PART III. THE SAURIA. (*Continued.*)

THE AVES.

THE MUSCLES OF THE BIRDS.

Eighteen birds have been dissected for this section of the work, but, as there is a marked similarity in the arrangement of the muscles, only those which present interesting features will be described in detail.

The conditions in *Gallus*, which is described fully, may be regarded as the normal, or typical, arrangement for the birds. The majority of those examined resemble it closely.

Gallus.

(Figs. 157–166.)

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The ventral constrictor, Csv.1, presents no division into parts. It consists of a sheet of transverse fibres which arise on each side from the inner surface of the mandible for the greater part of its length and which are inserted into a median raphe.

Innervation.—This is, of course, by the mandibular ramus of the Vth nerve. The course of this nerve is almost exactly as in the Reptilia. The main trunk passes deeply between the pterygoid and temporo-masseteric groups of masticatory muscles, the terminal, mandibular, branch enters the canal in the mandible. The first branch of this to perforate the jaw-bone breaks up into three to five twigs as soon as it emerges; one of these supplies the whole of the motor fibres to the Csv.1.

Lubosch (1933, fig. 14) depicts the posterior margin of this muscle as trending caudad. I have dissected, in all, about forty specimens, and in every one of them I find the posterior margin to be almost exactly transverse, but I also find that the posterior limit of the origin is placed further back than he depicts it, whilst the posterior limit of the insertion is a little further forward.

The muscles of mastication are essentially similar to those of the reptiles. I have not, however, found any trace of the retractor anguli oris in any one of the many birds examined.

The Masseter muscle is a relatively thicker muscle in the fowl than it is in any reptile examined. It arises from a very strong fascia which is bound to the outer surface of the post-orbital process of the skull and to the anterior wall of the fibrous external auditory meatus.

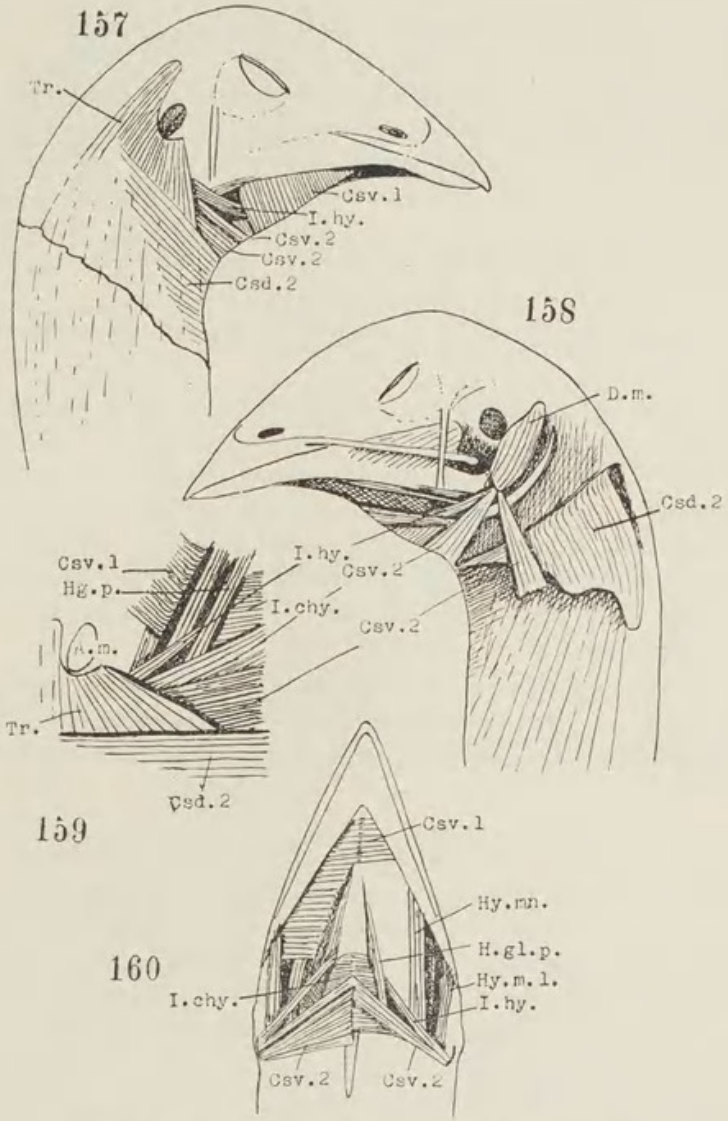
This fascia is, as it were, continued forward and ventrally along the superior margin of the muscle for about two-thirds of the length of that margin. The fasciculi arise from the outer surface of the post-orbital process and from the continuation of the fascia along the whole of its length. Their direction is ventrad and rostrad and they are inserted directly into the outer surface of the mandible well in front of the jaw joint.

The Temporalis muscle arises from the inferior margin and surface of the post-orbital process and from the skull in the temporal fossa deep to the M. masstericus. This temporal muscle is roughly pyramidal in shape. The apex of the pyramid is a short tendon which is inserted into the upper edge of the mandible, actually to the little tubercle upon that edge immediately above Meckel's fossa and which may be regarded as a much reduced coronoid process. The pyramid is, then, upside down, and the base is the origin of the muscle as described.

As the final portion of this work goes to the press I feel that some explanation of the absence of references to recent work is called for. The work was commenced in 1933 and progressed steadily till its completion in 1939. Delay in publication resulted from lack of available funds and the general uncertainty of conditions associated with the declaration of war. In 1942 the Trustees of the Australian Museum agreed to publish sections of the work from time to time as funds became available, and in 1944 a grant from the Commonwealth Scientific Publications Committee helped to expedite the completion of publication. I should like to express my gratitude to both those bodies, as well as to the Director of the Museum, Dr. A. B. Walkom, and to the Librarian, Mr. W. A. Rainbow, for invaluable assistance in the editing and printing of the memoir.

As a result of the delay, the work, in its reference to current research in comparative anatomy and embryology, is to a certain extent out of date. This has been unavoidable because my time has been wholly taken up in the discharge of my duties as Director of Medical Services of the Allied Works Council of the Commonwealth of Australia, and consequently I have had no opportunity of bringing the work up to date.—H.L.K.

The Quadrato-mandibularis muscle arises from the anterior process of the quadrate, and its fasciculi pass almost directly ventrad to be inserted on to the outer surface and lower edge of the mandible between the insertion of the M. massetericus and the joint. This muscle is a flat ribbon of tissue of no great thickness.



Figs. 157–160.—*Gallus*. Superficial muscles.

The pterygoideus externus muscle is a rounded bundle of fasciculi which arise from the wall of the skull below and just in front of the root of the post-orbital process. The muscle is clothed upon its anterior surface by a strong band of fascial fibres, and it is into this that the greater part of the fasciculi are inserted. The fascia gives the muscle a short tendinous insertion into the upper edge of the mandible medial to the insertion of the temporalis muscle.

The pterygoideus medius muscle appears as though it were an anterior extension of the M. quadrato-mandibularis. It arises from the upper edge and lateral surface of the anterior process of the quadrate bone. Its fibres pass ventrad, laterad, and rostrad, and are inserted along the upper edge of the mandible and along an upper strip of the internal surface thereof. The insertion of these fasciculi commences behind at the anterior edge of the M. quadrato-mandibularis and terminates at the same point as the most anterior point of insertion of the M. massetericus.

At its origin this muscle appears to be quite continuous with the anterior fasciculi of the M. quadrato-mandibularis, and, indeed it cannot be dissected free from that muscle. There is, however, a strong tendinous band running from the posterior point of origin of the muscle almost to the posterior edge of its insertion. This marks the limits of the two muscles, which are further indicated by the fact that the most anterior, like all the rest of the fasciculi of the M. quadrato-

mandibularis, are inserted into the inferior edge of the external surface of the mandible, whilst the most posterior fasciculi of the M. pterygoideus medius stop short to be inserted into the superior edge.

The Pterygoideus internus is a very massive muscle and is best described in two portions. These two parts are intimately fused along their contiguous margins.

The Pars medialis arises from the posterior half of the inferior and median surfaces of the palatine bone and from the inferior and posterior surfaces of the pterygoid bone. The origin is in part directly from the palatine and pterygoid bones, and in part from a fascia which is attached to the inferior surface of the palatine bone and spreads out upon the inferior surface of the muscle. In the result the muscle receives an appearance of being spindle shaped and arising from the fascia. The muscle is inserted into the inner half of the inferior surface and posterior edge of the median half of the transverse process of the mandible, and also on to the whole of the superior surface of that process medial to the articular cavity. This last insertion is of the whole of the fibres which take their origin from the pterygoid bone, and there is a partial cleavage between this portion of the muscle and the rest of it, which suggests the imperfect separation of a M. pterygoideus posterior.

The Pars lateralis arises from the anterior half of the inferior and lateral surfaces of the palatine bone in a manner similar to the origin of the last muscle. In similar way it receives an appearance of being spindle shaped, as viewed from the inferior surface. Inferiorly these two muscles are intimately fused along their contiguous edges. Superiorly a cleavage exists between the muscles right to the ventral fascial membrane anteriorly and gradually becomes shallower as it is traced backwards. The insertion of the M. pterygoideus internus is into the inferior surface and posterior edge of the lateral half of the transverse process and the post-articular piece of the mandible.

The Spheno-pterygoideus muscle arises from the side wall of the skull medially to and only just above the pterygoid bone. It is inserted into superior and anterior surfaces of the pterygoid bone and into the upper edge and posterior surface of the anterior process of the quadrate bone.

THE MUSCLES OF THE HYOID SEGMENT.

In the course of his work upon the muscles of saurians, Lubosch (1933) describes and illustrates those of a few birds. His description of the superficial constrictor sheet in *Struthio* and in *Gallus* is accurate in respect of the morphology of the muscles. I find, however, that there is an error in his determination of the extent of the constrictor sheet innervated by the facial nerve.

The muscle which he regards as the hyoid portion of this sheet and indicates with the letters C.mv.hy. is innervated by the ninth nerve and the aboral portion of the sheet is not nearly so extensive as his illustrations depict. This last statement is based upon dissections and experimental investigation in the case of *Gallus*, but upon the dissections only for the birds generally.

The disposition of the various branches of nerves VII, IX and X were carefully determined in *Gallus* and their functions were then determined by stimulation.

Many experiments were carried out before all doubts as to the functions of the various branches were set at rest. In the early experiments the birds were pithed prior to the work, but later it was found that one had from twenty to thirty minutes in which to carry out the experiments after they were simply decapitated, before the muscles failed to respond to stimulation. In this work I had the able assistance of my son, Geoffrey L. Kesteven, and take pleasure in recording my indebtedness to him, and also to Professor H. Priestley for the loan of the electrical equipment for the work.

The facial nerve issues from its foramen behind the external auditory meatus medially to the fibrous posterior wall thereof. It at once gives off two twigs to the depressor mandibulae muscle. After a very short course against the posterior surface of that muscle the nerve crosses to the fascial plane in front of the hyoid cornu and divides into two branches. Both of these reach the deep surface of the dorsal facialis constrictor (Csd.2) in front of the anterior margin of the M. trapezius. The posterior, or more dorsal, branch is distributed entirely to the Csd.2. The more medial, and larger, branch gives off a branch anteriorly. This supplies the two portions of the Csv.2 and the M. interhyoideus. The rest of the nerve supplies only the ventral portion of the Csd.2.

The ninth and tenth nerves (Fig. 161) emerge close together deep to the emerging seventh. They are joined by a fairly thick commissure immediately outside their foramina of exit from the skull. Just a little way distal to this another commissure is present. This leaves the tenth and runs forward to join the ninth ; it also is quite short. Almost immediately beyond the point of junction of this last with the glosso-pharyngeal, the nerve which supplies the whole of the muscles of the floor of the mouth leaves this last. Experimental work showed this to be composed, as far as its motor fibres were concerned, of ninth nerve fibres only. If one severed the ninth nerve behind the second commissure, and then severed the first, one obtained no contractions of any of these muscles on stimulation of the proximal end of the vagus. Amongst the muscles which contracted was the " C.mv.hy." of Lubosch, present in *Gallus*, and precisely similar to that muscle in *Struthio* and *Dromaeus*.

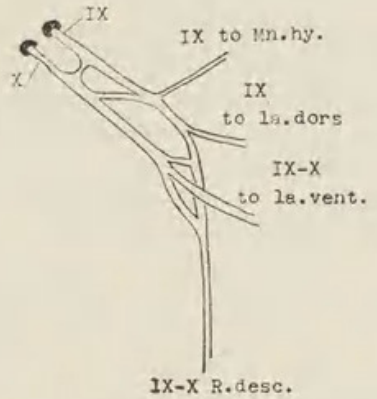


Fig. 161.—*Gallus*. Diagram of the main branches and anastomoses of the IXth and Xth nerves.
IX-X to la.dors., the nerve to the larynx ; IX-X to la.vent., the nerve to the deeper hypobranchial muscles ; IX to Mn.hy., the nerve to the superficial hypobranchial muscles ; IX-X R.desc., the descending gastro-intestinal trunk.

Beyond the nerve to the hypobranchial hyoid muscles, the ninth divides into its two terminal branches. One of these carries motor fibres to dorsal pharyngeal muscles, the other is the descending branch of the nerve.

Beyond the second commissure, and at an appreciable distance from it, the vagus divides into three. Two of these join the descending branch of the ninth. The third carries motor fibres to ventral pharyngeal muscles and the recurrent laryngeal fibres.

These same nerves were dissected out in *Struthio*, *Dromaeus*, *Anas*, *Phalacrocorax* and *Calyptorhynchus* ; they were also studied in serial sections of a number of late embryos, and in no case was any difference worthy of record noted. It is, therefore, assumed that the innervation of similar muscles is the same throughout the birds.

Stimulation of the two branches of the seventh nerve to the Csd.2 produced contractions only over the small region occupied by the muscle depicted in my figure 157. Actually, the extent of the muscle so depicted was determined by dissection before the experimental work was carried out, as also was the innervation of the " C.mv.hy." by the ninth nerve, and it was these discrepancies which caused me to undertake the experimental work.

The greater portion of the " C2.dv.abor." of Lubosch is portion of the general platysma myoides and may be designated constrictor colli spinalis, since it is probably completely homologous with the similarly named muscle in the Chelonians and some other reptiles.

The innervation of the deeper muscles presumably innervated by the ninth nerve, as indicated by dissections, was not definitely determined by the experimental method. That complete and clean exposure of the muscles necessary for quite satisfactory observations could not be completed before the muscles failed to respond to nerve stimulation.

The three parts of the Superficial constrictor are placed upon successively deeper planes, from behind forward.

The posterior portion of the superficial facialis constrictor (Csd.2) lies immediately beneath the skin. Its anterior border is found immediately behind the posterior margin of the depressor mandibulae muscle. It arises from the fascia dorsalis about one-third of the distance down from the mid-dorsal line to the mid-lateral line of the neck. This is the level of origin of the more

anterior fibres ; as one proceeds caudad one finds that the origin is placed gradually lower and lower. In other words, the fibres lose in length at the expense of their upper ends. They are all inserted into a medial ventral raphe. Their direction is almost precisely at right angles to the long axis of the neck, with a very slight inclination caudad. The fibres of this muscle lie upon the extensive trapezius muscle (Tr.), and the anterior fibres are nearly parallel with the most median fibres of that muscle as they tend to a transverse direction on either side of the mid-line.

The Csv.2 is present in two parts, the more superficial portion of the muscle (Csv.2) arises from a short line upon the outer surface of the post-articular piece of the mandible. From this origin the fasciculi pass ventrad and mediad to be inserted into the mid-ventral raphe. The muscle is broader at its insertion than at its origin, and the anterior fibres have an inclination rostrad. The muscle is placed upon a deeper plane than the Csd.2. At its origin it lies deep to the trapezius muscle, which, in turn, lies deep to the Csd.2. At its insertion, careful dissection reveals that there is a definite fine fascia overlying it which continues forward the plane of the Csd.2, although the median raphe of the one becomes intimately blended with that of the other.

The deeper and more anterior portion of the muscle arises from a similar short line in front of the last muscle and its fibres pass mediad and ventrad to be inserted into a mid-ventral raphe. The more posterior fibres of this muscle lie dorsally to the anterior fibres of the last and their respective median raphes do not combine. On the other hand, the insertion of the anterior portion is very intimately bound to the ventral surface of the body of the hyoid.

The Depressor Mandibulae muscle is a solid oblong mass of fibres which arise from the posterior, fibrous, wall of the external auditory cavity and from the surface of the skull dorsally thereto. The muscle lies deep to the anterior end of the M. trapezius. Its direction is, from its origin, ventrad and laterad, with a slight curve rostrad in its posterior fibres. It is inserted into the upper part of the external surface and practically the whole of the internal surface of the post-articular piece of the mandible.

It should be noted that this depressor mandibulae can represent only the pars cephalognathica of the muscle in the reptiles ; there is no trace of any division into two heads. It will save repetition to state that no representative of the pars notognathica has been found in any bird investigated.

The Interhyoideus muscle arises in front of the Csv.2, and deep to the deeper portion, from the articular bone ; it is a thick cord-like muscle which runs forward and mediad. It crosses the M. hyo-mandibularis superficially and then passes deep to the M. hyo-glossus posterior to reach the dorsal surface of the rod-like anterior portion of the hyoid body. The two muscles of opposite sides meet in a common line of insertion along the centre of this surface.

Muscles Innervated by the Ninth Nerve.

(Figs. 160–167.)

The M. hyomandibularis arises from the posterior half of the length of the hyoid cornu, clothing it completely with its fasciculi. The muscle divides into medial and lateral portions which are inserted, one behind the other, into the inner surface of the mandible. The smaller, lateral, portion is inserted superficially to the Csv.1, the medial portion deep to it.

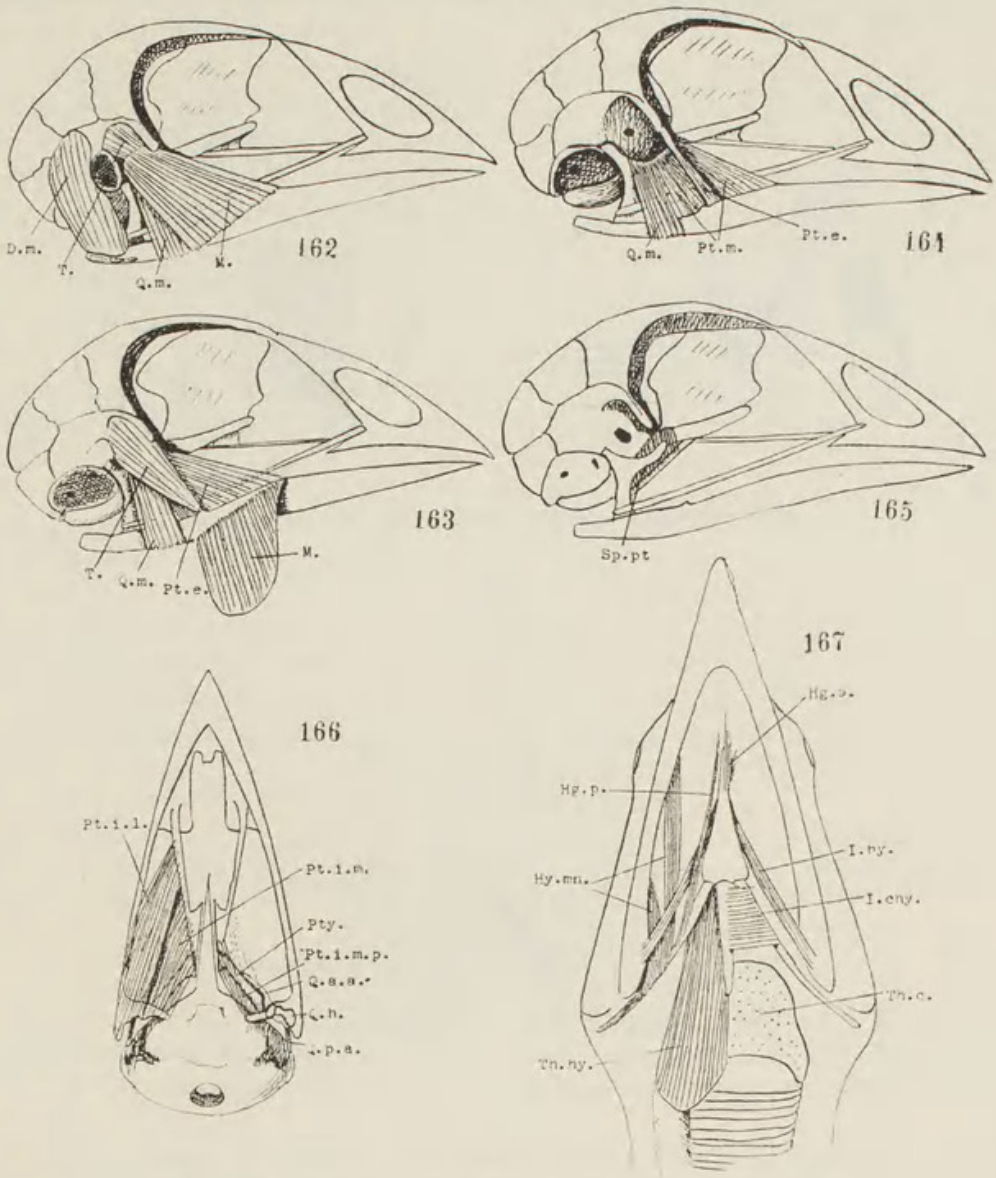
The M. hyoglossus posterior arises from the anterior half of the length of the hyoid cornu. Although this is a thin, cord-like muscle, its origin clothes all those surfaces of the cornu in this part of its length not covered by the M. intercerato-hyoideus. The fasciculi are inserted into a very fine tendon which loses itself in the tough tissues of the anterior end of the tongue.

The M. Thyro-hyoideus is a massive muscle which arises from the ventral surface of the thyroid cartilage, from a small area of the thyreo-tracheal membrane and from the wall of the pharynx close to these two structures. Its fibres pass directly forward, converging slightly to be inserted into the dorsal surface of the body of the hyoid behind the insertion of the M. inter-hyoideus.

The Interceratohyoideus muscle is a remarkably thick sheet of fibres which arise from one hyoid cornu, cross the urostyle, and are inserted into the other cornu. The muscle commences, in front, just behind the body of the hyoid and its posterior margin is about two-thirds of the length of the urostyle further back.

The Hyoglossus anterior muscle arises from the anterior end of the body of the hyoid and is inserted into the fibrous tissue of the tongue. The most ventral fibres of this muscle are

differentiated from the rest ; they run directly forward along the ventrum of the tongue between the tendons of the posterior hyoglossus muscle. The other fibres have a direction forward, dorsad and slightly laterad, outside the tendons.



Figs. 162–166.—*Gallus.* The muscles of mastication.
Fig. 167.—*Gallus.* The hypobranchial muscles.

Dromaeus and *Struthio.*

(Figs. 168–171.)

These two birds resemble one another so closely that they may be described together.

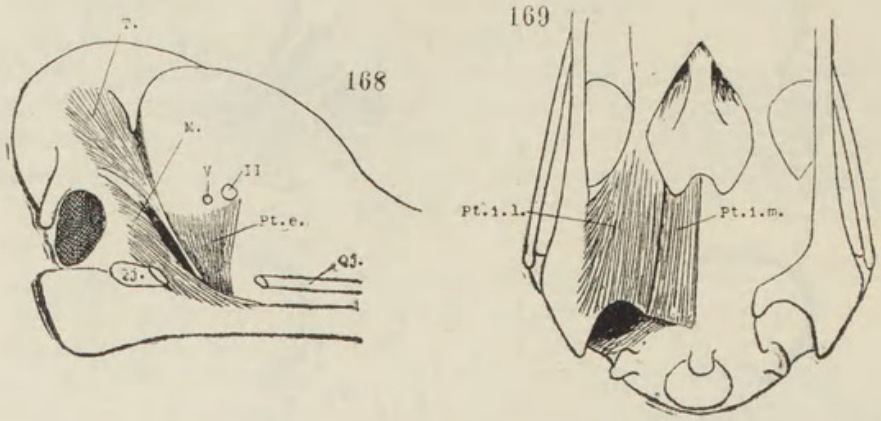
THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a is not to be found.

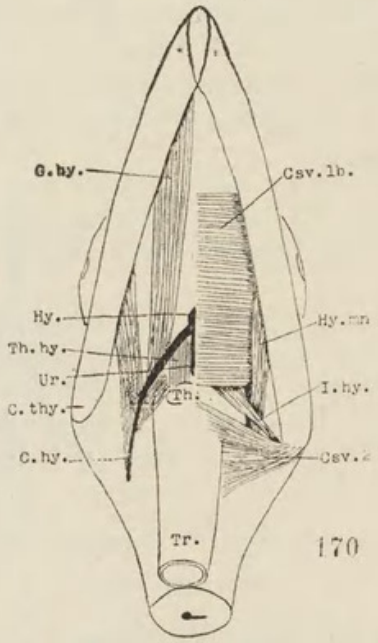
The Csv.1b is a very typical muscle. All the fibres pass directly transversely and are inserted into a median raphe. The line of origin is placed fairly high on the inner surface of the mandible, about one-third of its depth from the dorsal edge. This line commences behind just in front of the insertion of the muscles of mastication and extends forward to near the junction of the middle and anterior thirds of the length of the mandible.

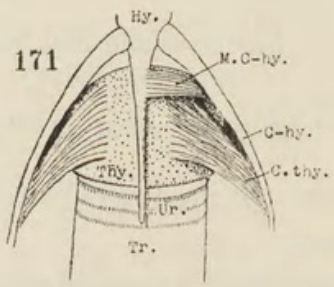
The Masseter muscle arises from the lower part of the temporal fossa and from the inferior post-orbital process above the quadrate. The fibres run forward and ventrally and are inserted on to the upper edge of the mandible and a narrow area on the outer surface close to the dorsal edge and into a more extensive area on the inner surface.

The Temporalis muscle arises from the upper part of the temporal fossa, from the inner surface of the superior post-orbital process, and from a small area of the surface of the alisphenoid bone in the posterior wall of the orbit. The fibres are all inserted into a strong rounded tendon which is inserted into the inner surface of the mandible below the foramen for the mandibular branch of the fifth nerve.



Figs. 168, 169.—*Struthio.* The muscles of mastication.





Figs. 170, 171.—*Dromaeus.* The ventral muscles.

The Quadrato-mandibularis muscle is apparently completely fused with the deep surface of the M. massetericus ; that portion of the muscle which arises from the inferior post-orbital process actually arises almost in the situation of the origin of the quadrato-mandibularis muscle in other birds. It will be remembered that the otic process of the quadrate, which stands out freely in the great majority of birds, is very nearly covered by the inferior post-orbital process in the Emu and the Ostrich and their allies.

The Pterygoideus externus muscle arises from the area of origin, is quite narrow, and commences in front of the optic foramen and extends back to the junction of the presphenoid to the basisphenoid bone. It is a flat sheet of fibres which pass, almost horizontally, laterad, converging to be inserted into a narrow area along the inner surface of the mandible below the insertion of the M. massetericus.

The Pterygoideus medius muscle is quite continuous with the deep surface of the M. pterygoideus externus ; it arises from the lateral surface of the palatine process of the quadrate. Its fasciculi run horizontally laterad, with a caudad inclination, to be inserted below the M. pterygoideus externus.

The Pterygoideus internus muscle is exceedingly massive. As is usual in the birds, medial and lateral parts may be recognized, although they are but poorly delimited. The pars lateralis arises from the lateral margin and inferior surface of the posterior plate of the palatine bone. The fibres run caudad and are inserted on the ventral edge of the ramus of the mandible and on the ventral surface of the expanded articular bone. The pars medialis arises from the inner margin of the expanded plate of the palatine and of the posterior plate of the vomer and from the ventral surface of the pterygoid bone immediately behind it. The insertion of the lateral fibres of this portion of the muscle is on to that portion of the ventral, expanded surface of the articular bone not occupied by the insertion of the pars lateralis. The remainder of this muscle probably represents the M. spheno-pterygoideus, which is, otherwise, not represented. The portion in question constitutes about the medial half of the muscle. All these fibres are inserted into a strong fascial band which binds the articular to the basisphenoid, behind the basipterygoid process, and also extends across the basisphenoid bone almost to the midline, just in front of the eustachian canal, where that leaves the tympanic cavity, and the anterior opening of the canal which carries the ramus palatinus facialis and the palatine artery. It will be noted that, if this be the spheno-pterygoideus muscle, its origin and insertion have both been shifted ; its situation alone justifies the suggestion. In view of the fact that the palate is rigid, it appears possible that this muscle functions in some way to assist deglutition.

The Levator quadrati muscle is composed of short fibres which arise from the basisphenoid bone in front of and above the basipterygoid process and pass to the concave, medial surface of the pterygoid process of the quadrate bone.

THE MUSCLES OF THE HYOID SEGMENT.

The Csd.2 was not found, but this was possibly because the muscle is very fine, poorly developed, and was not distinguishable on the roughened surface caused by the deep insertion of the feathers and by their erector and depressor muscles, specialized slips of the general platysma myoides.

The Csv.2 is the only representative found of the constrictor colli facialis. Its fibres arise, close together, from the fascia dorsalis just behind the angle of the jaw. The fasciculi diverge backwards and forwards as they pass ventrad and mediad. The muscle is imperfectly divided into anterior and posterior parts. The pars posterior is made up of those fibres which diverge caudad and those with a direct transverse direction. The pars anterior, with forward trending fasciculi, extends across the ventral surface of the trachea, its most anterior fibres meeting their antimeres in the midline.

The Interhyoideus muscle arises beneath the Csv.2. Its fasciculi are gathered to form a rounded, almost cord-like, muscle which runs forward and medially to flatten out somewhat and be inserted into the urostyle immediately behind the body of the hyoid and under cover of the posterior fasciculi of the Csv.1b.

The Depressor mandibulae muscle is a perfectly typical avian muscle which arises from the skull behind and above the external auditory meatus and from the posterior fibrous wall of that cavity, and is inserted into the articular bone. There is no trace of any division into two parts.

The facial nerve is essentially similar in all respects to that of *Gallus*, but the course of the ramus palatinus is of interest. I have previously recorded the fact that this nerve, in *Dromaeus*, runs forward below the basipterygoid process (Kesteven, 1941*a*). It was then suggested that Brock (1937) had mistaken a small branch of the nerve which runs forward below the process for the ramus itself, in *Struthio*. I have now to record that the course of this nerve and its branches is absolutely the same in both forms.

Muscles Innervated by the Ninth Nerve.

The Hyomandibularis muscle arises from the posterior third of the length of the hyoid cornu and its fibres run straight forward to be inserted into the inner surface of the mandible superficially to the posterior half of the Csv.1b.

The Geniohyoideus muscle is a flat sheet of fibres which arises from the outer side of the anterior two-thirds of the length of the hyoid cornu. Its fasciculi run straight forward to be inserted into the inner surface of the mandible along a line which commences in front at the symphysis and runs back along about one-half of the length of the ramus of the lower jaw and is situated just deep to the line of insertion of the Csv.1b. The two median edges of this pair of muscles are appreciably thicker than the lateral edge. The muscle lies between the mucosa of the mouth and the upper surface of the Csv.1b.

The Thyro-hyoideus muscle is a relatively thick sheet of fibres which arise from the posterior margin of the ventral surface of the thyroid cartilage and are inserted into the hyoid cornu close to the body of the hyoid.

The Ceratohyoideus muscle is a short bundle of fibres which arise from the anterior end of the hyoid cornu and pass directly transversely to be inserted into the proximal end of the urostyle.

The Ceratothyroideus arises from the hyoid cornu opposite the upper end of the trachea and is inserted into the ventral surface of the thyroid cartilage. This is the C2.mv.hy. of Lubosch.

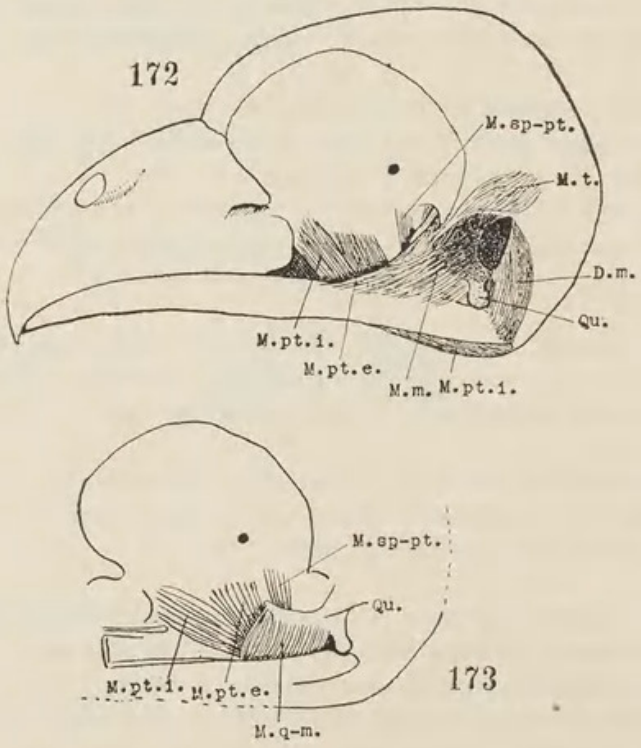
The last two muscles lie deep to the M. thyrohyoideus.

Podargus.

(Figs. 172–173.)

The Frog Mouth Owl is one of the birds in which the fronto-parietal joint functions to permit of the elevation of the upper beak. The movement is by no means as free as in the Parrots and Cockatoos, but is quite definite. This form was, therefore, dissected in order to compare its muscular mechanism with that of those other birds ; contrary to expectation, there was no trace of the peculiar modification of the arrangement of the pterygoid muscles which the parrots exhibit.

Before proceeding to the description of the muscles of mastication, it may be recorded that the other muscles present only minor differences from the typical avian arrangement.



Figs. 172, 173.—*Podargus*. The muscles of mastication.

THE MUSCLES OF MASTICATION.

In both the Owls and the Eagles the posterior wall of the orbit is made nearly complete by the extensive post-orbital process. This extends so far ventrad that it closes the temporal fossa from the orbit and, as a result, when the eye and its muscles have been taken from the orbit, little is seen of the muscles which, in the generality of birds, form its posterior wall. Although this is so, the muscles of mastication conform fairly closely to the typical avian arrangement.

The origin of the Temporal and Masseteric muscles is, as usual, from the temporal fossa. They and the M. quadratomandibularis are so intimately fused at their contactual surfaces that it is not possible to define them one from the other. Their origin is from the whole of the temporal fossa, the front wall of the external auditory meatus (here supplied by the extensive post-orbital process), the roof of the meatus, and the posterior and lateral surfaces of the quadrate and its articular ramus. Those fasciculi arising from the temporal fossa and the walls of the meatus may be regarded as constituting the M. temporalis. These fibres are inserted into a bifid tendon whose fan-like proximal ends lie buried in the muscle, and which is inserted, itself, into the inner side of the mandible above the foramen for nerve V3. The mass of fibres which arise from the outer surface of the more superficial of the bifurcations of the tendon and find their insertion into the dorsal edge and outer surface of a small area of the hinder end of the mandible, may be regarded as constituting the M. massetericus. All the fibres arising from the quadrate and its articular ramus are inserted into the posterior end of the mandible behind and below the insertion of the M. temporalis tendon. These fibres constitute the M. quadratomandibularis.

A short length of the temporalis tendon is visible below the post-orbital process between the masseteric fibres behind it and the anterior fibres of the M. quadratomandibularis in front.

The pterygoid muscles are also intimately fused at their contactual surfaces so that they may not be accurately defined.

The M. pterygoideus externus may be regarded as being constituted by fibres which arise from the whole of the lateral surface of the pterygoid bone. The fibres converge as they pass caudad and laterad to be inserted on to the inner edge of the expanded articular portion of the mandible.

The M. pterygoideus internus arises from both surfaces of the posterior end of the palatine bone and, by a small separate head, from the fascia joining the palatine bone to the mandible just behind the posterior point of contact of the two bones. The posterior half of the superior surface, the anterior half of the inferior surface, and the whole of the lateral edge of the muscle are clothed by a strong fascial sheath. The fasciculi of the anterior portion of the muscle are inserted into the dorsum of the ventral sheath, whilst the fasciculi of the posterior portion arise from the ventrum of the dorsal sheath and are inserted on to the inferior surface of the articular bone and edge of the mandible in front of it.

The M. sphenopterygoideus is intimately fused with the medial edge of the M. pterygoideus internus and the inferior surface of the M. pterygoideus externus. An examination of the inferior surface of the M. pterygoideus internus reveals a muscle which, at first sight, appears to be quite similar to the pars medialis of this muscle, as seen in the generality of birds. More careful examination discloses that the majority of the fasciculi of this muscle arise from the inferior surface and a narrow area along the inferior edge of the lateral surface of the pterygoid bone. These fasciculi pass forward to be inserted into the ventral fibrous sheath of the muscle. The sheath itself is attached in front to the inner margin of the palatine bone.

Apparently we have here a modification of the pterygoid muscles, whereby the pars medialis of the internal pterygoid and most of the fibres of the sphenopterygoid muscle have been converted into a depressor of the upper jaw.

A few perfectly typical fibres of the M. sphenopterygoideus pass laterad and caudad from the hinder end of the sphenoid bone to the pterygoid close to the pterygo-sphenoid articulation.

Eurystomus.

(Figs. 174–175.)

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1 is of particular interest because it is more definitely divided into the Mm. submentalis and intermandibularis than in any other bird dissected.

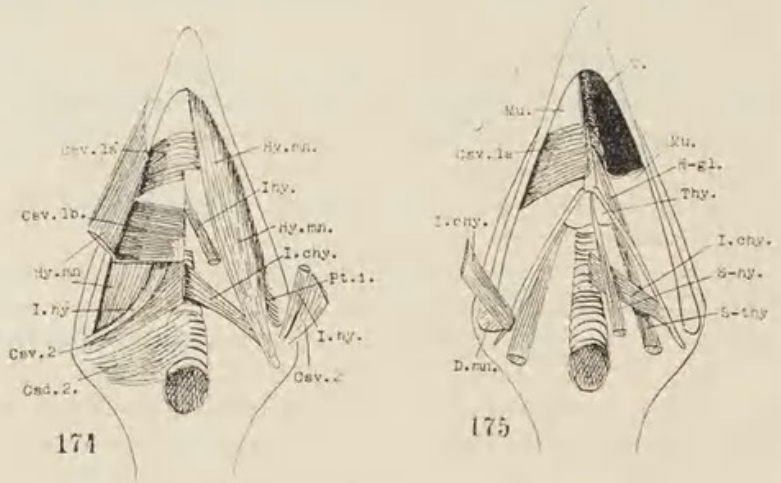
The M. submentalis (Csv.1a) is composed of a thin layer of fasciculi which extend uninterruptedly from one mandible to the other. These do not constitute a continuous muscle layer

except at their posterior margin, but each fasciculus is separated by a space as wide as the fasciculus is broad. The fibres do not run straight across but are curved forward to the centre.

The M. intermandibularis (Csv.1b) is a much thicker sheet of fibres which run directly transversely. The posterior half of these are inserted into a median raphe, the rest are uninterrupted.

Both these muscles are inserted deep to the M. hyomandibularis.

The M. massetericus arises from the lower and posterior portion of the temporal fossa and from the upper end of the otic process of the quadrate. The greater part of the fibres arising from the temporal fossa are inserted into the upper edge and a narrow area close thereto on the outer side of the mandible. The deeper of these fibres and those arising from the upper part of the temporal region are inserted on to the tendon of the M. temporalis, which runs ventrad and rostrad along the anterior edge of the muscle. Those fibres which arise from the quadrate bone are inserted into the medial surface of the surangular, above and behind the foramen for nerve V. There is no cleavage plane between the last fibres and the posterior fibres of the M. pterygoideus medius.



Figs. 174, 175.—*Eurystomus*. Ventral muscles.
D.m., M. depressor mandibulae; H.gl., M. hyoglossus; Hy.mn., M. hyomandibularis; I.chy., M. interceratohyoideus; I.hy., M. interhyoideus; Mu., mucosa of the mouth seen from below; Pt.i., M. pterygoideus internus; S.hy., M. sternohyoideus; S.thy., M. sternothyroideus.

The M. temporalis arises from the upper portion of the temporal fossa and from the posterior surface of the post-orbital process. The fasciculi are all inserted into a strong tendon which is inserted into the mandible just above and in front of the foramen for the nerve V3.

The M. quadratomandibularis arises from the lateral surface of the pterygoid process of the quadrate, and its fasciculi run horizontally to be inserted into the medial surface of the mandible. The area of this insertion is almost equal in length to the area of origin, but is situated a little posteriorly to it.

The M. pterygoideus externus arises from the wall of the orbit dorsally and laterally to the prootic foramen. Its fasciculi are all inserted into a tendon which is inserted into the dorsal surface of the mandible just behind and medial to the foramen for nerve V3.

The M. pterygoideus medius may be most conveniently described in two portions. The pars posterior arises from the outer surfaces of the body, the processus oticus and the ramus articularis of the quadrate. The more ventral fibres are nearly horizontal, the more superficial nearly vertical as they pass to their insertion on to the mandible. This portion of the muscle is only partially separated from the deep surface of the M. massetericus by a narrow, very strong fascial band which extends from the tip of the otic process of the quadrate to the mandible, deep to the posterior end of the area of insertion of the M. massetericus. The pars anterior arises from the ventral edge of the pterygoid process of the quadrate in front of and deep to the M. pterygoideus externus. The fasciculi run ventrad, caudad and laterad to be inserted, with those of the pars posterior, into the dorso-medial surface of the mandible medially to the insertion of the M. massetericus and behind that of the M. pterygoideus externus.

The M. pterygoideus internus presents the usual avian feature of incomplete division into medial and lateral parts. The pars lateralis arises from both surfaces of the expanded posterior end of the palatine bone. On the dorsal surface this area extends forward to underlie the hinder end of the nasal capsule. On the ventral surface it stops short at the transverse level of the planum ant-orbitale above it. A plane of incomplete separation between dorsal and ventral portions of the muscle is formed by a delicate fascia which extends back for some distance in the plane of the edge of the palatine bone. The pars medialis arises from a medial strip of the area just described and from the dorsal, ventral and lateral surfaces of almost the full length of the pterygoid bone and from a small area on the side of the presphenoid just in front of the spheno-pterygoid articulation. The whole of the fasciculi are inserted into the anterior surface of the articular bone, without any trace of division.

The M. spheno-quadratus arises from the lateral surface of the sphenoid bone medially to the pterygoid process of the quadrate. It is into the medial and part of the dorsal surface of this process that all the fasciculi are inserted.

The Fifth Nerve and its Branches.

The foramen prooticum comes into view when the last-mentioned muscle is pulled forward and medially. The nerves to the temporalis and masseterieus muscles pass dorsad and rostrad against the anterior surface of the M. temporalis, which lies in contact with the M. pterygoideus externus. A sensory branch of the fifth nerve also emerges from between these muscles but at a higher level. The twigs of this sensory branch are distributed to the temporal region of the head. The nerve to the M. pterygoideus internus runs forward medially to and below the tendon of its muscle, whilst the main ramus mandibularis runs ventrad and rostrad between its tendon and that of the M. temporalis. The nerves to the M. pterygoideus externus itself and to the M. pterygoideus medius are very short and reach their destination under cover of the former.

The maxillary ramus of the fifth nerve emerges between the tendons of this muscle and the M. temporalis and then turns rostrad superficially to the tendon of the former. In its further course across the floor of the orbit it lies upon the dorsal surface of the M. pterygoideus internus. As it crosses the M. pterygoideus externus it, of course, also passes externally to the more deeply placed M. pterygoideus medius.

The " myloid " branch of the fifth nerve emerges from the medial surface of the mandible about the middle of the width of the M. Csv.1b and superficially to that muscle. Three twigs are given to this muscle, and the main branch then continues forward just medially to the medial border of the M. hyomandibularis. The terminal branch gives four small twigs to the M. Csv.1a and then finally breaks up in front of that muscle. No twigs were observed to terminate on or in the M. hyomandibularis.

THE MUSCLES OF THE HYOID SEGMENT.

The Constrictor colli facialis dorsalis (Csd.2) is a thin sheet of diverging fibres, which arise from the fascia dorsalis behind the angle of the jaw, and slightly dorsal thereto, and spread out as they pass ventrad, curving rostrad, to reach the mid-ventral line below the anterior end of the trachea, where they are inserted into a median raphe.

The Constrictor colli facialis ventralis arises from the fascia of the M. depressor mandibulae and from the postero-ventral and medial corner of the os angulare. The fasciculi run mediad and curve rostrad to be inserted into a median raphe which lies below the M. interceratohyoideus which, in turn, lies beneath the extreme anterior end of the trachea. There is no indication of any division of this muscle into two parts as in *Gallus*.

The M. interhyoideus arises just in front of the origin of the last muscle and partly under cover of its anterior edge. This muscle arises as a narrow thin ribbon compounded of much fibrous tissue, but rapidly increases in thickness and slightly in width, to form a relatively stout cord which runs forward and medially to be inserted into the lateral edge of the posterior end of the body of the hyoid and into the anterior end of the cornu just behind its articulation with the body.

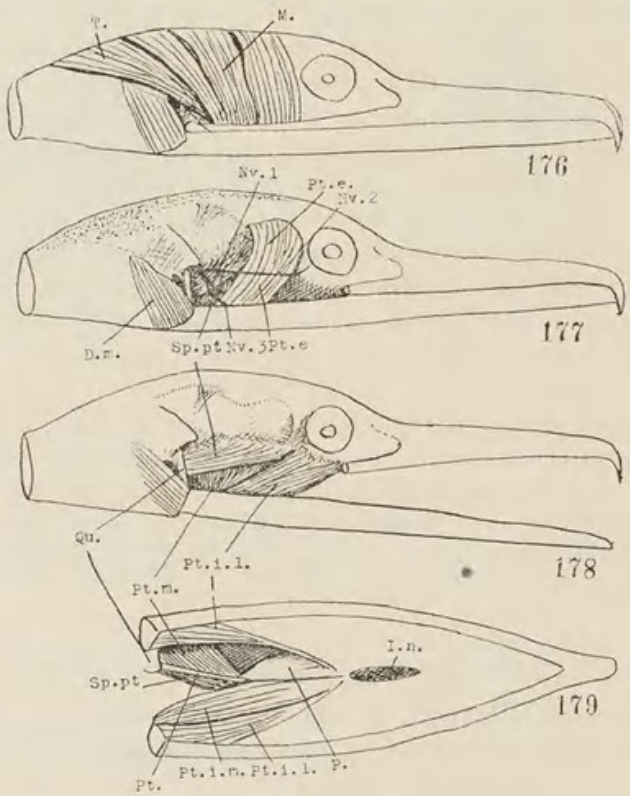
The M. depressor mandibulae is a perfectly typical avian muscle.

The Facial nerve emerges behind the depth of the external auditory meatus, between the M. depressor mandibulae and the posterior end of the hyoid cornu, and divides into its several branches almost at once. The two nerves to the M. depressor mandibulae are very short and

enter the postero-medial edge of the muscle. The nerve to the M. Csd.2 runs dorsad and caudad along the posterior edge of the M. depressor mandibulae, crosses the posterior end of the hyoid cornu, then, reaching the anterior margin of the M. Csd.2, it turns rostrad and ventrad beneath the muscle to break up into several fine twigs. The motor nerve to the M. Csv.2 and the M. interhyoideus crosses the muscle-covered hyoid cornu superficially and then runs forward and mediad along its medial border. The nerve finally breaks up into its terminal twigs on the deep surface of the two muscles.

The Muscles Innervated by the Ninth, Tenth and First Spinal Nerves.

The M. hyomandibularis is a more extensive muscle than is common amongst the birds and includes the genio-hyoideus completely fused with it. It arises, as usual, from an origin which completely clothes the posterior end of the hyoid cornu and extends forward along about one-third of its length. The fibres run forward and are inserted along a line on the inner surface of the mandible which extends from just in front of the area of insertion of the M. pterygoideus internus right forward to the symphysis. Posteriorly the muscle lies deep to the Mm. Csv.2 and interhyoideus ; anteriorly it is superficial to the insertions and lateral portions of the Mm. Csv.1a and Csv.1b.



Figs. 176–179.—*Phalacrocorax*. Muscles of mastication.
D.m., M. depressor mandibulae ; I.n., internal naris ; M., M. massetericus ; Nv^1., the profundus branch of the Vth nerve ; Nv^2., the maxillary branch of the Vth nerve ; P., palatine bone ; Pt., pterygoid bone ; Pt.e., M. pterygoideus externus ; Pt.i.l. & Pt.i.m., partes lateralis and medialis of the M. pterygoideus internus ; Pt.m., M. pterygoideus medius ; Qu., quadrate ; Sp.pt., M. sphenopterygoideus ; T., M. temporalis.

The M. interceratohyoideus arises from a short line on the medial surface of the hyoid cornu well towards the posterior end thereof. Its fibres spread out to form a relatively thin sheet deep to the Csv.2. Their insertion is into a median raphe.

The M. hyoglossus arises from the outer, dorsal and ventral surfaces of the anterior one-third of the length of the hyoid cornu. The fasciculi are gathered into a rounded cord-like muscle which runs forward, mediad and dorsad to be inserted into the tough fibrous matrix of the tongue, reaching it, of course, from below.

There is no M. thyrohyoideus present in this bird.

The M. sternohyoideus is a long oval cord-like muscle which (it is believed) arises from the anterior margin of the sternum and runs forward beneath the Mm. constrictor colli spinalis, constrictores colli fascialis dorsalis and ventralis to be inserted by a fine tendon into the postero-medial margin of the body of the hyoid just medially to the articulation of the cornu.

The M. sternothyroideus is a similar but slightly thicker muscle which lies laterally to the last, and (probably) has a similar origin. This muscle is deep to the M. interceratohyoideus as well as to those mentioned as superficial to the last. Its insertion is into the postero-lateral corner of the thyroid cartilage.

Phalacrocorax.

(Figs. 176–179.)

The muscles of mastication of *Phalacrocorax* are of particular interest. They resemble those of the Lacertilia more closely than do those of any other avian type examined. So closely do they resemble the muscles of the Lizards that there is no room for doubt as to the serial homology of the muscles in the two groups, and *Phalacrocorax* and its allies serve as the interpreter of the masticatory muscles of the whole of the Aves.

In this bird, as in *Physignathus*, we recognize at once two main groups of these muscles; one, the temporo-masseteric, lying superficially to the second and third divisions of the Vth nerve, the other, the pterygoid, lying deep to those nerves.

Although three members of the temporo-masseteric group of muscles are quite certainly present, as indicated by differences in the direction of their fasciculi and of origin and insertion, they are so intimately fused that it is not possible to indicate with any degree of confidence what may be the real limits of these three muscles. The three which are present are the Masseter, the Temporalis and the Quadrato-mandibularis. Of the three the M. massetericus is the most bulky and most superficial. It arises from a large area of the skull wall behind the orbit and extending up to the mid-dorsal line. Its insertion is entirely fleshy. The M. temporalis arises further back, extending beyond the posterior limit of the skull to arise from the mid-dorsal septum. Its fibres run rostrad, ventrad and laterad and are, for the most part, gathered on to a tendon which burrows forward between the fasciculi of the other two muscles to be inserted on to the upper edge of the mandible. The Quadrato-mandibularis muscle arises from the quadrate and from the skull wall close to it, and its fibres run ventrad to the mandible, passing deep to the last muscle.

The M. pterygoideus medius arises, again in the same sense, quite typically from the pterygoid bone and its fibres pass nearly horizontally but with an inclination ventrad and caudad to be inserted into the inner surface of the mandible behind the insertion of the last muscle.

The M. pterygoideus internus, though essentially similar to the lacertilian muscle, introduces a feature not present in any reptile, but apparently characteristic of, and certainly very prevalent amongst, the birds. The muscle is incompletely divided into lateral and internal parts. The pars lateralis arises from the lateral edge and upper surface of the os palatinum. This origin is largely tendinous and the inferior surface of the muscle is clothed by a membranous expansion of the tendon. This membrane gives their point of origin to the greater part of the fibres. The insertion is into the inner surface and lower edge of the mandible far back near the joint. The pars medialis arises from the inferior surface of the expanded palatine plate of the os palatinum. The greater part of this origin is fleshy, but there is also a strong membranous origin from the antero-lateral edge of the plate. Here also this membrane clothes the ventral surface of the muscle and gives origin to many fibres. The insertion is into the inferior surface of the laterally expanded articular process of the mandible. (Note.—In the illustration of the ventral aspect of these muscles, the articular process of the mandible has been removed from the right-hand mandible, in order the better to display the other muscles.)

The M. spheno-pterygoideus arises from the wall of the skull, low down along a line immediately dorsal to the level of the pterygoid bone. The fibres pass nearly horizontally caudad and laterad to be inserted into the pterygoid bone and into the shaft of the os quadratum.

There are here two completely fused muscles, the M. spheno-pterygoideus and the M. levator quadrati. We are enabled to make this statement at this stage because dissections upon other avian types have shown that both muscles are usually present. We may also remark that a M. pterygoideus posterior is also quite well differentiated in some birds.

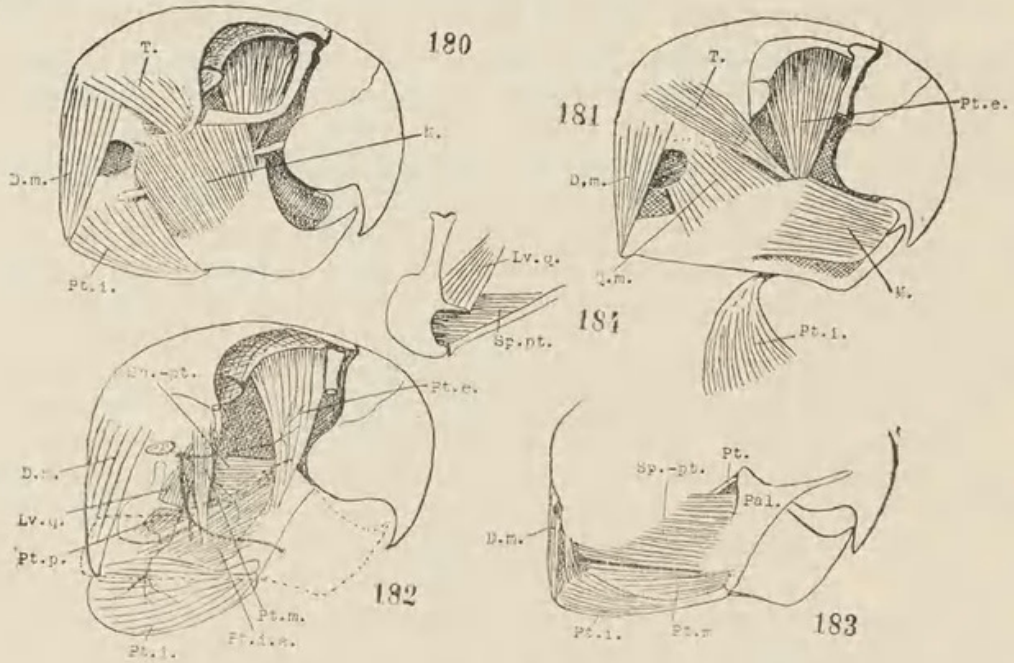
Calyptorhynchus, Cacatua and *Polytelis.*

(Figs. 180–184.)

The muscles of mastication of the parrots and cockatoos differ markedly from those of the fowl and the heron, and are peculiar.

The Masseter muscle is an extensive sheet of fibres which arise from the quadrato-jugal arch, from the fascia attached to the lower margin of the sub-ocular portion of the pre-orbital bone, and the post-orbital process, and from a fascia which is attached above to the inferior margin of the last process and below to the upper margin of a short pre-otic process. This extensive muscle encloses almost the whole length of the quadrato-jugal bar within its thickness. Its deeper fibres arise from the fascial sheets deep to the bar, whilst its superficial fibres arise from the fascia superficial to it.

The fibres are inserted directly upon the outer surface of the mandible along a line which begins close to the inferior margin and runs diagonally upward and forward to end close to the upper margin just behind the angle of the gape.



Figs. 180–182.—*Calyptorhynchus.* Muscles of mastication, lateral view.
D.M., M. depressor mandibulae; Lv.q., M. levator quadrati; M., M. massetericus; Pal., palatine bone; Pt., pterygoid bone; Pt.e., M. pterygoideus externus; Pt.i.l. & Pt.i.m., partes lateralis and medialis of the M. pterygoideus internus; Pt.m., M. pterygoideus medius; Pt.p., M. pterygoideus posterior; Sp.pt., M. sphenopterygoideus; T., M. temporalis.

Fig. 183.—*Calyptorhynchus.* Muscles of mastication, medial view.
For explanatory letters see Figures 180–182.

Fig. 184.—*Calyptorhynchus.* The Mm. levator quadrati and sphenopterygoideus seen from the lateral side.

The Temporalis is a longer and narrower muscle which arises from a shallow depression upon the side wall of the skull below and behind the post-orbital process. The most posterior and inferior fibres take their origin from the side wall of the skull above the upper edge of the area of origin of the M. depressor mandibulae. The direction of the fasciculi is ventrad, rostrad and laterad, and, as the muscle passes toward its insertion, on to the upper edge of the mandible just behind the upper limit of the insertion of the M. massetericus, it grows thinner and its fasciculi are all inserted into a fine tendon which in turn is inserted on to the edge of the mandible.

The Quadrato-mandibularis muscle arises from the anterior surface of the ascending body of the quadrate bone and from the skull wall above and in front of it. It is a relatively thick sheet of fasciculi which pass ventrad with an inclination rostrad and laterad to be inserted into the upper edge and outer surface of the mandible under cover of the M. massetericus.

The Pterygoideus externus muscle is exceedingly well developed. It is a solid muscle of triangular outline and considerable thickness. It arises from the upper part of the surface of the strong bony int-orbital septum and from the under surface of the roof of the skull. It is, in

Cacatua and *Calyptorhynchus*, but not in *Polytelis* and other small parrakeets, incompletely divided into two heads. Of these the larger and more anterior arises from the septum, the other from the skull roof. The whole of the fasciculi are gathered into a short tape-like tendon which is inserted into a tubercle upon the inner surface of the mandible a little distance below the upper edge. This tubercle is the upper end of a ridge which marks the anterior limit of the insertion of the internal portion of the M. pterygoideus internus.

The Pterygoideus medius is a quite small, spindle-shaped muscle which arises from the wall of the skull immediately below the post-orbital process. Its fibres are gathered into a thread-like tendon inserted into a small tubercle developed at the anterior end of the ridge which is continued forward from the shelf on which the articular facet is placed. This tubercle is placed about the middle of the depth of the inner surface of the mandible a little way in front of the mid-point between the posterior end of the ramus and the posterior end of the gape.

A quite separate Pterygoideus posterior is developed. This is a small sheet of fibres which arise from the inferior edge of the anterior process of the quadrate bone and pass back to be inserted on to the ridge which passes back and down from the articular process of the mandible.

The Pterygoideus internus is a most massive muscle and must be described in two parts, " lateral " or internal and " medial " or external. The Pars lateralis arises by fleshy fibres from both the internal and external surfaces of the mandible. The areas of its origin are approximately similar to and opposite each other, and are confined to the posterior end (see Figs. 180–183, Pt. i). These fibres converge towards the inferior edge of the mandible as they pass ventrad and rostrad, and are there gathered on to a fascia upon the exposed surfaces of the muscle. The fascia finally becomes a short narrow tape, which is inserted into the antero-inferior spur of the palatine bone.

The Pars medialis is a mass of relatively short fibres which arise from the lateral surface of the os palatinum and pass ventrad and caudad to be inserted into an extensive area upon the inner surface of the mandible. Of these fibres, those which arise from the upper end of the palatine bone gather, with those behind them arising along the postero-superior margin, into a relatively thick fleshy strand which is inserted on to the inferior surface of the outstanding articular process of the mandible. In Fig. 182 the muscles are shown as though the mandible were transparent, and practically the whole of the inner surface of it over the area occupied by the parallel lines used to indicate the pars medialis of this muscle (Pt.i.s.) affords attachment to the muscle, whilst the portion of the palatine bone encroached upon by those lines indicates the area of its origin.

The Spheno-pterygoideus is another particularly massive muscle in these birds. It arises from the lateral wall of the skull, low down, below the otocrane and forward from this site to the posterior end of the int-orbital septum, where that fuses with the rostrum basisphenoidei. From this origin the fibres pass horizontally forward to be inserted into the full length of the pterygoid bone, and, passing beyond that bone anteriorly, into a sulcus along the postero-superior margin of the os palatinum in its upper half. This portion of the muscle, in its passage antero-laterally beyond the os pterygoideum, encloses that bone entirely.

The Levator quadrati muscle is a well developed bundle of fasciculi which arise from the side wall of the skull ventrally to the origin of the M. pterygoideus medius and pass ventrad with an inclination laterad and caudad to be inserted into the upper edge of the short anterior process of the os quadratum.

The Depressor mandibulae mandibularis is a short rounded bundle of fasciculi which take their origin from the skull immediately behind the posterior limit of the origin of the M. spheno-pterygoideus and pass directly ventrad to be inserted on to the upper surface of the inner part of the shelf behind the articular process of the mandible. In *Polytelis* and other small parrakeets I find that this muscle lies horizontally, and that its fibres pass from their origin directly forward to be inserted on to the inferior edge of the articular process itself. In the larger cockatoos the insertion of this muscle is immediately in front of the M. depressor mandibulae and median to it. As the two muscles pass downward to their respective insertions they converge, and one gains the initial impression that one is in the presence of two heads of the M. depressor mandibulae. This muscle is, however, innervated by a twig from that nerve which innervates the spheno-pterygoideus muscle, whilst the M. depressor mandibulae is, of course, innervated by the VIIth.

A feature wherein the M. pterygoideus externus of the parrots and cockatoos differs from that of all the rest of the Sauropsida, or for that matter from all the vertebrates other than the fishes, has deliberately not been mentioned in the above description because I have deemed

it so important as to call for separate attention. It is that the muscle, at its origin, lies anteriorly to the optic nerve, and is to that extent pre-orbital. To my mind this is a feature of prime importance, because one of the strongest arguments against the acceptance of my contention, that the M. levator labii superioris of the sharks and rays is the homologue of the pterygoid group of muscles in the higher vertebrates, is the pre-orbital situation of the shark muscle.

Now, its situation deep to the second and third branches of the Vth nerve leaves us no doubt whatever that this muscle in the parrots is one of the pterygoid group. Its pre-orbital situation in these birds is proof positive that it is possible for a pterygoid muscle to have a pre-orbital origin. If we are able to accept as an accomplished fact the forward migration of a muscle post-orbital in other birds, there can no longer be any reason to doubt the possibility of a caudal migration of the same muscle in the progress of the modifications in masticatory mechanism which took place as between the fishes and the higher vertebrates.

Review.

Besides the birds whose musculature is described with more or less detail in the preceding pages, the following have been dissected : *Centropus*, *Hypotamidia*, *Halcyon*, *Struthidia*, *Nycticorax*, *Strepera*, *Anhinga*, *Corcorax*, *Anas* and three unidentified Eagles. In all, twenty-one birds have been dissected. In addition, a number of late embryos have been studied in serial sections.

This selection of birds covered, it is believed, a completely representative series, so that one is justified in believing that a composite picture based upon the common arrangement of the muscles in these, and omitting the isolated variations, may be regarded as presenting the typical avian arrangement.

Such a composite picture would reveal the following features :

THE MUSCLES OF MASTICATION.

These are divided into two groups, one superficial to the second and third branches of the fifth nerve, the other deep to those nerves. The superficial group would be divisible into massetericus, temporalis and quadratomandibularis muscles. Of these the first would be the most superficial and the last the deepest. The second group would be divisible into external, median, and internal pterygoid muscles and a spheno-pterygoid muscle.

The only superficial constrictor muscle innervated by the fifth nerve commonly present would be the Csv.1b. This would be found to be attached to the mandibular ramus deep to the line of insertion of the hyomandibularis muscle.

THE MUSCLES OF THE HYOID SEGMENT.

The constrictor colli fascialis dorsalis (Csd.2) would be found to be a relatively poorly developed muscle whose line of origin from the fascia dorsalis was placed just a little above the mid-lateral line.

The constrictor colli fascialis ventralis (Csv.2) would present itself in two portions, both arising from the post-articular lateral surface of the mandible and inserted, one beneath and slightly in advance of the other, into a mid-ventral tendinous intersection beneath the larynx or just in front of it.

The interhyoideus muscle would be found to arise just in front of the last two muscles and to pass forward and mediad to an insertion into the body of the hyoid or the hyoid cornu just behind it.

The depressor mandibulae muscle would be found to be comparable to the pars cephalognathica only of the reptiles.

THE MUSCLES INNERVATED BY THE NINTH NERVE.

The M. hyomandibularis would be found to arise from the hinder end of the hyoid cornu and to be inserted into the inner surface of the mandible, superficially to the posterior portion of the Csv.1b. It would also be found to be superficial to the Csv.1a when that muscle is present, and this extending so far forward.

The M. geniohyoideus arises from the lateral aspect of the fore end of the hyoid cornu and is inserted into the fibrous tissue of the ventrum of the tongue.

The M. interceratohyoideus lies deep to the Csv.2. It arises from one cornu and is inserted into a median raphe in which its fibres meet their antimeres. In certain birds, e.g. *Dromaeus*, this muscle is divided into two portions.

A M. thyrohyoideus is present in some birds, in others, apparently, its place is taken by the sterno-pharyngeal muscles.

So much, then, for what may be regarded as the typical arrangement of the avian cephalic muscles, but the departures from this " norm " are not without interest.

A typical M. Csv.1a appears to be present in *Eurystomus*.

In the cormorants, *Phalacrocorax* and *Anhinga*, and in some other birds, not so closely related but with equally long and narrow beaks, e.g. *Nycticorax* (Fig. 185) there is no deep layer to the Csv.2 and the anterior fibres of the superficial layer are woven through those of the opposite side, so that they appear to be woven through the posterior fibres of the Csv.1 (Fig. 185) and to be continued on to an insertion into the mandible deep to the M. hyomandibularis. In these forms one also notes that the Csv.1 is more extensive than is usual.

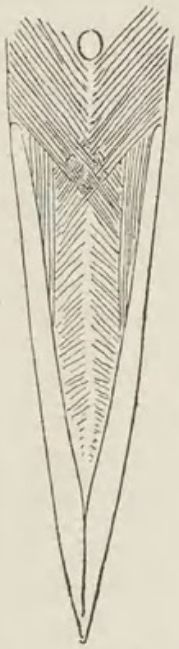


Fig. 185.—*Nycticorax*. The ventral superficial muscles.

It has not been possible to determine the limits of the Csv.2 and Csv.1 in these birds by the experimental method, but it is improbable that the Csv.2 fibres are really continued forward and across the mid-line. In *Eurystomus* the M. Csv.2 resembles one only of the two layers commonly present.

The variations in the muscles of mastication though (except in the parrots and their allies) never very extreme have, as a matter of fact, provided the means to the identification of the several muscles in the group. For it was only the occasional complete definition of one or more of the members of the group in various birds, which permitted the definition of the muscles in those birds in which the various muscles were more or less intimately fused.

COMPARISON WITH THE MUSCLES OF THE REPTILES.

It has been possible to recognize all the main divisions of the masticatory muscles found in the reptiles. The M. retractor anguli oris alone is missing. It will be remembered that it was not present in those reptiles in which the covering of the face region was rigid. That it should not be present in the birds is peculiar ; they have, covering the face, a skin which is freely movable upon the deep fascia. Reviewing the reptilian muscles, it was suggested that the M. retractor anguli oris might, perhaps, be that portion of the temporo-masseteric muscle which, in the Bony Fishes and in the tadpole of the frogs, functions as a depressor labii superioris. If that should be the fact, then it is further suggested that its absence from the Aves might be explained on the assumption that they have been evolved from forms with rigid face covering.

Although a Csv.1a has been identified in the Dollar Bird, *Eurystomus*, it is not quite certain that this is not merely an anterior portion of the Csv.1b. The reason for the identification adopted is : it was found that in the generality of the birds, when the Csv.1b is continued far forward, its fasciculi were not continuous from side to side but were inserted, in the typical manner, into a median raphe. On the other hand the anterior fibres of the Csv.1b in *Eurystomus* itself are uninterrupted in the mid-line.

There is, however, still another interpretation to be placed upon the whole muscle in the Aves. There is no doubt that this muscle is inserted more dorsally than is the Csv.1b in the Reptilia, and in view of the fact that in some of those the Csv.1a fibres were interrupted at the mid-line, it is not entirely unreasonable to suggest that we have here only the Csv.1a. Though a possible alternative interpretation of the muscle, it is not adopted here.

All three of the reptilian muscles of the hyoid segment are constantly present in the Aves.

The division of the Csv.2 into two layers is of particular interest, as we shall find when we come to inquire into the origin of the posterior belly of the digastric muscle and the M. stylo-hyoideus in the Theria.

Turning now to the muscles innervated by the ninth nerve, we find that the question of their identity has been complicated by a further reduction in the branchial skeleton. At first sight it seems obvious that the muscle which, in the Aves, we have designated the M. hyomandibularis, must be completely homologous with the M. thyreomandibularis of the Reptilia. On the other hand there is quite a possibility that it is that muscle in complete fusion with one or more of the juxtaposed muscles.

It was this difficulty, and uncertainty in the identity of the avian muscles which caused me to give them designations other than those used in the work on the reptilian muscles.

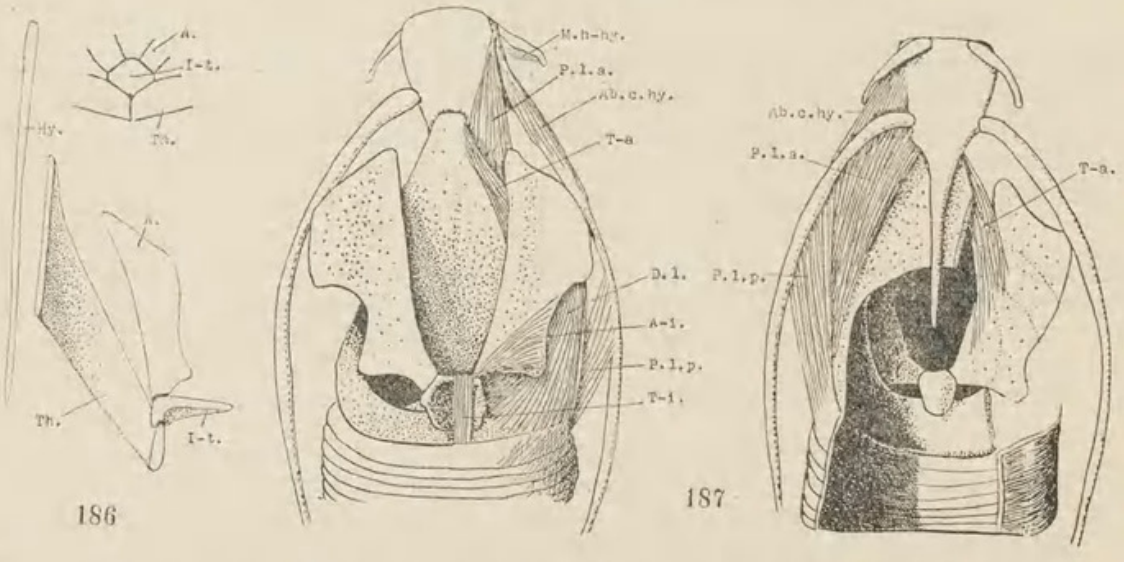
THE LARYNX AND ITS MUSCLES.

Dromaeus.

(Figs. 186–187.)

(*a*) *The Cartilages.*

The Thyroid is a complete hoop of cartilage which is split in the mid-line dorsally and rejoined by fibrous tissue. The ventral plate of the hoop is nearly three times as deep antero-posteriorly as the dorsal plate. As the use of the term " plate " probably implies, the hoop is dorso-ventrally flattened, and the lateral portions taper from the broad ventrum to the narrow dorsum. As indicated in the figures the dorsal plate is situated behind the caudal margin of the ventral plate. Anteriorly, the ventral plate is produced into a short spathulate process.



186 187

Fig. 186.—The larynx of *Dromaeus* in median sagittal section, semi-diagrammatic.
A., arytenoid cartilage ; I.t., interthyroid cartilage ; Th., thyroid cartilage.

Fig. 187.—*Dromaeus*. Dorsal and ventral view of the larynx, hyoid skeleton and related muscles.
A-i., M. arytenointerthyroideus ; D.l., M. dilator laryngis ; M.h.hy., M. hypohyalis ; P.l.a., M. protractor laryngis anterior ; P.l.p., M. protractor laryngis posterior ; T.a., M. thyroarytenoideus (constrictor laryngis) ; T.i., M. thyro-interthyroideus.

The Interthyroid is a small plate of cartilage which is articulated to the anterior margin of the split ventral plate. The area of this articulation is increased by sinuation of the edge of the thyroid, so that the interthyroid is let into the sinuation. The base of the little cartilage is relatively thick at the place of articulation, and from this it tapers as it projects dorsad and rostrad.

The Arytenoids are two plates of cartilage, flattened in the coronal plane of the head, but with a concavity on the ventral surface and a thickened medial border which forms a ridge ventrally. Their shape is clearly shown in the figures. They articulate with the antero-lateral corners of the interthyroid.

(*b*) *The Muscles.*

(i) *The muscles moving the larynx as a whole.*—It will have been obvious that there are certain of the muscles which are innervated by the ninth nerve which must act to carry the larynx to and fro with the hyoid apparatus. In addition to those, there are several small muscles which act to move the larynx in relation to the hyoid skeleton.

The M. protractor laryngei anterior arises from the dorsal surface of the lateral edge of the hyoid body in front of the larynx, and is inserted into the lateral curve of the ventral plate of the thyroid.

The M. protractor laryngei posterior arises from the hyoid cornu, along a length which is placed anteriorly to the posterior end of the larynx, and is inserted into the lateral curve of the ventral plate of the thyroid behind the line of insertion of the last muscle.

The M. abductor cornu hyoidei is an adjuvant to the last muscle. It arises from the ventral surface of the lateral edge of the anterior end of the hyoid body, below the area of origin of the M. protractor laryngei anterior, and is inserted along the outer and dorsal surfaces of the anterior end of the hyoid cornu. Acting alone, it would abduct the cornu but in conjunction with the M. protractor laryngei posterior it would ensure that that muscle pulled the larynx forward instead of merely abducting the cornu.

Attached to either side of the ventral surface of the anterior tip of the hyoid body there are two little rods of cartilage. These have been provisionally designated hypohyals. From each of them there arises a small sheet of muscle fibres which pass mediad and rostrad to be inserted into the deep surface of the thick mucosa of the under side of the anterior end of the tongue. The anterior end of the hyoid lies in the butt of the tongue. This muscle can only function to keep the hyoid in position relative to the ventral mucosa.

(ii) *The Intrinsic Muscles of the Larynx.*—The M. thyro-arytenoideus arises from the dorsal edge and lateral surface of the anterior portion of the thyroid cartilage and runs caudad and laterally to be inserted on to the arytenoid cartilage along a narrow area on the ventral surface close to the medial edge.

The M. aryteno-interhyoideus arises from the dorsal surface of the arytenoid cartilage over an area towards its posterior end. The fibres converge to be inserted into the edge and half the anterior surface of the interhyoid.

These two muscles, acting together, act as a constrictor laryngei.

The M. dilator laryngei arises from the whole of the ventral surface of the arytenoid cartilage not occupied by the last muscle, and is inserted on to the dorsal plate and contiguous surface of the postero-lateral part of the curve of the thyroid cartilage.

The M. thyro-interthyroideus arises from a small area alongside the fibrous junction of the two halves of the thyroid cartilage and is inserted into the posterior surface of the interthyroid cartilage close to the articulating base.

General Discussion.

The larynges of a number of other birds were dissected, but the Emu was selected for detailed description because its peculiar arytenoid cartilage has caused the almost complete separation of the Mm. aryteno-hyoideus and dilator laryngei and permits their clear description.

In the great majority of the birds the arytenoid cartilage presents its surfaces medially and laterally. The dorsal edge is usually convex whilst the ventral is straight, the cartilage is plate-like and curved, with the convexity laterally placed. All the intrinsic muscles take their origin from, or are inserted on, this surface, covering it completely.

In most cases the superficial muscles are the two constrictors, the aryteno-interhyoideus being placed medially to the other. The dilator is usually covered by these. The only departure of importance from the arrangement of the muscles as seen in the Emu is that it is not uncommon for the more superficial fibres of the dilator muscle to be continuous with those of the muscle of the other side, crossing behind the interhyoideus cartilage and superficially to the little thyro-interhyoideus muscle.

The laryngeal skeleton in all the examples examined presented the same cartilages as in the Emu. In several instances it was found that the interhyoideus cartilage was interposed between the two arms of the thyroid separating them completely. In not a few birds this little cartilage was ossified. No ossification was observed in any of the other cartilages.

SUMMARY AND REVIEW OF SAUROPSIDAN MUSCLES.*

THE MUSCLES OF THE MANDIBULAR SEGMENT.

Two ventral superficial constrictors are constantly present. The M. submentalis (Csv.1a) lies far forward between the mandibular rami ; it may be completely araphic so that its fibres extend uninterruptedly from one side to the other, as in the crocodiles. This is probably the primitive form of the muscle, since it resembles that of the fishes and amphibians, but if we are correct in regarding the raphic form as completely homologous with it, then this latter becomes the more important for our future studies, because there is no araphic muscle between the jaws of the Therians. In this connection an important feature of its location is that it always lies more deeply than the M. intermandibularis. Though, of course, the Ophidian muscle is not ancestral to any in the Theria, the form of the submentalis in the Snakes is of particular interest. It presents the extreme modification of the raphic form of the muscle, and the fact that the muscle has taken an almost antero-posterior direction in these reptiles must be accepted as evidence that such a modification was not an impossibility in the Theria. It is also important to recall that the M. submentalis is innervated by a branch of the fifth nerve independently of the M. intermandibularis.

The M. intermandibularis (Csv.1b) presents a division into anterior and posterior portions in some reptiles, but there is not the constancy in this subdivision that there is in the subdivision of the Csv.1 sheet as a whole, that is into Mm. submentalis and intermandibularis. Further than this the manner of this division of the M. intermandibularis is not one which may be regarded as inherited from the fishes or amphibians, but, rather, it should be regarded as a peculiar specialization in those reptiles in which it appears. This is important, because it might well be that if this subdivision of the M. intermandibularis had to be regarded as an inherited feature carried down from the elasmobranch fishes, then the expectation would be that such a feature would be portion of a muscular pattern so firmly established in the course of evolution that it should be looked for in further evolutionary changes in the Theria.

There is no doubt that the posterior of the portions of the M. intermandibularis in the majority of the Lacertilia closely resembles the posterior portion of the muscle in the Selachii. Lightoller, whose reptilian examples all presented this division of the muscle, designated the posterior portion " pars extramandibularis ", which term he had also applied to the posterior portion in the Selachians. This pars extramandibularis, however, is found only amongst the Lacertilia and in *Sphenodon*. Study of the development of several Lacertilians (*Physignathus*, *Tiliqua*, *Lygosoma*, *Varanus* and *Diporopherus*) reveals that the intermandibular muscle develops as a single sheet attached on each side to the medial face of the mandible throughout its length. Later, as the M. pterygoideus internus increases in bulk and extends its area of attachment below the posterior end of the mandible and then up over its external surface, the origin of the posterior portion of the M. intermandibularis is carried with it. This extramandibular origin for the muscle is, then, a peculiar, individual, ontogenetic and secondary character, of no phylogenetic significance.

THE MUSCLES OF MASTICATION.

Of particular interest was the discovery of most of the muscles of this group which were found in the Anura. The persistence of this pattern, of which we can now recognize some indication amongst the Selachian representatives, a further progress in certain of the bony fishes, and

* The avian conditions have been compared with the reptilian on the previous pages and in the following review they will not be included.

the very definite inception in the Urodela, must surely mean that it had by this time become a fixed pattern in the arrangement of the vertebrate muscles of mastication. We anticipate finding, at least, the main features of this pattern preserved in the Therian arrangement.

The M. retractor anguli oris of certain of the reptiles may be simply an individual peculiarity. On the other hand it must be recognized that it is not without fairly close resemblance to the protractor labii superioris of the bony fishes and of the anuran tadpole. In all these it is a superficial portion of the temporo-masseteric mass. It is, therefore, just possible that it is in reality the complete homologue of that muscle : beyond question it is completely analogous, but, though its derivation is the same, or at least very similar, it may yet be only a parallelism and not an homology.

THE MUSCLES OF THE HYOID SEGMENT.

The Superficial Constrictor (Csv.2).—Neglecting, for the moment, the anterior portion of this, which, as in the Amphibia, has been modified to act as a post-articular levator mandibulae, this sheet presents a fascicular continuum from the mid-dorsal to the mid-ventral line. In some reptiles the sheet is in two layers and the fibres of the deeper layer swing forward below the ramus of the lower jaw and extend some distance before being inserted into the superficial fascia superficially to the Csv.1b. The question arises in connection with these fibres, as to whether they are not a pars notognathica of the M. depressor mandibulae whose insertion has been transferred to the ventral fascia.

Behind the Cs.2 there is commonly an extensive superficial constrictor which is innervated by spinal nerves. In some reptiles the line of partition between the " M. Constrictor Colli Facialis " and the " M. Constrictor Colli Spinalis " is quite definite. In other forms it is impossible, by dissection, to define these muscles, one from the other. Experimental work, however, demonstrates that there is no portion of the two muscles with dual motor innervation.

The M. Depressor Mandibulae.—Lightoller's designations, partes cephalognathica and notognathica, have been used again for the divisions of this muscle, but his homologies for the two parts are not unreservedly accepted. The majority of the reptiles have both portions of the muscle well developed, but a large minority have only the pars cephalognathica. Certain of the Lacertilia which have only the pars cephalognathica present that division of the Cs.2 into two layers, and Lightoller has suggested that the deeper layer is the pars notognathica of this muscle, with a transferred insertion. The suggestion appears entirely reasonable. It is not uncommon for the pars notognathica to lie deep to the Cs.2 at its insertion. Whether this be the correct interpretation of this deeper portion of the Cs.2 or not, it is of particular interest to be able to record, quite definitely, that a portion of the superficial facial constrictor sheet has shown itself capable of taking up an almost antero-posterior direction. Such a modification, and such an extension forward of this sheet in a reptile prepares the way to the recognition of part of the sheet in the Theria.

With reference to the derivation of the pars cephalognathica, the discussion on the homology of the muscle in the Amphibia will apply equally to that of the Reptilia.

The M. interhyoideus.—This muscle has been recognized in the majority of the reptiles studied. Peculiarly, it is not present in either of the two Lacertilians studied by Lightoller (1939), although well developed in some other lizards. Its absence from *Tiliqua* and *Varanus* associated with the peculiar pars notognathica suggested, at once, that this latter was the M. interhyoideus. As against that identification it is to be remarked that the M. interhyoideus in the remainder of the Sauropsida arises further forward (from the angle of the jaw, Lacertilia, *Sphenodon* and Aves, or from the ceratohyoid, Chelonians) and is always inserted deep to the superficial sheets. The Crocodilia are peculiar, amongst the Reptiles, in that they have the primitive, expanded form of the muscle, arising and inserted deep to the superficial Cs.2.

THE MUSCLES INNERVATED BY THE NINTH NERVE.

It is not intended to review these muscles at length ; they have been introduced here only to stress the fact that experimental investigation failed to demonstrate any fifth nerve motor supply to the superficial longitudinal hyomandibular muscles. This work was carried out with *Tiliqua*, *Varanus*, *Chelodina* and *Gallus*. In every instance motor response to fifth nerve stimulation was obtained from the Csv.1b, and Csv.1a, if present, but none from the longitudinal muscle.

The importance of these observations will become apparent when we are discussing the homologies of the Digastric muscle.

REVIEW OF THE SAURIAN MUSCLES.

This review, originally written before the Therian work was commenced, has been rewritten because it was felt that the features which have been deemed of particular significance in their bearing on the interpretation of the Therian muscles should be drawn attention to at this stage of my work.

Unlike all the other reviews of the previous sections this one looks ahead instead of only backwards.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

Probably one of the most interesting and important results of the investigation of the muscles of the Reptilia has been the discovery that the M. submentalis is very constantly present. This muscle first made its appearance in the Selachii, where it was recognizable, in some forms only, as an anterior portion of the Csv.1 only in that its fibres were araphic. Throughout the Bony Fishes the muscle was found to be of very constant occurrence and always to lie deeply to the rest of the Csv.1. Again, in the amphibians, though but poorly developed in many instances, the muscle was very constantly present, its fibres were araphic, and it was situated deep to the remainder of the intermandibularis muscle. Here in the reptiles the muscle is always placed more deeply than the Csv.1b and also deep to the insertion of the ventral longitudinal muscles. Its fibres may be araphic or they may be inserted into a median raphe. They may run directly transversely or they may have a very marked caudal trend. This last feature is most marked in the Ophidians.

The M. intermandibularis does not present any division into anterior and posterior portions except in certain of the Lacertilia. In these particular forms the growth of the M. pterygoideus internus around and on to the external surface of the mandible has carried the origin of the M. intermandibularis up on to the outer surface of the same bone. This portion was regarded by Lightoller (1939) as being homologous with the pars extramandibularis of the Selachian muscle, and he accordingly applied to it the same designation. Whilst the homology is, in all probability, just as Lightoller believed, the extramandibular origin of the muscle is quite adventitious, certainly in these Lacertilia, and probably also in the Selachians, so that a separate designation appears undesirable, because it may tend to give undue weight to a secondary character which is not of phylogenetic significance.

More important than this occasional extramandibular origin is, apparently, the occasional marked antero-posterior direction taken by the fasciculi of the muscle. This is not regarded as phylogenetically important because it has been handed on to the Theria directly, but because it is definite evidence that the muscle was capable of being modified to take up the direction we believe it to have taken in the Therians. There is no doubt whatever that it is the Csv.1b which in certain of the reptiles has been thus modified, therefore, when, in the Theria, we meet a muscle which on other grounds may be regarded as a modified Csv.1b, the fact that its fasciculi take a direction nearly parallel to the ventral longitudinal muscles cannot be counted as evidence against its recognition as the Csv.1b.

THE MUSCLES OF MASTICATION.

Throughout the Sauria these present themselves in the same two groups we became familiar with in the lower Vertebrata, and more especially in the Amphibia. One group in front of and deep to the second and third rami of the trigeminal nerve (or behind those nerves as a result of their area of origin having been extended back along the base of the skull and/or the pterygo-palatine arch) and the second group superficial to those nerves.

This constant division of the muscles of mastication cannot be regarded in any other way than as an inherited character of phylogenetic importance and it will be thus that we must regard it in our study of the muscles in the Therians.

There has been a tendency in the past to homologize the Therian muscles with those of the lower Tetrapoda on the evidence of their origin and relation to one another without reference to the nerves (see especially Brock, 1938). We have now followed the varying relations of the muscles to one another and their varying areas of origin throughout the whole of the lower Tetrapoda and have found these to have extended beyond the limits set by such a basis of classification. The wide variation in the Aves, remembering particularly the cockatoos, and the Reptilia, with special emphasis on the crocodilian conditions, was of such a graduated kind

that we were always able to recognize, with confidence, not only the homologous groups but also the homologous muscles within those groups. Repeatedly the relations were such as would run counter to the suggested basis of classification of Brock.

It is, however, of interest to observe that this other basis of classification would be found to lead us, in the Therian studies, to the identification of the same two groups and individual muscles, as would the identification by reference to their relation to the nerves.*

MUSCLES OF THE HYOID SEGMENT.

Perhaps the most interesting and significant fact which emerges from the study of the hyoid muscles in the Saurians is that no settled plan of their relations to contiguous skeletal or muscular structures has been evolved. Amongst the component muscles, the pars cephalognathica of the M. depressor mandibulae is the only one which presents constancy of shape, origin, insertion and location generally. It was found that the fasciculi of the Csv.2 may run ventro-mediad without any obliquity, or they may take a marked rostrad inclination. They may be confined to the region of the neck behind the mandibles, or they may sweep forward between those bones for a considerable distance. They may be inserted in series with the Csv.1b or they may be inserted either deeply or superficially to that muscle. Finally the fasciculi may be arranged in a single or in a double layer. The muscle may arise as a continuous sheet from the dorsal fascia, or its anterior portion may arise more ventrally from other structures.

The M. interhyoideus may, apparently, be absent altogether or, in the alternative, be so modified and incorporated into other muscles that it is unrecognizable, or it may be well developed. When present it may arise from the ceratohyoid anywhere along its length, from the middle to the extreme distal tip, or being transferred to cranial structures, may arise from the otocrane, the quadrate or the post-articular piece of the mandible. It may be inserted superficially, in series with the Csv.1b and/or the Csv.2, into a mid-ventral raphe, or deeply to those muscles, either into a median raphe or to some part of the hyoid skeleton.

It is, moreover, of particular interest to observe that these variations are not characteristic of the several groups. Similar arrangements were observed in unrelated forms and dissimilarities in related.

In most instances it was not difficult to recognize the correlation of the observed arrangement of the muscles with an underlying modification of the skeletal structures or modification of the tongue. These characters in turn, however, were not, recognizably, of phylogenetic importance, but appeared to be individual variations.

The conclusions which one draws from these observations is that the Saurians have not yet reached stability of organization. They must still be in a plastic condition, and if this be so, then even more strongly must the same conclusion be expected to have applied to the Theriodontia.

If the musculature of the Theriodonts was in a plastic condition, then it would have readily been adapted to the profound modifications in the jaw articulation which took place in the evolution of Theria. It is of interest to note that in the course of those skeletal modifications the area of insertion of the only stable muscle, the pars cephalognathica, took up a completely new position. Thus was the way made clear for a complete rearrangement of the hyoid muscles.

Thus far we can carry our study of the comparative myology of the vertebrate head with a high degree of confidence that we have correctly identified the successive modifications of the primitive piscine muscles, but it is with far less confidence that we offer identifications of the components of the nine-twelve nerve-muscle associations.

Amongst the higher Tetrapoda the identification of these muscles is complicated by intracerebral nerve fasciculation (Kappers and others) and extracerebral nerve anastomoses, which have more or less completely obscured the original nerve-muscle pattern. The complications of this problem have recently been stated by Brock (1938). As she states, apparently identical muscles, functionally and topographically, " are quite distinct in origin and innervation ".

It is not proposed to discuss these muscles here ; that discussion will be taken up when we can include in it the mammalian muscles (see page 306).

* Lightoller's derivation of the M. pterygoideus from the levator maxillae superioris (L.1) of the Elasmobranchii has been discussed in a previous section. The evidence against the derivation appeared to be both positive and negative. Positive in that it appeared that one could definitely trace the evolution of the muscle from the levator labii superioris (add.) of the Selachians ; negative in that the M. pterygoideus as here derived appeared to be present in Bony Fishes as well as the M. levator maxillae superioris (the M. levator palatini) and that there appeared no explanation of the altered relation of the first ramus of the fifth nerve.