

# AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Leighton Kesteven, H., 1944. The evolution of the skull and the cephalic muscles: a comparative study of their development and adult morphology. Part III. The Sauria. Reptilia. *Australian Museum Memoir* 8(3): 237–269. [19 May 1944].

doi:10.3853/j.0067-1967.8.1944.512

ISSN 0067-1967

Published by the Australian Museum, Sydney

nature culture **discover**

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PART III. THE SAURIA.

THE REPTILIA.

INDEX OF THE ABBREVIATIONS USED ON THE ILLUSTRATIONS TO PART III.

A., Arytenoid cartilage; A-i., M. aryteno-interthyroideus; C.c.s., M. constrictor colli spinalis profundus; Chy., Ceratohyoid cartilage; C.la., M. constrictor laryngis; Clm., M. cleidomastoid; Csd.2a & 2b, The dorsal hyoid superficial constrictor muscle; Scv.1a & 1b, M. intermandibularis; Csv.1b', M. interhyoideus; Csv.2a & 2b, The ventral hyoid superficial constrictor muscle; Csv.2', The ventral hyoid superficial constrictor muscle; Csv.2'', Constrictor colli spinalis; C.thy., M. ceratohyoides; D., the dentary bone; Di.la., M. dilator laryngis; D.m., M. depressor mandibulae; D.m-m., M. depressor mandibulae mandibularis; G.g., Gasserian ganglion; G.gl., M. genio-glossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.g.l.a., M. interhyoideus; H.g.l.p. & H.g.p., M. hyoglossus posterior; Hy., The body of the hyoid; Hy.m.l. & Hy.mn., M. hyomandibularis lateralis and medialis; I.ch. & I.chy., M. interceratohyoides; I.hy., M. interhyoideus; Ins.mass., The area of insertion of the M. massetericus; I.t., Interthyroid cartilage; Ju., The jugal bone; L.d., M. latissimus dorsi; Lg.d., M. longissimus dorsi; Lv.Oc., M. levator bulbi oculi; Lv.q., M. levator quadrati; M. & Mm., M. massetericus; M.e., M. interhyoideus; M.chy., M. ceratohyoides; M.hy.h., M. hypohyalis; M.hy.m., M. hyomandibularis; M.q-m., M. quadratomandibularis; M.sp.pt., M. sphenopterygoideus; M.t., M. temporalis; Mx., The maxilla; Nv.d.p., The nerve to the M. depressor palpebrae; Nv.pt.int., The nerve to the M. pterygoideus internus; Nv', The ophthalmicus profundus branch of the fifth nerve; Nv'', The maxillary branch of the fifth nerve; Om., M. omohyoideus; P. & Pal., The palatine bone; P.c., P.n. & P.n.o., Partes cephalognathica and notognathica of the M. depressor mandibulae; Pila.ant., The pila antotica; P.l.a., M. protractor laryngis anterior; P.l.p., M. protractor laryngis posterior; Po., The postorbital bone; Pr.la., M. protractor laryngis; Pt.ex., M. pterygoideus externus; Pt.int., M. pterygoideus internus; Pt.m., M. pterygoideus medius; Pt.i.l. & Pt.i.m., Lateral and medial parts of the M. pterygoideus internus; Pt.p., M. pterygoideus posterior; Q.a.a., The anterior arm of the quadrate bone; Q.h., The articular head of the quadrate; Q.J., The quadratojugal bone; Q.m., M. quadratomandibularis; Q.p.a., The posterior arm of the quadrate; Qu., The quadrate bone; R.a.o., M. retractor anguli oris; Re.la., M. retractor laryngis; Sc., The scapula; S-m., M. sternomastoideus; S.m., The symphysis menti; Sp.pt., M. sphenopterygoideus; Sq., The squamosal bone; S.t., The sheath of the tongue; St., The sternum; St.hy., M. sterno-thyroideus; St.hy.m. & St.m., M. sterno-thyroideus medius; St.l., M. sterno-thyroideus lateralis; St.p., M. sternothyroideus posterior; T. & Temp., M. temporalis; T.a., M. thyro-arytenoideus; Th., the thyroid cartilage; Th.gl., M. thyro-glossus; Th.mn., M. thyro-mandibularis; Th.ph., M. thyro-pharyngeus; Thy. & Th.hy., M. thyro-hyoideus; Thy. & Th.c., the thyroid cartilage; Th.v., M. geniohyoideus; T.i., M. thyro-interhyoideus; T.m., M. thyromandibularis; T-m., M. temporo-massetericus; Tr., M. trapezius; Ty. & Ty.m., The tympanum; Ur., The urostyle.

ELASMOBRANCHIATA.	SAUROPSIDA
Csv.1a .. .. .	M. submentalis.
Csv.1b .. .. .	M. intermandibularis.
Dsv.1b <sup>2</sup> (p. extramandibularis)	Not a separate entity
Pterygoideus .. .. .	Mm. pterygoideus externus, medius and internus, and depressor mandibulae mandibularis
Quadratmandibularis ..	Mm. retractor anguli oris and temporo-massetericus, i.e. Mm. temporalis, massetericus and quadrato-mandibularis
Levator maxillae superioris ..	Mm. pterygo-quadratus, sphenopterygoideus and levator-quadrati
Csd.2a .. .. .	M. depressor mandibular pars notognathica
Csd.2b .. .. .	Mm. depressor mandibulae pars notognathica. Constrictor colli facialis (dorsal part)
Cpr.d2 (pars quadrato-hyoidea)	M. depressor mandibulae, pars cephalognathica
Levator hyoidei .. .. .	? Cerato-hyoideus capitis of <i>Chelodina</i>
Interhyoideus .. .. .	Interhyoideus
Csv.2a and 2b .. .. .	M. constrictor facialis ventral part

## 1. Lacertilia.

*Physignathus.*

(Figs. 130-134.)

This is a large Agamid lizard; the species here described, *P. lesueurii*, is very common along the streams in the neighbourhood of Bullahdelah, N.S.W. The eggs are deposited in early November along the elevated banks of the stream. As many as twelve have been found in the one hole. It would appear that all are deposited before the hole is filled in, for a lizard caught in the act of oviposition had laid eight and they were not covered at all. The hole is about six inches deep, and the top eggs are only one to two inches below the surface. The eggs hatch out during the following February. I have been fortunate in obtaining nearly two hundred of these eggs in various stages of development. Two full sets of twelve were obtained immediately after being laid, and these were hatched for definite periods and then fixed. Two eggs collected as soon as laid hatched out in 109 and 105 days.

My developmental stages are numbered 1 to 100, the numbers indicating actually or very closely the number of days hatched. The series is complete from day to day, for the period three days to twenty-six, thereafter the hatching period was determined by comparing the state of development of single specimens from groups already partly hatched, with this early series and letting the remainder hatch on; as sets comparable with those already dated came to hand I was able to extend my series with close approximation to accuracy.

## THE MUSCLES OF THE MANDIBULAR SEGMENT.

(Figs. 130-131.)

## THE DEPRESSOR PALPEBRAE INFERIORIS.

This is a very thin sheet of radiating fibres which arise from a restricted area of the fibrous wall of the orbit, behind and laterally to the investment of the optic nerve as it enters the orbit, and spreads out in the lower eyelid superficially to the tarsus.

*Innervation.*—This is by a fine branch of the ramus mandibularis V which is given off from the gasserian ganglion before the R. mandibularis and R. maxillaris separate, but it may be traced through the ganglion to the mandibular ramus. It passes directly forward to the orbit, deep to the lower part of the pterygoideus externus muscle.

The Mandibular ventral constrictor (Cv.) is in two separate sheets, a smaller deep, the Submentalis, and a more extensive superficial, the M. intermandibularis.

The Intermandibularis (Fig. 130, Cv.1b) arises from the inner surface of the mandible anteriorly and from the outer surface posteriorly. The origin from the inner surface commences one-quarter of the full length of the mandible behind the symphysis, and terminates a little way behind the mid-point of the length of the mandible. This line of origin is fairly high up along the inner surface and is interrupted by four slips of the thyromandibularis which, coming from a deeper position posteriorly, perforate the intermandibularis to gain insertions on to the inner edge of the narrow inferior surface of the mandible.

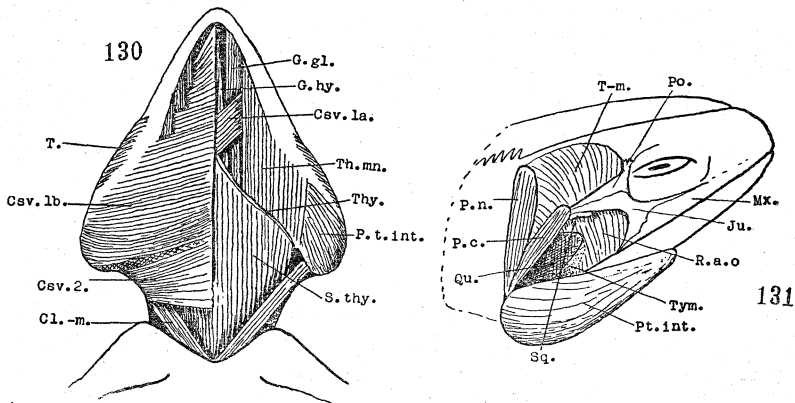
The origin of the muscle from the outer surface of the mandible commences where the other origin terminates and extends back to the tip of the post-articular process. In its anterior portion this origin is from the mandible between the M. pterygoideus internus and the insertion of the M. temporo-massetericus. Behind this the origin has been carried dorsally, by the swelling of the body of the former muscle and its insertion, to the inferior margin of the tympanic ring; behind this again the origin returns to the mandible between the depressor mandibulae above and the pterygoideus internus below.

*Innervation.*—This is by two separate branches of the R. mandibularis. After giving off the various branches to the masticatory muscles, the nerve enters the mandible on its inner side behind the coronoid process through Meckel's fossa, a small sensory branch being given off from its outer side just before it enters the canal. Inside the canal, after a short course, a branch is given off which passes down internal to Meckel's cartilage and then turns medially and perforates the bone. This is, apparently, entirely motor, and it spreads its twigs out over the ventral surface of the muscle; it issues from the mandible ventrally to the last section of the origin of the muscle from the internal surface of the jaw. This, which Lightoller designates the mylo-hyoid nerve, supplies the motor twigs to the greater part of the intermandibularis.

After giving off this motor twig the main nerve continues forward in the canal till it reaches almost to the anterior limit of the origin of the intermandibularis pars superficialis. Here two more twigs are given off in quick succession. The first is the larger; like the mylo-hyoid nerve, these also emerge from the bone ventrally to the origin of the muscle. The first of these two twigs is the lingual nerve, it perforates both superficial and deep intermandibular muscles and joins the hypoglossal nerve in the sublingual ganglion. The second may be termed the anterior mylo-hyoid nerve; it divides into two branches, the first of which spreads out on the surface of the superficial intermandibular muscle to supply the anterior portion. The other branch perforates the superficial muscle and spreads out on the ventral surface of the deep part of the muscle (*M. submental*) supplying its motor nerves.

The Submental (*Csv.la*) is a much smaller sheet of fibres which arise from the inner surface of the jaw dorsally to the origin of that portion of the superficial muscle which arises in front of the first perforation by the thyro-mandibularis.

*Innervation.*—This has been given in connection with that of the intermandibularis muscle.



Figs. 130-131.—*Physignathus*.

*Insertion.*—Both muscles are inserted into the mid-ventral raphe. The anterior fibres of the intermandibularis run sharply forward and are inserted almost at the symphysis, those immediately behind gradually, but rapidly, assume a directly transverse direction, and this is maintained to the posterior margin of the muscle. The fibres of the submental pass obliquely caudad, towards the mid-line and they are inserted into the same raphe deep to that part of the superficial muscle which arises in relation to the first, second and third perforations by the thyromandibularis. There is no indication of an interruption in the continuity of the superficial sheet immediately on either side of the mid-line.

The Retractor Anguli Oris is a muscle which, so far as I am able to learn, has not previously been recorded in any reptile. It is probably homologous with the massetericus minor of the Anura.

The muscle is a flat, roughly quadrangular, sheet which arises from the inferior edge of the squamosal bone and the inferior edge and deep surface of the jugal bone. The fibres pass directly ventrad to be inserted into the tissues of the lips at the angle of the mouth. There is no merging of this muscle with the underlying *M. temporo-massetericus* or *pterygoideus externus* muscles.

*Innervation.*—This is by a branch of the *R. mandibularis V* which reaches the muscle by passing rostrad and ventrad, deep to the temporo-massetericus, and then, turning laterad and rostrad between that muscle and the *pterygoideus externus*, it turns caudad around the anterior surface of the temporo-massetericus, to reach the deep surface of the retractor anguli oris.

The Temporo-massetericus is a very massive muscle which arises from the anterior surface of the quadrate, the anterior and dorsal surfaces of the parotic process, the anterior membranous wall of the auditory meatus, the lateral wall of the skull, both inner and outer surfaces of the posterior arm of the parietal and of the little post-temporal plastered to its ventral edge laterally, and finally from the upper part of the inner surface of the jugal and inner surface of the posterior arm of the post-orbital. The mass of the muscle fills almost the whole of the superficial area of the supra-temporal space, only a quite small area of the *pterygoideus externus* being visible

in the antero-medial corner of the space. The whole of the fibres converge to be inserted on to the superior edge and outer and inner surfaces of the mandible from the tip of the coronoid process almost back to the joint. The insertion on to the outer and inner surfaces extends about half-way down the depth of the mandible; the insertion on to the coronoid tip is in part effected by the tendon of the pterygoideus internus as was seen in some urodeles.

*Innervation.*—This is by several short branches which leave the R. mandibularis V just after that nerve separates from the ganglion.

The rest of the masticatory muscles form an exceedingly complicated and powerful pterygoid muscle which is not divided into parts by any definite cleavage planes. It is, however, necessary to describe it in three portions, anterior, medius and posterior. The Anterior, Pterygoideus externus, arises from the side of the body of the parietal and from the posterior surface of the post-orbital arm of that bone and from the greater part of the length of the epipterygoid bone. These fibres are gathered to a central tendon by which they gain an insertion on to the coronoid process of the mandible and the inner surface below it. This latter insertion is behind the coronoid process and also just behind the ventral process of the pterygoid and transverse bones.

This portion of the muscle corresponds very closely, and is doubtless homologous with the anterior portion of the pterygoid muscle of the amphibians.

The median portion, Pterygoideus medius, arises from the outer surface of the posterior process of the pterygoid bone and from the lower half of the anterior membranous wall of the auditory meatus as well as from the lower part of the anterior surface of the quadrate. These fibres are all inserted directly into the inner surface of the mandible over its full depth behind the coronoid and below the insertion of the temporo-masseteric fibres inserted on the inner side of the mandible. There is no clear plane of separation between these and the more superficial temporo-masseteric fibres.

The posterior portion is the homologue of the muscle which, in *Sphenodon*, Edgeworth designates the pterygo-mandibularis, and which has been described in various reptiles as the pterygoideus internus. It is completely homologous with the pterygoideus internus of the Caecilians.

The Pterygoideus internus muscle arises by an exceedingly strong band of tendon from the posterior surface of the os transversum, the descending process of this and the os pterygoideum, and from the margin of the last bone between the process and the articulation with the epipterygoid bone. This band widens rapidly as it passes back, forming a strong tendinous investment for the ventral and lateral surfaces of the muscle. Its lateral edge is much thickened and winds round the ventral edge of the mandible caudad, ventrad, and laterad, vertically below the coronoid process, without becoming bound to the mandible. A few of the most anterior and superior of the fibres of the muscle arise directly from the posterior surface of the descending process of the os pterygoideum above the origin of the tendon; the whole of the rest arise from the upper surface of the tendinous sheathing. They are inserted on to both inner and outer surfaces and ventral edge of the mandible. On the outer side there is no insertion in front of the joint, but internally the insertion commences immediately behind Meckel's fossa. The fibres thus inserted are intimately fused with those of the pars anterior, and those inserted into the inner surface of the mandible behind them are in similar relation to the pars medius. Behind the joint facet the mandible is almost entirely enswathed by the muscle, only the extreme tip, where the depressor mandibulae is inserted, not being so covered.

There yet remains for description a portion of this muscle which must act as a depressor of the lower jaw, Depressor mandibulae mandibularis. These fibres arise from the posterior surface of the quadrate along the superior margin of the articular surface, actually from the upper part of the joint capsule. They pass directly back to be inserted into the superior edge of the mandible in front of the insertion of the (hyoid) depressor mandibulae. On the inner side the origin of these fibres is continued ventrad and rostrad on to the inner surface of the posterior arm of the os pterygoideum and they gradually assume a more vertical direction as their point of insertion is also carried forward along the mandible, and ultimately they are merged with the posterior portion of the temporo-masseteric muscle.

*Innervation.*—The whole of the muscles of mastication are innervated by branches of the R. mandibularis V which leave the nerve close to the ganglion. That to the pterygoideus internus runs down parallel and very close to the main inferior mandibular branch and internal to it. Just before the main nerve enters Meckel's fossa this motor nerve turns caudad and mediad. It is a nerve of some size and was traced back through the muscle for a considerable distance.

The Pterygo-quadratus muscle arises from a fine, but very strong, ligament which is attached above to the skull immediately below the incisura prootica and below to the pterygoid bone immediately behind the articular facet for the lower end of the epipterygoid. This ligament lies medially to and parallel with the epipterygoid. This muscle also arises from the lower edge of that flange of the prootic bone which forms the upper part of the lateral wall of the tympanic recess. This latter origin is confined to a very short length of the edge below and behind the incisura prootica. The fibres pass caudad, parallel to the posterior process of the pterygoid bone, and are inserted on the upper edge and inner surface of that process. The insertion extends back to the capsule of the pterygo-quadratus articulation.

*Innervation.*—This is by a twig from the Vth nerve, given off from the infero-posterior surface before the nerve breaks up into its three main rami.

No trace was found of a separate Spheno-ptyergoideus muscle, though it was sought for in several specimens.

The function of this muscle is difficult to understand; both at its origin and insertion it is attached to rigid structures. The ligament of origin forms the lateral margin of the anterior aperture of the eustachian canal, but it does not seem that contraction of the muscle could affect the size of the aperture. The inner surface of the muscle in its upper one-third is covered by the tympanic mucosa, but as the muscle is straight from origin to insertion its contraction cannot change the size of the tympanic chamber.

#### THE DEVELOPMENT OF THE MUSCLES OF THE MANDIBULAR SEGMENT.

(Fig. 132.)

At stage 15 the ventral constrictor sheet is represented by a band of muscle fibres which extend along the middle third of the length of the short flexed Meckel's cartilage. These arise on each side from the periosteum of the cartilage and pass directly towards the mid-line, but do not reach their antimeres; a gap nearly one-quarter of the distance between the two cartilages is left between the muscles. The separation of this sheet into deep and superficial layers is apparent in places only; for the rest it appears as a single layer.

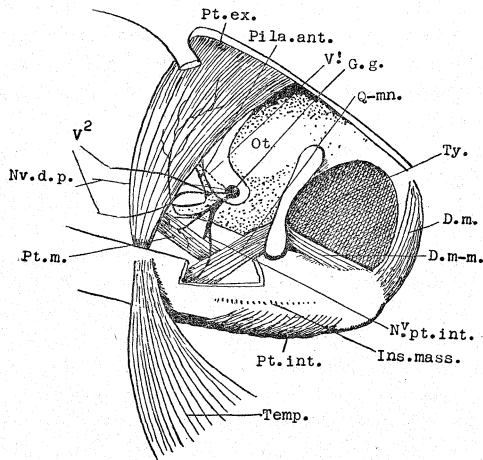


Fig. 132.—*Physignathus* embryo, stage 80.

At Stage 20 the sheet is a little longer antero-posteriorly, the fibres reach nearer the mid-line, and the separation into two layers has taken place completely. The deeper layer extends a little anteriorly to the superficial but does not extend quite so far back.

At stage 50 the superficial sheet extends back almost to the posterior end of the cartilage and it is to be noted that its origin throughout is from the cartilage. At this stage the origin of the muscle is perforated by the thyro-mandibularis in four places. The pterygoideus internus lies still entirely above the ramus of the jaw and to its inner side.

At 73 the pterygoideus internus has extended round below and laterally to the jaw and now is inserted on to the outer surface of the angular and surangular, and it has pushed the origin of the intermandibularis up on to the outer surface of the surangular and articular above it.

At 100 these two parts of the Csv.1 muscle are as in the adult.

The development of the adductor muscles of the lower jaw is particularly interesting, in as much as the later stages indicate very clearly the influence of the amphibian ancestry.

At 20 the primordium of these muscles consists of a "V"-shaped, exceedingly cellular, faintly striated and somewhat gelatinous mass of tissue. The point of the "V" is at the base of the ascending process of the palato-quadrate but lateral thereto. One arm extends dorsad and caudad behind the gasserian ganglion and the R. mandibularis V, and this is the larger arm. The other extends directly dorsad in front of the above nerve and ganglion but deep to the R. maxillaris V. It was quite impossible by dissection to demonstrate that the upper end of either arm was definitely attached. The posterior arm at its upper end lay upon the otic capsule; the anterior reached up to the taenia marginata in front of the capsule.

It is possible that a swelling seen on the anterior edge of the anterior arm was the primordium of the depressor palpebrae inferioris. This suggestion arises from the fact that it is assumed that the muscle in question is one of the mandibular muscles because it is innervated by the Vth nerve. I have been unable to find any stage in which the muscle was distinctly connected to the other muscles of the segment.

The insertion of the base of the two arms was into the perichondrium of Meckel's cartilage at the point where the coronoid process subsequently develops.

At 35 the muscles had increased in size and there was found a projection from the anterolateral and ventral end of the anterior portion. This extends back some little distance between the posterior end of Meckel's cartilage and the posterior end of the palato-quadrate; it does not reach the cartilage of the lower jaw, but appears to end freely. This is the primordium of the pterygoideus internus, and its development is very much as Edgeworth (1931) describes the development of the muscle in *Sphenodon*.

The actual derivation of the several very definite components of the adult musculature, which are found in later stages, is exceedingly difficult to follow. The complete separation of the muscles by the rami of the fifth nerve, however, permits one to assert with a high degree of confidence that the three pterygoid muscles and the depressor mandibulae mandibularis are developed from the anterior arm and the rest of the muscles from the posterior.

At stage 80 (Fig. 132) there are no less than eight quite distinct muscles developed, most of which are already indicated at 50.

The Retractor Anguli Oris is a small muscle, relatively, just as in the adult.

The Masseter is exposed by the removal of the last muscle. This is a flat sheet of muscle which arises from the lower margin of the supratemporal arch just in front of the tympanum, and passes ventrad with an inclination rostrad, to be inserted on to the outer surface of surangular above the upper margin of the pterygoideus internus. This muscle is very readily demonstrable. One detaches the insertion and the whole sheet peels off the subjacent temporalis without the derangement of a single fibre on the contiguous faces of the two muscles.

The outer surface of the Temporalis is exposed by the removal of the masseter. Removal of the posterior boundary of the orbit exposes the anterior margin of the temporalis muscle, and the maxillary nerve may then be seen entering the orbit from beneath the margin. Using the nerve as a guide, the fibres are turned back and the muscle gradually detached from its origin. When the gasserian ganglion is exposed, the deep surface of the muscle is reached, and, turning this outward, the detachment of the muscle is completed. It is now seen that the muscle arises from the upper portion of the inner surface of the supratemporal arch, both surfaces of the posterior process of the parietal bone, the outer surface of the upper part of the otic capsule, and the upper part of the anterior surface of the quadrate. It is further found that, where the muscle is in contact with the pterygoideus externus in front, the two separate quite cleanly, and that at no other place is there any fusion between the deep surface of this and any subjacent muscle. When the temporalis is thus reflected outward and forward its two, relatively large, motor nerves are put on the stretch and brought very plainly into view. They leave the R. mandibularis V just distal to its emergence from the ganglion. The muscle is inserted on to the inner surface of the surangular, above Meckel's fossa.

The Quadrato-mandibularis is a quite separated little group of short muscle fibres which arise from the lower end of the quadrate across the anterior surface just above the articular end, and run forward and ventrad to be inserted along the top of the mandible and down each side a little way a short distance in front of the joint.

The Pterygoideus Externus arises from the posterior surface of the post-orbital bar, from the lower edge of the anterior end of the posterior process of the parietal, and from the greater part of the length of the epipterygoid bone. The fibres are inserted into a tendon within the depth of the muscle, and the lower end of the tendon is inserted into the tip of the coronoid and into the inner surface of the coronoid bone, in front of Meckel's fossa.

The most anterior fibres of the temporalis are inserted into this same tendon, in a manner precisely similar to that observed in the Urodele, *Necturus*.

The Pterygoideus Medius is a small muscle which arises from the outer surface of the posterior process of the pterygoid bone and is inserted into the articular bone below Meckel's fossa. This muscle is almost in contact with the quadrato-mandibularis posteriorly, but a small gap separates their margins.

The Pterygoideus Internus arises from the os transversum and pterygoid bone as in the adult, and is inserted into the articular bone below the insertion of the pterygoideus medius and also, on the outer side of the mandible, into the articular, angular and posterior portion of the surangular below the insertions of the Mm. massetericus, quadrato-mandibularis, depressor mandibulae mandibularis and depressor mandibulae muscles. The whole of the fibres of the muscle are horizontal in direction, almost at right angles with the other muscles.

The Depressor Mandibulae Mandibularis is quite distinct from the surrounding muscles. It arises from the upper margin of the posterior wall of the Q.-M. joint capsule and passes back to be inserted into the dorsal edge of the post-articular process of the mandible in front of the insertion of the depressor mandibulae. In its proximal half this muscle lies in the floor of the tympanic cavity, and this half may be clearly seen through the transparent tympanic membrane after the removal of the skin covering that membrane. This muscle may well be the precursor of the M. depressor mandibulae of the Monotremes.

#### THE COURSE AND RELATIONS OF THE RAMI OF THE FIFTH NERVE.

The Gasserian ganglion lies upon the outer surface of the membrana spheno-obturatoria immediately in front of the otic capsule. Apparently only two rami leave this ganglion, but it actually lies in a pocket of the dura which is extruded through the incisura prootica, and the R. ophthalmicus profundus turns inward and runs forward on the inner surface of the membrana spheno-obturatoria quite a distance before perforating it to enter the orbit.

The R. maxillaris leaves the anterior surface of the ganglion, carrying a short diverticulum of the dura with it. After a very short course laterad and rostrad against the posterior surface of the pterygoideus externus, it perforates the diverticulum and bears a ganglion. From the distal side of the ganglion two branches spring. One turns ventrad and rostrad, the other rostrad, both passing externally to the M. pterygoideus externus.

The nerve to the M. depressor palpebrae inferioris leaves the anterior surface of the gasserian ganglion distal to the R. maxillaris and runs forward deep to the M. pterygoideus externus.

Immediately the R. mandibularis emerges from the dural sheath, the two nerves to the M. temporalis are given off from the dorso-medial surface of the nerve, then the nerve to the M. pterygoideus externus leaves the anterior surface; and at the same level, from the posterior face, the nerve to the M. pterygoideus medius is given off. The main ramus now continues ventrad against the deep surface of the M. temporalis, and a branch, apparently sensory, is given off which perforates the Mm. temporalis and massetericus and reaches the subdermal tissues of the lips at the angle of the mouth. Immediately after this the large nerve to the M. pterygoideus internus is given off from the ventro-medial surface and thereafter the main nerve enters Meckel's fossa. Its further course has been described as far as the departure of the anterior mylo-hyoid and the lingual nerves. These, it will be remembered, did not pass beneath Meckel's cartilage as did the mylo-hyoid nerve itself. After the two anterior nerves are given off the main nerve continues on its way along the upper edge of Meckel's cartilage within the mandible, diminishing as each of three more branches perforate the inner wall of the canal, and the terminal branch escapes in similar manner.



## THE MUSCLES OF THE HYOID SEGMENT.

(Figs. 130-131.)

The Superficial Constrictor (Csd.2 and Csv.2) is continuous from the mid-dorsal to the mid-ventral line. The origin is from the dorsal intermuscular septum commencing just behind the transverse level of the posterior margin of the *M. pterygoideus internus* and extending thence for a distance equal to about one-third of the antero-posterior length of the head. The insertion, slightly wider than the origin, is into the mid-ventral raphe. The anterior fibres are parallel to the posterior fibres of the *pars extramandibularis* of *Csv.1b*, but are separated from them by a definite interval. Dorsally these fibres are similarly separated from the *pars notognathica*.

*Innervation.*—The anterior fibres are innervated by a small branch from the seventh nerve, which reaches the deep surface of the muscle behind the posterior margin of the *pars notognathica*. The greater part of the muscle is innervated by two nerves which come from the first two spinal nerves. The ventral rami of these two nerves join below the exit of the second, without, as far as I can see, giving off any branches. The compound nerve passes laterally and ventrally between the lower margin of the median and superior margin of the ventral trunk muscles; it then turns laterad and appears behind the posterior-superior margin of the sterno-cleido mastoid muscle and immediately breaks up into several branches. One of the largest of these reaches the deep surface of the *Cs.2* and again divides into three or four branches. Two of the larger of these penetrate the muscle and are probably sensory nerves. The remainder terminate in the muscle itself. Experimental work reveals that the spinal nerves do not supply motor fibres to the muscle.

The Depressor Mandibulae presents *partes cephalognathica* and *notognathica* very similar to those parts of the muscle in the *Anura*.

The *Pars Cephalognathica* arises from a small area of the squamosal and from the perimysium of the *M. temporo-massetericus* above and behind the tympanum. From this origin the fasciculi pass ventrad and caudad to be inserted into the post-articular process of the mandible in front of the insertion of the *pars notognathica* and above the insertion of the *M. pterygoideus internus*, and behind that of the depressor mandibulae mandibularis muscle. The area of origin is relatively small and all the fasciculi pass uninterruptedly from origin to insertion, except for a few posterior fibres which are fused with those of the *pars notognathica* just above the mandible.

The *Pars Notognathica* is similar to the *pars cephalognathica* but is larger; it arises from a short length of the edge of the posterior process of the parietal bone close to the body of the bone, from a small pit lateral to that for the ligamentum nuchae (dorsal intermuscular septum) on the back of the body of the parietal, and from a short length of the dorsal intermuscular septum just behind this. The direction of the muscle is ventrad, caudad and slightly laterad, to its insertion on to the extreme dorso-posterior tip of the post-articular process of the mandible.

Superiorly the posterior corner of the *M. temporo-massetericus* lies between the two parts of this muscle; inferiorly they are side by side.

*Innervation.*—This is by separate branches of the VIIth nerve which reach the muscle on its deep surface.

## THE MUSCLES OF THE BRANCHIAL SEGMENTS.

(Figs. 133, 134.)

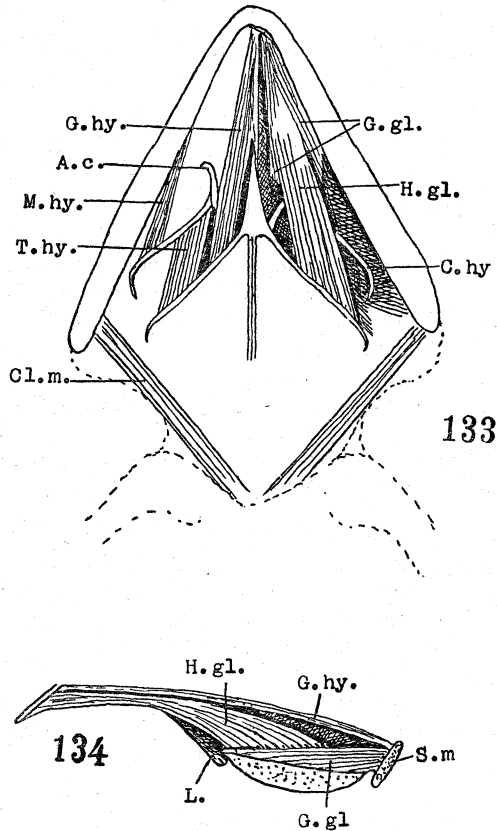
## THE HYPOBRANCHIAL SPINAL MUSCLES.

The Hyoid skeleton consists of (1) a median and anterior *pars entoglossus* of fibrocartilage, (2) a urohyal, also of fibrocartilage and double throughout its length, (3) paired slender hypohyals which are firmly attached, not jointed, to the median elements where urohyal and *pars entoglossus* join, and whose direction is laterad and rostrad from their origin, so that their distal ends come to lie close to the inner surface of the mandible a little in front of the middle of its length, (4) paired stylohyals attached by fibrous tissues to the distal end of the hypohyal and extending thence caudad nearly parallel to the ramus of the jaw, (5) paired thyrohyals which are articulated to the median elements immediately behind the attachment of the hypohyal and pass caudad and laterad, with a sinuous curve concave outward first and then concave inward, to terminate a little in front of the transverse level of the posterior end of the mandible and a short distance medially thereto.

In the adult lizard, when the superficial constrictors have been removed from the neck, and ventral to the hyoid skeleton, there appears to be a single, relatively thick, sheet of muscle

arising from the clavicle, episternum and antero-ventral margin of the epicoracoid and passing thence to be inserted along the posterior edge of the thyroid cartilage. When, however, in the emergent embryo (stage 100) the muscle is freed from its origin, commencing at the lateral margin, a lateral and superficial portion of the sheet may be peeled from the rest without breaking any intermingled fibres. It is now found that in such juvenile specimens there are three separate sterno-thyroid muscles and, moreover, it is found that these three muscles may be demonstrated in the adult.\*

The Sterno-thyroideus Lateralis muscle arises from the ventro-medial edge of the epicoracoid and from the episternum and clavicle for the greater part of the length of the latter. This origin is in part by the intermediation of the connective tissues superficial to the pectoral girdle and in part directly from the clavicle itself. The origin of the sterno-mastoid muscle is superficial to the medial portion of the origin.



Figs. 133-134.—*Physignathus*. Fig. 133. The deeper ventral muscles.  
Fig. 134. Median section of the tongue and floor of the mouth.

The insertion is into the posterior edge of the thyroid cartilage along almost its full length.

The Sterno-thyroideus Medialis is a narrow strip of muscle which arises from the clavicle and episternum to one side of the mid-line and passes forward to be inserted into the base of the urohyal and a very short length of the thyrohyoid cartilage alongside of it.

These muscles are placed so closely side by side that, in the adult no line of separation is obvious. The origin of the sterno-mastoid muscle is placed superficially to the contiguous margins.

\* Although partly fused there can be no doubt that these three muscles are the same as those more completely defined muscles found in this situation in *Varanus* and other reptiles.

The medial muscle and portion of the lateral muscle are visible between the two sterno-mastoid muscles and behind the posterior margin of the Csv.2, whilst the posterior end of the lateral muscle is visible lateral to the sterno-mastoid and behind the Csv.2 when the skin is removed.

The Sterno-thyroideus profundus muscle is a thin sheet of fibres which arise from the anterior margin of the clavicle along its median two-thirds under cover of the origin of the above superficial muscles. From this origin the fibres pass rostrad, the lateral fibres with a laterad inclination, to be inserted along the posterior edge of the thyroid cartilage under cover of the origin of the same muscles. In the adult it is difficult to separate the superficial and deep muscles, but in the emergent embryo and slightly earlier developmental stages there is a definite difference in the direction of the more lateral fibres. Those of the superficial muscle have a slight inclination mediad from behind, whilst those of the deep muscle are inclined laterad. The deep muscle lies against the ventral surface of the trachea along its median edge and below the mucosa of the pharynx laterally.

The Thyro-mandibularis muscle arises from the lateral three-quarters of the length of the anterior edge of the thyroid cartilage and is inserted into the inferior edge of the mandible in front of the M. pterygoideus internus and into the outer surface of the mandible between this muscle and the portion of the M. temporo-massetericus, under cover of the insertion of the Csv.1b. Anteriorly, as already mentioned, this muscle perforates the Csv.1b in three of four slips to gain its insertion.

The Genio-hyoideus is placed on the same plane and lies medially to the thyro-mandibularis muscle. The origin is from the medial one-quarter of the anterior edge of the thyroid cartilage. Quite separate from its fellow of the opposite side at its origin, the muscle inclines towards the mid-line and about half-way forward of its length becomes fused with its fellow, the two being inserted together by a short narrow tendon into the back of the symphysis menti.

The Hyo-glossus muscle is a flat muscle which arises, under cover of the last two muscles, from the greater part of the length of the same, anterior, edge of the thyroid cartilage. It runs forward superficially to the thyro-hyoideus, as far as the stylo-hyal and then turns dorsad to end in the tissues of the tongue, reaching far forward.

The Thyro-hyoideus muscle arises from the same edge of the same cartilage under cover of the hyoglossus and passes rostrad to be inserted into the posterior edge of the stylohyal. This is a thin flat muscle.

The Hyo-mandibularis muscle arises from the inner edge of the mandible in company with the insertion of two of the perforating slips of the thyro-mandibularis, and passes caudad to be inserted into the anterior edge of the stylohyal laterally to the insertion, on the posterior edge, of the thyro-hyoideus muscle. The slips of origin of this muscle perforate the Csv.1b in the same manner as the slips of origin of the thyro-mandibularis muscle.

The Genio-glossus arises from the anterior end of the inner surface of the mandible, and its fasciculi pass caudad and dorsad at varying angles to be inserted into the tissues of the tongue. The greater part of these are inserted laterally to the hyoglossus muscle but a large minority are inserted medially to that muscle, which thus, as it were, splits this muscle into partes medialis and lateralis.

#### *Amphibolurus.*

This is an agamid lizard, allied to *Physignathus*. As was anticipated, its musculature is essentially similar to that just described. The only point of difference worthy of note is that the M. sterno-thyroideus profundus is very completely differentiated from the superficial muscle laterally. Its median fibres run directly antero-posteriorly and are fused with the deep surface of the medial superficial muscle. The rest of the fibres incline more and more laterad till the most lateral pass almost directly laterad. This lateral direction is made possible by the greater posterior extension of the thyroid cartilage. The lateral limit of the origin of the sterno-thyroideus lateralis lies deep to the insertion of the anterior fibres of the M. trapezius.

#### *Anolis.*

*Anolis* is one of the Iguanidae. I have for study seven specimens of the genus; three each of *A. carolinensis* and *A. cristatellus*, and one of an unnamed species. They are all so closely similar that no differences worthy of note were observed.

## THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1 presents superficial and deep portions as in the agamid lizards and, as in those, the superficial is divisible into intermandibular and extramandibular portions.

The muscles of mastication are intermediate in their state of differentiation between that of the adult and young *Physignathus*, and in addition one other muscle is present.

The Retractor Anguli Oris muscle is as in the Agamidae.

The Mm. temporalis, massetericus and quadrato-mandibularis are very completely fused.

The Depressor mandibulae mandibularis is not recognizable.

The three pterygoid muscles are well differentiated. The M. pterygoideus externus and internus are essentially as in the young *Physignathus*, the pterygoideus medius rises higher on the anterior portion of the otic capsule than in that form.

The Pterygo-quadratus muscle is a small triangular sheet of fibres which arises by its broader end from the posterior edge of the processus pterygoideus and from the skull immediately below the incisura prootica and extends horizontally caudad and slightly laterad to be inserted into the infero-medial corner of the quadrate. This muscle lies along the outer side of the eustachian passage and may well be the forerunner of the tensor tympani muscle of the mammals.

*Innervation.*—This is by a twig from the Vth nerve given off before that breaks up into its component rami.

The Spheno-pterygoideus muscle is a fine round strand of fasciculi which arise from the skull above the incisura prootica and pass directly ventrad to be inserted into the pterygoid bone immediately posterior to the articular facet for the epipterygoid bone.

*Innervation.*—This is by a twig from the ramus mandibularis V which leaves the nerve very close to its departure from the ganglion.\*

## MUSCLES OF THE HYOID SEGMENT.

The Csv.2 is essentially as in the Agamidae, but the peculiar posterior prolongation of the urohyal passes superficially to the muscle, issuing from beneath the posterior margin of the pars extramandibularis of the Csv.1b.

The Depressor Mandibulae is not divided into partes noto- and cephalo-gnathica; the origin of the muscle from the mid-dorsal intermuscular septum extends back almost to the anterior edge of the epicoracoid. The most posterior fibres run forward superficially to the pterygoideus and to the Csv.1b and terminate in a membrane which gives them insertion into the outer surface of the mandible in front of the M. pterygoideus internus.

The Hypobranchial Spinal muscles are essentially similar to those of the Agamidae.

*Basiliscus.*

This is another of the Iguanidae. It is a much larger lizard than the species of *Anolis*, but unfortunately I have only the head and part of the neck of a single specimen. This is perfectly preserved, and permits me to describe with confidence as much of the muscles as are present, but the absence of the anterior end of the pectoral girdle renders the account somewhat incomplete. So far as the material permits, one is enabled to say that there is a very close resemblance to the smaller iguanids just described. The urohyal, however, is not prolonged posteriorly and does not become superficial to the Csv.2.

## THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a (M. submentalis) is continued right forward to the symphysis menti; anteriorly its fibres are directly transverse, but not araphic; further back they incline caudad and mediad beneath the anterior portion of the Csv.1b, M. intermandibularis.

The muscles of mastication are essentially similar to those of *Anolis*, the anterior fibres of the pterygoideus medius being fused with the deep fibres of the pterygoideus externus. This last muscle is remarkably developed. The parietal bone is produced backwards into a large laterally compressed supra- and post-occipital crest. From the side of this crest the pterygoideus externus muscle gains an additional area of origin, so that it projects back beyond the skull proper and high above the general contour of the head.

\* There is little doubt that these two muscles represent the spheno-pterygo-quadratus mentioned by Edgeworth (1931, p. 804). It is, however, quite erroneous to describe them as a single muscle in the Iguanidae; their fibres are almost at right angles to one another.

## THE MUSCLES OF THE HYOID SEGMENT.

As in *Anolis*, the Csv.2 is somewhat more extensive than in *Physignathus*.

The Depressor Mandibulae is smaller than that of *Anolis*; its origin does not extend nearly so far caudad along the mid-dorsal line.

Actually the whole of the dorsal origin of the muscle, that from the mid-dorsal septum, lies under cover of the posterior extension of the pterygoideus externus muscle. The mid-dorsal septum actually extends forward to the usual terminal point at the back of the parietal bone ventrally to, and attached to, the ventral edge of the supra-occipital crest. It is not possible to recognize any division of the muscle into partes noto- and cephalo-gnathica, nor are any of the fibres inserted elsewhere than into the postarticular process of the mandible.

The Hypobranchial Spinal muscles are essentially as in *Physignathus*.

*Chameleon.*

(Fig. 135.)

Of this genus I have a single perfectly preserved specimen of *C. etienni*, from the Belgian Congo.

## THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a (M. submentalis) is small, as in *Physignathus*.

The Csv.1b is represented by the pars intermandibularis only. The muscle arises from fairly high up on the inner surface of the mandible. Its posterior margin is just in front of the anterior end of the pterygoideus internus muscle as that curls around the lower edge of the mandible. The muscle is not perforated by any slips of the hypobranchial spinal muscles.

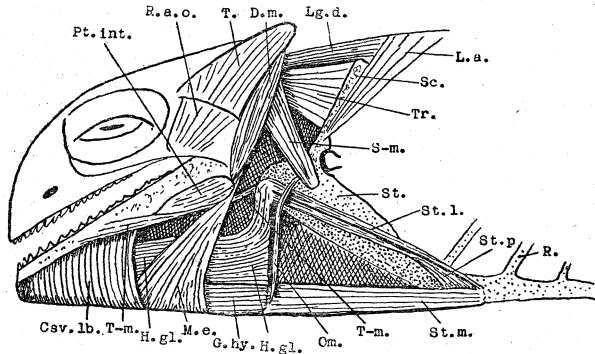


Fig. 135.—*Chameleon.*

The muscles of mastication are essentially as in the Agamidae. The occipital crest in *Chameleon* is more complex than that of *Basiliscus*. The median element is formed mainly from the parietal, but in part also from the supraoccipital, and there is, on each side, a supporting flying buttress formed by a posterior prolongation from the squamosal bone. The muscle that fills all the space between the components of the crest on each side is, not the pterygoideus externus (which is actually reduced in size), but the temporo-massetericus.

Pterygo-quadratus and Spheno-ptyerygoideus muscles are not definable.

## THE MUSCLES OF THE HYOID SEGMENT.

The post-cephalic constrictor sheet (Cs.2) appears to be divided into two portions. Behind the depressor mandibulae there is a relatively broad, and exceedingly thin, diaphanous sheet of fibres which arise from the dorsal septum and pass right to the mid-ventral line. This sheet appears to be innervated only by fine twigs from a branch of the VIIth nerve which reaches the muscle from beneath the posterior margin of the reduced depressor mandibulae. Behind this diaphanous sheet is a second. This arises as a narrow band of fibres from the subdermal surface of the coracoid just behind the insertion of the M. trapezius. After a very short course ventrad, this band of fasciculi widens out, the fasciculi becoming separated, and this diverging of the fibres is continued to the mid-ventral line where they form a relatively broad sheet in front of the pectoral girdle.

The innervation of this posterior sheet appears to be entirely by fine twigs from the first two spinal nerves.

This is possibly a constrictor colli spinalis, portion of the panniculus carnosus, similar to that of the Chelodina.

The Depressor mandibulae is quite a small muscle. It arises from the back of the quadrate and from the postero-inferior edge of the "flying buttress" formed by the squamosal. There is no trace of any division of the muscle into two parts.

*Innervation* is by the VIIth nerve.

Musculus interhyoideus arises from the perimysium on the lower part of the posterior surface of the depressor mandibulae. At its origin the fibres of the muscle are gathered into a flat strand which passes ventrad behind the depressor mandibulae, then ventrad and rostrad behind and partly under cover of the pterygoideus internus, and finally ventrad and mediad. As soon as the fibres pass from beneath the last muscle they begin to spread out till, at the mid-ventral raphe, into which they are inserted, they form a tolerably wide superficial sheet. The posterior margin of this sheet lies in the transverse plane of the origin of the muscle, that is, at the posterior margin of the depressor mandibulae, the anterior fibres incline forward to be inserted into the median raphe deep to the posterior fibres of the *Csv.1b* pars intermandibularis.

*Innervation.*—This is by a fine branch from the VIIth nerve which curls around the posterior edge of the depressor mandibulae muscle to reach it.

One cannot but draw attention to the remarkable similarity of this muscle to the median portion of the pars interhyoidea of the elasmobranchian *Csv.2*, and its general similarity to the anterior portion of the *Csv.2* of the amphibians. The origin, of course, is different from both of these. The origin of the muscle is strongly suggestive of that of the missing *Csv.1b* pars extramandibularis, but the situation of the anterior fibres mid-ventrally, deep to the pars intermandibularis, is not that of the anterior fibres of the pars extramandibularis in other lacertilians. The resemblance of this muscle to the *M. interhyoideus* in other reptiles confirms its identification.

#### THE HYPOBRANCHIAL SPINAL MUSCLES.

The Hyoid Skeleton is peculiar, and like the muscles to be described next, it is apparently modified in association with the remarkable protrusible tongue.

The pars entoglossus, as in other lizards, is a fibro-cartilaginous structure. It is here peculiar in that it is not tapered but is of the same thickness from end to end. The posterior end of the entoglossal part joins the short hyaline cartilaginous body of the hyoid. To this latter a short cerato- and slightly longer thyro-hyal are articulated. The former extends laterad and dorsad towards the ramus of the jaw a short distance in front of the joint. No trace of a separate, or any, stylohyal was found. The thyrohyal is also a relatively short rod of cartilage; its direction from the body of the hyoid is laterad and dorsad, with a very slight inclination caudad to terminate immediately behind the posterior end of the mandible, almost in contact with the insertion of the depressor mandibulae and pterygoideus internus. Both pairs of hyoid processes form incomplete half-hoops which conform to the contour of the deep throat at the root of the remarkable sheath of the tongue. These two half-hoops are very close together at the mid-line, where the processes are articulated to the hyoid body, but diverge slightly as they depart from their origin.

The Sterno-thyroideus lateralis arises from the mid-line of the sternum between the first and second sternal ribs. The muscle is a narrow ribbon of no great thickness, and it passes rostrad and laterad to be inserted into the extreme tip of the thyroid cartilage.

The Sterno-thyroideus medialis arises from the sternum just behind the origin of the *M. sternothyroideus lateralis*. This also is a relatively narrow ribbon, but somewhat thicker than the last muscle. It passes directly rostrad, alongside of its fellow, to be inserted into the root of the thyroid cartilage and back of the body of the hyoid. Its outer margin is strengthened by a tendinous strand which, continued rostrad past the hyoid, gives origin to some of the lateral fibres of the *M. genio-hyoideus*.

The Sterno-thyroideus profundus arises from the mid-line of the sternum for a short distance in front of the sterno-thyroideus lateralis. It is very similar to the last muscle and runs forward under cover of it to be inserted into the end of the thyroid cartilage.

The Omo-hyoideus muscle has not been found in any other lizard examined. It arises from the epicoracoid under cover of the insertion of the M. sterno-mastoideus. This is a very narrow and thin strand of fibres which passes nearly transversely, but with an inclination rostrad, superficially to the three sterno-thyroid muscles, to be inserted into the back of the body of the hyoid.

The Hyoglossus muscle arises from the greater part of the length of the ventral surface and anterior edge of the thyroid cartilage and passes forward to be inserted into the mandible far forward, on each side of the symphysis and under cover of the Csv.1. The fibres which arise farthest out, at and near the end of the cartilage, have a direction mediad and only slightly rostrad, until they join, and become bound up with, the more medial fibres, when they turn forward.

The Genio-hyoideus muscle arises from the symphysis menti and passes rostrad alongside of its fellow, and medially to the last muscle, to be inserted into the inner end of the thyroid cartilage.

The Thyro-mandibularis muscle is a narrow ribbon of fibres which arises from the extreme end of the thyroid cartilage and passes forward under cover of the "swelling" of the pterygoideus internus muscle. In front of this last muscle the thyro-mandibularis becomes superficial to the posterior margin of the Csv.1b, and its membranous tendon is continued forward some distance before finally being inserted along the lower edge of the mandible.

The Thyro-hyoideus muscle arises from the anterior edge of the thyroid cartilage and is inserted into the posterior edge of the ceratohyal. The direction of the fibres is from their origin mediad with an inclination rostrad. This muscle is blended with the deep surface of the hyo-glossus.

No Hyomandibularis muscle was found.

The Genio-glossus muscle arises from the symphysis menti and runs back along the side of the sheath of the tongue for the greater part of the length thereof. A little in front of the hyoid body the muscle turns dorsad and is inserted into a median raphe on the dorsal surface of the sheath between the body of the hyoid and the posterior end of the larynx.

In comparing the above description with that of Lubosch, it will be noted that I find a thyro-mandibularis in the situation of the branchio-mandibularis visceralis of this author. I have not been able to find the branch of the IX nerve to this muscle. Lubosch has failed, in his specimen, to find the interhyoideus muscle but has found a deep, dorsal, part of the Csv.1 in, nearly, the situation of the interhyoideus (Lubosch, Fig. 9, C<sub>2</sub> mv.dors.).

#### Geckos.

(Fig. 136.)

Two genera of Geckos have been dissected, several specimens of *Gymnodactylus phyllurus* and one of an unnamed species of *Thecadactylus*. They are almost identically similar in their musculature.

Particular interest attaches to the ventral musculature.

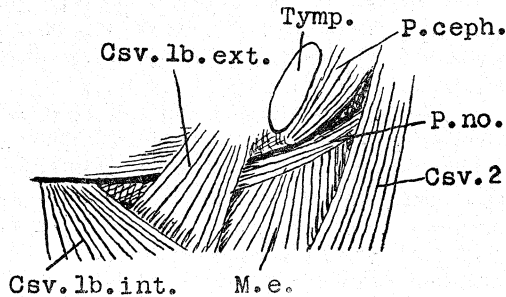


Fig. 136.—Gecko.

The two portions of the Csv.1b are quite separate. The pars intermandibularis arises from a little less than the middle one-third of the mandible, and its fibres radiate, the anterior mediad and the posterior caudad. The separated pars extramandibularis rises from the perimysium of

the pterygoideus internus and its fibres trend mediad and rostrad, forming an angle with the posterior fibres of the pars intermandibularis.

The Interhyoideus muscle arises, deep to the pars cephalognathica of the depressor mandibulae, from the internal, vertical edge of the quadrate near the dorsal end of the bone. The fibres trend mediad, radiating so as to produce a relatively wide band of muscle at the mid-line. As the muscle passes from beneath the post-articular portion of the mandible, they pass deep to the anterior end of the pars notognathica of the depressor mandibulae.

*Innervation.*—This is, as in *Chameleon*, by a branch of the VIIth nerve which reaches it from beneath the depressor mandibulae muscle. This innervation would seem very definitely to indicate that the muscle must be regarded as a deeply situated portion of the hyoid constrictor.

The Pars cephalognathica of the depressor mandibulae is as in the generality of lacertilians.

The Pars notognathica is peculiar. It arises from the dorsal intermuscular septum under cover of the hyoid constrictor sheet. The insertion is not into the post-articular portion of the jaw; the fibres pass forward ventrally and medially to the angle of the jaw and become lost in the connective tissue deep to the pars extramandibularis of the C<sub>sv</sub>.1b.

The post-cephalic hyoid constrictor fibres are essentially similar to the whole of the C<sub>s</sub>.2 in *Physignathus*.

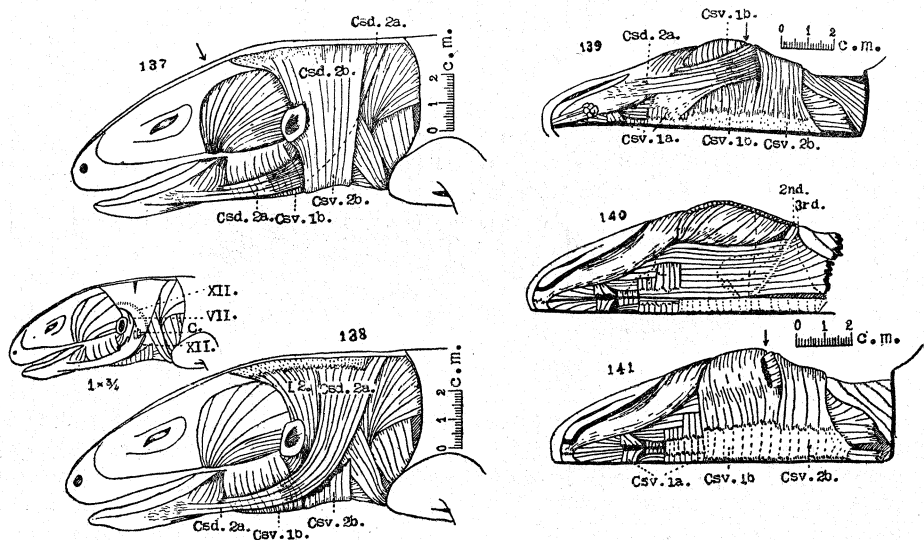
The muscles of mastication may be briefly dealt with. There is no retractor anguli oris recognizable, the M. pterygoideus is small, no depressor mandibulae mandibularis is recognizable. The M. pterygo-quadratus and the M. speno-pterygoideus are present.

The hypobranchial spinal muscles are essentially as in typical lacertilians, except that a complete transverse tendinous inscription interrupts the continuity of the lateral and medial sterno-thyroid muscles, and these two are not definable, one from the other.

#### *Tiliqua*.

(Figs. 137–141, from Lightoller.)

*Tiliqua* is one of the genera of the Scincidae. I have been able to dissect, also, two other members of the family, both belonging to the genus *Lygosoma*. They are all essentially alike. Lightoller has described most of the cephalic muscles of *Tiliqua scincoides*, and for the most part they are similar to those forms already described.



Figs. 137-141.—*Tiliqua* (from Lightoller).

The M. submentalis (C<sub>sv</sub>.1a) is represented by small triangular sheet of fibres which arise by a fine tendon from the median surface of the mandible close to the symphysis menti. The fasciculi trend caudad and mediad and are inserted into a median raphe. The posterior end of the muscle lies deep to the anterior end of the pars superficialis of the same muscle.



The Pars notognathica of the depressor mandibulae resembles that muscle in Iguanidae in that it is not inserted into the mandible, but is continued forward to be inserted into the superficial fascia on the ventrum of the mouth, and by this medium becomes attached to the lower margin of the mandible anterior to the extramandibular portion of the Csv.1b. The origin of this portion of the depressor lies deep to the Csd.2, but anteriorly the muscle lies superficially to the pars extramandibularis of the Csv.1b.

The muscles of mastication are more completely fused than in any other lacertilian studied. There is recognizable only the division into temporo-masseteric and pterygoid portions as described by Lightoller.

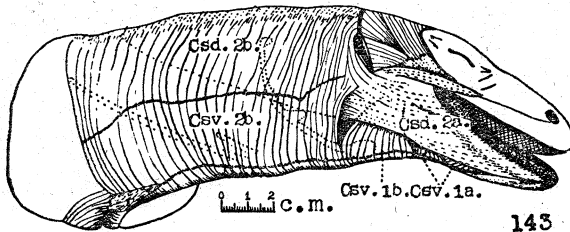
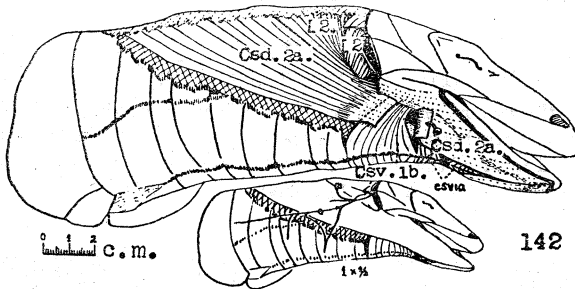
The hyobranchial spinal muscles are similar to those of *Physignathus*.

*Varanus*.

(Figs. 142-143, from Lightoller, 144-147, from Bradley.)

The superficial constrictor muscles of *Varanus varius* have been described by Lightoller and the muscles of mastication of *V. bivittatus* by Bradley.

Lightoller's description of the superficial muscles is complete and accurate and I have reproduced his drawings.\* It should be noted, however, that he includes the M. submentalis and the M. intermandibularis of the ventral mandibular constrictor as portion of the Csv.1a, whilst I regard the latter as being portion of the Csv.1b. This difference of interpretation arises from the fact that in none of the reptiles dissected by Lightoller was the M. submentalis developed as a distinctly separated muscle such as is present in *Physignathus*, and many other reptiles.



Figs. 142-143.—*Varanus* (from Lightoller).

I find that the anterior portion of the Cs.2, both dorsally and ventrally, is innervated by the VIIth nerve as Lightoller describes, but I find that the greater part of the muscle is innervated, like that of *Physignathus*, by the conjoined first and second spinal nerves. Here again experimental work reveals the absence of motor fibres to the muscle in the spinal nerves.

Bradley's description of the muscles of mastication of *V. bivittatus* might almost serve as a description of those of *V. varius*. The retractor anguli oris, indicated by Bradley, is quite readily dissected off the subjacent M. temporo-massetericus (capiti-mandibularis of Bradley). The Mm. pterygo-quadrata and speno-ptyergoideus (Mm. pterygo-sphenoidalis posterior and pterygo-parietalis of Bradley) are essentially similar to those muscles in *Anolis*.

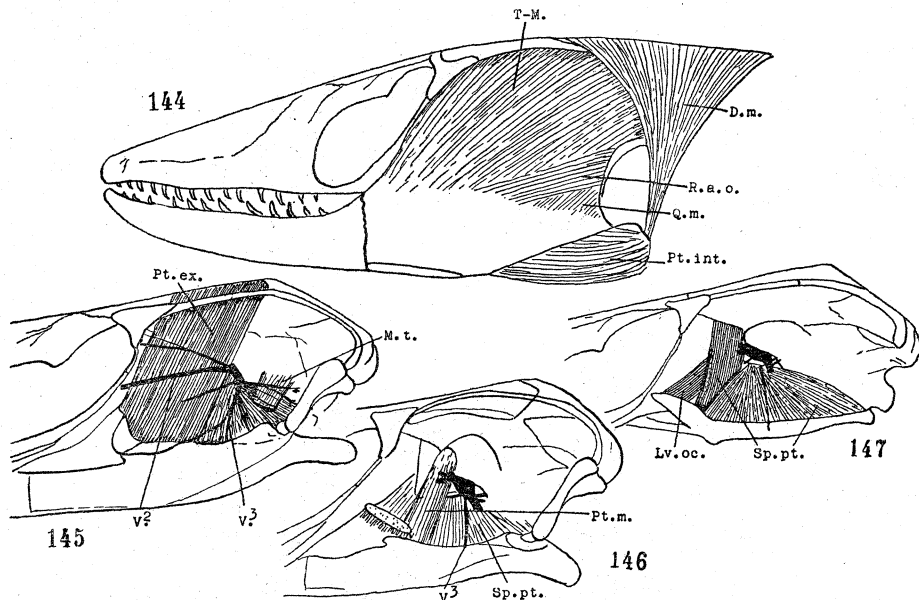
\* This has been made possible by his kindness in giving me advance proofs for the purpose, and I have to thank him for the same assistance with the illustrations of *Sphenodon*.

## 2. Rhynchocephalia.

(Figs. 148-149, from Lightoller.)

*Sphenodon* is, of course, the only recent representative of this group. Osawa (1898), Lubosch (1933), and Lightoller (1935) have described the cephalic muscles. I reproduce illustrations from Lightoller.

The superficial ventral constrictor muscles are, in my specimens, very similar to those in his. In my specimens, however, the partly separated posterior slip of the C<sub>sv</sub>.1b which arises under cover of the depressor mandibulae (C<sub>sv</sub>.1b<sup>1</sup> of Lightoller, Vb of Lubosch), is quite distinctly continuous with the more deeply placed "M. interhyoideus" of Lightoller's description. This latter muscle is undoubtedly the homologue of that which I have described in *Chameleon* and other lacertilians as the M. interhyoideus. I find that in the specimen of *Sphenodon* which I

Figs. 144-147.—*Varanus* (from Bradley).

have dissected it is not difficult to free the origin of the muscle from the stylohyoid bone, and that when this is done it is found that a fascial sheet carries the origin of the muscle up to the posterior edge of the quadrate. One might therefore describe the muscle as having this last origin, and as being bound to the stylohyal as it passes over it.

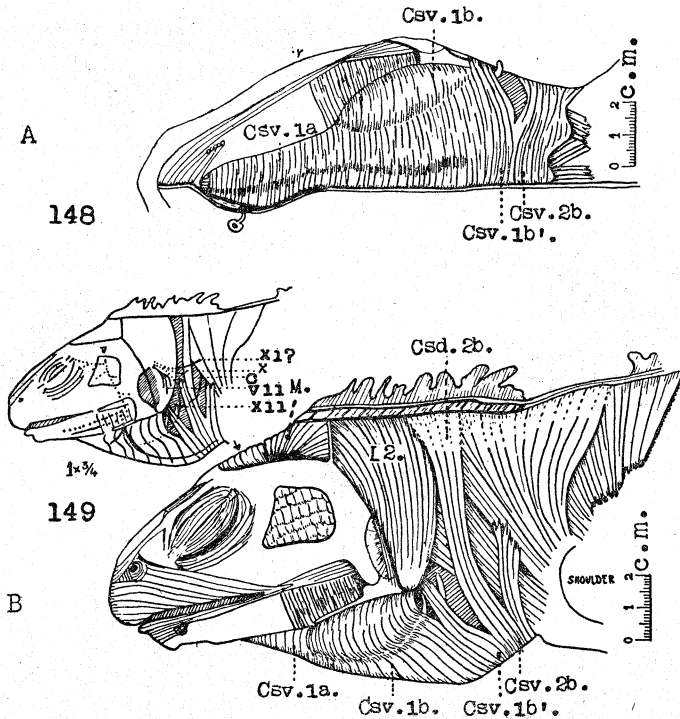
This is the first reptile I have dissected in which no trace of the M. submentalis (C<sub>sv</sub>.1a) could be found.

Whilst the form of the superficial ventral constrictors in my specimen is very much as described by Lightoller, differing only in that the posterior, shorter portion is rather more extensive, I find that the innervation is as described by Lubosch. I therefore agree with the latter that the C<sub>sv</sub>.1b of Lightoller's description is the anterior portion of the C<sub>sv</sub>.2; herein *Sphenodon* resembles Crocodiles.

Immediately after the VIIth nerve leaves the tympanic cavity, as described by Lightoller, it divides into four branches. Three of these pass directly into the overlying Depressor mandibulae, the fourth and largest branch runs ventrad against the deep surface of that muscle, passes through the origin of the M. interhyoideus from the stylohyal cartilage, and reaches the deep surface of the last-mentioned muscle. It then breaks up into very fine branches. The most anterior of these to be detected, passes directly mediad along the M. interhyoideus. No branch of this was observed to reach the anterior margin of the muscle. The rest of the branches of the nerve pass caudad on the deep surface of the C<sub>sv</sub>.2.

I would agree with Lightoller that the Csv.1 is innervated only by the Vth nerve, but must agree with Osawa and Lubosch that the interhyoideus and the Csv.2 are innervated by the VIIth.

I find, moreover, that the posterior, shorter, fasciculi of the Csv.2 are very definitely innervated by a twig from the ventral ramus of the second spinal nerve. The main nerve issues from between the dorsal and ventral trunk muscles a little anteriorly to the anterior margin of this posterior portion of the Csv.2. The twig to the muscle turns caudad and ventrad around the upper margin of the cleido-mastoid muscle, and terminates by breaking up on its deep surface. Whether the second cervical nerve anastomoses with the first was not determined by actual observation, but in as much as that the nerve to the M. cleido-mastoid was observed to leave the emergent main trunk, it is confidently believed to do so. Material has not been available for experimental work, but the results in the lacertilian examples suggest very emphatically that the spinal innervation of the muscles is sensory only.



Figs. 148-149.—*Sphenodon* (from Lightoller).

The Depressor mandibulae muscle is precisely as described by Lightoller. The absence of the pars notognathica is peculiar, but not unique; its absence has been noted in *Chameleon*, and in *Anolis* the muscle, though extensive, is not divided into two portions.

The Retractor anguli oris muscle appears to have been overlooked by previous workers. It is possible that the ease with which I was able to detach the bones of the facial arcades after they had been decalcified, together with my practice of staining my dissection subjects, permitted me to find a small muscle which others had missed. The muscle arises from the deep surface of the jugal bone along its length, and also from the deep surface of the post-orbital bone at the level of the upper margin of the posterior ramus of that bone.

The insertion is into the tissues of the upper lip.

This muscle is a triangular sheet of fibres, quite thin posteriorly, where the fibres have a direction ventrad and rostrad. Anteriorly the muscle becomes thicker, and that portion arising high up behind the orbit passes down between the eye and the temporalis muscle as a definite rounded strand of fibres which increase in bulk and spread out in the longitudinal plane, before reaching the corner of the mouth, as they descend ventrad to their insertion.

The innervation is by a fine twig, presumably of the fifth nerve, which perforates the temporo-massetericus muscle about the middle of its antero-posterior length and a short distance above the upper margin of the jugal bone.

The muscles of mastication are as described by Lightoller and Osawa, and in this respect *Sphenodon* is very similar to *Physignathus*. There is a further resemblance to that lizard in the form and situation of the *M. pterygo-quadratus* (*Spheno-ptyerygo-quadratus* of Edgeworth, 1931). The muscle is well developed and it differs from that of *Physignathus* only in that the fibres trend more ventrad to their insertion.

The Pterygo-mandibularis of Edgeworth is the pterygoideus internus of this work. That of *Sphenodon* differs from that of *Physignathus* only in that its origin is continued rostrad along the dorsal surface of the pterygoid bone anteriorly to the os transversum.

The remaining cephalic muscles of *Sphenodon* are so essentially lacertilian in character that they do not call for detailed description.

### 3. Crocodilia.

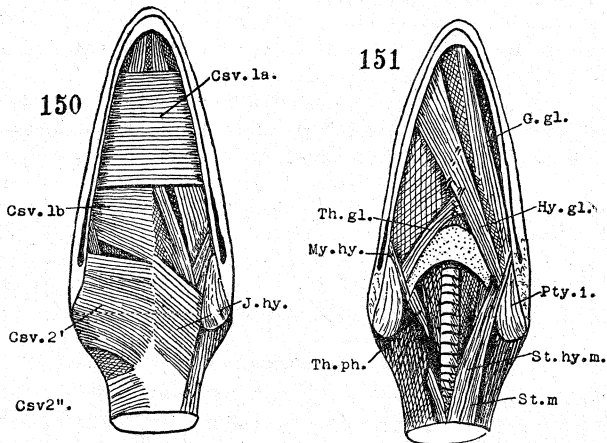
(Figs. 150-151.)

*Material.*—The following account of the cephalic musculature is based upon the dissection of two specimens of Alligator. These are but recently hatched young; the larger measures 4 cm. from tip of snout to occiput, the other is a few millimetres shorter, both are, unfortunately, cut off in front of the shoulder girdle.

#### MUSCLES OF THE MANDIBULAR SEGMENT.

Csv.1.—The small size of my material made it quite impossible to determine with confidence the innervation of most of the muscles, and this difficulty arose in connection with the ventral constrictor sheets. There is a very clear definition of these sheets into four parts. It is believed that the first two only are mandibular.

Csv.1a.—The Submentalis.—A relatively extensive sheet of araphic fibres is thus identified. It is composed of transverse fibres which are quite continuous from side to side. They arise from the inner surface of the mandible along a line which is closer to the dorsal than the ventral edge. This line commences a short distance behind the mentum and ends a little way behind the middle of the length of the lower jaw.



Figs. 150-151.—Alligator.

Csv.1b.—The Intermandibularis.—The origin is from a similar line along the mandible immediately behind the Csv.1a., but only about half as long. These fibres have a direction slightly caudad; they are inserted into a median raphe, many of them cross the mid-line and form a narrow strip of latticed fibres.

No Retractor anguli oris was found.

The Temporo-massetericus muscle is not so massive as was the general rule in the Lacertilia.

Origin is from the outer part of the ventral surface of the quadrate, and from the ventral surface of the quadrato-jugal and jugal as far forward as the suture with the os transversum.

Insertion is on to the inner surface of the surangular along the posterior half of its length.

The Pterygoideus externus muscle presents the usual clean face of contact with the more superficial temporo-massetericus muscle, with the ramus maxillaris trigemini lying upon it between the two muscles.

Origin is from the inferior surface of the extreme upper end of the quadrate, from the whole of the bones surrounding the supra-temporal fossa and from the adjacent ventro-posterior surface of the alisphenoid.

Insertion: The fibres arising from the supratemporal fossa curve rostrad and ventrad, the rest of them pass directly ventrad, all with a slope laterad, to be inserted on to the inner surface of the surangular in front of the insertion of the temporo-massetericus.

Pterygoideus medius has an extensive origin from the greater part of the inferior surface of the quadrate, from the inferior surface of the alisphenoid, and from the ascending lamina of the pterygoid bone.

Insertion: The fibres pass ventrad and laterad to be inserted into the surface of the angular which bounds the fenestra in the mandible.

Pterygoideus internus.—Origin is from the edges and contiguous area of the upper surfaces of the bones surrounding the palatal vacuity, and from the anterior bony margin of the interorbital vacuity.

Insertion: The fibres pass caudad and ventrad to be inserted on to the inner surface of the angular in front of the insertion of the pterygoideus medius.

Pterygoideus inferior (Pty.i.).—This is a massive group of fibres which bulges subdermally medial to posterior end of the jaw.

Origin: This is from the upper surface of a strong fascial membrane which is attached to the posterior edge of the palatal lamina of the pterygoid bone.

Insertion: The fibres pass caudad and slightly ventrad, and then dorsad to be inserted into the inferior surface of the angular behind the joint. The most dorsally placed of these fibres lie immediately below the lowest fibres of the pterygoideus medius muscle, namely, those arising from the lower part of the ascending lamina of the pterygoid bone; the two sets of fibres are at right angles to one another, and they separate leaving clean faces to the muscle. These superior fibres of the pterygoideus inferior pass almost directly rostrad to their insertion on to the angular.

Pterygoideus anterior.—This is a small bundle of fibres which appear to be quite separate from the rest of the complex pterygoid muscle. They arise by a very strong fibrous membrane from the lower edge of a meniscus of cartilage which is attached to the lateral edge of the palatine lamina of the pterygoid bone.

Insertion: The little brush of fibres passes directly ventrad to be inserted on to the inner surface of the dentary bone in front of the fenestra in the lower jaw, and, where the laminate suture permits, the surangular to extend forward on the outer surface of the hinder end of the dentary.

*Innervation* of the muscles of the mandibular segment.—Branches of the ramus mandibularis have been observed innervating all parts of the muscles of mastication except the last. The usual innervation of the anterior portion of the ventral constrictor, by twigs from the main nerve as it courses along Meckel's canal, was observed also. It was not possible to trace any of these last on to the intermandibularis muscle, nor was any other possible course of innervation observed.

#### Discussion.

The identification of the submentalis rests upon the complete absence of the median raphe. Throughout the Amphibia and in certain of the cartilaginous and bony fishes there was observed an anterior ventral mandibular constrictor which differed from the rest of that sheet in the absence of a median raphe. Though, in those forms, the muscle in question lies always, as far as at present known, close behind the mentum and differs from the muscle in the Alligator in that it is a relatively thick muscle, still it is believed that the very distinctive feature which characterizes this muscle so constantly in those other vertebrates justifies the present identification.

The Muscles of mastication resemble closely those of the Lacertilia. The separation of the lower portion of the pterygoideus internus, forming the pterygoideus inferior, may be regarded as a direct concomitant with the extreme posterior transportation of the jaw articulation.

The absence of any pars extramandibularis in the crocodilian Csv.1 is of interest. Even if that muscle which I have identified as the Csv.2' (pars anterior) be in its anterior portion innervated by the Vth nerve, and this I regard as being extremely unlikely, it is still not extramandibular in its origin. It certainly resembles the pars extramandibularis of many lacertilian forms in that it covers the portion of the pterygoid muscle which, in those forms, is inserted on the outer surface of the jaw. The correlation of the absence of the pars extramandibularis and of any insertion for the pterygoideus upon the outer surface of the mandible is of interest. It will be remembered that the extramandibular origin of the constrictor sheet in the lacertilians was regarded as being a secondary condition brought about by the growth of the pterygoid muscle outside the jaw, and as not being of phylogenetic significance. The conditions in the Alligator appear to support this view.

#### THE MUSCLES OF THE HYOID SEGMENT.

The Superficial Hyoid Constrictor sheet extends further forward than it does in the lacertilians or in *Sphenodon*. It is very distinctly divided into two portions.

The Pars anterior.—This arises for the most part from the inferior edge of the mandible (Fig. 150, Csv.2'), but in its posterior portion it arises from the ligamentum nuchae by a membranous extension. The fasciculi themselves do not extend dorsad above the level of the mandible. This muscle occupies the situation of that which Lightoller designates the pars extramandibularis of the Csv.1. It lies superficially to that portion of the complex pterygoid muscle which corresponds to the posterior end of the pterygoideus internus of the lacertilians, but in this reptile the insertion of either of the muscles does not extend on to the external surface of the mandible. The direction of the fibres is mediad and caudad. The anterior fibres are at an angle with the posterior fibres of the Csv.1b and are separated from them throughout their length. The insertions of the M. sterno-mandibularis and of the M. mylo-hyoideus lie in the gap between the Csv.1 and Csv.2'.

Insertion: This is into a median ventral raphe. The greater part of the fasciculi extend right to the mid-line, but posteriorly they fall short.

Pars posterior (Csv.2').—This is a much smaller sheet of fibres which arise from the dense fibrous tissue which invests a group of subdermal cervical glands placed at the mid-lateral line of the neck in front of the shoulder girdle. Their direction is mediad and rostrad. The most anterior fibres do not reach the mid-line, the posterior do.

Insertion: Into a median raphe continuous with that of the pars anterior.

Innervation.—This is by a branch facial nerve.

The Interhyoideus muscle of the Alligator (L.hy.) is a remarkably well developed and extensive muscle. Its origin, however, is peculiar.

This is a sheet of fasciculi which lies immediately deep to the Csv.2 on either side of the mid-line, but which burrows very deeply for its attachment. The two muscles of either side together enclose the ventral capiti-nuchal muscles, the pharynx, the trachea, and the hypo-branchial spinal muscles, in a tube which, however, is incomplete above, where the two ventral capiti-nuchal muscles lie on each side of the mid-line. The muscle extends from the posterior margin of the thyroid cartilage backwards for a distance of 1.5 mm. (The full length of the mandibles is 4.2 mm.)

Origin: This is from an intermuscular septum which separates the lateral and ventral capiti-nuchal muscles. The septum is quite short and the fasciculi of the interhyoideus extend up between these trunk muscles. A few of the most anterior fasciculi have an origin from a fine membrane which passes dorsad laterally to the lateral capiti-nuchal muscle and is attached above to the posterior edge of that lamina of the quadrate which covers the lateral surface of the exoccipital bone.

Insertion: The anterior fibres are inserted into a very short length of the posterior margin of the thyroid cartilage immediately below the trachea, the fibres behind these, about one-third of the full number, are inserted into a median raphe of their own, which lies in contact with the trachea. The rest of the fasciculi are inserted into the same raphe as the pars anterior of the Csv.2'.

From their origin the fasciculi pass ventrad. Posteriorly they lie first between the trunk muscles, then between the lateral trunk muscle on the outer side, and the pharynx, trachea and spinal hypobranchial muscles on the inner side. Anteriorly the same structures lie to the inner

side, but the pterygoideus inferior lies to its outer side. It thus reaches the deep surface of the Csv.2' and at once turns mediad to its insertion, superficial to all the structures which lie medial to it.

The Depressor Mandibulae.—This muscle appears to be divided into anterior and posterior parts when viewed upon the removal of the skin, but no plane of separation could be demonstrated.

Origin : From the lateral half of the postero-superior surface of the quadrate, the ridge of the squamosal above that, and then along the dorso-posterior edge of the parietal and supra-occipital to the mid-line, and finally back along the ligamentum nuchae for a short distance.

Insertion : The direction of the anterior fibres is caudo-ventrad and slightly laterad, that of the posterior fibres ventrad and laterad. They are all inserted on to the dorsal surface of the post-articular piece of the articular bone.

Innervation of the muscles of the hyoid segment.—These appear to be innervated only by the facial nerve. That nerve leaves the acoustico-trigeminal fossa by perforating the prootic bone in the roof of the fossa. It thus reaches the anterior wall of the tympanic cavity, it rises on this wall till it meets the anterior margin of the tympanum, and then turns back around the median margin of the tympanum, and at its posterior margin bends ventrad and enters a canal between the dorsal surface of the quadrate and the parotic process of the exoccipital, and which is enclosed immediately behind the tympanic cavity by the squamosal laterally and above, the exoccipital medially, and the quadrate below. The posterior aperture of this canal is about half-way down the shaft of the quadrate and just on the dorsal surface above the median edge. Immediately the nerve emerges from the canal it gives off three small twigs which enter the M. depressor mandibulae. They were not traced far into the muscle—one did well to find them at all—but were assumed to be entirely motor nerves to that muscle. The main nerve turns ventrad and mediad, running behind and slightly laterally to a vessel which accompanies it through the canal, and which is taken to be the vena capitis lateralis. In this situation the nerve lies against the upper and then the deep surface of the M. pterygoideus inferior. It thus reaches the anterior margin of the M. interhyoideus, and at once breaks up into fine branches. Of these, three small ones break up upon the lateral surface of the muscle. The largest branch runs ventrad parallel with the fasciculi of the muscle till the under surface of the Csv.2' is reached, and on this surface its branches trend both back and forward and terminate. The other branch of size passes caudad along the lateral surface of the M. interhyoideus, between it and the lateral trunk muscle, but trending ventrad.

There remains for description another muscle, probably hyoid. This may be provisionally designated the Depressor Auricularae. The tympanic recess in the Alligator is protected by a thick flap of skin. This is attached, along the dorso-median margin of the recess, to the squamosal bone and to the same bone along the upper half of the posterior margin. The flap is thickest behind, and in this thickened portion there is lodged a small pyramidal muscle. The base of the pyramid is muscular and is attached to the lateral surface of the squamosal bone near its posterior end. The apex of the pyramid is tendinous and is inserted into the quadrate at the postero-lateral margin of the tympanic recess. The obvious function of this interesting little muscle is to pull the tympanic covering flap close against the edge of the recess.

#### Discussion.

Passing from the lacertilian muscles to those of the Alligator, it was at once thought that the muscle which has just been designated Csv.2' was the pars extramandibularis of the Csv.1. Its situation is exactly that which one would have anticipated for a pars extramandibularis. It would seem, however, that there can be little doubt that it is the homologue of the more posterior muscle. This seems to be quite conclusively proven by its innervation. It is true that in certain of the Elasmobranchs Lightoller observed an invasion of the Csv.1 by the VIIth nerve, but nowhere in the amphibians or in the lacertilians is there such an invasion. Osawa has stated that a branch of the facial nerve innervates the Csv.1 in *Sphenodon*, but, as already noted, Lightoller was unable to find such in his dissection, nor could I find any twigs of the VIIth nerve (supplying the Csv.2) running forward into the Csv.1 territory. In the present dissection it has been possible to demonstrate the innervation of this muscle by the VIIth beyond question, and in a manner very similar to the innervation of the Csv.2 not only in *Sphenodon* but also in the Lacertilians. There is, however, no trace discoverable of any innervation by spinal nerves in this reptile.

The manner of innervation of the C<sub>sv</sub>.2 is in itself distinctive, quite apart from the actual source of the nerve, when it is compared with the manner of innervation of the C<sub>sv</sub>.1. The hyoid muscle is innervated by a nerve which reaches its deep surface and spreads thereon, whilst the components of the C<sub>sv</sub>.1 are supplied with motor nerves upon their superficial surface.

The origin of the *M. interhyoideus* alone causes one to hesitate in so identifying this muscle in the Alligator. It is, however, significant that this peculiar origin is correlated with the complete loss of the wide-spreading hyoid cornua. Another little feature, perhaps not without its significance in this respect, is that there is a small anterior bundle of fasciculi of this muscle with an origin from the skull in close proximity to the upper end of the stylohyal. May it not be that the loss of the hyoid cornua has, in this reptile, caused the muscle to find a new point of origin, and that the last portion to do so was that attached to the tip of the stylohyal? This, perhaps, became divorced from the cartilage when that was completely taken into the tympanic cavity. The attachment of part of the fasciculi to the same raphe as the C<sub>sv</sub>.2 recalls conditions observed in the Elasmobranchs.

The Depressor Mandibulae muscle calls for little comment. It were mere speculation to suggest whether or no the undivided muscle represents one of both the parts so often present in the Amphibians and Lacertilians.

It appears more than probable that the Depressor Auriculae is a separated portion of the depressor mandibulae, but as no trace of its innervation was found, this is not certain. Its situation, completely separated from the muscles of the mandibular segment, and almost continuous with the deep anterior border of the depressor, certainly points to its origin from that muscle.

In view of the fact that the depressor mandibulae has been regarded as the muscle from which the post-auricular muscles of the Mammalia are derived, it would be of interest to find it forming such a muscle in one of the reptiles.

#### THE HYPOBRANCHIAL SPINAL MUSCLES.

The reduction in the hyoid apparatus appears to have been responsible for marked changes in the origins and insertions of these muscles as compared with their probable homologues in the Amphibia and Lacertilia. It is unfortunate that both my small specimens have been cut off in front of the shoulder girdle. I am, therefore, unable to determine the origin of those of these muscles which arise from the girdle.

The Sterno-thyroideus medialis (St.hy.m.) is inserted on to the little posterior wing of the thyroid cartilage.

The Sterno-mandibularis (St.m.) is probably the homologue of the sterno-thyroideus lateralis. It is inserted on to the inner surface of the mandible in the gap between the C<sub>sv</sub>.1 and C<sub>sv</sub>.2'. These are narrow thick strap-like muscles which taper from behind forward to their insertions.

The Hyomandibularis (My.hy.) muscle lies deep to the sterno-thyroideus. It arises from the tip of the posterior wing of the thyroid and is inserted on to the mandible just behind the overlying muscle.

The Hyo-glossus (Hy.gl.) muscle also arises from the wing of the thyroid cartilage by a short strong tendon. Passing forward, it broadens out and crosses the mid-line in front of the thyroid cartilage, and is inserted into the tissues of the tongue well forward along the lateral area thereof. As this muscle crosses the mid-line it interlaces with its antimere.

The Thyro-glossus (Th.gl.) appears to be a separated portion of the last muscle. It arises from the wing of the thyroid cartilage in front of the other muscles and, interdigitating with its antimere, is inserted into the tissues of the tongue around the anterior wall of the laryngeal depression. Its function is, fairly certainly, to pull the anterior wall of the depression against the posterior and to cover in completely the laryngeal opening.

The Genio-glossus (G.gl.) muscle arises from the inner surface of the mandible on either side of the mid-line and, passing back, its fibres spread out to be inserted into the tissues of the side of the floor of the mouth behind the insertion of the *M. hyoglossus*.

The Thyro-pharyngeus (Th.ph.) muscle arises from the dorsal edge of the posterior wing of the thyroid cartilage. Relatively broad at the origin, the fasciculi converge as they pass caudad and dorsad around the side of the pharynx to be inserted into the tissues thereof slightly dorsal to its mid-lateral line.



## Crocodilus.

The Trustees of the Australian Museum presented me with a specimen of *Crocodilus* sp. about two feet long. The careful dissection of this specimen failed to disclose features wherein its cephalic musculature differed materially from that of the Alligator.

My thanks are tendered to Dr. C. Anderson, the former Director, and to the Trustees for the specimen.

The contribution of Lubosch on the visceral musculature of the Sauropsida reached me after my own work upon the Reptilia had been completed. When it was found that his description of a number of forms differed from my own, the dissections in question were either repeated or, having been preserved in sufficiently complete condition, the dissections already made were examined again.

Whether the marked difference between his description of the muscles of Alligator and my own are explainable as the differences between the young individuals and the adults I am not in a position to say, but that appears hardly possible. After going over the dissections again most carefully, I am unable to find that my original descriptions were at fault.

Outstanding among the differences is the fact that Lubosch failed altogether to find the remarkably well developed muscle which I have identified as the *M. interhyoideus*. The *M. mylohyoideus* of my description is very much more developed in the adult; Lubosch identified it as the third constrictor (C.3, Fig. 30) and regards that which I have designated the *M. thyropharyngeus* as a deeper, more dorsal portion of the same muscle (Fig. 34).

It has not been possible to confirm the statement of Lubosch that these two muscles are innervated by the IX nerve; on the other hand, it cannot be denied. "Failure to find", in specimens so small as mine, cannot be relied upon as negative evidence.

## 4. The Chelonia.

*Chelodina longicollis*.

(Figs. 152-153.)

*Material*.—This reptile is quite common in the streams throughout New South Wales and I have been able to avail myself of a practically unlimited supply of adults. I have also had a number of specimens taken from the egg a little while before hatching.

## MUSCLES OF THE MANDIBULAR SEGMENT.

The Intermandibularis muscle (Cv.1) shows no division into separate portions.\* It arises from the inner surface of the mandible. Commencing in front, alongside of the symphysis, the line of origin is almost at the inferior margin; as this line passes caudad it rises steadily and terminates, well toward the upper margin of the dentary, just in front of the insertion of the temporalis muscle. The whole of the fibres have a direction mediad and caudad.

*Insertion*: Anteriorly the fasciculi are inserted into the floor-plate of the mouth at some distance from the mid-line. Posteriorly they are inserted into a median raphe.

*Innervation*.—This is by three small branches of the mandibular ramus of the Vth nerve which perforate the mandible and spread over the superficial surface of the muscle.

The Temporalis muscle is by far the most massive component of the muscles of mastication. It arises from the dorso-lateral surface of the alisphenoid lamina of the parietal bone and from the whole of the dorsal surface of the depressed area of the skull behind and above the prootic foramen.

The insertion is into the upper edge and outer surface of the coronoid process of the mandible.

There is a fibro-cartilaginous meniscus attached to the inner edge of the upper surface of the coronoid process. This meniscus is folded down alongside of the coronoid process, between it and the upturned edge of the antero-lateral corner of the pterygoid bone. The lateral surface of the meniscus is lined by buccal mucosa and lies against a similar surface. Between it and the pterygoid bone there is a synovial cavity, the bone being covered with a layer of cartilage and that in turn by the synovial membrane.

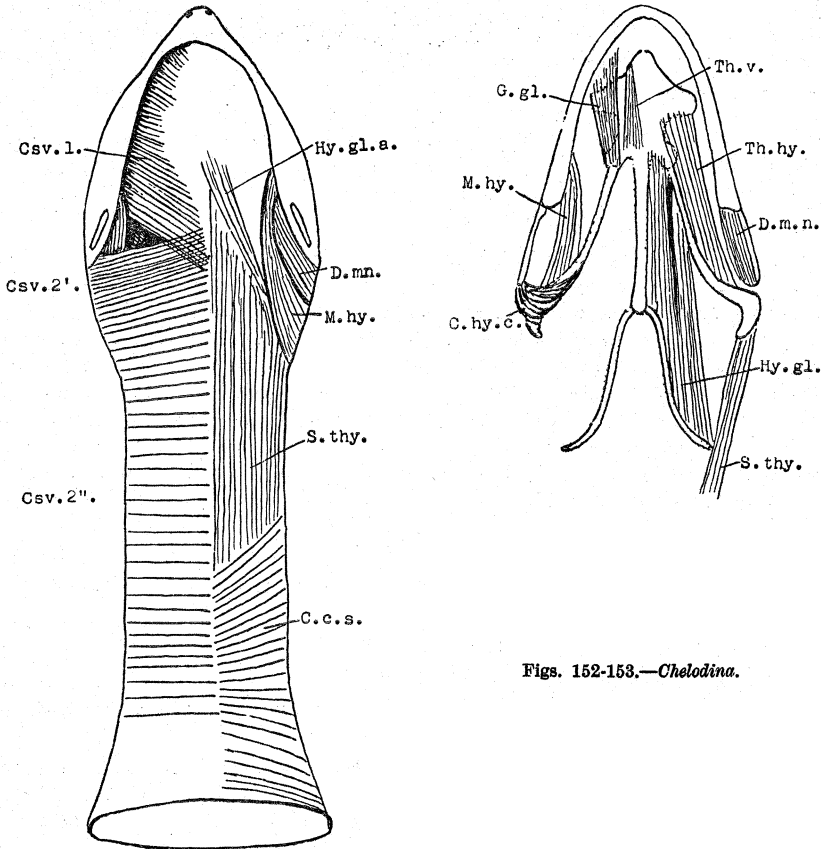
The Pterygoideus externus lies entirely under cover of the *M. temporalis*. It arises from the anterior surface of the alisphenoid lamina of the parietal bone medial to, and in front of, the prootic foramen.

\* In the late embryo there is a small submentalis muscle. This is a compact rounded bundle of fibres which pass from one ramus of the jaw to the other without any median raphe.

The insertion is into the articular bone very close to the inferior edge of the inner surface and well back just in front of the joint.

The muscle is crossed superficially, along its upper line of origin, by the maxillary ramus of the Vth nerve and below, just above its insertion, it is crossed diagonally by the mandibular ramus just before that reaches Meckel's fossa on the inner side of the mandible.

The Pterygoideus medius arises from the upper surface of the pterygoid bone laterally to and in front of the prootic foramen, behind the via masticatoria, and also from the anterior surface of the quadrate in front of and below the origin of the M. temporalis.



Figs. 152-153.—*Chelodina*.

The insertion is into the surangular bone above Meckel's foramen.

The Pterygoideus internus arises from the upper surface of the pterygoid bone in front of the via masticatoria.

The insertion is into the inner surface of the angular immediately in front of the insertion of the M. pterygoideus medius and below Meckel's fossa.

*Innervation.*—The muscles of mastication are innervated by branches of the ramus mandibularis V which leave the main nerve close to the gasserian ganglion.

#### MUSCLES OF THE HYOID SEGMENT.

The Hyoid superficial Constrictor Sheet is very definitely divided into two portions.

*Pars anterior (Csv.2').*—The fibres arise from a membrane which is attached to the subdermal margin of the posterior bony wall of the tympanic cavity and supratympanic bulla, and then extends across the supratemporal trough, superficially to the posterior end of the temporalis muscle, to become attached to the crest of the supraoccipital, and is also attached for a short distance behind this to the ligamentum nuchae. The muscle fibres do not extend dorsad of the line of the jaw.

The insertion is into a median raphe. The direction of the fasciculi is mediad and rostrad and the first few pass beneath, deep to, the posterior fasciculi of the C<sub>sv</sub>.1.

*Innervation.*—By the two terminal branches of the motor division of the VIIth nerve.

*Pars posterior (Constrictor Colli Spinalis\*) (C<sub>sv</sub>.2'').*—This muscle should, in all probability, not be described as one of the hyoid muscles. It is, however, included in this section because it is so closely similar to the posterior portion of the C<sub>sv</sub>.2 of other reptiles already described. Its separate identity was determined by stimulation experiments. These yielded a very definite boundary between this and the "constrictor colli facialis" in front. This is an extremely extensive sheet of muscle which extends, from just posterior to the jaw, back along almost the full length of the neck. It arises from the ligamentum nuchae for the anterior two-thirds of its length, and here the muscle fibres extend right round the neck from mid-dorsal to mid-ventral lines. The posterior one-third of the fasciculi arise from an intermuscular septum at the mid-lateral line. This line of origin is immediately below the tendon of the plastro-nuchal muscle. This tendon is attached by three digitations to the hinder ends of the lateral processes of the second, third, and fourth cervical vertebrae. The anterior limit of the mid-lateral line of origin of the constrictor colli spinalis is at the attachment of the posterior digitation.

The insertion is into a mid-ventral raphe.

*Innervation.*—This is by a strong branch from the united first and second spinal nerves. The ventral ramus (no dorsal ramus of the nerve was found) of the first spinal nerve runs backward below the longer dorsal trunk muscles and joins the second, apparently without giving off any branches. The ventral ramus of the second spinal nerve divides immediately after it issues from its foramen. These pass side by side, first caudad and ventrad, then ventrad, and finally rostrad and ventrad. The anterior of the two branches thus comes to meet and unite with the first spinal nerve. The conjoint nerve continues rostrad and reaches the deep surface of the constrictor colli spinalis from between the sterno-thyroideus and the cerato-hyoideus-capitis. It at once turns caudad and runs back along the deep surface of the neck so as to continue along the deep surface of the shorter posterior fasciculi of the muscle, giving off small twigs all the way, the nerve grows steadily finer and finer.

The Depressor Mandibulae presents no division into separate parts. It arises from the posterior surface of the squamosal where that bone forms the hinder wall of the supratympanic bulla.

The insertion is into the post-articular piece of the articular bone.

*Innervation.*—Two twigs from the motor division of the VIIth nerve.

The Interhyoideus muscle would probably not have been recognized as such had the adult *Chelodina* only been studied.

In the adult (Fig. 152, Hy. gl.a.) the muscle is a small triangular fan of fasciculi which arise from the median border of the ceratohyal immediately in front of the insertion of the lateral portion of the *M. hyoglossus*. The muscle lies against the deep surface of the C<sub>sv</sub>.2'.

The insertion is into the posterior edge of the floor plate of the mouth.

*Innervation.*—This is by a twig from one of the terminal branches of the motor division of the VIIth nerve. This leaves the deep surface of the C<sub>sv</sub>.2' at the outer edge of the interhyoideus and breaks up upon the superficial surface of the muscle.

The true nature of this muscle was discovered in young specimens almost fully developed, taken from the eggs. In these, the muscle is inserted into the same median raphe as the C<sub>sv</sub>.2'. Its innervation was determined by separating the whole of the C<sub>sv</sub>.2' together with the posterior portion of the C<sub>sv</sub>.1 and the anterior portion of C<sub>sv</sub>.2'' and the interhyoideus, and slicing off and detaching with them the superficial layers of the *Mm. depressor mandibulae*, *ceratohyoideus-capitis* and posterior end of the *M. hyoglossus*. These last three were then carefully dissected off the constrictor sheet from the deep side and the remainder of the preparation stained and mounted for examination under high magnification. The nerve could not be found in the adult.

\* The muscle is a portion of the *panniculus carnosus*, but has been given this designation after much of my work on the *Theria* has been completed. A muscle which is deemed to be completely homologous with it is present in the *Cetaceans*, but, in them, extending very much further forward (Kesteven, 1941*d*). The reason for the introduction of this term is to emphasize the presence of a superficial constrictor innervated by spinal nerves as well as the facial constrictor. This, and the designation *constrictor colli facialis*, will be found in later sections of the work and used with the same intent.

## THE COURSE AND MOTOR BRANCHES OF THE FACIAL NERVE.

Together with the Vth nerve the facial leaves the cranial cavity through the prootic foramen. In the trigemino-facialis fossa the facial lies above the trigeminal and the geniculate ganglion lies above the separated trunk of the trigeminal. From the ganglion the facial nerve swings laterad and then caudad through the prootic bone. Passing above the columella auris near its inner end, the nerve enters a short canal and appears on the base of the skull just below the posterior corner of the squamosal. In this situation it lies against the deep surface of the depressor mandibulae, and gives to that muscle two twigs. The nerve now divides into two branches and these turn dorsad and laterad around the posterior surface of this muscle, and reach the deep surface of the C<sub>sv</sub>.2'. Both the branches are distributed to the C<sub>sv</sub>.2'. None were observed to reach fibres of the C<sub>sv</sub>.2'' or to extend on to the C<sub>sv</sub>.1.

## SPINAL MUSCLES.

The Constrictor Colli Spinalis Profundus.—This name is applied to a constrictor muscle not observed in any of the vertebrates previously dissected.

The muscle arises from the same intermuscular septum as do the short posterior fibres of the constrictor colli spinalis, but extends right back to the last cervical vertebra so that it here lies above the clavicle.

Insertion: The direction of the fibres is ventrad and mediad with a slope caudad in front and a slight inclination rostrad posteriorly.

*Innervation.*—By a branch of the ventral ramus of the third spinal nerve.

In the young specimens this muscle was found to be inserted, as to its anterior fasciculi, into the deep surface of the anterior margin of the plastron, and as to the rest of the fasciculi, into a strong facial sheet which is attached medio-ventrally to the plastron behind the first insertion and laterally to the scapula. This insertion suggests strongly that the muscle is really the cleido-mastoid, which otherwise is not developed.

## THE HYPOBRANCHIAL SPINAL MUSCLES.

The larynx in this reptile has been brought right forward so that it lies in the floor of the mouth anterior to the middle of the length of the jaws. The forward migration of the larynx has, of course, been accompanied by the thyroid cartilage; it has also resulted in the abolition of a fleshy tongue. It would appear that the latter has been replaced by a tough fibro-cartilaginous plate which lies ventrally to the thyroid cartilage, and which has been here designated the "floor plate". The thyroid cartilage has short anterior wings, to which, however, the ceratohyal is not attached. It is suggested that another of the results of the forward migration of the thyroid has been the transfer of the articulation of the ceratohyal to a more posterior situation. Posteriorly the thyroid is produced into a long median rod, and to the end of this the two posterior cornu are articulated.

The forward migration of the larynx and its cartilage has also, apparently, resulted in an arrangement of the hypobranchial spinal muscles which is very different from that of the Lacertilians. In the following description the designations adopted are those which reflect the homologies of these muscles with those of the Lacertilians, in so far as such are determined; in some cases, however, the homologies have not been determined, even tentatively, and in these instances noncommittal descriptive names are used.

The Genio-hyoideus (G.gl.).—This muscle lies deep to the floor plate, between it and the thyroid cartilage. It arises from the inner surface of the mandible to one side of the symphysis. The direction of its fibres is caudad and slightly mediad. They are inserted on to the posterior margin of the thyroid cartilage and on to the perimysium of the hyoglossus at its insertion.

The Hyo-glossus (Hy.gl.) arises from the whole of the outer surface of the posterior cornu of the hyoid. It is incompletely divided into medial and lateral portions. The former is inserted into the posterior edge of the thyroid cartilage between the bases of the two cornua. The lateral part is inserted into the anterior one-third of the inner surface of the ceratohyal.

The M. genioglossus (Th.v.).—The muscle thus identified arises from the anterior edge of the hyoid cartilage. Its fasciculi run directly caudad and are inserted into the deep surface of the floor plate.

The thyro-hyoideus muscle (Th.hy.) is a thick rounded bundle of fasciculi which arise from the lateral surface of the greater part of the length of the ceratohyal and pass forward and slightly

mediad to be inserted on to both ventral and dorsal surfaces of the anterior wing of the thyroid cartilage.

The Hyomandibularis (M.hy.) muscle arises posteriorly to the last muscle from the remainder of the lateral surface of the ceratohyal. The solid bundle of fibres pass forward to be inserted into the inner face of the mandible anterior to the joint.

The Cerato-hyoideus-capitis (C.hy.c.) muscle arises from the outer edge of the tip and from the anterior edge of the ventral surface of the lateral end of the ceratohyal and, passing dorsad and rostrad superficially to the outer end of the Mm. mylohyoideus and depressor mandibulae, is inserted on to the flange of the squamosal bone which stands out above and behind the supra-tympanic bulla.

The Sterno-thyroid (S.thy.) muscle arises from the dense subdermal fascia along a line which commences ventrally at the mid-line a little behind the middle of the length of the neck, and inclines forward as it rises dorsad to the mid-lateral line. It is a thin sheet of fasciculi which pass directly forward to be inserted, for the most part, into a membrane and tendon which attach it to the ventral surface of the thyroid and the perimysium of the muscles inserted thereon. A few of the more lateral fibres are inserted on to the outer end of the ceratohyal, and these are also firmly bound to the tip of the posterior cornu of the hyoid as they pass over it.

*Innervation.*—The very complete fusion of the hypoglossal with the vago-accessorius trunk renders it impossible to be confident as to the innervation of these muscles. It appears that the greater part of the hypoglossal fibres leave the fused trunk on its inner side shortly after the nerves emerge from their bony canals, but of this one cannot be certain. A further complication is introduced by the fact that branches from the two separate trunks join the other before the nerve to the hypobranchial spinal muscles separates from the rest of the resultant network.

The Glossopharyngeal nerve was dissected out and the branch to the larynx found to turn ventrad and mediad around the posterior margin of the ceratohyoideus-capitis, then to run forward along the median edge of the ceratohyal, and then to turn dorsad between the ceratohyal and the lateral margin of the hyoglossus posterior.

#### *Emydura macquariae.*

I am indebted to the Trustees of the Australian Museum for a specimen of this tortoise, and tender them my thanks.

The Submentalis muscle is quite clearly differentiated from the intermandibularis. It takes the form of a small sheet of fibres, continuous from side to side, situated deep to the anterior end of the M. intermaxillaris.

The M. interhyoideus is similar to that of the young *Chelodina*.

The M. constrictor colli spinalis profundus is not differentiated from the M. constrictor colli spinalis superficialis. There is a continuous sheet of fibres extending as far back as in *Chelodina*, but there is no overlapping of two sheets.

Apart from these differences the cephalic musculature of these two fresh-water Chelonians is essentially similar.

### 5. Ophidia.

(Figs. 154–156.)

*Material.*—A practically unlimited supply of specimens of two common snakes has permitted a very complete survey of the adult myology. The two are *Python variegatus* and *Pseudechis porphyriacus*. These resemble one another and published descriptions of other snakes so closely that it has been confidently assumed that there was no necessity to dissect any other species.

It has not been possible to study the development of the muscles. In serial sections, those of young *Notechis scutatus* were observed to present no marked differences from those of the adult species studied.

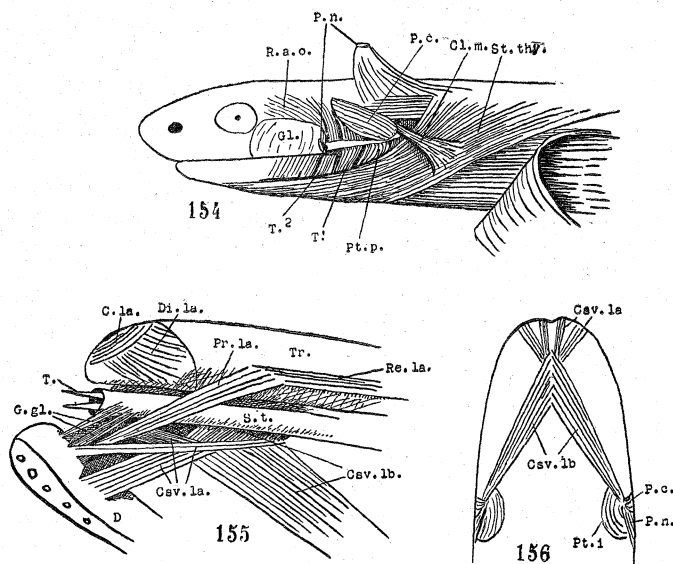
### THE MUSCLES OF THE MANDIBULAR SEGMENT.

The ventral constrictor is sharply divided into anterior, submentalis, and posterior, intermandibularis, parts as in other reptiles.

The Submentalis (Cv.1a) resembles the pars profunda of the anterior portion of the mandibular constrictor of the Lacertilians.

In *Pseudechis* it consists of two portions, both of them quite small. The larger of these consists of a small quadrangular sheet of fibres which arise from the inner surface of the dentary close to the anterior end of the bone. The fasciuli pass caudad and mediad to be inserted into a median raphe which is placed above the submental crease, and which in its posterior part is common to this muscle and the Csv.lb, the latter being the more superficial of the two muscles. The smaller part of the muscle arises from the extreme tip of the dentary and passes caudad, dorsally to the fibres of the other part of the muscle, to be inserted into the same median raphe, but posteriorly to the other fibres.

In the *Python* the muscle is undivided and its fibres interlace with those of the Csv.lb at their insertion into the median raphe so that the two muscles appear to be continuous and interlacing at the mid-line. In fact it was thus that Hoffmann, following D'Alton, treated the conjoint Csv.la and Csv.lb, designating them the intermaxillaris. Comparison with *Pseudechis* and the reptiles generally leaves no doubt that there are the two separate muscles blended at their insertions.



Figs. 154-156.—*Pseudechis*. T., tongue; T<sup>1</sup>. & T<sup>2</sup>., Mm. massetericus major and minor.

The Intermandibularis (Csv.lb) is similar in the two forms. It arises from the inner surface of the posterior end of the dentary and surangular, and also from an aponeurotic ribbon which is attached to the inferior margin of the tendon of the pars notognathica of the M. depressor mandibulae and to the inferior edge of the angular below the insertion of the pars cephalognathica of the same muscle. The fasciuli pass sharply forward, and gradually reach the mid-line, to be inserted into the median raphe already described in connection with the Csv.la, and superficially to that muscle in *Pseudechis*, but interlacing with it in *Python*.

The dissections of Lubosch indicate a greater variation in the disposition and extent of the parts of this muscle, amongst the snakes, than might have been anticipated from the facts revealed in my two dissections. There is, however, a fundamental similitude in all the dissections.

#### MUSCLES OF MASTICATION.

These are exceedingly complex and their action has been studied by students of snake-bite. In the course of their studies they have described the anatomical form and relations of the muscles, but unfortunately these descriptions are, for the most part, given without any explanation of the nomenclature used as compared with that of other workers.

The latest of such works, and the most careful, is by N. H. Fairley (1929). I tabulate below his nomenclature, that of Hoffmann and the nomenclature of this work.

This work.	Hoffmann.	Fairley.
Retractor anguli oris	Parietali-quadrato-mandibularis, 1a	Anterior temporal muscle
Masseter minor	Not noted	Anterior temporal muscle, mandib. part
Masseter major	Par.-quadr. mand. 1b	Middle temporal muscle
Temporalis	Par.-quadr. mandib. 1c	Posterior temporal muscle
Pterygoideus externus	Par.-quadr.-mandib. 1d	?
Pterygoideus medius	Occipito-quadrato-mandibularis 2b	Pterygoideus internus
Pterygoideus internus	Transverso-maxillo-pterygo-man- dibularis	Pterygoideus externus
Spheno-pterygoideus anterior	Pterygo-parietalis	Pterygo-palatine
Pterygo-quadratus	Pterygo-sphenoidalis posterior	Spheno-pterygoideus
Spheno-pterygoideus	Pterygo-sphenoidalis anterior	Parieto-pterygoideus
Median slip of the Spheno- pterygoideus	Vomero-sphenoidus	?

The Retractor Anguli Oris (R.a.o.) is a very extensive muscle. In *Python* it arises from the parietal and post-orbital bones just behind the orbit. The fasciculi pass ventrad and laterad, with an inclination caudad, to be inserted into the tissues of the lower lip immediately behind the angle of the mouth.

In *Pseudechis* the muscle is more extensive; its origin extends back along the parietal, and behind that bone the muscle arises from an aponeurosis superficial to the other muscles. The fibres pass ventrad and laterad, and are inserted into the dorsal and posterior margins of the capsule of the venom gland.

In both snakes there is a very strong quadrato-maxillary ligament which occupies, superficially to the muscles, the situation of a quadrato-jugal bone. This ligament crosses the tendinous lower end of the retractor anguli oris muscle in the Boidae and lies along the lower margin of the capsule of the venom gland in the Colubrine snakes.

*Innervation.*—This is by a branch of the mandibular ramus of the Vth nerve which leaves the main trunk soon after it emerges through its foramen in the side wall of the cranium, and reaches the muscle from beneath the anterior border of the Mm. temporalis and masseter.

The Masseter muscle is not differentiated from the temporalis in *Python variegatus*, but in *Pseudechis* one can recognize two portions, of the masseter and also the temporalis as quite separated muscles. Hoffmann's reproduction of D'Alton's illustrations of the muscles of *Python bivittatus* indicates that therein the entities of the masticatory muscle group are almost as well differentiated as in the colubrine snake *Pseudechis*.

Masseter minor (T<sup>2</sup>).—This muscle arises from the deep surface of the retractor anguli oris. It is a relatively small muscle and its fibres pass directly ventrad to be inserted into the outer surface of the mandible.

Fairley describes this muscle as the mandibular slip of the anterior temporal muscle. That is to say, he regarded it as a partly separated portion of the retractor anguli oris. The insertion into the mandible, however, indicates quite definitely that it is not a portion of that muscle. Fairley failed to observe that the retractor anguli oris of the Boidae is not inserted into the mandible, and this explains the confusion.

*Innervation.*—This is by a branch of the mandibular ramus of the Vth nerve which leaves the main trunk along with all the other nerves to the muscles of mastication.

Masseter major (T<sup>1</sup>).—This muscle has an aponeurotic origin from the supraoccipital bone. It is a fairly massive muscle and its fibres pass ventrad and laterad to be inserted into the upper edge and outer surface of the surangular.

The Temporalis muscle is larger and thicker than the more superficial masseters. It arises from the lateral, descending, plate of the parietal, and its fibres are inserted into the upper edge of the surangular, medial to the insertion of the masseter minor muscle.

*Innervation.*—By a branch of the mandibular ramus of the Vth nerve which breaks up into several smaller twigs as it enters the muscle.

The foregoing description of the Mm. masseter minor, masseter major and temporalis is based upon the muscles of *Pseudechis*. In *Python variegatus* there is a temporo-masseteric mass of muscle which arises from the area of origin of the three muscles in *Pseudechis*, but in which the three components are but poorly indicated by superficial depressions and intervening membranous partitions from both sides of which the fasciculi arise.

The Pterygoideus externus.—This is a quite small muscle which takes its origin from the anterior end of the lateral plate of the parietal bone, and from there its fibres pass ventrad deep

to the maxillary ramus of the Vth nerve to be inserted into the lower edge of the internal surface of the angular. In *Python* the muscle is reduced to a thin ribbon of fasciculi, which, moreover, are of a dark grey colour, recalling the degenerating muscles of the developing tadpole.

*Innervation.*—By a branch from the ramus mandibularis similar to that innervating the other muscles.

*Pterygoideus medius.*—This muscle is reduced in both of the snakes studied; that is, reduced when compared with the muscle in other reptiles. In *Pseudechis* the muscle is still separated from the pterygoideus internus, but in *Python* it is completely fused therewith.

The muscle arises from the posterior end of the pterygoid bone and its fibres pass caudad and laterad to be inserted into the inner surface of the angular behind Meckel's foramen.

The *Pterygoideus internus* (Pt.p.) muscle arises from the anterior end of the os transversum by a very strong, rounded, tendon. The muscle rapidly swells into a thick rounded mass of fibres which pass back beneath the mandible, to be inserted on to its inferior surface below the joint.

*Innervation.*—In *Pseudechis* the nerve to the M. pterygoideus internus passes down between it and the pterygoideus medius, that to the latter muscle leaving the other at the superior margins of the two.

The Spheno-ptyerygoideus anterior is very similar in the two snakes. It arises from the anterior surface of the basitrabecular process of the basisphenoid bone and passes forward, its fibres diverging somewhat, to be inserted into the anterior end of the pterygoid bone.

*Innervation.*—A twig from the mandibular ramus of the Vth nerve.

The *Pterygo-quadratus* is very similar to the same muscle in the Lacertilians. It arises from the posterior surface of the basitrabecular process of the basisphenoid and, passing caudad and laterad, is inserted into the posterior end of the pterygoid and lower end of the quadrate bone.

The Spheno-ptyerygoideus muscle is similar to, but more extensive than, the muscle in other reptiles. It arises from the palatine above the basitrabecular process of the basisphenoid and, its fibres radiating back and forth, is inserted into the middle third of the pterygoid bone.

*Innervation.*—These three muscles are all innervated by twigs from a common branch of the ramus mandibularis of the Vth nerve.

Hoffmann, following D'Alton, described a "Vomero-sphenoideus" muscle in *Python bivittatus*. In both the snakes I have studied I find a small muscle, which I would regard as a slip of the anterior spheno-ptyerygoideus muscle, which fits his description.

#### MUSCLES OF THE HYOID SEGMENT.

The Superficial ventral constrictor, Csv.2, is that muscle which Hoffmann described as the M. atlanto-epistropheo-hyoideus, but in the snakes which I have dissected it is much more extensive than in the *Python* as described by D'Alton, and on which Hoffmann's description is based. It is more than probable that the use of magnifying spectacles has enabled me to recognize more of the muscle than could be recognized without them.

The sheet of fibres is extremely tenuous, the origin is from the ligamentum nuchae and posterior end of the skull by means of the subdermal aponeurosis and the perimysia of the muscles of mastication. In *Pseudechis* the origin is almost confined to the aponeurotic structures over the depressor mandibulae, and the fibres pass from the origin, beginning with the more anterior of them, ventrad, then ventrad and caudad, and finally, almost directly caudad blending with the superficial longitudinal muscular sheath of the body. In *Python*, the Csv.2 is more distinct; it arises from the ligamentum nuchae for a short distance behind the skull, and there is no actual origin from the aponeurotic structures over the depressor mandibulae. From their origin the fibres pass ventrad and swing rostrad towards the mid-line, but fade out before reaching it.

*Innervation.*—The anterior fibres of the muscle in both snakes are very definitely innervated by fine twigs from the motor division of the VIIth nerve which reaches the Csv.2 between the partes noto- and cephalo-gnathica of the depressor mandibulae.

The presence of a Constrictor Colli Spinalis in the *Python* is very doubtful. It has not been possible to demonstrate any spinal nerve supply to the muscle; on the other hand, in the more extensive muscle of the colubrine snake, innervation by the first and second spinal nerves separately was demonstrated in every specimen dissected. There is, however, no indication of any boundary between the Sphincter colli facialis and the spinal sphincter. Experimental work is needed to determine boundaries.



The Depressor Mandibulae muscle recalls that of the Lacertilians, and more especially that of the Monitor lizard.

*Pars Cephalognathica.*—This is a remarkably massive and a compact muscle which arises from the back of the skull close to the mid-line, and from the posterior surface of the quadrate. The muscle is always separable into anterior, more superficial, and posterior, deeper, portions, and of these the latter is the larger. The plane of separation extends down almost to the mandible. The insertion of both portions is into the post-articular part of the surangular.

*Innervation.*—This is by several small twigs from the motor division of the VIIth nerve, which enter the muscle on the surface exposed on separation into its two parts.

*Pars Notognathica.*—This has an extensive origin by means of the aponeurosis, from the ligamentum nuchae for some distance behind the skull. The fasciculi converge as they pass rostrad, and ventrad, to be inserted by a very strong tendon into the surface of the anterior end of the quadrato-mandibular ligament.

*Innervation.*—This is by a single large branch of the motor division of the VIIth nerve which reaches its deep surface from behind the posterior margin of the pars cephalognathica.

#### THE HYPOBRANCHIAL SPINAL MUSCLES.

The absence of the sternum alone would render the identification of these muscles a matter of some difficulty, but in addition to the loss of that structure their identification is made more difficult by the reduction in the hyoid apparatus and the transportation of the larynx very far forward and the development of the long protrusible tongue and its sheath.

The Hyoid apparatus is reduced to a narrow bow with a short anterior spur. This last lies just forward of the transverse level of the two jaw joints; the thin arms of the bow extend back along the neck for some distance. This single hyoid arch is probably the second; it appears too far back to be the ceratohyal.

The superficial sterno-hyoid and hyomandibular muscle is a forward continuation of the rectus abdominis. As it passes over the hyoid cornu its deeper fibres are bound thereto; its anterior insertion is into the skin superficial to the parotid gland and to the lower edge of the mandible almost along its full length.

The lateral, Cervico-hyomandibular, muscle has an aponeurotic origin from the ligamentum nuchae behind the origin of the pars notognathica of the *M. depressor mandibulae*. Its fibres sweep forward ventrad and mediad, and have an aponeurotic insertion into the skin and posterior end of the mandible. The union of this aponeurosis of insertion with that of the pars notognathica gives the muscle an attachment to the lower edge of the quadrato-mandibularis ligament.

The muscle which is, in all probability, the homologue of the sterno-mastoid arises, in the snakes, from the deep surface of this last muscle about the middle of its length and passes rostrad and slightly dorsad. Tapering rapidly, the muscle is inserted, by a fine strong tendon, into the upper end of the quadrate between the two portions of the pars cephalognathica of the *M. depressor mandibulae*. Hoffmann designated this muscle the retractor ossis quadrati.

The Genioglossus appears to be represented by a small muscle which has not heretofore been observed, but which is present in both the snakes studied. The muscle arises from the inner surface of the mandible superficially to the *Csv.1a*. Its fibres pass more directly mediad and dorsad between the two halves of the submentalis to be inserted in part into the sheath of the tongue and in part into the side of the trachea just posterior to the larynx. In *Pseudechis* the latter fibres are quite separate from the former throughout their length and, moreover, in this form those inserted into the sheath of the tongue are distinctly gathered into a posterior and an anterior group.

The Geniohyoideus (*pr.1a*) is that muscle which Lubosch designated "geniotrachealis", and Goppert "protractor laryngis". It arises from the fore end of the dentary behind the origin of the *M. genioglossus* and, passing back and dorsally, is inserted into the side of the trachea a short distance behind the larynx.

The Hyo-glossus muscle ("Genio-hyoideus" of Lubosch) is apparently that which Goppert designated the retractor laryngis. The muscle is a narrow thin band of fibres which arise from the deep surface of the curve of the hyoid apparatus and, passing forward along the side of the trachea, are inserted thereinto just behind the insertion of the protractor.

A muscle which arises from and surrounds the free end of the hyoid cornu and passes forward to be inserted into the base of the sheath of the tongue was termed the hyo-glossus by Hoffmann. It appears more probable that it is the homologue of the thyro-hyoideus of the Lacertilians.

## 6. Review.

The Ventral Superficial Constrictors.—Of these there are, constantly present in all the Lacertilian genera examined, three portions of the mandibular sheet and a continuous hyoid sheet. In addition there is, in some forms, the muscle which has been designated *M. interhyoideus*.

The obvious division, in a number of forms, of the *Csv.1* into three parts raises the question of the homology of these to the divisions of the muscle observed in the Anamniota.

Past writers have failed altogether to recognize that the muscle does present itself in more or less well defined portions, excepting only Lightoller. He expresses the opinion that only two parts of the muscle call for recognition, a *pars intermandibularis* and a *pars extramandibularis*, and these he homologizes with the similarly-named portions of the *Csv.1* in the Selachians.

Unfortunately, Lightoller did not study the bony fishes at all, believing them to be specialized, and on that account not throwing any light upon the serial homologies of the muscles throughout the vertebrata.

Lightoller, however, has drawn attention to the fact that the *pars intermandibularis* of the *Csv.1* already, in certain of the Selachii, shows a division into anterior and posterior portions. Throughout the bony fishes, it will be remembered, this division of the anterior part of the *Csv.1* into *submentalis* and *intermandibularis* muscles is of constant occurrence. Again, in the great majority of the Amphibia, the *Csv.1* is divided very completely into these two components. In the Amphibia it was further observed that no *pars extramandibularis* is ever developed, and in this respect the Amphibia resemble the bony fishes. It was also observed that the *submentalis* of the amphibian muscle is placed on a slightly deeper plane than the rest of the muscle.

Now, taking all these facts into consideration, it would appear that the *M. submentalis* of the Lacertilian is probably the homologue of the *submentalis* of the Crocodilia, Emydura, and of the Amphibia. Like the last, it is placed in front of the rest of the muscle and occupies a deeper plane.

The *partes intermandibularis* and *extramandibularis* I have regarded as being, together, the homologue of the *pars intermandibularis* of the Amphibia.

To this conclusion I am led by the following considerations. There is no *pars extramandibularis* developed in any bony fish, any of the Dipnoi, or any other Amphibian. Further than this, the whole of the *Csv.1* of the Lacertilians is developed medially to the rami of the lower jaw, and in early stages of the development it is attached on either side to the median surface of Meckel's cartilage. In these early stages there is no extension laterally to these cartilages, no *pars extramandibularis*. The extension laterally and dorsally to the ramus of the jaw appears to be conditioned entirely by the growth of the *M. pterygoideus internus* around the ventral edge and up over the lateral surface of the jaw. It is noteworthy that it is only after this muscle has so extended, and only as it does so, that the *Csv.1* comes to have the *extramandibular* extension. There is, so far as my material permits me to judge, no example of any portion of the *Csv.1* in any Lacertilian having an *extramandibular* attachment anteriorly to the anterior margin of the *M. pterygoideus internus*, nor in any reptile which has no portion of the *M. pterygoideus internus* arising on to the outer surface of the mandible, e.g. Chelonians and Crocodilia, and *Chameleon*.

It will be remembered that the *Csv.1* of the Selachians was not divided, in any of the genera examined, into anterior and posterior divisions, except to the extent that the origin of the posterior portion was *extramandibular*, whilst that of the anterior portion was *intermandibular*. Even in this respect it was not possible to recognize any definite line of demarcation between the two parts. The origin, in nearly every case, extended gradually across the outer surface of the mandible. Actually, it will be remembered, the division was quite clearly stated to be one of anatomical convenience and not of actual separation, or definition.

In view of all the facts it appears probable that the posterior portion of the *Csv.1*, behind that which contributes to the *submentalis* of the Bony Fishes, the Amphibia and the Reptilia, is homologous throughout.

The following are the dates of publication of the four numbers of this MEMOIR :

Number 1, pages 1-62 and i-iv : 30 June, 1942.

Number 2, pages 63-132 : 30 June, 1943.

Number 3, pages 133-268 : 19 May, 1944.

Number 4, pages 268-310 : 13 June, 1945.

#### CORRIGENDA.

Page 36, line 3. For *Taeniura lymna* read *Taeniura lymma*.

Page 82, line 10 from bottom. For Coccillans read Coecilians.

Page 187, lines 10 and 15. For Caecilians read Coecilians.

Page 100, line 15. For Bridge . . . (1879) read Bridge . . . 1878.

Page 200, line 26. For Bridge in 1893 read Bridge in 1898.

Page 253, line 4. For Lightoller (1935) read Lightoller (1939).

Page 267, line 18. For spheeno-pterygoideus anterior read pterygoideus anterior.