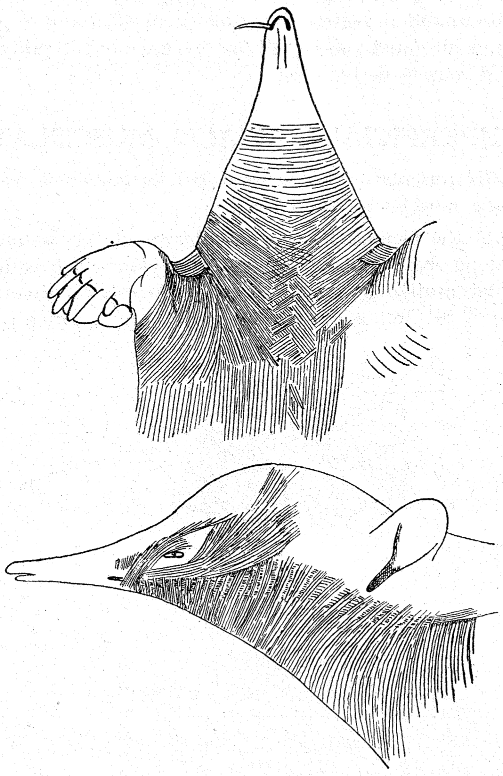


Fig. 189.—*Echidna.* The superficial facial muscles and the panniculus carnosus (after Ruge).

In the monotremes, except for the end of the snout, the whole head is covered by a flexible cuticle, and there is a wide range of movement of the neck and head upon the trunk. The need of orderly folding and control of the cuticle in harmony with the head and neck movements has, demonstrably, been met by the development of extensive sheets of muscle fibres.

Whilst the panniculus carnosus, originating from trunk myotomes, contributes in part to this nucho-cephalic sheet in its posterior part, the major portion of it is innervated by the seventh nerve and must be regarded as hyoid muscle.

Comparison of either of the monotremes, but especially the Platypus, with the lower forms mentioned above will, it is believed, reveal that the differences in the superficial hyoid muscle sheets in them are differences of degree rather than of kind.

Although previous workers have bestowed definite names on various parts of the hyoid muscle sheet in the monotremes, in actual fact no one of these is, even imperfectly, delimitated from another. It will be remembered that in a number of instances amongst the lower forms, it was found impossible to state definitely where the boundaries between components of the superficial constrictor sheets were ; they were defined by their origins and insertions only. Just in this same way, it is permissible to recognize component parts in the hyoid sheet of the monotremes.

Briefly, in the monotremes the superficial hyoid sheet of muscle fibres has spread forward and dorsad on to the side of the face and head, and various parts of it are functionally differentiated by their origins and/or insertions, but these are not anatomically differentiated by separation of their margins. The important thing to appreciate is that these muscles have not as yet been differentiated, though, in the light of the conditions in the marsupials and mammals, we may say that they are very definitely forecasted.

The origin of the facialis musculature of the Theria, and especially the superficial muscles of expression, have engaged the attention of several previous workers, and as a result there are now six outstanding explanations of their origin.

Gegenbauer was of the opinion that the whole of the superficial muscles were derived from a primitive cervico-facial platysma.

Ruge recognized that the primordial facial muscle plate divided into deep and superficial parts. The deep, he stated, gave rise to the stapedius, the stylohyoideus, the digastricus posterior and the platysma.

Huber investigated the question in greater detail than his predecessors and concluded that only the first three of the above muscles were derived from the deep portion of the plate. He was of the opinion, however, that the superficial sheet presented a primitive division into sphincter colli profundus and platysma, and that the whole of the retroauricular superficial facialis muscles were derived from the latter and the pre-auricular from the former division (Fig. 190).

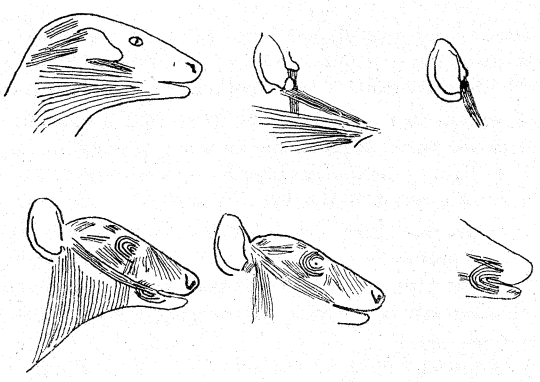


Fig. 190.—Huber's diagrammatic presentation of his theory of the origin of the various facial muscles. Those derived from the platysma, in the upper three drawings, those from the sphincter colli profundus in the lower.

Futamara (*vide* Lightoller) believed that he could demonstrate the division of the primitive cervico-facialis sheet into superficial and deep layers, that the deep yielded all the pre-auricular muscles, and the superficial, the platysma and the rest of the retro-auricular muscles. He thus combined the theories of Gegenbauer and of Huber.

Edgeworth believes that the whole of the facialis musculature of the Theria is an entirely new formation. He regards these muscles as being differentiated from the mesoderm *in situ, de novo,* and as not being portion of the facialis muscle plate with which we are familiar in the lower vertebrata. For Edgeworth only those muscles which lie deeply are survivals of the facialis musculature of the lower Vertebrata. It is not quite clear whether he regards the superficial muscles of those lower forms as having been lost, or whether he believes their anlagen are incorporated into the plate which gives rise to the deep muscles.

Lightoller has endeavoured to trace the evolution of the primitive branchial musculature of the Elasmobranchs through the changes in the hyoid and mandibular arches and then throughout the whole of the Vertebrata. Like all previous investigators except Edgeworth, he is of the opinion that the whole of the facialis musculature of the Theria has been inherited from the lower animals. Lightoller's approach to the subject has been very similar to my own, and I had the very good fortune of discussing the work with him as we both studied many identical species. There are many points on which we agree completely, but on others we agreed to differ. Lightoller's homologies are given in the following table.*

---

* The nomenclature of this work is given between brackets, where it differs from that of Lightoller.

	Elasmobranchii.	*Mammalia.*
Csd.1c.	Pars nucho-maxillaris (csd.1).	Notoplatysma
Csd.2a.	Pars epihyoidea (csd.2pr)	Portion of retro- and pre-auricular musculature
Csd.1c.	Pars mandibularis (csv.1b)	Sphincter colli profundus and trachelo-platysma
Csv.2a.	Pars interhyoidea (M. interhyoideus)	Stylohyoideus and digastricus posterior falsus
Csv.2b.	Pars inscriptionalis	Sphincter colli superficialis (the M. caninus)
L.2.	Levator hyoidei	Portion of the retro- and pre-auricular facialis musculature and digastricus posterior.

Of the above muscles the first and the third are, in the lower vertebrata, innervated by the fifth nerve, with a possibility by the seventh also in the Elasmobranchii.

The Stapedius muscle is derived by Lightoller from the M. stapedius of the crocodile.

Thus Gegenbauer, Ruge, Huber, Futamara, Edgeworth and Lightoller have all offered theories as to the origin of the facialis musculature. Of these, the simple explanation of Gegenbauer appears to state the probability as far as it *can* be stated in relation to the lower Vertebrata.

The therian facialis musculature includes superficial and deep components; the superficial have been classified as pre-auricular, retro-auricular, platysma and sphincter colli superficialis, and of the deep there are three separate muscles, the stapedius, the stylohyoideus and the posterior belly of the digastric.

In the Saurians the facialis musculature is made up of a continuous superficial sheet, a separated portion of this (the post-articular levator of the lower jaw) and a deep component, the M. interhyoideus. In the birds portion of the superficial sheet is in two layers.*

There is, therefore, except in the birds, no evidence of the existence of two layers in the superficial musculature in the hyoid segment of the lower Vertebrata, so that, apparently, the most we can say as to the origin of the therian superficial facial muscles, is that they were derived from the superficial constrictor sheet of the Reptilia and lower vertebrates generally.

There is no animal below the Theria existing today which is in possession of the primitive platysma and sphincter colli profundus postulated by Huber. It is hardly possible to recognize the condition in certain of the birds as presenting these two primitive sheets, although there is here definite evidence that already in the Sauria the single sheet had shown an ability to divide, at least partly, into two layers.

It is a fact that, with full knowledge of the muscles of the Eutheria, and searching for their equivalents, one may, by careful dissection, demonstrate portions of the superficial sheet of the Prototheria which conform to the requirements of portions of one or other of the two postulated sheets. This, however, is not evidence of the presence of the two sheets, but, rather, that all the superficialis muscles of the Eutheria have been derived from the single sheet in the lower forms. Futamara's (Lightoller) embryological findings are not evidence of the pre-existence of the two sheets, but are simply the ontogenetic differentiation of the primitive single sheet. The separation into deeper and more superficial layers has undoubtedly taken place and it was this separation which Futamara (Lightoller) regarded as of phylogenetic significance.

Lightoller's detailed correlation of the component parts of the Therian superficial and deep facialis musculature with the constrictors and levators of the Elasmobranchiata lacks the evidence of the persistence of some of the fish muscles in the Amphibians and Saurians. Their reported reappearance in the Therians is, therefore, subject to grave suspicion.

Some of these instances must be discussed in more detail than others.

The Lacertilia are really highly specialized Saurians, and it is unfortunate that the abundance of lacertilian material should have led to their tacit acceptance as typical of the reptilian conditions. In the Lacertilia the growth of the pterygoid muscles below and then up on to the external surface of the jaw pushed the origin of the posterior portion of the M. intermandibularis dorsally and externally on to the mandibular ramus, producing a condition very similar to that present in the Elasmobranchs and, in them, brought about in very much the same way. Here, then, Lightoller recognized a pars (extra-) "mandibularis". Although differentiated from the pars intermandibularis in the elasmobranchian examples only by its origin, this muscle had appealed to Lightoller as of marked importance by reason of the fact that it is innervated by the seventh nerve in its posterior part.

---

* In a general survey such as the present, it would only cloud the issue to take cognizance of muscles which are only occasionally present, such as the deep facial cerato-hyoideus-capitis of *Chelodina.*

Amongst the Amphibians, as amongst the Bony Fishes, there is no example of a pars extramandibularis, and amongst the Sauria the muscle is found only in certain Lacertilia. In all these animals there is no evidence that the posterior end of the intermandibular constrictor is innervated by the seventh nerve ; always it appears to be innervated only by the fifth.*

This difficulty of the innervation of the muscle in the Reptilia was noted by Lightoller.

It is doubtful whether the pars (extra-) mandibularis was worthy of a distinctive name. In the reptiles its peculiar origin is an entirely secondary and adventitious result of the overgrowth of one of the muscles of mastication, in the Elasmobranchs it is probable that the forward migration of the hyoid skeleton forced the original floor of the mouth ventrad, and that the complete covering of the external surface of the ramus of the jaw by the muscles of mastication caused the origin of the posterior part of the M. intermandibularis to be transferred to the facial covering of the masticatory muscles. The question of the innervation of the pars extramandibularis in the Elasmobranchs will remain unsettled until decided by an appeal to experimental stimulation of the severed nerve trunks and roots. It will be remembered that, as noted by Lightoller, there is a very intimate communication between the roots and trunks of the fifth and seventh nerves in these fishes, so that there is a possibility that the hyomandibular nerve carries motor fibres of the fifth nerve as well as mixed fibres of the seventh to the M. intermandibularis and the skin between the jaws.

Even if it should prove that the pars extramandibularis in the Elasmobranchs is innervated by the seventh nerve, the absence of the muscle from the lower Tetrapoda, except the Lacertilia where it is innervated by the fifth nerve, renders it improbable that any muscle present in the Theria and innervated by the seventh nerve should be homologous with it.

This objection is further supported by the fact that there is no other instance of the reappearance in the Theria of an elasmobranchian muscle which cannot be traced through the intervening vertebrate classes.† In other words, it would be the one instance of complete discontinuity in the phylogenetic history of the Therian muscles of the head and neck.

It should also be remembered that the acceptance of the theory of the homology of the pars extramandibularis of the elasmobranchian Csv.1b with any component of the therian facialis musculature carries with it acceptance of a belief in the myotomic, or segmental, duality of the facialis musculature, in support of which there is no other evidence.

It is, therefore, to be concluded that there is not sufficient evidence to justify the acceptance of Lightoller's equation of the Csv.1b pars extramandibularis with the Mm. sphincter colli profundus and tracheloplatysma.

The same general line of argument applies against the proposal to regard the notoplatysma as the equivalent of the Csd.1. This muscle is not present in any one of the lower Tetrapoda, and, even if it be the fact that it is innervated by the seventh nerve in the Elasmobranchs, its complete absence from all these forms makes one doubt very much that it should reappear in the Theria.

It is believed that the variability of the situation and relative extent of the superficial facialis sheet of muscle amongst the Amphibia and Sauria justifies the belief that the Therian facialis superficial musculature is simply a further extension of that same variable sheet, and to such an extent that it is not possible to indicate, with any degree of confidence in one's identification, from which portion of the muscle sheet of the lower forms the various therian entities were derived.

The division of the facialis sheet of the Theria into deeper and more superficial layers is not novel to the Theria. In most birds this division is seen ventrally. It is not logical to regard this partial division in the birds as the starting-point of the therian condition, because the birds cannot be regarded as ancestral to the Theria.

The multiplicity of designs presented by the various mammals and marsupials in the arrangement of the superficial facialis muscles provides an added reason for believing that they have been derived from an undifferentiated sheet similar to that of the Prototherians. There is, moreover, reason to believe that the marsupials present a more primitive condition than the

---

* In the Bony Fishes, of course, the posterior portion of the M. intermandibularis is fused with the anterior portion of the hyoid superficial constrictor to form the protractor hyoidei, and there is dual innervation of the resulting muscle.

† Lightoller was of the opinion that the M. interhyoideus (pars interhyoidea of his nomenclature) is rarely represented in the reptiles. Unfortunately the muscle happens to be unrecognizable in the three reptilian types he studied, but a reference to the previous pages will remind the reader that the muscle is present in the majority of the Sauria.

mammals, reflecting, perhaps, the origin of some of the component muscles. Particularly, in this connection, we may single out the M. detrahens aureum of the wallaby (Fig. 191) and other diprotodonts. This certainly looks like portion of the saurian constrictor colli facialis which has gained an attachment to the ear.

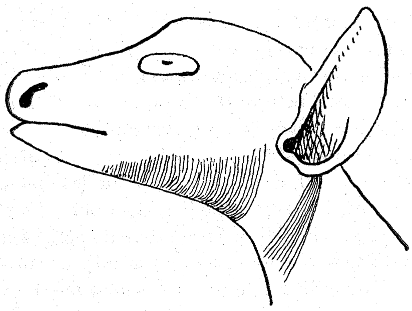


Fig. 191.—Wallaby. The M. detrahens aureum.

It seems reasonable to assume that there would have been a greater degree of similarity in the facialis muscle pattern in the mammals and marsupials, if the ancestral therian stock had already evolved a partially differentiated superficial facialis musculature. The basic pattern of this ancestral partial differentiation should, surely, be readily recognizable in all the Theria, if there had been one.

If, on the other hand, the primitive Theria had an undifferentiated sheet, similar to that of the Prototheria, then the wide degree of variation which we observe is completely understandable.

THE STYLOHYOIDEUS MUSCLE.

The whole of the arguments in favour of regarding this muscle as having been derived from the M. interhyoideus have been briefly and clearly stated by Lightoller (1939). With those views the writer is in complete agreement.

Edgeworth (1935) derives the posterior belly of the digastric muscle from the M. interhyoideus, but he states that in the higher Eutheria " . . . the interhyoideus separates into two parallel muscles, the stylohyoideus and the digastricus posterior . . . " This derivation of the muscles follows from his description of the early development of the hyoid muscle plate in the Mammalia. This, he states, " . . . separates into dorsal and ventral portions. The former is the primordium of the Levator hyoidei . . . the ventral portion is the interhyoideus."

This interpretation appears to assume the complete loss of the superficial components, and in the result he is forced to regard mammalian superficial facialis musculature as something quite new, and arising in the class without any precursor in the lower forms.

It appears, further, that Edgeworth assumes that when the myotome divides into a dorsal and a ventral part, the ventral must contain the anlagen of ventral muscles only, and the dorsal the dorsal anlagen only. This is a belief which, it seems, may easily be carried too far.

There are strong reasons for believing the M. depressor mandibulae of the Sauria to have been the precursor of the posterior belly of the M. digastricus. As will be pointed out later, its fibres have a tendency to extend beyond the mid-lateral line ventrally, and its origin to descend to a lower level than the origin of its precursor, the anterior fibres of the superficial hyoid constrictor. In this incomplete descent ventrad the muscle has come to lie across the mid-lateral line. If the digastricus posterior is derived from this muscle, then there has been a further descent, and an erstwhile dorsal muscle has become a ventral muscle. Not only is this so, but, if the homology is correct, from what we know of the ontogeny of the digastricus posterior in the Theria, the muscle plate was ventrally situated before it divided into its component parts.

In this connection it is noteworthy that the muscle which Edgeworth identifies as the levator hyoidei in the monotremes is placed wholly ventrally to the ventral limit of the similarly named muscle in the lower forms. It is placed ventrally to the quadrate and to the posterior end of Meckel's cartilage, and is derived from the primordium of the hyoid muscles *in this location* ;

therefore, it is arguable that only the ventral moiety of the primordium is present at all, and that all the dorsal muscles of the hyoid segment have been lost. That is, of course, if the location of the primordial muscle plate at the time of its splitting be regarded as determining what muscles are developed from it.

THE POSTERIOR DIGASTRIC MUSCLE.

It is believed that this muscle is derived from the M. depressor mandibulae of the Sauria. It, therefore, becomes necessary to discuss briefly the probable origin of that muscle once again.

There is no apparent reason why we should doubt that the M. depressor mandibulae of the birds is completely homologous with that of the reptiles.

Throughout this work it has been assumed that every muscle in the higher forms has been derived from some muscle in the lower, and in the result there has been available to us the method of identification *per exclusionem*. In the present instance that method would be unsatisfactory ; the M. digastricus posterior appears, at first sight, to be placed altogether too far ventrally to be the homologue of the remaining facial muscle, the M. depressor mandibulae, and also too deeply.

Let us consider first the point of origin of the muscle. In the Elasmobranchii the muscle arises from the side of the head at the level of the upper limit of the branchial muscles. In the bony fishes the origin is placed much more ventrally. In the Holocephali the dorsal limit of the muscle is variable, but is lower than in the majority of the Selachii. In the Dipnoi the muscle rises far toward the dorsum, perhaps, to some extent carried there by the dorsal situation of the vault of the branchial recess at the back of the skull. In the Euamphibia the origin of the depressor mandibulae is placed high up towards the dorsum of the posterior end of the head and neck, but in the reptiles one finds it arising lower down on the side of the head ; the pars notognathica is commonly not developed. Lastly, in the birds, the pars notognathica is never present and the origin of the muscle is from the back of the skull behind the external auditory meatus.

An examination of the site of origin of the M. digastricus posterior in the Theria reveals that it is very closely just that of the M. depressor mandibulae in the birds and certain of the reptiles. The fact that it is so is, however, disguised somewhat by the increase in the size of the skull above and behind the otocrane. This has caused the area of skull behind the external auditory meatus to be overhung, so that the muscle appears to take its origin from a new situation altogether, whereas, as a matter of fact, there is but very little difference in the two locations. It would be foolish to deny that the site of origin of the therian muscle is not more ventrally situated than is that of the saurian ; it is, but not nearly so much so as appears. Compared with the amount of migration of the site of origin of certain other muscles, particularly those of mastication, whose homology is unquestioned, the amount of migration of the site of the origin of this muscle is small and is not such as to constitute a reason why we should refuse to admit that the muscles are homologous.

Whilst the location of the origin of the muscle in the Theria calls for careful examination in view of its apparent novelty, the manner of its insertion presents nothing new. In several of the Reptilia, e.g. *Tiliqua* and *Varanus*, it was observed that portion of the Csv.2 extended almost to the mid-ventral line to gain an insertion into the superficial fascia. Whilst these were fasciculi of the pars notognathica and on that account, perhaps, not completely homologous with the therian muscle, which is regarded as having been derived from the pars cephalognathica, their ventral insertion bears very directly upon the question.

It will be remembered that in the Selachii the Csd.2 and Csv.2 formed a continuous sheet, in which we defined three parts by their origin, insertion, or relation to certain structures. In the Batoidei these parts were less easy to define. In the Chondrostei and in the Bony Fishes the identity of the three parts was almost completely lost, or at least profoundly modified.

In the Amphibia the M. depressor mandibulae fairly constantly presents a division into two parts, justifying a belief that it was derived from two muscles, but the contribution of the levator to this muscle was not a constant feature, though, possibly, that component was present in some forms. In the Sauria the muscle was found in two parts in some of the Lacertilia and Ophidia, but in other Reptilia and in the birds only the pars cephalognathica was present. Since the amphibian depressor was, very definitely, derived from superficially placed precursors, and since those form a continuous sheet in the Selachians and are profoundly modified in other ways in the bony fishes, the most that can be stated with confidence is that it was derived from the Csd.2 with a possible inclusion of the hyoid levator in some Urodela.

In the Reptilia, there is no evidence that a hyoid levator is ever present, at no time does the primordium of the M. depressor mandibulae show any division into deeper and more superficial layers. Indeed the separation into anterior and posterior parts, seen in some Lacertilia, is a relatively late happening. Although there is this definite splitting into partes noto- and cephalognathica in a number of lizards and snakes, the complete absence of such division from other lizards, from most, if not all, other reptiles, and from all the birds leads to the conclusion that the muscle is derived from one muscle only, and this conclusion is supported by the developmental history of the muscle.

The manner of innervation of the muscle in the Theria appears to have been regarded by previous observers as an obstacle to the homology accepted here. This does not appear as an obstacle to one who comes to the Theria from the lower Vertebrata. On the contrary, one finds complete conformity with the Saurian conditions. It is innervated by a post-auricular branch of the facial nerve.

One objection to regarding the M. depressor mandibulae of the lower Vertebrata as the homologue of the M. digastricus posterior of the Theria is the difficulty of accounting for the retro-auricular facialis muscles if they have not been derived from the depressor.

A critical examination of the varying areas of origin dorsally of the saurian M. constrictor colli facialis (Csd.2–Csv.2) will reveal that it is not uncommon for the origin of this muscle to lie superficially to the depressor.

Once the Csd.2 had obtained an origin superficially to, and overlying the depressor mandibulae the way was clear for it to invade the whole of the area occupied by the retro-auricular facialis muscles.

In both the Prototherians a muscle is found which is strictly comparable with the constrictor colli facialis, and which, indeed, has been designated constrictor colli by Huber. This takes its origin dorsally in a plane which is superficial to the situation of the M. depressor mandibulae.

It is concluded that there are no vital objections to regarding the M. digastricus posterior as having been derived from the M. depressor mandibulae of the lower Vertebrata.

It is, therefore, concluded that the M. digastricus posterior has been derived from the anterior fibres of the dorsal portion of the hyoid constrictor of the Elasmobranchii, for these alone are deemed to have contributed to the formation of the M. depressor mandibulae of the Saurians.

THE MANDIBULAR MUSCLES.

In order to maintain continuity of discussion the derivation of the M. digastricus anterior will be considered next.

The majority of workers have, in the past, derived this muscle from the M. mylohyoideus, the M. intermandibularis of this work. The latest review of the question is that of Lightoller who would derive the muscle in part from the intermandibularis and in part from the ventral longitudinal muscles. In this latter he is in agreement with the work of Rouvier (1906) and of Toldt (1907).

The ventral longitudinal muscles are innervated by spinal nerves, whilst the anterior belly of the M. digastricus is innervated by the fifth nerve only. Lightoller states : " . . . the lateral fibres of the ventral longitudinal muscle are pierced and apparently innervated by the N. mylohyoideus " and refers to his own observations to that effect in *Tiliqua*, and to the work of Chaine and Rouvier.

I have been able to confirm the observation in *Tiliqua* and have found the same distribution of the nerve in *Varanus* and in *Chelodina*. However, experimental stimulation of the distal and of the severed nerve fails to cause contraction of the longitudinal muscles in any one of the three forms ; nor is there any contraction of the longitudinal muscles on stimulation of the nerve in the common fowl.

It is concluded that the twigs of the fifth nerve which reach the longitudinal muscles do not carry any motor fibres.

Perhaps the way to a proper understanding of this muscle has been obscured by a failure to realize that it is the Csv.1a portion, alone, of the amphibian and saurian mylohyoid muscle which is represented by the therian M. mylohyoideus.

This—submentalis—muscle first makes its appearance in the Elasmobranchs as an araphic portion of the Csv.1. In those fish it is placed on the same plane as the rest of the muscle. The M. submentalis is commonly well defined in Bony Fishes, but is variable in its relation to the insertion of the longitudinal muscles and to the posterior portion of the Csv.1 itself. In some species it is superficial, in others deep to these other muscles.In the Amphibia the submentalis is present in Urodela and Anura, but absent from the Coecilians and Dipnoi. It always lies deep to the plane of the M. intermandibularis, mylohyoideus of authors generally. Throughout the Reptilia there is an anterior part of the intermandibularis cleanly separated from the rest of the muscle and always placed dorsally, deeply, to it. The fibres of this reptilian M. submentalis may be araphic and directly transverse in their direction, or they may be inserted into a median raphe and have a direction diagonally posteriad and mediad, from their origin far forward on the inner side of the mandible. In most of the birds the Csv.1 is not differentiated into anterior and posterior parts in any way ; the submentalis muscle is not present.

The deeper situation of the anterior part of the Csv.1 in the Lacertilia led the writer to designate it the " pars profunda " until the araphic form was met in the Crocodilia and the true character of the muscle was recognized.

The situation of the M. submentalis is quite comparable with that of the Therian M. mylohyoideus, whereas the M. intermandibularis lies in a more ventral superficial plane.

The presence of this deeper portion of the M. intermandibularis in the reptiles appears to have been completely overlooked by previous workers.

Once we have recognized that this variable muscle was present in the Reptilia we are at liberty to assume that it was also present in the primitive mammal and it is easier to believe that it gave rise to the M. mylohyoideus than it is to understand how the superficially placed M. intermandibularis came to occupy a situation deep to other muscles of the mandibular segment.

If this be the correct interpretation of the mylohyoideus, it remains to determine what has become of the main portion of the intermandibularis, and one very naturally turns to the only other muscle in the region innervated by the fifth nerve, the anterior belly of the digastric.

Viewed from the saurian aspect it appears highly probable that the intermandibularis is represented in the mammals by the anterior digastric. This appears a much more likely interpretation of the facts than would be the assumption that the intermandibularis has been aborted.

The comparison of the M. intermandibularis with a M. digastricus anterior in such a form as *Homo* must lead to the rejection of the homology proposed here, but that is, of course, the extreme modification of the muscle. The early condition in the process of adaptation is presented in the Cetaceans, amongst others. That of *Delphinus* is illustrated here (Fig. 192). Comparison of this with the Csv. of lower Tetrapoda, and especially in those forms (*Varanus, Sphenodon, Crocodilus, Chelodina* and *Dromaeus*) in which the fibres have a direction caudad and mediad, reveals at once that there is really very little difference between them. Even the firm insertion of the mammalian muscle into the hyoid is definitely foreshadowed by the binding of the mid-ventral raphe to the hyoid apparatus in a number of Saurians.

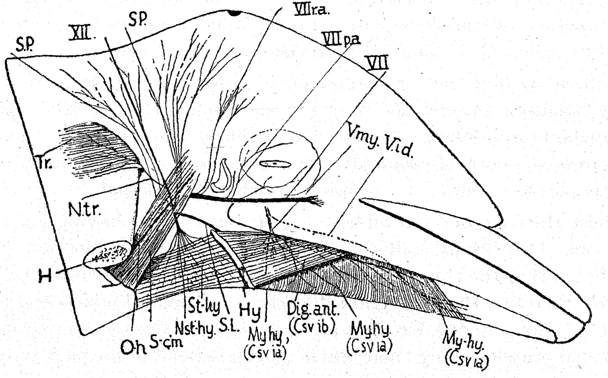


Fig. 192.—*Delphinus.*

Csv.1b, M. digastricus anterior ; H., humerus ; Hy., hyoid cornu ; Csv.1a, M. mylohyoideus ; N.st.-hy., the nerve to the M. stylohyoideus ; N.tr., the nerve to the M. trapezius from the cervical plexus ; O.h., M. occipitohumeralis ; S-c.m., M. sterno-cleido-mastoideus ; S.l., the superior laryngeal nerve ; Sp., sensorimotor nerves to the panniculus and dorsal trunk region from the cervical plexus ; Tr., M. trapezius ; V.i.d., the inferior dental nerve ; V.my., the myloid branch of the inferior dental nerve ; VII p-a., preauricular twigs of the facial nerve ; VII r-a., retroauricular twigs of the facial nerve. (From Kesteven, 1941*d*.)

The mammalian M. mylohyoideus presents itself in two layers in a number of species (*vide* Bertelli, 1927). It might appear that its two layers are homologous with the two layers of the Saurian Csv.1, the Csv.1a and Csv.1b. There is no doubt that this interpretation of the muscles is a completely admissible interpretation and there is no evidence to negate it completely.

On the other hand, if the two portions of the first ventral superficial constrictor have been so modified, we are forced to look to extramandibular muscles for the homologue of the M. digastricus anterior.

Since the only experimental work carried out to test the nature of the fifth innervation of the longitudinal muscles which have been homologized with the digastricus anterior has shown that innervation not to be motor, it is concluded that those muscles probably did not contribute to the formation of this. We are therefore left without any forerunner to the M. digastricus anterior in the lower tetrapods. But, inasmuch as the M. digastricus anterior has been demonstrated to be genetically a mandibular muscle (Edgeworth, 1935), we are constrained to return to the only mandibular muscles of this region in the lower Tetrapoda, and we are once more forced to look to the Csv.1b.

It is, of course, possible that only portion of the Csv.1b has been converted into the anterior digastric and that the remainder has contributed to the formation of the M. mylohyoideus. Against this, however, it must be pointed out that the line of origin of the digastric alone is in the situation of the line of the origin of the Csv.1b, whilst the line of origin of the mylohyoid is deep to that and is in the position of the line of origin of the Csv.1a.

THE MUSCLES OF MASTICATION.

The discussion of these muscles may be made very brief. There is no reason why we should not homologize the two groups of these muscles in the Theria with those we are familiar with in the lower Tetrapoda. This is, of course, in conformity with past practice. The origins and insertions satisfy the equations perfectly, as also do the relations to the branches of the fifth nerve.

THE BRANCHIAL AND HYPOBRANCHIAL MUSCLES.

Looking back over these muscles in the lower Vertebrata it appears as though there had been little congruence amongst them, but, if we omit from our review the muscles of occasional occurrence and tabulate those which may be regarded as characteristic of each group, it is found that there is a relatively high correspondence amongst them. This agreement is further brought out by the diagrammatic presentation of the muscles in Figs. 193 and 194.

The peculiar specialization of the Bony Fishes may be regarded as excluding them from the evolutionary history of the Tetrapoda, and we may, therefore, neglect them in the present discussion and pass from the Elasmobranchii direct to the Urodela.

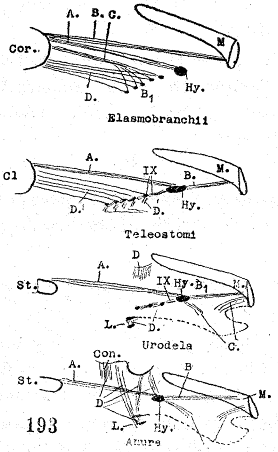
Comparing these we find that the continuous coraco-mandibularis muscle of the fishes has been replaced by a muscle interrupted at the hyoid arch. On the other hand there is present in the elasmobranchiate musculature a shorter coracohyoideus as well as the long muscle. Deep to this again there is the coracobranchialis communis, and all three are hypobranchial muscles and are innervated by the composite occipito-spinal " hypoglossal " nerve.

In the Urodeles the coracomandibularis may be regarded as having been cut off short at the hyoid, and the coracobranchialis communis as having lost its connection to the coracoid also. It will be remembered that the three elasmobranchian muscles are intimately fused for the greater part of their length, therefore the suggestion that the coracomandibularis and the hyomandibularis should have been modified in the Urodela as suggested involves a comparatively slight change. The fusion of the two muscles along their whole length instead of for part only is all that is called for.

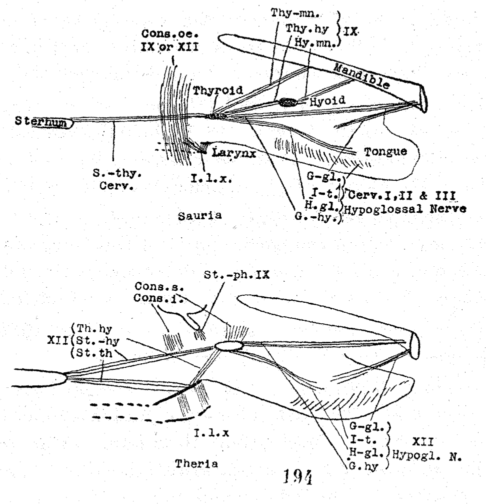
If further we assume that the coracobranchialis communis also became fused for a much greater length, its extension into the region of the tongue may be regarded as an easy step. The genioglossus may be regarded as a modification of the deep portion of the geniohyoideus.

It is not contended that any of these muscles is the homologue of any other, but it is believed that these hypobranchial spinal muscles of the Urodela are directly derived from those of the Elasmobranchii.

Whether this be the fact or not, it is of interest to note that the arrangement of the principal hypobranchial muscles of the Tetrapoda remains unchanged throughout the whole series. The pattern is slightly disguised amongst the Reptilia by the varying presence or absence, and varying relations, of certain muscles which lie ventrally to them.



193



194

Fig. 193.—Diagram of the branchial and hypobranchial muscles in the lower Tetrapoda. A., Mm. coracohyoideus, claviculohyoideus and sternohyoideus; B., Mm. coracomandibularis and geniohyoideus; C., Mm. genioglossus and hyoglossus; D, branchial muscles; L, larynx.

Fig. 194.—Diagram of the branchial and hypobranchial muscles of the Sauria and of the Theria. Cons.i. & Cons.s., the inferior and superior constrictor muscles of the pharynx; G.gl., M. genioglossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.mn., M. hyomandibularis; I.l., intrinsic muscles of the larynx; I.t., intrinsic muscles of the tongue; St-hy., M. sternohyoideus; St.thy., M. sternothyroideus; Th.hy., M. thyrohyoideus; Th.mn., M. thyromandibularis; IX, X and XII, the nerves innervating the muscles.

Though it is possible to recognize the sternohyoideus and geniohyoideus in the great majority of the Tetrapoda, it is the fact that the muscles so identified are not always innervated by the same nerve. In the Lacertilia, there are two other muscles which pass from the hyoid apparatus to the mandible and one other which passes from the thyroid cartilage to the hyoid. These are longitudinal muscles and they are innervated by the glossopharyngeal nerve. In the birds, there is always a muscle which passes from the hyoid to the mandible, and not uncommonly this muscle is divided into a lateral shorter part and a medial which may extend right to the symphysis menti. It is functionally a geniohyoideus and has been so named in the body of this work. It also is innervated by the IXth nerve.

In the Theria, in addition to the sternohyoideus and geniohyoideus, there are sternothyroid and thyrohyoid muscles innervated by the glossopharyngeal nerve.

In all the Tetrapoda, there is a constrictor pharyngis, innervated by the vagus. In the Theria, the muscle is present in superior and inferior divisions.

Comparing the Anura and the Reptilia, one finds in the former three branchial muscles—craniohyoideus, craniolaryngeus and dorsolaryngeus—innervated by the Xth and/or IXth nerve. These might appear to be the forerunners of the three muscles which we have found in the Reptilia situated ventral to the hypobranchial muscles and innervated by the glossopharyngeal nerve.

Actually, however, these two trios have little in common to support such a suggestion. The amphibian muscles are demonstrably branchial, their development from typical branchial muscles, during the metamorphosis of the tadpole, is readily observed. The reptilian muscles, on the other hand, are developed from the same stroma as the typical hypobranchial muscles.

Edgeworth would regard their innervation by the IXth nerve as secondary, as also would he regard the glossopharyngeal innervation of the Avian geniohyoideus and hyomandibularis (branchiomandibularis).

This interpretation appears to be entirely reasonable, but it is suggested that the "secondary" character of the innervation may be more apparent than real. It is possible that the true explanation of their innervation is that their motor fibres have taken a shorter, new, intracranial course and issue with the IXth instead of with the rest of the Xth nerve.

That which is here suggested is the converse of the explanation of Straus and Howell (1936) for the innervation of the accessorius muscles by spinal nerves in the long-necked Ungulates. Their suggestion is that true accessorius fibres still innervate those muscles, but that they have taken a new intraspinal course and now issue with the cervical nerve fibres.

It is an interesting fact, probably not without significance, that, with the exception of the intrinsic muscles of the larynx, the branchial muscles throughout the whole of the Vertebrata are constrictor muscles. Even the interarcualia recti act to bring the branchial arches together and assist in the more perfect compaction of the branchial basket.

After the most careful study of these muscles in the extensive series of animals whose muscles have been described in the earlier parts of this work one can only record the impression that the evidence is not available on which to determine with confidence the origin of the branchial muscles in the higher Tetrapoda with any degree of exactitude.

Embryological evidence appears to indicate different segmental origins for apparently identical muscles in more than one instance.

The outstanding phenomenon in the changes in the branchial region as we have traced the muscles from fish to Theria has been the gradual reduction in the number of segments which have been carried forward from group to group. This reduction has obscured the sequence of inheritance so much that it is not always possible to determine which segments remain; much less is it possible to determine which muscles have persisted in the altered conditions observed.

It is concluded that the most one can say with confidence is that the vago-glossopharyngeal muscles, as a group, are homologous throughout the Vertebrata, but that owing to the possibility, if not the probability, of fasciculation of the nerves in this region, it is not possible to separate the muscles into vagus and glossopharyngeal groups.

Not only is this so, but there is reason to believe that certain of the muscles innervated by the glossopharyngeal nerve are really hypobranchial and not branchial in origin, as already stated.

The final conclusions of this part of the work are conveyed by the tabulation below. A reference to the earlier tables of similar kind, conveying the conclusions of each section will give the homologies, as the writer sees them, of the Therian muscles with those of each of the groups of the lower Tetrapoda.

	Hypobranchial Muscles Innervated by Nerves behind the Vagus		Branchial Muscles Innervated by the IXth and Xth Nerves.	
Elasmobranchii	Coracohyoideus	A		
	Coracomandibularis	B	Intrinsic branchial muscles	D
	Coracobranchialis communis	C		
Teleostei	Claviculohyoideus	A	Intrinsic branchial muscles	D
	Geniohyoideus	B		
Urodela	Abdominohyoideus	A	Intrinsic branchial muscles Intrinsic laryngeal muscles Constrictor pharyngis	D
	Geniohyoideus	B		
	Hyoglossus Genioglossus	C		
Anura	Abdominohyoideus	A	Tadpole Intrinsic Branchial muscles	D
	Hyoglossus	B		
	Hyoglossus Genioglossus	C	Adult: Craniolaryngeus Craniohyoideus Dorsolaryngeus Intrinsic laryngeal muscles Constrictor pharyngis	D

	Hypobranchial Muscles Innervated by Nerves behind the Vagus		Branchial Muscles Innervated by the IXth and Xth Nerves	
Sauria	Sternothyroideus	A	Thyromandibularis Thyrohyoideus Hyomandibularis	B
	Geniohyoideus	B		
	Hyoglossus Genioglossus Intrinsic muscles of tongue	C	Intrinsic laryngeal muscles Constrictor pharyngis	D
Theria	Sternohyoideus Sternothyroideus Thyrohyoideus	A	Stylopharyngeus Constrictor pharyngis sup. Constrictor pharyngis inf. Intrinsic muscles of larynx	D
	Geniohyoideus	B		
	Hyoglossus Genioglossus Intrinsic muscles of tongue	C		

I have, in conclusion, to acknowledge gratefully the receipt of several grants from the Trustees of the Commonwealth Council of Scientific and Industrial Research, which have helped very materially to make this work possible.

POSTSCRIPT.

(Added 29th July, 1944.)

In this year of grace 1944, some five years after the work was finished, years packed full of civilian war work and away from microscope and scalpel, a critic has asked me what remains to be done to correct or confirm my conclusions. The reply seemed obvious to me. I have offered working theories only, and have proven nothing. The whole field needs covering again, not once but probably many times, before sufficient types and varieties of arrangement have been studied anatomically and embryologically, and sufficient evidence will have been amassed on which to establish a sound and completely satisfactory explanation of the evolution of the cephalic muscles and of the skull.

My critic then suggested that at least I should be able to indicate where I had wished more evidence had been available to me. That information, he thought, would be useful guidance and perhaps provide inspiration for future students.

I have, therefore, endeavoured to revive the mental atmosphere in which the work was done by reading it through. I have not succeeded, for my recollection is of a constantly recurring sense of frustration due to absence of conclusive evidence whilst the work was in progress. I feel that, had I been keeping notes with a view to compiling such a chapter as this, many more lines of research would have been suggested.

On pages 3 and 4, I discussed the constant association of segmental nerve and muscle-plate derivatives and offered an explanation of this constancy. It would be interesting to test both the explanation offered and the apparent exceptions. Examples of " heterogeneous " innervation are the branchial levators in Selachii (pp. 12–13), the protractor hyoidei in Teleostei (pp. 72–77) and also in certain constrictor colli muscles in the Sauria. The " explanation " could, it is believed, be tested in the manner suggested, the apparent examples of heterogeneous innervation, by stimulation of the motor nerves.

A careful study of the development of the mandibular muscles of the Selachii would yield interesting results. The study should be carried out with serial sections of the very early stages, and, of course, reconstruction from the sections. Actual three-dimensional vision of the structures is essential for their proper understanding. This study of early stages would need to be supplemented by actual dissection under high magnification of the earliest stages to which the method is applicable, and further dissections of later stages until the adult form is reached. I think that such a study would either confirm or correct my belief that the quadratomandibularis is derived from the primitive middle adductor, and the rest of the muscles of mastication from the primitive dorsal adductor.

In view of the many cranial and muscular similarities of the Chondrostei to the Selachii, suggesting comparatively recent divergence from the parent elasmobranchiate stock, a re-survey of the development of the branchial muscles would be interesting. It is possible that such a survey would lead to the recognition of evanescent traces of some of the missing elasmobranchian branchial muscles.

The history of the origin of the laryngeal and pharyngeal muscles in the Anura is still largely wrapped in mystery. I have no doubt that much could be learned by actual dissection of larger tadpoles. This problem would be most easily solved if the development of the muscles were studied backwards. Complete familiarity with adult form and disposition should be acquired first, then this condition should be seen in the youngest tadpole in which it is attained. Then would follow a search for successively earlier and earlier stages, perhaps ending with reconstructions of the earliest from serial sections. This work would be very tedious and difficult if attempted on ordinary small tadpoles, but some tadpoles (e.g. *Myxophyes* and one of the *Hyla* species) attain relatively monstrous size long before metamorphosis commences, and these are relatively easy to dissect.

Very naturally, I should like to see my theories relative to the correct interpretation of the fourth and sixth nerves tested in some way. Being neither an experimental embryologist nor a neurologist, I can make no suggestion as to how they might be tested.

I feel that full use has not yet been made of fossil skulls. Few, if any, of them have been studied by the application of our method of serial section and serial plate reconstruction. There is no reason to believe that even those encased in friable matrices, or coal, would not yield perfect sets of serial sections if carefully encased in a cement envelope, and if each section were firmly stuck to a glass slide with canada balsam before being cut from the block. Outline drawings of the bones, with sutures and small foramina carefully marked on them, could then be traced from both sides of each section on to sheets of blotting paper of appropriate thickness, and the whole assembled just as is done in the reconstruction of embryonic skulls. This method would be infinitely preferable to that of attempting to clean the bones *in situ* and/or " restoring " the unseen parts. In the reconstructed model, the whole skull, including the bones of palate, suspensarium, and jaw, could be handled and taken apart, in fact " disarticulated " if required.

In conclusion, having acted on his criticism, it is only right that I thank my son, Geoffrey L. Kesteven, for having given it.

INDEX.

LITERATURE SUPPLEMENT.

Brock, Gwendolen T., 1937.—The Morphology of the Ostrich Chondrocranium. *Proc. Zool. Soc. Lond.*, (B) 107, pp. 225–243.

Fairley, N. H., 1929.—Dentition and Biting Mechanism of Australian Snakes. *Med. Journ. Australia*, March 9, 1929, pp. 313–327.

Futamura, R., 1907.—Beiträge zur vergleichenden Entwicklungsgeschichte der Facialismuskulatur. *Anat. Heft*, 32, pp. 479–575.

Gaupp, E., 1906.—Die Entwickelung des Kopfskelettes. *Hertwig's Handbuch der vergleichenden und experimentalen Entwickelungslehre der Wirbeltiere*, iii, 2 Teil, pp. 573–874.

Goodrich, E. S., 1909.—Vertebrata Craniata : Cyclostomes and Fishes. Lankester (ed.). *A Treatise on Zoology*, part ix. Oxford, 1909.

Lubosch, W., 1933.—Untersuchungen über die Visceralmuskulatur der Sauropsiden. *Morph. Jahrb.*, lxxii, pp. 584–666.

Lightoller, G. H. S., 1939.—Probable Homologues. A Study of the Comparative Anatomy of the Mandibular and Hyoid Arches and their Musculature. Part I. Comparative Myology. *Trans. Zool. Soc. Lond.*, xxiv, pp. 349–426.

Luther.—*Fide* Edgeworth, *Journ. Anat.*, lix, 1925, pp. 225–264.

Norris, H. W., 1908.—The Cranial Nerves of *Amphiuma means*. *Journ. Comp. Neurol.*, xviii, pp. 527–568.

Osawa, G., 1898.—Beiträge zur Anatomie der *Hatteria punctata*. *Archiv. mikr. Anat.*, li, pp. 481–691.

Pollard, H. B., 1892.—On the Anatomy and Phylogenetic Position of *Polypterus*. *Zool. Jahrb.* (*Anat.*), v, pp. 387–428.

Regan, C. Tate, 1923.—The Skeleton of *Lepidosteus*, with remarks on the Origin and Evolution of the lower Neopterygian Fishes. *Proc. Zool. Soc. Lond.*, pp. 445–461.

Sagemehl, M., 1891.—Beiträge zur vergleichenden Anatomie den Fische. IV. Das Cranium Cyprinoiden. *Morph. Jahrb.*, xvii, pp. 489–595.

TAXONOMIC LIST AND INDEX OF THE SPECIES AND GENERA OF WHICH THE MUSCLES HAVE BEEN STUDIED.

- Pisces. Pp. 11–104.
  - Elasmobranchii. Pp. 11–43.
    - Selachii Pp. 11–28.
      - *Acanthias* (*Squalus*) *megalops* Macleay=*Flakeus megalops* (Macleay).
      - *Brachaelurus modesta* Gunther=*Brachaelurus waddi* (Bloch and Schneider).
      - *Carcharinus* sp.
      - *Chiloscyllium punctatum* Muller and Henle.
      - *Mustelus* sp.=*Emissola antarctica* (Gunther).
      - *Orectolobius maculatus* (Bonnaterre).
      - *Pristiophorus cirratus* (Latham).
      - *Sphyrna blochii* Cuvier=*Sphyrna lewini* (Griffith).
    - Heterodontidae. Pp. 28–35.
      - *Heterodontus portusjacksoni* (Meyer).
    - Batoidei. Pp. 36–52.
      - *Dasyatis brevicaudatus* Hutton=*Bathytoshia brevicaudata* (Hutton).
      - *Hypnarce subniger* Dumeril=*Hypnarce monopterygium* (Shaw and Nodder).
      - *Raja australis* Macleay.
      - *Taeniura lymma*=*Taeniura lymnia halgani* (Lesson).
      - *Urolophus testaceus* (Muller and Henle).
    - Chondrostei. Pp. 52–56.
      - *Acipenser* sp.
      - *Polyodon* sp.
      - *Psephurus gladius* Martens.
    - Holocephali. Pp. 56–63.
      - *Callorhynchus antarcticus*=*Callorynchus milii* Bory.
      - *Chimaera ogilbyi* Waite=*Psychichthys ogilbyi* (Waite).
  - Teleostei. Pp. 43–104.
    - Crossopterygii.
      - *Polypterus* sp.
    - Actinopterygii.
      - *Lepisosteus osseus* (Linné).
      - *Lepisosteus platystomus* Rafinesque.
      - *Armia calva* Linné.
    - Acanthopterygii
      - *Anguilla reinhardtii* Steindachner.
      - *Balistapus aculeatus* Linné.
      - *Cantherines ayraudi* Quoy and Gaimard=*Nelusetta vittata* (Richardson).
      - *Cnidoglanis megastomus* Richardson.
      - *Drepane* (*Drepanichthys*) *punctatus* Linné.
      - *Epibulus insidiator* Pallas.
      - *Fistularia petimba* Lacépède.
      - *Girella cuspidator* should be *Girella tricuspidator* Quoy and Gaimard.
      - *Gonorhynchus greyi* Richardson.
      - *Hemirhamphus intermedius* = *Reporhamphus australis* (Steindachner).
      - *Mugil cephalus* Linné=*Mugil dobula* Gunther.
      - *Platycephalus fuscus* Cuvier and Valenciennes=*Planipora fusca* Cuvier and Valenciennes.
      - *Tandanus tandanus* Mitchell.
      - *Zanclistius elevatus* Ramsay and Ogilby.

TAXONOMIC LIST AND INDEX OF THE SPECIES AND GENERA OF WHICH THE MUSCLES HAVE BEEN STUDIED.—*Continued.*

Amphibia. Pp.133–187.	Neoamphibia.	Dipneusti. Pp. 133–144.	*Neoceratodus.* *Leipdosiren.*
	Euamphibia.	Coecilia. Pp. 187–191.	*Herpele.* *Ichthyophis.*
		Urodela. Pp. 155–180.	*Amblystoma* (*Axolotl*) *tigrinum* Green. *Diemyctylus* sp. *Molge* (*Notophthalamus*) sp. *Necturus maculatus* Gray. *Plethodon* sp. *Spelerpes* sp.
		Anura. Pp. 143–154, 180–187.	*Hyla aurea* Lesson. *Hyla caerulea* Gunther. *Lymnodinastes peronii* Bibron. *Lymnodinastes tasmaniensis* Gunther. *Myxophyes fasciolatus* Gunther. *Rana pipens* Shreber.
Reptilia. .. .. .. Pp. 238–269.		Lacertilia. Pp. 238–253.	*Amphibolurus muricatus* Shaw. P. 246. *Anolis carolinensis* Dumeril and Bibron. Pp. 246–7. *Anolis cristatellus* Dumeril and Bibron. *Basiliscus* sp. Pp. 247–8. *Chameleon* sp. Pp. 248–250. *Gymnodactylus* sp. Pp. 250–251. *Lygosoma* sp. P. 251. *Physignathus lesueurii* Gray. Pp. 235–246. *Thecodactylus* sp. Pp. 250–251. *Tiliqua scincoides* Shaw. Pp. 251–2. *Varanus* sp. Pp. 252–3.
		Rhyncocephalia. Pp. 253–255.	*Sphenodon.*
		Crocodilia. Pp. 255–260.	*Alligator* sp. *Crocodilus.*
		Chelonia. Pp. 260–264.	*Chelodina longicollis* Shaw. *Emydura macquarii* Shaw.
		Ophidia. Pp. 264–269.	*Notechis scutatus* Peters. *Python variegatus* Gray. *Pseudechis porphyriacus* Shaw.