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PART II. THE AMPHIBIA.

The Cephalic Muscles of Branchiate Amphibians: 1. The Dipnoi; 2. The Anuran Tadpole; 3. The Urodele Larva; 4. The Perennibranchiate Urodele; 5. Review.

The Cephalic Muscles of the Abranchiate Amphibians: 1. The Adult Caducibranchiate Urodeles; 2. The Adult Anura; 3. The Adult Caecilians; 4. Review; Appendix. The Laryngeal Muscles of the Amphibians.

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The Origin of the Amphibia: 1. General considerations; 2. The Evidence of the Cephalic Muscles on the Phylogeny of the Amphibia; 3. The Serial Homology of certain of the Bones in the Skulls of the Amphibia, and their bearing on the Evolution of the Class.

THE CEPHALIC MUSCLES OF BRANCHIATE AMPHIBIANS.

INTRODUCTION.

The inclusion of the Dipnoi amongst the Amphibia and their discussion in this section of the work is in accord with the conclusions arrived at as a result of reviews of their anatomy and embryology published by myself elsewhere (Kesteven, 1931*a*, 1931*b* and 1941). Those conclusions were that the Dipnoi are the most primitive amphibians known. Therefore, since they may be regarded as the most primitive members of the group which next falls for description and discussion, they are dealt with first.

The nomenclature of the muscles will continue, as far as possible, to reflect the conclusions arrived at relative to their homologies throughout the vertebrate series. It may here be explained that throughout the whole of this work it has been my practice to become completely familiar with the musculature of each group before commencing the study of the next higher group. Thus, the musculature of the branchiate Amphibia was studied before any of the abranchiate forms were examined at all. The object was to avoid the possibility of interpreting the musculature of the lower groups in terms of the higher. This has involved the use of provisional nomenclature until the whole of the work was completed, and its alteration, where required, on the completion of the work. The revision of the typescript which was entailed by this policy has permitted the inclusion in a few places of paragraphs such as this and others which include references to observations made during later portions of the work.

The use of the designation "pterygoideus" for one of the muscles of mastication in the fishes is an example in illustration of substitution of a name conveying an intimation of the final conclusion arrived at and introduced only after the work on the Reptilia was completed.

There is, however, a limit to which this policy of introducing the final conclusion into the nomenclature may be carried. For instance, it is believed that the anterior belly of the M. digastricus was derived from the Csv.1b, the M. intermandibularis, but it would, clearly, be inadvisable to apply such a designation to a flat sheet of muscle fasciculi.

The Table of Homologies is introduced to bring the work up to date, as it were, and it is introduced at the beginning with a view to presenting the conclusions of the section on the Amphibia as an introduction indicating the trend of the work.

LIST OF ABBREVIATIONS USED ON FIGURES 70–99.

A.c., Arytenoid cartilage; A.hy., M. abdomino-hyoideus; At.sc., M. attrahens scapulae; Br. 1 & 2, Branchial cartilages; Br.cl., Branchial cleft; C.he. & C.hy.e., M. interhyoideus; C.hy., Ceratohyoid cartilage; C.hy.a., M. ceratohyoideus anterior; Co., M. claviculo-branchialis; Co.hy.br., M. claviculo-hyoideus; C.p. & C.ph., M. constrictor pharyngei; Csd., Superficial dorsal constrictors; Csv.1a, M. submentalis; Csv.1b, M. intermandibularis; Csv.2a & 2b, Anterior and posterior parts of the M. interhyoideus; Cu., M. cucullaris; Dep.mn., M. depressor mandibulae; D.hy., M. dilator hyoidei; D.l. & D.lh., M. dorso-laryngeus; D.la., M. dilator laryngei; D.l.s., M. depressor labii superioris; E.br., The base of the external branchiae; Ep., Epithelium of the buccal mucosa; F.pr., Foramen prooticum; G.gl., M. genioglossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.gl.a., M. hyoglossus anterior; Hy.ph., M. hyopharyngeus; I.br., Mm. interbranchiales; I.h. & I.hy., M. interhyoideus; I.l.c., Inferior labial cartilage; I.sp., M. infraspinatus; L.a.b., Mm. levatores arcuum branchialium; L.br., The dorsal superficial branchial constrictor muscle: L.d., M. latissimus dorsi; L.hy., M. levator hyoidei; L.sc.i., M. levator scapulae inferior; L.sc.s., M. levator scapulae superior; L.v., M. laryngeus ventralis; Mas., M. massetericus; M.c. & Mk., Meckel's cartilage; Mm., Mm. interbranchiales; O-a-hy., M. omo-abdomino-hyoideus; Omo., M. omohyoideus; P.c., Pars cephalognathica; Pet.p., M. petro-hyoideus posterior; P.h.o., Posthyoid ossicle; P.n., Pars notognathica; Pr., Procoracoid; Pr.m., Processus muscularis; Pt., M. pterygoideus; Pt.a. & Pt.p., Anterior and posterior parts of the M. pterygoideus; Q-m., M. quadrato mandibularis; Qu., Os quadratum; R.ab., M. rectus abdominis; Rh.a., M. rhomboideus anterior; S.a.o. & S.a.ob., M. subarcualis obliquus; S.a.r., M. subarcualis rectus; S.a.t., M. subarcualis transversus; Sc., The scapula; S.c-t., M. spino-capitis transversus; S.l.c., Superior labial cartilage; Sph., M. sphincter laryngei; St.hy., Ceratohyoid cartilage; T., M. temporalis; V.mn., The mandibular ramus of the Vth nerve.

1. The Dipnoi.

THE CEPHALIC MUSCLES OF NEOCERATODUS FORSTERI.

(Figs. 70–73.)

(*a*) MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1b (Fig. 70).—This is the only representative of the Csv.1 sheet; there is no trace of a Csv.1a. The muscle arises from the greater part of the medial surface of the mandible and is inserted into the relatively broad mid-ventral raphe. Although not extensive superficially, the muscle is really massive, for the surface of the mandible is fairly deep. The mid-ventral raphe is a very strong membrane and the fibres are inserted onto its ventral surface. The posterior fasciculi of this muscle lie superficially to the most anterior portion of the M. interhyoideus to the extent indicated on the right side of Fig. 75, where the Csv.1b fibres have been cut away to show the underlying Cpr.2. There is a clean plane of separation between the two muscles and their separation is rendered the more easy by the different direction of their two sets of fasciculi.

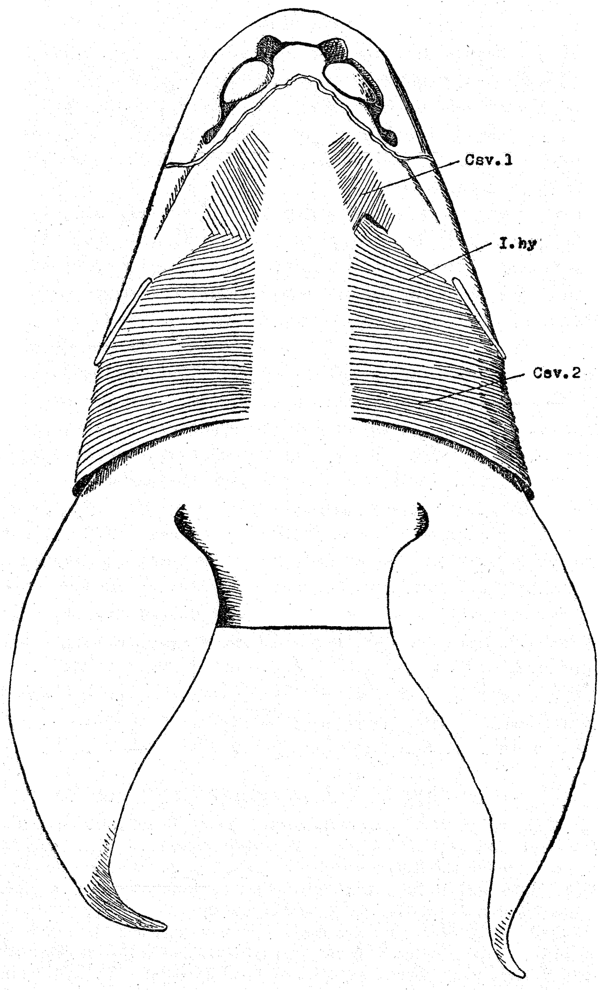

Fig. 70.—*Neoceratodus.* Ventral view of the superficial constrictors.

Innervation.—The only nerve found to give fibres to the Csv.1b was the posterior myloid nerve (Nv.my.1).

TABLE OF PROBABLE MUSCLE HOMOLOGIES.

Serial Designation.	Particular Designations.*						
	Selachians.	Holocephali.	Teleosts.	Dipnoi.	Urodeles.	Anura.	Caecillians (Apoda).
Csv.1a and Csv.1b	Submentalis. Pars intermandibularis	Protr. inf. lab. inf. and Intermandibularis	Submentalis and Intermandibularis	Intermandibularis	Submentalis and Intermandibularis	Submentalis and Intermandibularis	Intermandibularis
Csv.1b²	Pars extra-mandibularis	+	Protractor hyoidei (in part)	O	O	O	O
Pterygoideus	Levator labii superioris	+	+	+	+	+	+
Quadrato-mandibularis	+	+	Temporalis	+	Temporalis and Massetericus	Temporalis and Massetericus major, minor and minima	Temporalis and Massetericus
Levator maxillae superioris	+	Levator labii superioris (?)	Levator arcus palatini	O	O	O	Levator quadrati
Cd.1.pr.	+	O	O	O	O	O	O
Csd.2a	+	+	Hyohyoideus (upper part)	+	Depressor mandibulae Pars notognathica	Pars notognathica	Pars notognathica
Csd.2b	+	Dilator operculi	Hyohyoideus (upper part)	+	Pars notognathica	Pars notognathica	Pars notognathica
Cd.2.pr.	+	Depressor mandibulae	Hyohyoideus (upper part)	Retractor mandibulae	Depressor mandibulae, Pars cephalognathica	Pars cephalognathica	Pars cephalognathica
Levator hyoidei	+	O	Add. arcus palatini Add. hyomandibularis Add. operculi	+	Pars cephalognathica	+ in tadpoles O in adults	?
Cv.2.pr. or Interhyoideus	Interhyoideus	Interhyoideus	Protractor hyoidei (posterior part)	+	Cerato-hyoideus externus	+	+
Csv.2a	+	+	Hyohyoideus (anterior part)	+	+	O	+
Csv.2b	+	+	Hyohyoideus (anterior part)	+	+	O	+
Csd.3 to 6	+	O	O	O	+	+	?
Csv.3 to 6	+	O	O	O	O	?	O
C.pr. 3 to 6 Interbranchiales	+	+	O	+	+	+	?
Levatores arcuum branchialium	+	+	+	+	One present in one species, otherwise O	O	?
Epiarcualia obliqui	+	+	Epiarcualia recti, obliqui and transversi	O	O	O	O
Adductores arcuum branchialium	+	+	+	O	O	O	O
Ventral branchial muscles	O	O	Subarcualia recti, obliqui and transversi	Subarcualia recti, obliqui and transversi	Subarcualia recti, obliqui and transversi†	Subarcualia recti, obliqui and transversi†	Subarcualia recti
Coraco-branchiales	+	+	Claviculo-branchialis	+	?	+ (one slip only)	?
Coraco-mandibularis	+	+	O	+	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis
Coraco-hyoideus	+	+	Claviculo-hyoideus	+			

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* The + sign indicates that the muscle is present and that the serial designation has also been used as the particular. The O sign indicates that the muscle is probably absent.

† These muscles become the Petrohyoid, Dorsolaryngeus and Constrictor pharyngei muscles in the adult.

The mandibular adductors are very similar in all three Dipnoans. In addition to the two adductors of the lower jaws there are, in the Dipneumona, small retractores anguli oris, which Edgeworth (1926) describes as being developed from the adductor portion of the mandibular myotome. These are not present in *Neoceratodus.*

There are two main divisions of the mandibular adductor muscle mass, an internal and an external. Edgeworth (1911) followed Jacquet in designating the internal " temporal ", and the external " pterygoid ". These designations of Jacquet were most unfortunate, for it will appear later that it is the internal which is homologous with the pterygoid of the fishes and amphibians, whilst the external is homologous with the quadrato-mandibularis of the fishes.

THE PTERYGOIDEUS MUSCLE.

This takes origin from that part of the dorsum of the skull which is covered by the post-frontal bone (Kesteven, 1931*b*) and from the deep surface of that bone itself. It is a large nearly quadrilateral muscle with its antero-lateral and deep corner drawn out into a very strong short tendon which is inserted on to the upper edge of the lower jaw bone internal to the insertion of the quadrato-mandibularis. The tendon of insertion spreads out fanwise above, in the middle of the thickness of the muscle, so that the fasciculi arising from the skull are inserted into its deep surface and those from the post-frontal into its superficial surface. For a short distance above the insertion this tendon forms a sheath on the lateral surface of the muscle, separating it from the quadrato-mandibularis.

THE QUADRATO-MANDIBULARIS.

This takes origin from that area of the dorsum of the skull which is covered by the squamosal bone and from the deep surface of the squamosal, as well as from the anterior, free, surface of the descending process of that bone. This muscle also has a central tendinous sheet into which all the fibres, except those arising from the descending process of the squamosal, are inserted. As in the Pterygoideus, the sheet terminates anteriorly and inferiorly in a strong tendon which is inserted into the upper edge of the lower jaw bone. This insertion extends from the posterior edge of the teeth to just in front of the joint. The insertion of the Pterygoideus is medial to only the anterior half of this. The fibres arising from the descending process of the squamosal are inserted into a similar but much smaller tendon of their own, but this latter is completely fused with the other before its insertion.

Adams (1919) regarded these fibres arising from the descending process as a " masseter slip (adm.2) ". I find that the division I have described is much more in conformity with the division of the adductor mass itself. The division between the small posterior mass is much more incomplete than the other and there is no structure intervening between those two portions. On the other hand, the division I have described is much more complete, fusion only taking place between the short deep fibres of the two divisions just above the insertions. Those insertions are placed one internal to the other, and they are separable right down to the bone without the severance of any fibres or fasciculi. Finally, the maxillary and mandibular divisions of the fifth nerve, after issuing from the foramen prooticum externum, pass forward and ventrad between these two divisions, thus delimiting the primitive quadrato-mandibularis from the pterygoideus, exactly as was found in the fishes.

Edgeworth's (1926) description and illustration of these muscles and the related divisions of the Vth nerve are a little misleading. Actually, however, the discrepancy is only apparent. In the adult the origin of the quadrato-mandibularis, levator mandibulae posterior of Edgeworth, extends dorsad and mediad so that the proximal portion of the mandibular division of the nerve comes to lie internal to this muscle.

The use of the designation " levator " for this muscle, whilst mechanically correct, is, from the point of view of muscle homologies, quite wrong.

The two muscles of mastication are separated by an interval filled by loose fascial tissue, and, in their anterior portions, by the emerging second and third branches of the fifth nerve which lie in this tissue.

The fifth nerve presents the same relations to these two divisions of the muscles of mastication as was found in the fishes. The second and third emerge from the prootic foramen together and lie at once between the Mm. pterygoideus and quadrato-mandibularis. The nerve to the former muscle arises from the main division of the mandibular branch immediately outside the foramen and turns dorsad medially to the maxillary branch. The nerves to the latter muscle, two in number, leave the main branch a little later and reach the muscle laterally to the maxillary branch. The terminal myloid branch reaches the surface of the muscles close to their two tendinous ends, and immediately turns laterad and then caudad around the lateral surface of the M. quadrato-mandibularis tendon to reach the mandibular foramen. Immediately within the foramen it is joined by the mandibular branch of the seventh nerve, the chorda tympani, but does not fuse with it until the posterior myloid nerve to the Csv.1b has been given off (Fig. 72). The anterior myloid nerve (Nv.my.) gives off one more branch before itself emerging from the canal far forward.

(*b*) THE MUSCLES OF THE HYOID SEGMENT.

The Csv.2 and the Csd.2 are quite continuous posteriorly (Fig. 71). The origin of the Csd.2 is from the dorsal fascia just a little dorsally to the line of attachment of the opercular membrane. The posterior margin of the muscle is the free edge of the membrane. The insertion is per medium of the Csv.2 into the mid-ventral raphe. The continuity of the two portions of the sheet is interrupted in the region of the operculum and the suboperculum by two lines of insertion on to the deep surface of those bones. The antero-dorsal portion thus delimited is, apparently, homologous with the M. levator operculi of the bony fishes. The insertion of the fasciculi of this muscle is along a line a short distance below the dorsal margin of the deep surface of the operculum. A little distance below this line a second small sheet of fasciculi arises; these are inserted on to the deep surface of the suboperculum, and below them the Csv.2 takes its origin from the same surface.

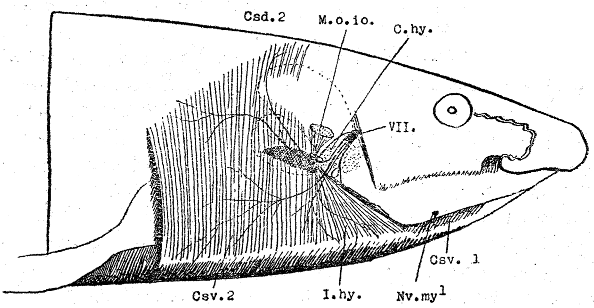

Fig. 71.—*Neoceratodus.* Lateral view of the superficial constrictors.

In addition to these small muscles beneath the opercular bones there is a small but remarkably massive muscle which arises from an oval area of the deep surface of the operculum infero-anteriorly. The fasciculi are all gathered to a short stout tendon which is inserted on to the upper edge of the deep surface of the suboperculum at its anterior end.

The Cpr.2, M. interhyoideus, is very similar to that muscle in the Elasmobranchia. It arises from a small area on the lateral surface of the ceratohyoid just behind the angle of the jaw and deep to the mandibulo-subopercular ligament. Its anterior fasciculi run forward at a sharp angle, the posterior fasciculi run directly transversely, those in between having intermediate directions. The muscle lies in the same plane as, and is inseparable from, the anterior fasciculi of the Csv.2. The most anterior fasciculi are inserted deep to the posterior fibres of the Csv.1.

These hyoid muscles are, of course, innervated by the motor twigs of the facial nerve. The location of these twigs over the surface of the muscles is shown in Fig. 71.

The seventh nerve gives off the palatine branch whilst it is within the facial canal. This palatine canal leaves the other a short distance from the cranial end and passes directly ventrad; just before it reaches the ventral surface, the canal turns rostrad and mediad and runs forward for a short distance within the cartilage and then reaches the surface of the cartilage so that the nerve lies in a parabasal canal whose walls and roof are cartilaginous and whose floor is supplied by the parasphenoid bone.

Continuing dorso-laterally with a slight caudal inclination, the ramus hyomandibularis issues from its canal between the otic and basal roots of the quadrate, as previously described

(Kesteven 1931*b*). Almost at once the nerve breaks into three branches. The first leaves the anterior side of the nerve, runs laterad and rostrad behind the otic root and ramus of the quadrate for a short distance and then, turning rostrad, plunges into a canal which tunnels the ramus of the quadrate, a short distance above the articular head, in a direction ventrad and rostrad. The nerve issues from this canal under those fibres of the M. quadrato-mandibularis which arise from the front of the quadrate. If these fibres be pulled inward, without disrupting their attachment, the nerve is brought into view as it runs forward along the lateral edge of the muscle to reach the myloid foramen in the mandible. A short distance within that canal, just beyond the departure of the posterior myloid nerve, this branch of the facial fuses with the myloid branch of the fifth nerve. This has been identified as the Chorda tympani (Nv.ch-t., Fig. 71).

The next branch of the hyomandibular trunk is the lateralis component. This leaves the anterior side of the main nerve and enters, almost immediately, the lateral line canal which lies nearly parallel with the posterior margin of the quadrate and anterior margin of the operculum.

A second inferior mandibular branch next leaves the same side of the main nerve and runs ventrad, laterad and rostrad, deep to the anterior margin of the operculum, then deep to the mandibulo-subopercular ligament and forward along the medial edge of the ventral surface of the mandible for a little distance. This probably communicates with the posterior myloid nerve, but the communicating twig was not found.

The hyomandibular nerve now breaks up into its several motor twigs to the hyoid muscles, whose distribution is shown in Fig. 76.

There is no reason to doubt the complete homology of the two superficial constrictor sheets, Csv.1b and Csv.2, with the first and second sheets in the fishes. One should, however, note that in *Ceratodus* the resemblance of the hyoid sheet is to the Selachians and Holocephali rather than to the bony fishes. In these latter the hyoid constrictor runs dorsad under cover of the opercular components, whilst in the dipnoan the sheet is, in its posterior portion, quite superficial. It is true that in *Ceratodus*, as in the teleosts, the anterior portion of the dorsal constrictor lies beneath the opercular bones, and it would appear that in the bony fishes the more complete bony equipment of the opercular flap had invaded the muscular sheet, but that the development of the branchiostegal membrane had captured the sheet whilst the opercular skeleton had grown backward in a fold superficial to that membrane. It is probable that the branchiostegal rays are really superficial to the muscle sheet in all the fishes. They are obviously so in the eels.

In *Neoceratodus* there is no branchiostegal membrane, the opercular skeleton is but poorly developed, and the conditions generally are as in the Holocephali.

Edgeworth (1911, p. 188) says that " In Ceratodus the myotome of the mandibular segment spreads upwards lateral to the Gasserian ganglion and separates from the lateral half of the intermandibularis . . . It divides into outer and inner portions . . . the former of which . . . arises from the trabecular wall and the latter from the outer and anterior surface of the quadrate. The intermandibularis joins its fellow in a median raphe and becomes attached laterally to Meckel's cartilage ; its posterior end extending backwards underlies the fore part of the interhyoideus ", and (p. 212) " The hyoid myotome and the interhyoideus spread backward in the opercular fold and form . . . anteriorly a levator hyoidei inserted into the upper end of the hyoid bar, and an interhyoideus, and posteriorly a continuous ventro-dorsal . . . sheet in the operculum . . . the anlage of the hyomaxillaris ligament is cut off from the upper edge of the interhyoideus and spreads forwards to the hind edge of Meckel's cartilage."

His description of the arrangement of the hyoid muscles in a 55 mm. specimen of *Protopterus* is also of interest here (Edgeworth, 1926, p. 724). " The levator hyoidei is inserted into the knee of the hyoid bar . . . The most posterior fibres of the constrictor hyoideus form a continuous dorso-ventral sheet, but the majority have separated into three portions—dorsal, middle and ventral. The dorsal portion passes from the auditory capsule to the operculum, the middle portion from the operculum to the suboperculum, and the ventral from the suboperculum to the mid-ventral line. The middle portion has extended forwards, and its anterior portion forms a separate muscle, the retractor mandibulae, of horizontal fibres easily distinguishable from the vertical fibres of the constrictor. The dorsal edge of the retractor rises and, in front of the dorsal portion of the constrictor, is attached to the auditory capsule. The posterior end of the retractor is attached to the operculum and suboperculum. The muscle extends forward in front of the hyoid bar and is inserted into the hind end of the jaw to the splenial and angular bones. The anterior edge of the ventral portion of the constrictor is slightly separated from, and overlaps, the hind edge of the interhyoideus."

Comparing these descriptions with the muscles in the adult *Neoceratodus*, we note that the levator hyoidei of the larval form is no longer present and that there is now no recognizable overlap between the contiguous edges of Csv.1 and Csv.2, but that they are indistinguishably blended. There is, however, a very close resemblance between the hyoid sheets in the adult *Neoceratodus* and the 55 mm. *Protopterus*, more particularly in the division of the upper end of the sheet beneath the opercular bones.

In front of this point in the adult *Neoceratodus* we find a muscle, which is essentially similar to the interhyoideus of the selachians, situated deep to the fore end of the superficial hyoid constrictor and to the posterior end of the intermandibularis.

It would appear from Edgeworth's Figure 19 that the overlap of the anterior portion of the interhyoideus beyond the posterior margin of the intermandibularis, in the 19 mm. *Protopterus*, is dorsal to that muscle.

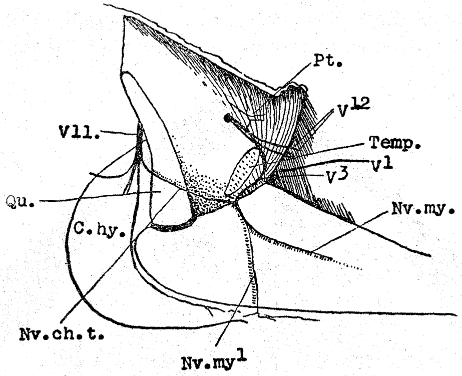

Fig. 72.—*Neoceratodus.* Semi-schematic presentation of some of the branches of the Vth and VIIth nerves. C.hy., Ceratohyoid; Nv.ch-t., Communicating branch of the VIIth to the myloid branch of the Vth; Nv.my., Myloid nerve; Nv.my^1., Posterior myloid nerve; Temp., Tendon of the tempo-masseteric muscle.

If this be so, then we may conclude that it is the anterior portion of the hyoid constrictor sheet which persists as the interhyoideus in the adult *Neoceratodus*. It also seems not unreasonable to assume, for the present, that the antero-posteriorly directed lateral fibres of the interhyoideus are homologous with the retractor mandibulae of the *Protopterus*.

Edgeworth (1926, p. 724) remarks that Rudge was of the opinion that the retractor mandibulae of the Dipneumona was homologous with that portion of the Csd.2 which Lightoller has since designated the pars quadrato-hyoidea. With this opinion Edgeworth is unable to agree. He points out that a pars quadrato-hyoidea is not present in the dipneumonous lungfishes, and that the retractor results from a relatively late forward growth from the middle portion of Csd.2.

To the present writer it appears that both the abortive muscle of *Neoceratodus* and the fully developed retractor of the Dipneumona are to be compared with the hyoid component of the retractor hyoidei of the bony fishes, the whole of the deep sheet to be regarded as homologous with the interhyoideus of the elasmobranchs, but presenting a partial modification and specialization. A deep intermandibular fascia which is present in *Neoceratodus* may be actually the homologue of the anterior portion of the protractor hyoidei. Unfortunately we do not know the later development, but if it be a forward extension of the "hyomaxillaris ligament" of Edgeworth then it is developed in a manner very similar to the protractor hyoidei of the bony fishes.

I have been able to dissect specimens of *Lepidosiren* measuring 48 to 50 mm. These, which I have to thank Professor W. E. Agar for, are young which have just completed the metamorphosis, and their muscular anatomy must be essentially similar to that of the adults.

The retractor mandibulae is an obvious little muscle lying along the outer edge of the skull, along the surface of the squamosal bone. There can be little doubt that it is completely homologous with the pars cephalognathica of the depressor mandibulae of the whole of the amphibians and reptiles. The homology of this muscle is discussed later, and it is regarded as the modified form of the pars epihyoidea.

(c) BRANCHIAL MUSCLES (Fig. 73).

Musculi Marginales. Interbranchial Muscles.

Cpr. 3, 4, 5 and 6.—Each of these has a fleshy origin from the under side of the cartilaginous roof of the gills near the lateral margin. From this origin each muscle passes almost vertically downward but with a curve first outward and then back medially. Where they take origin, the fasciculi of each muscle are gathered together to produce an oval fleshy belly, but on entering the interbranchial septum they are separated and spread out to form a thin layer immediately beneath the anterior gill filaments. As they are followed downward it is found that they spread steadily to form a slowly widening ribbon, then, a little more than two-thirds of the distance towards the inferior angle of the pouch, the muscle fibres quite suddenly give place to fine tendinous fibres which are continued to the inferior margin of the septum.

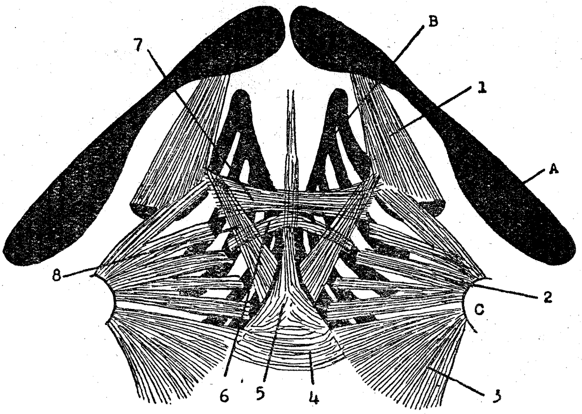

Fig. 73.—*Neoceratodus.* A semi-schematic presentation of the ventral branchial muscles, as seen from below. 1, M. subarcualis rectus; 2, The five Mm. coracobranchiales; 3, M. cucullaris; 4, M. sphincter oesophagi; 5, M. subarcualis transversus V; 6, M. subarcualis transversus III; 7, Mm. subarcuales transversi I and II; 8, Mm. subarcuales II-V; A, Hyoid arch; B, Branchial arches; C, The coracoid.

There is no seventh deep constrictor.

These muscles are designated constrictor branchiales by Edgeworth in his description of the development in *Protopterus* and *Lepidosiren* (1926, p. 727).

Their homology with the interbranchial muscles of the Selachii appears quite obvious, although they are no longer related to the superficial constrictors, these latter being absent. The resemblance to the interbranchial muscles of the Holocephali is very close. One observes that these dipnoan interbranchial muscles differ from those of the fishes in that they arise from the skull dorsally instead of from the upper elements of the branchial arches, extrabranchials or pharyngobranchials. On the other hand, it should be noted that this dorsal origin for these muscles is correlated with, and probably conditioned by the absence of the caudo-dorsal " return " direction of any part of the branchial arch skeleton dorsally. In the dipnoan the segments of the branchial arches are all in the same plane, so that a dorsal attachment for muscles external to them and in the same plane must of necessity be to skeletal or fascial structures dorsally.

We shall find essentially similar relations present in the anurous amphibian tadpoles.

It will be remembered that there are no interbranchial muscles developed in any of the bony fishes.

Levatores 3 to 7 (levatores arcuum branchialium) are very similar muscles. Each has a fleshy origin from the under surface of the temporal cartilaginous gill-roof just along the line where that merges with the side wall of the skull and otocrane. Each is a short, round muscle and its point of origin is directly above the point of its insertion into the dorsal end of the branchial arch, in front of and medial to the origin of the deep constrictor. The seventh is the longest of these muscles; the fifth branchial arch is not fully developed and does not reach so far dorsally as the others.

The Cucullaris (Fig. 73) arises immediately behind the seventh levator arcuum by a strong tendinous band of fibres which "fans" out at once, and also from the antero-ventral surface of the post-temporal immediately behind the origin from the skull and at a slightly lower level. From this origin the fibres spread out and, passing ventrally and medially, gain insertion into scapular and suprascapular regions of the pectoral arch. Inferiorly it is impossible to separate this muscle from the fifth coraco-branchial muscle. The two together form a strong muscular wall for the fleshy portion of the posterior wall of the atrium. The condition recalls that described in *Dasyatis* (p. 46).

These branchial levators recall more strongly those of the selachian fishes than those of the teleosts. In the latter the levators are closely bunched together at their origin from the skull, whilst in the Dipnoi, for the dipneumonous forms are similar to *Neoceratodus,* they are spaced out, one behind the other in regular sequence, as in the Selachii.

The extensive cucullaris recalls that of the bony fishes in its development from a single branchial myotome. Greil (1908) described the muscle plate of the fifth branchial arch as developing into four muscles dorsally, of which the most posterior is that which he designated the "levator scapulae". This is apparently the cucullaris of my description. So far as I am aware, the development of the cucullaris in the Dipneumona has not been observed, but Edgeworth (1926, p. 725) says of the larvae of *Protopterus* and *Lepidosiren* that "In the fifth arch there is a constrictor branchialis V which extends downwards through the arch and is continuous ventrally with the hinder part of the Coraco-branchialis V" and that in the 55 mm. specimen (of *Protopterus*) "Constrictor branchialis V and the corresponding portion of coraco-branchialis V have undergone a considerable extension backwards and form a broad sheet of dorso-ventral fibres, which arise from the back of the auditory capsule and, behind that, from the post-temporal bone which has now developed."

It is highly probable that later stages would reveal that this backward extension is the inception of the development of the cucullaris.

It would appear from Edgeworth's work (1911) that the cucullaris of the bony fishes is always developed from a single branchial muscle plate when present at all, but that in the Selachians (1911 and 1926*b*) the cucullaris is developed from small portions of the dorsal ends of several branchial muscle plates.

Whilst thus resembling the cucullaris of the bony fishes in its development, the muscle in the dipnoans, as observed in the adult, is more similar to that of the selachians. In the bony fishes the muscle is small and so closely resembles the levatores arcuum branchialium that it has been so designated by several writers. In the selachians it is an extensive muscle very similar to that of the dipnoans but, in the generality of instances, more massive.

(*d*) THE HYPOBRANCHIAL MUSCLES.

Subarcuales transversi (Fig. 73).—There are three of these. Numbers one and two arise together from the first two ceratobranchial cartilages and from a fibrous band between the two cartilages. The third arises from the third ceratobranchial. The three muscles incline toward one another at the mid-line and there form a continuous sheet immediately beneath the bases of the third and fourth ceratobranchial cartilages. There is no median tendinous raphe; the fibres are in part continuous and in part interlace at the mid-line. According to Edgeworth, Jacquet designated these Mus. chiasmique. They are the second and third interbranchial muscles of Greil.

Constrictor pharyngei (Fig. 73).—Edgeworth tells us that this is developed from the fifth subarcualis transversus; it is therefore included in this subsection, but the longitudinal fibres which enter so largely into its constitution suggest that there is also another component. The muscle arises from the median surface of the fifth ceratobranchial on each side, and forms a muscular layer to the floor of the pharynx between those cartilages. The posterior fibres pass transversely and either are continuous or interlace across the mid-line. The middle fibres bend forward and either interlace or are continued forward as two parallel, closely touching bundles of fasciculi which terminate in a common tendon ventral to the chiasmatic muscle. This tendon is inserted into the tough fibrous tissue in the floor of the mouth behind the hyoid copula.

Subarcuales recti.—Two pairs of recti are present, the posterior according to Edgeworth being composite muscles.

Subarcualis rectus 1 (hyo-branchialis) (Fig. 73) takes origin from the posterior face of the ceratohyoid near its median end. A stout fleshy muscle at its origin, it flattens out and broadens as it passes caudally and slightly laterally to be inserted on to the inferior edge of the first ceratobranchial along the middle third of its length.

Subarcuales recti 2, 3, 4 and 5 (Fig. 73) form one continuous ribbon of muscle which arises in front from the first ceratobranchial cartilage just medial to the median margin of the insertion of S.arc.r.1 and passes back beneath the other arches, being bound to each ceratobranchial as it passes below it, to be inserted on to the base of the fifth ceratobranchial cartilage.

The coraco-branchiales (Fig. 73).—These are five ribbon-like muscles which arise, one behind the other, from the middle of the length of the inferior surface of the ceratobranchial cartilage and converge to be inserted close together on to the coracoid portion of the pectoral arch at a little distance from the mid-line on each side. The last of these is much broader than the others, and, as already described, is inseparable from the lower and median margin of the cucullaris.

(*e*) THE HYPOBRANCHIAL SPINAL MUSCLES.

The Coraco-mandibularis (genio-hyoideus) arises behind from the coracoid arch on either side of the mid-line. It is a flat muscle and tapers to its insertion by a short ribbon of tendon into the symphysis.

The Claviculo-hyoideus is a massive tetrahedral muscle. The base of this tetrahedron is at its origin from the coracoid and from a membrane dorsal to the coracoid which is attached to the pectoral arch on each side. One of the sides of the muscle is exposed by the removal of the ventral constrictors and the coraco-mandibularis ; the other two sides lie against the coraco-branchial muscles. The apex is inserted into the hyoid copula.

The Genio-hyoid ligament is a short, round ligament which binds the hyoid copula to the symphysis.

There remains for description a slender fleshy rounded muscle which arises from under the edge of the dorsal squame of the squamosal (Kesteven, 1931). At its origin it lies above the outer edge of the first gill septum, just lateral to the origin of Cpr.3, the first interbranchial muscle, near the lateral margin of the cartilaginous atrial roof. From this origin the muscle passes medially, forward and ventrally, to be inserted into the epibranchial cartilage of the first arch along with but posterior to the first levator arcuum branchialium.

Actually this muscle arises almost in continuity with the first branchial deep constrictor and is inserted almost in continuity with the first branchial levator. Since the levator is developed from the medial and dorsal portion of the general constrictor sheet, it appears that this should be regarded as an aberrant piece which was situated at the line of fission between the two derivatives and has remained attached to both. It was only found on one side of the specimen dissected.

From the deeper layer of the branchial muscle plates there are developed, in the selachians, epiarcual branchial muscles and interbranchial muscles, in the bony fishes, epiarcual branchial muscles and subarcual branchial muscles, and in the dipnoans epiarcual, interbranchial and subarcual branchial muscles.

It has been demonstrated that the interbranchial muscles of the selachians and the subarcual muscles of the bony fishes are both developed from the same ventro-median portion of the primordial muscle plate. Ontogenetically, therefore, these muscles are homologous and they have been so regarded in a previous section of this work. We have now to consider in what light we must view the interbranchial and subarcual muscles of the dipnoans.

It appears to the writer that, beyond question, the subarcual muscles in the Dipnoi and Teleostomi are completely homologous, and it might, therefore, appear to follow that the interbranchial muscles of the Selachii cannot also be homologous with the subarcual muscles of the Teleostomi. It would certainly appear that we must regard the primordial muscle plate in the bony fishes as having grown down and given rise to the subarcual muscles and as having become completely aborted between these and the epiarcual muscles, whilst in the Dipnoi the intervening portion has persisted and given rise, as in the Selachii, to the interbranchials.

A strict interpretation of the facts is perhaps as follows. The Dipnoans present a more primitive condition than the bony fishes ; in them we are permitted to observe the intermediate stage in the evolution of the subarcual muscles. In this stage they arise as ventral extensions from the ventro-median portion of the deeper part of the primitive constrictor sheets. In the bony fishes a further stage has been arrived at. In this the connecting piece, which we designate the interbranchial muscle, has been lost.

If this be correct then, whilst there is ontogenetic evidence that the subarcual muscles are homologous with the interbranchials of the Selachians, phylogenetically the interbranchial muscles are homologous in the Dipnoi and the Selachians, as also are the subarcual muscles in the Dipnoi and the Teleostomi.

2. The Anuran Tadpoles.

(Figs. 74–78.)

The following description of the masticatory and branchial muscles of the anuran tadpoles is taken directly from dissections of the tadpole of *Mixophyes fasciolatus.* The illustrations are similarly derived. I was fortunate in the spring of 1932 to obtain a large number of these tadpoles and was able to rear them till some had acquired indubitable specific characters. They were of relatively large size, measuring 7 to 8 cm. in length, the heads being 1–5 cm. long and of equal width and only slightly less deep. I was able to dissect out most of the muscles after staining with picric acid and borax carmine. Doubtful points in the anatomy and innervation were checked or corrected by the study of thick lightly-stained sections rendered transparent by the Spalterholtz method. I have, moreover, made careful comparison with preparations of the smaller tadpoles of *Hyla aurea, H. cerulea, Crinia* sp.* and *Lymnodynastes* sp. The resemblance was so complete that no differences were observable. The primordial cranial and branchial structures were so similar one to another and to those of *Rana,* that one is justified in making the assumption that the description here given of these muscles may be accepted as being truly and completely one of the muscles of the anuran tadpoles generally.

The primordial cranium is so essentially similar to that of *Rana* that I have reproduced, only slightly modified, Gaupp's illustration thereof in illustration of that of *Myxophyes.* I have, however, preferred to designate the suprarostral cartilage " upper labial " and the infrarostral " lower labial " in order to convey their complete homology with the corresponding structures in the fishes.

The primordial visceral skeleton also is essentially similar to that of *Rana.* The hyoid, or first copula, is rather better developed and is articulated on each side to the anterior edge of the hyal cartilage. The two hyal cartilages are, as in *Rana,* broad and massive. They articulate one with the other in the mid-line, and on each side with the inferior edge of the muscular (antorbital) process. The second copula lies in contact with the median edges of the hyal cartilages in their posterior halves, these edges diverging to accommodate the copula. This second copula is a small quadrilateral plate which overlaps inferiorly the similarly shaped, but larger, planum hypobranchiale. This latter shows no division into right and left halves, as it does in *Rana.* The four branchial arches are articulated to the lateral margin of the hypobranchial plate much as in *Rana,* and have similarly serrated edges.

MIXOPHYES TADPOLE.

Stage A. (Figs. 74–76.)

The dimensions of this stage are those given above. There is as yet no sign of the development of either limb, and the lungs are but small, apparently functionless organs, for the little animals were observed not to swim to the surface for air as did those in which, at a later stage, the lungs were found to be much enlarged.

The Submentalis muscle (Csv.1a, Fig. 74) appears as a small nodular condensation of tissue which takes the picric acid stain well, and stands out quite clearly, immediately behind the symphysis of the inferior labial cartilages. As yet no definite muscle fibres are observable under the dissecting microscope.

The Intermandibularis muscle (Fig. 74, Csv.1b) is a very fine thin band of muscle fibres which arises on each side on the anterior and superior surface of Meckel's cartilage along the centre one-third of its length and passes round the lateral surface of the cartilage, and then passes caudally, ventrally and medially to be inserted with its antimere into a median ventral raphe.

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* Of these I have had some hundreds for study, presenting in all forty-seven stages of development from ovum to adult form.

In situation this muscle encloses a triangular area whose third side is the posterior margin of the inferior labial cartilages. Where the fibres leave Meckel's cartilage the band of fibres lies in the horizontal plane, but as they pass medially the more posterior fibres come to occupy a position dorsad to the anterior fibres so that the median raphe is almost in the vertical plane.

Innervation.—Both these two muscles are innervated by the mandibular ramus of the Vth nerve. The actual innervating branch to the Csv.1b was quite plainly seen leaving the main nerve just as that passed across the outer surface of Meckel's cartilage. The nerve to the Csv.1a was found in stage C described later.

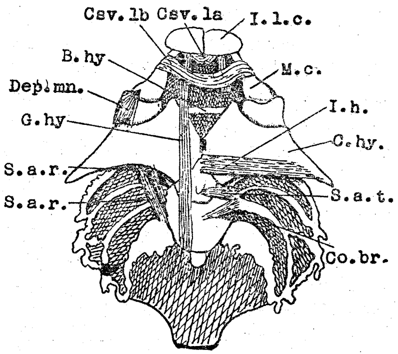

Fig. 74.—*Mixophyes* tadpole, stage A.—Ventral aspect.

The Interhyoideus muscle, Csv.2 (Fig. 74, I.h.), arises from the mid-ventral raphe and is inserted on each side on to the inferior, postero-lateral, corner of the hyoid cartilage. The muscle is fairly stout, oval in transverse section, and a certain number of the fasciculi cross the mid-line and arise amongst those of the opposite side.

Innervation.—The motor twig for this muscle leaves the hyomandibular ramus of the VIIth nerve after that has passed mediad and ventrad from between the two heads of the depressor mandibulae muscle.

The Dilator hyoidei muscle, Csd.2 (Figs. 75, 76, D.hy.), arises from the dorsal edge of the antorbital muscular process and passes caudad, laterad and ventrad across the external surface of the process, to be inserted into the ventral edge of the lateral margin of the hyoid cartilage immediately lateral to the joint with the process and in front of the origin of the interhyoideus muscle. The dilator hyoidei is a short, thick, relatively broad muscle and occupies practically the whole of the concave depression on the outer surface of the muscular process.

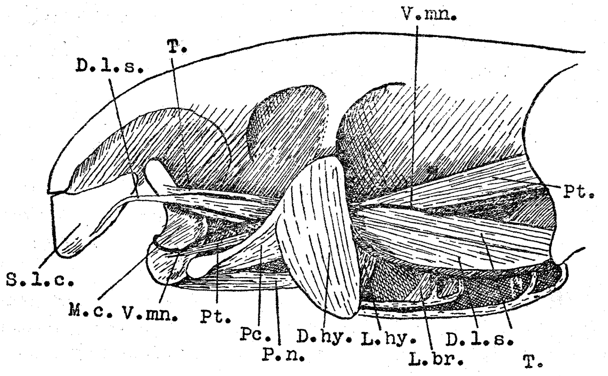

Fig. 75.—*Mixophyes* tadpole, stage A.—Lateral aspect.

Innervation.—The motor twig for this muscle leaves the hyomandibular trunk of the VIIth nerve before it passes beneath the depressor mandibulae muscle.

The Depressor Mandibulae muscle presents itself even in this early stage in the two portions which Lightoller has designated partes cephalognathica and notognathica. It must, however, be remarked that (though I have made use of those designations with a view to establishing their identity with the parts of the muscle in the adult frog) at this stage of its development the former is not entitled to its name, for it does not arise from the cranium but from the mandibulo-maxillary visceral skeleton.

The Pars Cephalognathica (Figs. 75, 76, P.c.) arises under cover of the dilator hyoidei, from the lower part of the outer surface of the muscular process.

The Pars Notognathica (Fig. 75, P.n.) arises from the lateral edge of the hyoid cartilage under cover of the anterior edge of the same muscle.

The two portions taper rapidly and are inserted by a short common tendon into a backward turned spur on the infero-lateral corner of Meckel's cartilage.

The contiguous edges of these portions are separated by a very narrow interval, and at their origins the joint between the process and the hyoid cartilage lies deep to the interval. The uppermost fibres of the pars cephalognathica have an inclination ventrad, the lowermost fibres of the pars notognathica an inclination dorsad, as they pass forward to their insertion.

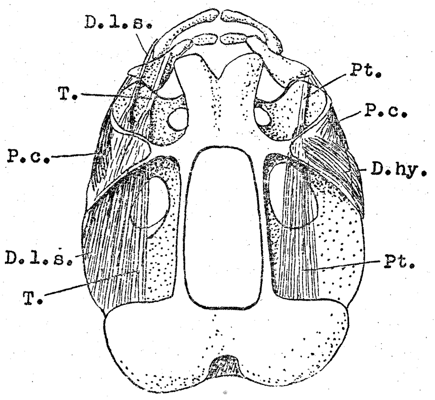

Fig. 76.—*Mixophyes* tadpole, stage A.—Dorsal aspect.

Innervation.—This is by twigs of the hyomandibular trunk of the VIIth nerve as it passes from beneath the dilator hyoidei muscle, that is to say, dorsally to it.

The mandibular adductor muscle mass presents five distinct components. Together they fill the space between the ethmoid region of the skull and the upturned antorbital muscular process, and, extending backward, cover the floor of the orbit. Although thus closely packed, they are quite readily dissected asunder.

The Depressor Labii Superioris Longus (Figs. 75, 76, D.l.s.) is an elongated ribbon of muscle fibres which takes origin from the outer margin of the floor of the orbit along its length. It tapers gradually as it extends forward and its fibres give place to a fine tendon as they reach the transverse level of Meckel's cartilage. The tendon is continued onward in the loose tissues of the side of the mouth and is inserted into the superior labial cartilage about the middle of its length, close to the inferior margin, whereon are set the horny larval teeth.

The Depressor Labii Superioris Brevis is a much shorter muscle which arises from the anterior edge of the muscular process and passes forward, covering the anterior end of the depressor longus to be inserted into the tendon of this latter muscle.

The Temporalis (Figs. 75, 76) arises from the floor of the orbit medially to the long depressor. As it extends forward it comes to lie ventrally to the anterior end of the long depressor. Like the other muscles, it tapers to a fine, but short, tendon which is inserted into the superior surface of Meckel's cartilage about the junction of the posterior and middle thirds of its length.

The Pterygoideus Muscle (Figs. 75, 76) is similar in shape to the temporalis. It arises from the cranial wall and orbital floor medially to the suborbital vacuity. It passes forward across the antorbital bar beneath the other three muscles and is inserted into the upper surface of Meckel's cartilage behind the temporalis.

The Massetericus is a very thin sheet of short muscle fibres which arise from the medial surface of the muscular process close to the anterior edge thereof and passes cephalad, ventrad and slightly laterad, to be inserted into the proximal end of Meckel's cartilage just in front of the insertion of the pterygoideus.

Innervation.—All these muscles of mastication are innervated by twigs from the mandibular ramus of the Vth nerve as it passes them.

The mandibular ramus of the Vth nerve appears on the floor of the orbit between the pterygoideus muscle on the inner side and the temporalis on the outer. It runs forward for a short distance along the medial border of the temporalis and then, above the antorbital transverse bar, it passes dorsally to the muscle, crossing it from within outward and forward. Under cover of the muscular process it perforates the depressor labii superioris longus. It next bends laterad and ventrad and crosses the outer and superior surfaces of Meckel's cartilage between the insertions of the temporalis and pterygoideus in front and the masseter and depressor mandibulae behind. Having crossed the cartilage of the lower jaw, it turns forward and was traced nearly to the symphysis ; the twig to the Csv.1b was clearly seen in several dissections. No twig was observed turning backwards to reach the interhyoideus muscle.

Hypobranchial Muscles.

Two subarcuales recti are recognizable (Fig. 74, S.a.r.), but, as they extend further than across a single interbranchial interval and both arise from the first ceratobranchial cartilage, it were only guesswork to attempt their segmental designation.

They are two narrow, thin bands of fibres which run parallel, separated by a narrow interval. The medial muscle arises from the first ceratobranchial cartilage a little distance from the lateral edge of the planum hypobranchiale and passes back to be inserted into the third ceratobranchial* and hypobranchial plate just where the two are articulated. The lateral muscle arises laterally to the other and passes back and medially to be inserted into the point of articulation of the hypobranchial plate and the fourth ceratobranchial.

Only one subarcualis transversus (Fig. 74, S.a.t.) was found in tadpoles of this stage. It is a short thin muscle which arises from a spur on the centre-point of the second copula, first basibranchial cartilage, by a fine short tendon. It rapidly becomes wider as it passes laterad to be inserted into the bases of the first and second ceratobranchial cartilages just beyond the margin of the hypobranchial plate.

A single marginal muscle (interbranchial muscle) is indicated only at this stage by a fine brightly-stained line of tissue along the external surface of the first branchial cartilage. This is in the position in which the muscle itself is developed in stage B.

Innervation.—I have not been able to determine the innervation of these muscles.

The Claviculo-branchialis (Fig. 74, Co.br.).—This name is applied to a muscle very similar to the subarcualis transversus, which takes origin immediately behind it from the hypobranchial plate just at and medially to the root of the third branchial arch and, tapering, extends mediad, slightly caudad and ventrad to be inserted into the tissues of the pericardial wall.

Innervation not determined.

The Levator Hyoidei (Fig. 75, L.hy.) arises from the lateral edge of the meta-pterygoid process. This is an exceedingly fine triangular sheet of muscle fibres. The origin from the meta-pterygoid presents a short gap dividing the muscle into anterior and posterior halves, and suggestive of a duality of the muscle. The insertion is by the point of the triangle into the hyoid cartilage. The point of insertion is on the postero-lateral edge behind the insertion of the dilator hyoidei and posterior to that for the origin of the interhyoideus.

Innervation.—This is by twigs from the ramus hyoideus VII after it has been joined by the communicating branch from the IXth, and as the nerve passes under cover of the muscle.

The Dorsal Superficial Branchial Constrictors (Csd.3–6) are represented by an inconstantly interrupted sheet of fibres (Fig. 75, L.hr.) which arise from the lateral edge of the meta-pterygoid process behind the levator hyoidei and extend ventrad to be inserted into the outer wall of the branchial chamber along the mid-lateral line. The number of fasciculi into which the sheet is

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* The four branchial arches are quite unsegmented so that the designation ceratobranchial or epibranchial is to be understood as purely topographical and one of convenience only. The distal or epibranchial ends of the arches are united by a serrated strip of cartilage which gives to them the appearance of having, each, bent posteriad till it came into contact and fused with that next behind.

divided by the interruptions is three or four, and the situation of the fasciculi is not sufficiently constant to allow one to hazard an opinion as to actual number of superficial dorsal constrictors represented, basing that opinion on the structure of the muscle. On the other hand one is reasonably justified in postulating a number equal to that of the branchial arches.

Innervation.—It can be stated that these muscles are innervated by twigs from the ninth and tenth nerves, because these nerves only were found in their proximity. The extreme tenuity of the twigs, however, renders it extremely difficult to determine their origin, they are so easily torn loose in the attempt to dissect them out.

The Constrictor Pharyngei muscle arises from the postero-lateral and ventral corner of the auditory capsule. It passes caudad, mediad and ventrad around the posterior wall of the branchial cavity.* It does not reach the mid-line, but is inserted a little distance therefrom into the posterior and ventral wall of the branchial cavity.

The Cucullaris muscle arises medially to the constrictor pharyngei from the inner corner of the postero-ventral angle of the auditory capsule. From this origin it passes mediad and ventrad between the posterior branchial and anterior abdominal walls. At its origin and for a little distance therefrom it is narrow and ribbon-like and in this part of its length it is more closely related to the branchial wall; at about the middle of the total length of the muscle it passes over the space between the two and becomes more intimately bound to the abdominal wall and, expanding fan-wise, it is inserted into a tendinous intersection, to the other side of which the anterior end of the rectus abdominis is attached. The line of this intersection is in the horizontal plane a little ventral to the middle of the dorso-ventral diameter.

Innervation.—The motor twig to the muscle was not found in any of the dissections of this stage, but, as it was subsequently demonstrated that this becomes the cucullaris muscle of the adult frog, one very naturally assumes that it is innervated, as is the adult muscle, by the Xth nerve.

The superficial ventral branchial constrictors.—Before describing the muscle which is believed to represent these muscles of the fish, it is necessary to recall the fact that the branchial arches bend ventrally as they extend laterally from their joint with the hypobranchial plate. The pericardium lies behind but in the plane of the triangular space thus formed below and between the branchial chambers. The whole of this space, which tapers to an apex immediately below and behind the second copula, is enclosed below by a relatively strong membrane which is attached on each side to the ventral convexity of the branchial arches, beyond this the arches are attached to the membrane as it rises on each side to gain an attachment to the lower margin of the meta-pterygoid process medial to the attachment of the levator hyoidei and superficial dorsal branchial constrictor muscles.

I return now to the ventral branchial constrictors (Csv.3). Traversing the floor of the pericardial space there are a series of transverse fasciculi which are inserted into a median raphe and which arise on each side along the lateral limit of the space. On each side posteriorly some of these fibres ascend further on the lateral wall of the branchial chamber to arise from a short longitudinal branchio-abdominal ligament which, later becoming attached to the coracoid, is recognizable in the adult frog as a coraco-cephalic ligament.

Innervation.—Though it cannot be definitely asserted, it is believed that this diaphanous muscle is innervated by twigs from the IXth and Xth nerves.

HYPOBRANCHIAL SPINAL MUSCLES.

The Geniohyoideus Muscle (Fig. 74, G.hy.) lies dorsally to the Csv.1a and 1b and to the interhyoideus. It is a narrow band of fibres which may be regarded as arising from the posterior margin of the hypobranchial plate. From this origin it passes directly forward, between the interhyoideus and the hyoid cartilage, and then dorsally to the two divisions of the first superficial ventral constrictor to be inserted into the inferior labial cartilage laterally to the tiny nodular primordium of the Csv.1a.

The Quadrato-abdominis Muscle is an exceedingly transitory structure. It was present in about 50% of the dissections of this stage, and provided evidence that they were not all in

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* When the skin has been removed from the venter of the tadpole it is found that one can quite readily separate the posterior branchial wall from the anterior abdominal wall on either side of and below the pericardium, and that this separation can be effected on each side right to the dorsal limit of the branchial cavity just below the cranial floor.

precisely the same stage of development. I have been unable to find the muscle in any of the earlier or later stages of this or other Anuran tadpole that I have been able to examine.

Lying superficial to all the other muscles, this takes its origin from a back-turned spur on the quadrate just behind the articular extremity. This spur projects ventrad, mediad and caudad, and carries the fine tendon of origin of the muscle quite clear of the depressor mandibulae, the cephalic head of which lies against its concavity. The tendon of origin begins as a fine thread and then becomes a ribbon which gives place to muscle fasciculi only after it has passed the posterior margin of the interhyoideus. The muscular part of the structure is extremely thin, little more than a single layer of fibres. These broaden out behind the interhyoideus and lose their identity on the surface of the anterior end of the rectus abdominis close on either side of the mid-line.

I am unable to homologize this muscle with any in the fishes. Innervation not determined.

Stage B. (Figs. 77, 78.)

Until the pectoral girdle is developed no changes in the musculature take place which call for description. The tadpoles of this (B) stage have, all of them, both limb-girdles developed. There is, however, so little change in size that the presence of the limbs alone serves to distinguish them from stage A before they are dissected. The mouth is as in stage A.

Intermediate stages display changes in the muscles which permit one to speak with confidence of the changes recorded in this. Those intermediate stages, it is believed, will be readily visualized by comparison of this with stage A.

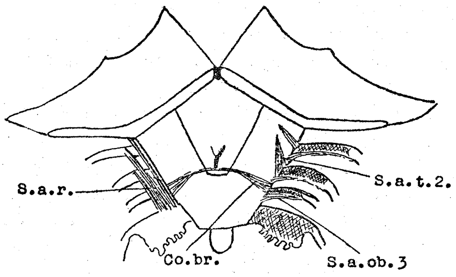

Fig. 77.—*Mixophyes* tadpole, stage B.—Ventral aspect.

The Csv.1a, though but very slightly increased in size, now shows quite clearly its muscular character.

The Csv.1b is somewhat broader antero-posteriorly but is not appreciably thicker.

The Interhyoideus also is changed only in that it is broader.

The Dilator hyoidei is unchanged, as also are the two heads of the depressor mandibulae.

The muscles of mastication present one particularly interesting change. The depressor labii superioris longus has become slightly shorter and it has acquired an insertion into the upper surface of Meckel's cartilage in front of that of the temporalis, as well as having still its original insertion into the superior labial cartilage. The temporalis muscle also is shortened slightly. The masseter is definitely enlarged. The remaining muscles of mastication are unchanged.

The subarcuales recti and transversi are unchanged.

The single interbranchial muscle is now definitely composed of muscle fibres, and the second and third interbranchials are recognizable at the same stage as this was observed in stage A.

The Coraco-branchialis now extends caudad to an insertion on the coracoid just medial to the glenoid cavity.

The Levator hyoidei is thicker than in stage A.

The Superficial Dorsal Branchial constrictors are also more definitely developed muscles, in that they are thicker and more compact.

The Constrictor Pharyngei is also thicker and now reaches nearer the mid-line.

There are now recognizable four muscles behind the branchial cavity. (These are semi-schematically represented in Fig. 78.)

The first of these is the Omo-hyoideus (Fig. 78, Omo.). It is a narrow ribbon of fibres which arise from the posterior wall of the cavity close to the ventral end of the fourth branchial cartilage and passes caudad to be inserted on to the scapula just laterally to the glenoid cavity.

The second is the Cucullaris (Fig. 78, Cu.). This is now much increased in thickness and is inserted on to the dorsal surface of the scapula laterally to the joint.

The third is the muscle which, in the adult, is the dorso-laryngeus. It arises under cover of the origin of the cucullaris and runs ventrad on the surface of the posterior branchial wall to terminate just laterally to the origin of the omo-hyoideus.

The fourth, and last, of these muscles (Fig. 78) arises from the ventral surface of the skull medially to the origins of the last two. It is a thin, relatively broad, band of muscle fibres which pass mediad and ventrad on the posterior branchial wall, near its dorsal limit, and ends thereon ventrally to the pericardium. The point of termination of this band of muscle fibres is near the middle of the curve of the fourth branchial cartilage but somewhat closer the mid-line. This band of fibres ultimately gives rise to the muscles which I have designated cranio-hyoideus and cranio-hyoideus anterior, two of the three posterior petro-hyoid muscles of Gaupp. These muscles are already indicated by incomplete divisions of the band of fibres.

The superficial ventral branchial constrictor sheet (Csv.3) is now more definite, it appears almost as a continuous sheet instead of as a wavy network of fibres as in stage A.

The Genio-hyoideus muscle has increased in width and almost reaches its fellow of the other side at the mid-line. It is also much shorter and terminates behind in a short tendon which is inserted into the hypobranchial copula.

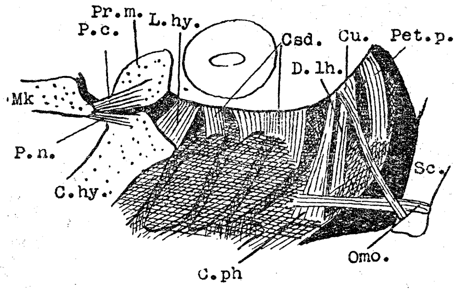

Fig. 78.—*Mixophyes* tadpole, stage B.—Lateral aspect.

The tiny genio-glossus, recognizable in earlier stages as a brightly stained tissue condensation, now appears as a definite muscle. It arises from the inferior labial cartilage superficially to the genio-hyoid on either side of the submentalis and terminates in an irregular brush of fibres amongst the tissues of the floor of the mouth, passing dorsad between the two genio-hyoid muscles to reach that tissue.

The Quadrato-abdominis muscle has disappeared.

The Infraspinatus and levator-scapulae muscles are recognizable. Though small, they are already quite as in the adult.

The final stages in the metamorphosis of these muscles into those of the adult frog have been studied in three later stages of *Mixophyes* and in a very complete set of stages in the development of *Limnodynastes*. It has been possible to compare stages in the development of the smaller *Limnodynastes* with stages A, B, C, D and E of the larger tadpole. This comparison revealed a very complete similarity and enabled one to use these stages as " mile posts " in the wider comparison.

The Csv.1a gives rise only to the small compact submentalis of the adult.

The Csv.1b extends first caudad on either side of the mid-line giving rise to the Csv.1b^1, then later, as the lower jaw lengthens backwards, a deeper layer of this muscle is carried back by the elongating lower jaw, and it is this which gives rise to the Csv.1b^2.

The Interhyoideus gives rise to the muscle which I have designated Csv.2, and which Gaupp terms the subhyoideus. No change is found in this muscle until the hyoid cartilage commences to assume definitely its elongated, curved and slender adult form. When this is first initiated the interhyoideus appears to become broader at the expense of its thickness, and its origin is carried dorsad, and caudad with the curving upper end of the stylohyal cartilage. This change commences after the tail has shrunken to about one-third of its full size. The final stages in the development of this muscle are those during which it increases in thickness and becomes folded on itself as described in the adult.

The Csv.3 appears to be entirely aborted. It is, however, possible that some of its anterior fibres are incorporated along the posterior margin of the Csv.2.

The Dilator Hyoidei is another caducous muscle. As the point of articulation of the lower jaw is carried posteriad the muscular antorbital process is gradually reduced in size, and just before the last stages in this transportation the hyoid cartilage loses its articulation with the inferior surface of the process and becomes attached loosely to the ventral surface of the auditory capsule. The dilator hyoidei becomes progressively reduced in keeping with the reduction of the muscular process, and finally disappears rapidly just prior to the alteration in the attachment of the stylohyal.

The Depressor mandibulae is developed directly from the two heads already present in stage A.

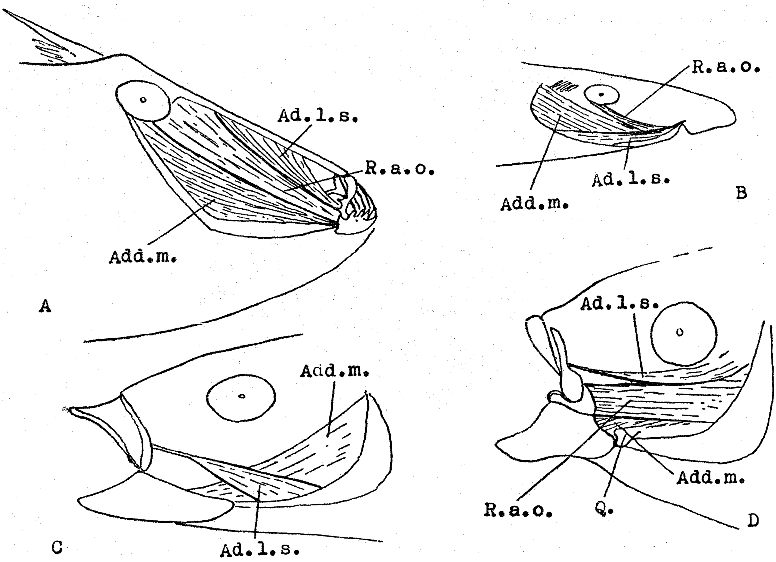

Fig. 79.—Four illustrations to show different origins of the same muscles in fishes.

The origin of the Pars Cephalognathica spreads so as to occupy the whole of the posterior edge of the muscular process under cover of the levator hyoidei. When the process has been transported caudad, this head of the muscle extends dorsad and caudad across the interval between the process and the auditory capsule to reach the site of origin it has in the adult.

The origin of the Pars Notognathica also is carried caudad as the hyoid articulation to the subocular arch is carried back. When the hyoid plate of the tadpole is transformed into the stylohyal cartilage of the adult this head of the muscle loses its origin from the cartilage and retains its superficial position, the origin being transferred to the subcutaneous deep fascia as in the adult.

The muscles of mastication change their direction as the jaw articulation is carried backward and slightly laterally.

The Depressor Labii Superioris Brevis has completely lost its identity in stage C of *Mixophyes* in which the mouth is just beginning to extend back and along the side of the skull, and whilst the superior labial cartilages still function as the upper jaw.

The Depressor Labii Superioris Longus retains its insertion into the upper labial cartilage until that disintegrates and is absorbed. This takes place very rapidly just after the tail has been completely absorbed and the tiny frog has left the water. During the change the animals are very lethargic and lie hidden beneath stones and other cover at the water's edge. For this reason I failed to observe the transition amongst the specimens of *Mixophyes* and was only successful with the *Limnodynastes* by fortunate chance. Several specimens at this stage of development were washed out whilst cleaning up the aquarium late in December, 1933.

After the upper labial cartilages are absorbed, the long depressor of the upper lip becomes partly incorporated with the Temporalis but, even in the adult, it is still readily separable as a superficial and lateral portion of that muscle.

The Pterygoideus and Temporalis alter only in their changed direction ; the former becomes the Pterygoideus of the adult. The Massetericus retains its primitive origin from the muscular process till that is aborted ; it then gains an origin from the inferior edge of the post-orbital bar and from the inferior and anterior margin of the tympanic annulus.

The Quadrato-mandibularis (Masseter) and Masseter minima first make their appearance whilst the last half of the tail is being absorbed, and they were found from the first in the situation they occupy in the adult frog.

The whole of the subarcual muscles are caducous, and they are aborted when the branchial skeleton is metamorphosed into the hyoid apparatus. A third subarcualis rectus and a second subarcualis transversus are developed at the time the fore limbs are formed but before they are protruded, and at this time the three interbranchial muscles are also fully developed.

The metamorphosis of the branchial skeleton is also accompanied by the complete abortion of the levator hyoidei, and the superficial dorsal branchial constrictors.

At this time also the Constrictor Pharyngei extends further mediad, meets its fellow of the other side behind the larynx and some of its fibres obtain a point of origin on the posterior horn of the hyoid skeleton.

The three petro-hyoid muscles also reach the adult condition as the branchial skeleton is metamorphosed, whilst the hyo-glossus appears and reaches the adult form and the genio-hyoideus becomes divided up into the component parts of the adult during the same period.

The laryngeal muscles of the late tadpole consist of a dorso-laryngeus and a Sphincter Laryngei, this latter being incomplete anteriorly and dorsally.

In addition to these the posterior fibres of the constrictor pharyngei are inserted into the same tissue as the anterior ends of the sphincter.

COMPARISON WITH *NEOCERATODUS* AND THE FISHES.

Watson (1926, pp. 194–5) wrote : " The extremely close resemblance between the Dipnoi and the Urodela, a resemblance covering the respiratory and circulatory systems, the urogenital apparatus, the brain, the skull, the histology and the embryology throughout, indicates them as the first fishes to be considered in the search for the Amphibian ancestors.

" These resemblances are specifically between the Dipnoi and the Urodela, they appear most strikingly in a comparison of Lepidosiren with a perennibranchiate Urodele, and are not nearly so pronounced if Ceratodus be compared with a frog or a Cœcillian."

This insistence on comparison with adult forms and the neglect of the larval stages of the remaining Urodeles and of the Anura is peculiar. Watson is probably correct in his statement on a later page of the same work that the aquatic amphibians are in all probability descended from terrestrial forms. But that he should overlook the fact that the aquatic forms may be regarded as having been arrested at one of the stages of development common to all Amphibia is regrettable. Had he not done so he would have found the Dipnoi to be comparable with all the recent Amphibia, with the possible exception of the aberrant Caecilians. Even in the latter, as we shall see later, the adult structures of the head indicate quite clearly that they too are comparable with those most primitive amphibians, the Dipnoi. Watson's description of *Neoceratodus* as a " modern fish " is quite incomprehensible.

The muscles of the anuran tadpole present a somewhat bewildering resemblance to the Dipnoi on the one hand and to the fishes on the other.

Let us consider first the muscles of the mandibular segment. The submentalis is unquestionably completely homologous with the similarly named muscle of the bony fishes. Behind this we find a very well defined intermandibularis equally unequivocably homologous with that of *Amia* or *Polypterus*. On the other hand, this last muscle is as clearly homologous with the intermandibularis of the Dipnoi. This is the more apparent when the tadpole muscle is compared with that of the 19 mm. larva of *Protopterus* (*vide* Edgeworth, 1926, plate IV, fig. 19). The Dipnoans, however, have no submentalis muscle.

Whilst the muscles of mastication may be broadly divided into two main groups, those arising medially to the rami mandibularis and maxillaris V, and those arising laterally thereto as in the Dipnoi, there has been a remarkable division of the latter group of muscles which can only be compared with that which has taken place amongst the fishes.

We may begin by recognizing as probably completely homologous the muscle having its origin medial to and in front of the nerve in all of these forms. It has been consistently designated the Pterygoideus in every description.

Several modifications of the M. levator labii superioris were observed amongst the Selachians. These are apparently illustrative of possible stages in the conversion of that muscle into the pterygoid adductor of the lower jaw. These were observed and described in various members of the Selachii and confirmed, it appeared, in the Holocephali and *Neoceratodus*. At the time of my study of the muscles of *Callorhynchus* (Kesteven, 1933) I was particularly struck with the fact that the masticatory muscles of the generality of the bony fishes might be divided into three components, which were then designated adductor labii superioris, retractor anguli oris and adductor mandibulae. The figures which were then published are reproduced again here (Fig. 79). They depict four stages in the change of the origin of the pterygoid muscle from anterior to the orbit to behind it. In all four instances the ramus mandibularis of the Vth nerve lies between the parts of the pterygoid muscle below and the temporo-masseteric muscle superficially.

In the tadpole the Pterygoideus muscle retains its primitive origin medial to the nerve and, as in the Dipnoi, it passes forward to its insertion on the lower jaw anterior to the point where the nerve crosses the jaw. Resembling in its origin also all those fishes which retain the primitive origin of the muscle.

The Temporalis is either the adductor labii superioris or the muscle which, in the work on *Callorhynchus*, I designated the retractor anguli oris. The insertion of this latter muscle is, in the great majority of the bony fishes, into the lower jaw and, per medium of a more or less definite tendinous condensation of the maxillo-mandibular fascia, into the maxillo-labial bone as well.

It now becomes clear that the origin of this muscle in the tadpole lateral to the nerve, and its dual insertion into both Meckel's cartilage and into the superior labial cartilage should be interpreted, in the light of our present knowledge, as indicating not only the complete homology of the muscle with part, at least, of the M. temporo-massetericus of the bony fishes, but also the complete homology of the superior labial cartilage of the cartilage of the tadpole and the maxillo-labial bone of the fishes.

These homologies are of particular interest as confirming the views already expressed that the labial bones of the fishes are not homologous with the maxillae and premaxillae of the tetrapods.

The homologies of the remainder of the muscles of mastication of the tadpole with those of the fishes are not subject to separate determination. The most that can be said at present is that they are, as a whole, to be regarded as derivatives of the M. adductor mandibulae.

The recurrence of the division of the adductor muscles of the jaw into two groups by the emergent rami of the Vth nerve, which was observed throughout the fishes, must surely be regarded as inherited by both fishes and amphibians from a common ancestor. If this be a reasonable assumption, it constitutes a complete justification for the opinion expressed in the last paragraph.

In the hyoid segment there are in the tadpole the interhyoideus, dilator hyoidei, the levator hyoidei and the depressor mandibulae, and, of these, the first and last give rise to adult muscles, the other two are entirely caducous.

Comparison with the larval *Protopterus* leads to the suggestion that the muscle which is here designated the levator hyoidei is that which Edgeworth terms the levator hyoidei, and if that be so, and if Edgeworth's identification be correct, then that which I have designated dilator is identifiable as the superficial dorsal hyoid constrictor. The interhyoideus is, apparently without doubt, homologous with the similarly named muscle in the *Protopterus* larva.

It is probable that the muscle which I have designated the Csv.3 is homologous with the constrictor hyoidei of Edgeworth's description. Edgeworth accepts the statement of Rudge that the muscle in question is innervated, in *Protopterus*, by the ramus hyomandibularis VII. Though unable to state so definitely, I am of the opinion that in the tadpole the Csv.3 is innervated by twigs from IX and X.

The superficial and deep ventral hyoid constrictors have been so exceedingly modified in the bony fishes that comparison of the tadpole muscles with them is difficult. This is the more so in view of the fact that the whole of the interhyoideus muscle becomes, in the tadpole, converted into a superficial constrictor in the adult, whilst in the bony fishes the primitive single muscle becomes developed into superficial and deep muscles. The very definite attachment of the muscle in the tadpole, to the lateral end of the hyal cartilage, would appear to be evidence that we have to deal with a true interhyoideus, as we know that muscle in the elasmobranch fishes, and that the posterior portion of the pars primitiva, which gives rise to the superficial muscle in the elasmobranchs, is not developed in the tadpole at all.

If it should subsequently be shown that the Csv.3 is really a caducous Csv.2, then it will also have been proven that the superficial ventral hyoid constrictor of the adult frog is developed from the interhyoideus, and is a deep constrictor which has acquired a superficial situation in replacement of the lost posterior portion of the pars primitiva ventralis hyoidea.

In the branchial segments we may first of all discuss and dismiss those muscles whose homologies are apparently quite clear. The musculi marginales are without reasonable doubt completely homologous with the interbranchial muscles of the Dipnoi and Elasmobranchs. The subarcualia obliqui and recti are also fairly certainly homologous with the similarly named muscles in the Dipnoi and bony fishes.

Although in the tadpole there is but one single slip representing the several present in both the Dipnoi and the Elasmobranchii, there is no reason to doubt that this single slip is homologous with one or other of the components of the coraco-branchialis.

The homology of the muscles which I have designated superficial dorsal branchial constrictors is by no means clear. In their situation on the wall of the branchial chamber, which is essentially an opercular fold, they would appear to be hyoid muscles and comparable with the dorsal end of the hyoid constrictor of the Holocephali and Dipnoi. On the other hand, they very definitely do not appear to be innervated by the VIIth nerve and they are quite definitely placed more deeply. They arise, not from a deep fascia, but from the edge of a cartilaginous shelf, the metapterygoid process, which stands out behind the quadrate, and above the branchial chamber. Now whilst this process is quite clearly not in any way homologous with that which overhangs the branchial chamber of the Dipnoi, one cannot entirely overlook, and disregard, the fact that it has come to occupy that situation. This gives rise to the suggestion that the muscles may be the levatores arcuum branchialium. It will be remembered that there is good reason to believe that the branchial levators are to be regarded as the deepest portion of the primitive constrictor sheet dorsally; it is therefore not surprising that it should be difficult to decide, as the sheet is progressively reduced, just which part remains. It may, however, be observed that in the most primitive Elasmobranchs the branchial levators are found to continue the deep constrictors dorsad; they are, as it were, the dorsal continuation of the interbranchial muscles. In the tadpole the musculi marginales, which we have seen to be homologous with the interbranchial muscles of the elasmobranch fishes, are placed more deeply than those which I have designated the superficial dorsal branchial constrictors.

In the Axolotl we shall find that the muscles which have been designated the branchial levators are definitely more superficially placed than the musculi marginales of the Axolotl. There appears every reason to believe that these muscles of the Axolotl are homologous with the muscles under discussion. In the Axolotl they arise from the fascia dorsalis, the deep fascia, and therefore arise in similar manner to the superficial constrictors of the elasmobranch fishes.

Although the evidence is not conclusive, it is believed that the designation which I have given these muscles is more correct than it would be to designate them branchial levators.

RANA.

After the work on the development and adult anatomy of the cephalic musculature of the Australian frogs had been completed I received ten stages in the later development and metamorphosis of *Rana pipens* from Professor H. W. Norris. I have again to express my gratitude to him for his continued assistance. My work on the Amphibia is based very largely on material he has presented to me.

The youngest of these is a tadpole, fully grown, with small hind legs and very small fore-limbs tucked deeply beneath the surface. The most advanced has but a mere stump of a tail, the mouth, relatively, is of adult size; the last (almost amorphic) remnant of the gill filaments remains as a strand of tissue in front of the pectoral girdle on each side. In short, metamorphosis is almost complete. The other eight stages are intermediate between these, and each is slightly more advanced than the one before it. They are in fact a thoughtfully selected series of the most instructive stages in the late steps of the development of the cephalic and capiti-pectoral muscles.

Being of large size these specimens were all good dissection subjects, and they were excellently preserved. Before dissection they were carefully skinned and then stained with picric acid.*

These ten stages have been preserved, after dissection, in my collection and are marked *Rana pipens*, Nos. 1 to 10.

They are so essentially similar to comparable stages in the development of the Australian frogs that it were almost mere repetition to describe them. This essential similarity permits one to believe that the description which has been given on the previous pages of the development and metamorphosis of the cephalic and capiti-pectoral muscles may be accepted as being applicable to the Anura generally.

The metamorphosis of the mandibular muscles is very clearly presented in stages 4 to 10. It is noteworthy that all the divisions of the adductor muscles of the lower jaw found in *Mixophyes* and *Hyla* are to be found here with even greater ease than in those forms. The depressor labii superioris brevis is better developed. In stage 10 all the muscles elevating the lower jaw of the adult Australian frogs are quite well developed.

The ventral constrictors develop just as in *Mixophyes.*

The levator hyoidei is rather weaker in *Rana* than it is in *Mixophyes* ; its evanescence is presented in the four stages 5 to 8.

The migration of the two heads of the depressor mandibulae is quite clearly shown in stages 6 to 10, and in stage 9 the last semi-transparent remnants of the dilator hyoidei are to be seen posterior to the tympanic annulus, superficial to the depressor. Earlier stages in its absorption are seen in stages 8 and 7.

The M. interhyoideus develops as in the Australian frog. Behind the interhyoideus, and separated from it by a marked interval, there is, in stages 1 to 5, the muscle which I have designated the inferior branchial superficial constrictor. In *Rana* this muscle arises from the dorsal fascia behind the skull at the mid-lateral line as a narrow ribbon. The fibres diverge slightly, so that, at their insertion into a raphe at the mid-ventral line, the muscle is broader than at its origin.

In no case can I detect any innervation by twigs wandering caudad from the interhyoideus. The muscle is entirely caducous ; its reduction and final disappearance without ever making contact with the interhyoideus is quite strikingly presented in the stages 5, 6, 7 and 8.

The position of this muscle in this series appears to confirm my identification.

In *Rana* there is no question whatever that the muscles which I identified, in the Australian frogs, as the superficial branchial dorsal constrictors are completely caducous. They are rather more weakly developed than in *Mixophyes*, but are still at their full development at stage 5. Now at this stage the crowding together of the branchial arches, characteristic alike of the Holocephali, Teleostei and Amphibia, has placed the long axis of the gill slits right across the path these muscle fibres would have to take were they to grow down to reach the outer ends of the fibres of the constrictor pharyngei, and moreover the first gill slit extends well posteriorly to the posterior margin of the muscle fibres in question. From stage 5 to stage 10 one observes the gradual closure of the gill slits and the absorption of the gill filaments. They close from before backwards one after the other. The two edges are brought close together and partial closure results in a row of small perforations along the line of closure ; later the perforations are closed. In stages 6 and 7 the gill clefts are almost completely closed and the gill filaments form a crowded spongy-looking mass between the posterior margin of the interhyoideus and the pectoral girdle. In stage 7 the superficial dorsal branchial constrictors have lost their staining properties to a slight extent, as all the muscles do as they commence to be absorbed. The strand of muscle fibres which is to give rise to the anterior petro-hyoid muscles is seen passing ventrad and mediad behind and deep to the degenerating gill filaments. In stage 8 the dorsal superficial constrictors have faded to a shadow and have acquired the semi-transparent appearance of late absorption stages. The anterior petro-hyoid muscles are differentiated from the common strand. The degenerating gill filaments form a narrower, more compacted, granular-looking mass.

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* Experience has taught me that dissection specimens which have been stained in picric acid should be very thoroughly washed with several changes of spirit before being put away to keep. If this precaution is not taken they darken very much and the differential staining is almost entirely lost, all the tissues turning a dark bronze-green. I have also found that a better differential colouring is obtained by staining with carmine first and with picric acid afterwards, than is obtained with picrocarmine mixtures, but great care must be taken that the carmine stain is very light ; for dissection purposes carmine very readily overstains in the absence of the picric acid.

The development of the Omohyoideus in *Rana* is as in *Mixophyes*, as also is the development of the Cucullaris.

3. **The Urodele Larva.** (Figs. 80–82.)

The following description and the illustrations are based upon a numerous collection of Axolotls for which my thanks are due to Professor H. W. Norris. Not only have I to thank him for the collection of Axolotls and adult *Amblystoma tigrinum*, but he has also given me sets of serial sections, cut in all three planes, of larvae from 6 mm. to 47 mm. in length.

The dissected specimens varied in length from 8 to 16·5 cm. and showed no noteworthy differences in their musculature.

In larvae six to ten millimetres long there is not sufficient differentiation of the mesoderm to permit of the identification of the muscle plates with any degree of confidence. In those measuring thirteen to fourteen millimetres in length, practically all the muscles of the largest larvae are recognizable. The differentiation of the mesoderm into the muscles apparently takes place very rapidly between the ten and thirteen millimetre lengths.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Submentalis, Csv.1a (Fig. 80), appears in the 13 mm. larva as a compact little bundle of transverse fibres placed immediately behind the anterior tips of Meckel's cartilages. This muscle alters with age only by increasing in size, at no time is there any median interruption of the continuity of the fibres from side to side. The origin is from the perichondrium of Meckel's cartilage in the larva and from the periosteum of the dentary in the older specimens.

The Intermandibularis, Csv.1b (Fig. 80), is also developed in the 13 mm. larva, and has the form it retains throughout life. On each side it arises from the cartilage, or bone, of the lower jaw for almost the whole length of the lower jaw, forming a complete intermandibular sheet. The fibres are inserted in the mid-line into a raphe.

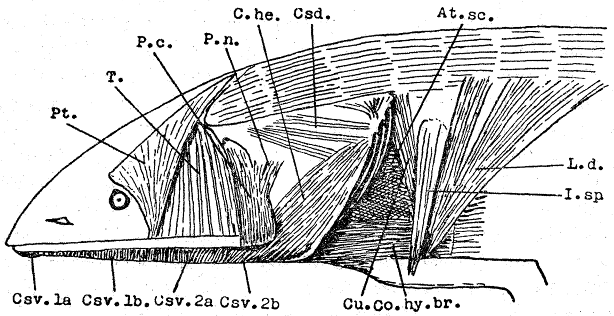

Fig. 80.—The Axolotl.—Lateral aspect of the subdermal muscles.

The adductor muscles of the lower jaw are not so much differentiated as in the anuran tadpole, only three being recognizable.

The Pterygoideus (Fig. 80, Pt.) is the muscle which previous writers have designated temporalis ; Lightoller alone has recognized that it was not correctly so designated, and he recognized that it is really a pterygoid muscle.

The muscle has an extensive origin from the side and dorsum of the cranium in front of the quadrate, and above and medial to the auditory capsule so far back as the posterior dorsal ridge of the skull. In front the origin of the muscle extends forward of and above the orbit. From this extensive area the fibres converge to a tendon which is inserted on to the inner and upper edge of the mandible in front of the insertion of the temporalis.

The Temporalis Muscle (Fig. 80, T.) arises from the surface of the quadrate and auditory capsule between the depressor mandibulae and pterygoideus muscles. Its origin rises to a point at the level of the lateral intermuscular septum a little in front of the origin of the superficial dorsal constrictors and the apex of the area of origin of the depressor mandibulae. The fibres are gathered to an insertion on to the outer surface of the mandible close to its upper margin just a short distance in front of the joint. This insertion is effected by a very short tendon.

The Quadrato-mandibularis arises from the quadrate and auditory capsule under cover of the temporalis and laterally to the deeper portion of the pterygoideus. The insertion is into the inner surface of the upper edge of the mandible a short distance behind the insertion of the temporalis, with the ramus mandibularis V, penetrating between the dentary and Meckel's cartilage, placed between the two insertions. The fibres of the temporalis muscle have a general direction from above ventrad, cephalad and laterad, but they do not tend cephalad as acutely as the fibres of the underlying quadrato-mandibularis, which latter are thus recognizable from those of the more superficial muscle by the difference in direction, as well as by the fact that the ramus mandibularis V lies, in part of its course, in the cleavage plane between the two muscles.

The presence of this muscle has apparently not previously been discovered.

Innervation.—All three of the muscles of mastication are innervated by twigs from the ramus mandibularis V as it passes between them.

The Course of the Rami of Nerves V and VII.

The situation of the main divisions of the Vth and VIIth relative to the skull and the muscles is of interest and will be quite briefly reviewed.

The V-VII ganglionic mass is found partly embedded in the anterior wall of the auditory capsule close to the lateral wall of the neurocranium. From this ganglionic mass the two main divisions, V and VII, depart, the former antero-laterally, the latter postero-laterally.

The Nervus Trigeminus.—The first ramus to leave the trunk of the nerve is the ophthalmicus profundus. This runs forward along the inner wall of the orbit close to the floor. The maxillary ramus and ramus ophthalmicus superficialis next depart together. There is no reason to doubt that the ramus maxillaris is joined by the ramus buccalis VII in the Axolotl, as it is in *Siren*, and that a ramus ophthalmicus superficialis VII joins the ramus ophthalmicus superficialis V. Norris designates the combined trunks " infraorbitalis " and " supraorbitalis " in *Siren* (1913, p. 283).

The two nerves course alongside one another laterad and dorsad between the origin of the temporalis muscle and the anterior wall of the auditory capsule, posterior wall of the orbit, and come into view together beneath the skin high up behind the orbit. They turn forward at once over the surface of the pterygoideus muscle. The ophthalmicus superficialis courses directly forward above the orbit. The maxillary nerve turns ventrad across the muscle and then runs forward along the upper margin of the upper jaw below the orbit.

From the point of departure from the common nerve trunk of these last two rami the remainder of the Vth nerve, the ramus mandibularis, courses ventrad and slightly forward between the quadrato-mandibularis deep to it and the pterygoideus superficial to it, then between the quadrato-mandibularis and temporalis. Between the insertions of these two muscles it turns ventrad across the external, lateral, surface of Meckel's cartilage between it and the internal surface of the dentary bone. It thus reaches the ventrum of the mouth and breaks up into its terminal branches, which radiate mediad and forward from this point.

The Nervus Facialis.—The rami ophthalmicus superficialis and buccalis are, without reasonable doubt, incorporated with the last two rami of the Vth nerve.

The Ramus Palatini is given off close to the ganglion and courses straight forward beneath the cranial floor after a short course ventrad, mediad and forward.

I have not found the ramus alveolaris which Norris describes, but do not regard my failure as evidence of the absence of the nerve.

The main trunk gives off a relatively large communicating branch, the lateralis components, to the IX-X ganglion and then the large ramus hyoideus ; this, after a short course laterad and ventrad between the otic process of the quadrate and the cephalic head of the depressor mandibulae, turns backwards through that muscle and reaches the surface of the interhyoideus behind it and is distributed to structures on the ventrum of the mouth.

The two rami mentales are bound together for a short distance. After their separation they course together laterad and slightly dorsad between the quadrate and the cephalic head of the depressor mandibulae, and come into view beneath the skin fairly high up along the exposed margin of the quadrate. The ramus mentalis internus now runs down and forward along the exposed edge of the quadrate and then turns forward along the lower jaw. The ramus mentalis externus curves backward around the margin of the depressor mandibulae and then runs ventrad and slightly caudad on the surface of that muscle near its anterior margin. Finally it turns forward behind the insertion of the muscle and crosses the muscle in a cephalo-dorsad direction. It crosses superficially to the ramus mentalis internus behind the angle of the mouth and runs forward in the upper lip to just in front of the orbit where it receives a communicating branch from the ramus maxillaris V-VII. I have failed to find that branch of this nerve which, in *Siren*, runs along the ventral border of the lower jaw, or, it may be, I have failed to find the ramus mentalis internus, but if the latter, then the division of the ramus mentalis into two branches certainly takes place as just described. I have traced these nerves in several specimens.

THE MUSCLES OF THE HYOID SEGMENT.

In the 9–10 mm. larva the hyoid mesoderm forms a complete plate in which the differentiation into muscle plate and procartilage is not obvious, and in this respect it resembles the mesoderm of the remaining cephalic segments. It is, however, believed that certain more closely gathered strands of cells, which are slightly more granular and placed nearer the mid-line on each side, are to be regarded as the ectoderm from which the cartilage will later develop. There is certainly no division of the primordial muscle plate into its later components. In the 13 mm. larva (Fig. 81) the hyoid musculature consists of (1) a thin sheet of transverse fibres which extends from the posterior margin of the Csv.1b to the posterior edge of the opercular fold and extends upward on each side to the dorsal limit of the fold, arising from the deep subcutaneous tissues in this situation, and inserted into a median raphe ventrally, (2) a compact bundle of fibres which arise from the tissues dorsally to the end of the dorsal end of the hyoid cartilage and extend forward and ventrally beneath that cartilage to be inserted into its anterior tip, and (3) the depressor mandibulae.

The Csv.2 (interhyoideus of Drüner) is the continuous sheet, whilst the compact diagonal muscle is the Interhyoideus (cerato-hyoideus externus of Drüner).

In the larger Axolotls one can distinguish two portions of the Csv.2.

The Csv.2a (Fig. 80).—The anterior and major portion of the ventral superficial hyoid constrictor is very similar to the Csv.1b. It arises from near the dorsal end of the cerato-hyoid cartilage behind the jaw, and its fibres pass ventrally and forward, from above and posterior to the mandible, and then mediad and forward to be inserted into the median raphe. The great obliquity of the more anterior fibres carries them forward deep to the posterior half of the Csv.1b at their insertion. As these fibres come forward and ventrally from above and behind the posterior end of the jaw they have a very deceptive appearance of arising from the inner surface of the jaw itself.

The Csv.2b (Fig. 80).—This posterior portion of the hyoid constrictor arises from the superficial surface of the interhyoideus muscle behind the mandible and also from the dorsal tip of the first epibranchial cartilage. In the older larvae the two muscles are fused, but in the smaller it is possible to dissect the Csv.2b free from the interhyoideus right up to the tip of the epibranchial cartilage. The fibres of Csv.2b are parallel with those of Csv.2a and are inserted behind them into the median raphe. The most posterior fibres lie in the free edge of the opercular fold.

The Depressor Mandibulae in the 13 mm. larva presents (Fig. 81) a pars cephalognathica (Pc.) which is a compact bundle of fibres that pass almost directly dorsad to their origin from the connective tissues above the postero-lateral corner of the auditory capsule, and a very short and much smaller little bundle of fibres, the pars notognathica (P.n.), which arise from the cerato-hyal cartilage just behind and a little above the posterior end of Meckel's cartilage. Both parts are inserted into the posterior end of Meckel's cartilage.

In the larger larvae the muscle presents only a pars cephalognathica. This arises from the dorsum of the skull behind the auditory capsule and in line with the intermuscular septum between the dorsal and lateral trunk muscles. Some of the posterior fasciculi arise from the connective tissue of the gill cover ventrally to the superficial dorsal branchial constrictors, and in front of the origin of the posterior fibres of Csv.2b. This, however, is only found in the largest specimens. The insertion of the muscle is on to the outer surface and posterior end of the mandible behind the joint. In the largest specimens (Fig. 80) the insertion is by a short stout tendon on to the extreme posterior end of the mandible.

The Interhyoideus (Figs. 80–82).—This is the muscle which has been designated cerato-hyoideus externus by Drüner (1903) and other observers. The muscle arises from the deep fascia close to the dorsal end of the first epibranchial cartilage just posterior to the top of the first gill cleft. It passes ventrad and cephalad in the opercular membrane, along the ventrum of the ceratohyal, to be inserted into that face of the cartilage from the angle thereof to the anterior tip. The two muscles do not meet in the mid-line.

Innervation.—The muscle is innervated by twigs from the ramus jugularis of the hyoid trunk of the VIIth nerve.

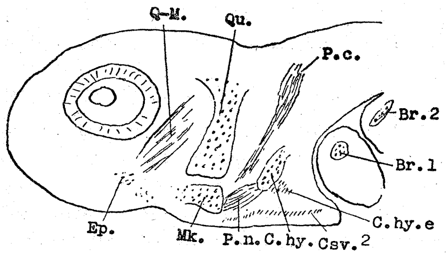

Fig. 81.—The Axolotl.—Sagittal section from a 13 mm. embryo.

MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Dorsal Branchial Constrictor muscles (Fig. 80, Csd.) number four. They are narrow bands of fibres which arise close together from the lateral intermuscular septum and fascia dorsalis behind the depressor mandibulae. From their origin they pass with varying degrees of obliquity to be inserted into the free edge of the opercular membrane between the branchial septa. The first of these passes deep to the dorsal end of the Csv.2b to reach the base of the first external branchia, the second and third reach the bases of the second and third external branchiae without passing beneath any other muscle, the fourth, Csd.6, ends in the free edge of the membrane ; there is no fourth external branchia.

Innervation.—Twigs of the IXth and Xth nerves were traced to these muscles in the larger larvae.

The Interbranchial Muscles (Musculi marginales) (Fig. 82, Mm.1–3) or first, second and third branchial muscles of Drüner, arise from connective tissues close to the tips of the second, third and fourth epibranchial cartilages and pass thence, parallel to the interhyoideus, to be inserted, the first into the base of the first epibranchial cartilage, the second and third along the length of the respective interbranchial septum, between the second and third epibranchial cartilages and the free edge of the septum. The second is shorter and more slender than the first, and the third than the second. Each of these muscles, at its insertion, is apparently in continuity with one of the dorsal superficial constrictors, but closer examination discloses that whereas the constrictor is placed quite superficially across the roof of the branchial chamber, these are placed on the deep side of the opercular membrane and pass more deeply as they extend ventrad and mediad.

Innervation.—These muscles are innervated also by twigs of the IXth and Xth nerves.

The Constrictor Pharyngei (M. transversus ventralis of Lightoller) (Fig. 82, C.ph.) appears in the larger larvae as a single muscle, but in the smaller larvae, from 40 mm. to 13 mm., there is a definite division of the muscle into anterior and posterior positions. According to Drüner the muscle represents fourth and fifth interbranchial muscles.

In the larger larvae it arises on each side from a little more than the middle third of the length of the fourth epibranchial cartilage and passes mediad to meet its fellow of the other side. The insertion along the mid-line is into the posterior one-half of the elongated basibranchial cartilage and into a median tendinous strand for a similar distance behind it. The muscle is a good deal broader antero-posteriorly at its insertion than it is at its origin.

Innervation.—It has not been possible to find the motor nerves to this muscle in any of the dissections. On the other hand, in a very fine series of horizontal sections of a 30 mm. larva stained with iron haematoxylin, it has been possible to trace the nervus intestino-accessorius and to observe its division, and finally to follow the ramus intestinalis recurrens sufficiently far to feel confident that the innervation of the muscles by this nerve in the Axolotl is probably as described by Norris (1913) in *Siren lacertina.*

The Dorso-laryngeus Muscle arises from the lateral intermuscular septum and fascia dorsalis immediately behind the fourth dorsal superficial constrictor and superficially to the antero-dorsal corner of the origin of the cucullaris. It passes ventrad and comes to lie parallel with, but deep (dorsal) to the posterior margin of the constrictor pharyngei and follows these around to be inserted into the median raphe on the floor of the pharynx just in front of the larynx. The fibres of this muscle are absolutely continuous from origin to insertion. Stained and cleared preparations show no sign of any interruption across the muscle.

Innervation.—This is probably by twigs from the nervus intestino-accessorius as in *Siren.*

HYPOBRANCHIAL MUSCLES.

All these muscles are innervated by the ramus intestinalis recurrens. Norris (*l.c.*, p. 233) points out that there is here an invasion and capture of the territory of the primitive post-trematic rami of the branchial nerves by this nerve, which, he says, is accordingly much enlarged.

The Subarcualis obliquus 1 (Fig. 82, S.a.r.^{1}).—This is the muscle which, following Drüner, writers have designated the cerato-hyoideus internus. I have made use of the above designation in order to preserve in the nomenclature its homology with the muscle in the fishes and Dipnoi.

It arises from the ceratohyal close to the insertion of the interhyoideus, and passes backwards and slightly laterad to be inserted on to the ventral surface of the enlarged base of the first epibranchial cartilage.

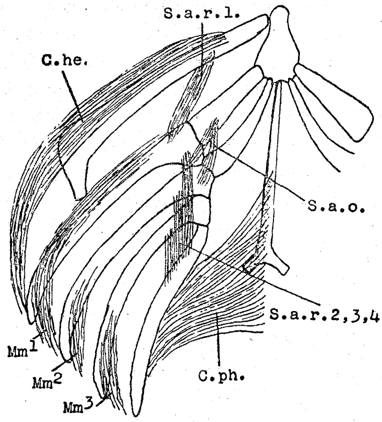

Fig. 82.—The Axolotl.—Ventral aspect of the branchial skeleton and its muscles.

Innervation.—This is by a twig which leaves the post-trematic branch of the glossopharyngeal nerve just before it passes beneath the muscle. Norris states that in *Siren* there is also a motor supply to this muscle from the ramus intestinalis recurrens. I have not found this second motor nerve, but would not imply that it does not exist.

The Subarcualis Obliquus 2 (Fig. 82, S.a.o.) arises from the outer end of the first cerato-branchial cartilage and is inserted in two separate bundles of fibres into the proximal end of the second epibranchial cartilage. This is the subarcualis obliquus of Drüner and others.

Innervation by the Xth nerve is as described by Norris.

The Subarcualis Rectus of Drüner (Fig. 82, S.a.r.) is clearly composed of three small muscles which are confluent along their contiguous margins. They arise from the bases of the first, second and third epibranchial cartilages and are inserted alongside of one another into the base of the fourth epibranchial.

Innervation is the same as that of the last muscle.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The Genio-hyoideus is a narrow muscle which arises from the mandible just laterally to the submentalis and passes directly caudad, beneath the superficial ventral constrictors, to be inserted on to the anterior edge of the short cornu of the elongated rod-like basibranchial cartilage, and to be then continued caudad by a similar but much shorter section which arises from the posterior edge of the same cornu and is inserted into the first tendinous inscription of the rectus abdominis.

The Claviculo-hyoideus (Fig. 80, Co-hy-br.) muscle has been designated by previous writers the omo-arcualis and the procoraco-arcualis ; I have preserved in my designation its homology with the muscle in the Dipnoi and bony fishes.

The muscle arises from the inferior surface of the basihyal, the inner ends of the first and second ceratobranchial cartilages, from the side of the elongated, rod-like basibranchial and both surfaces of the small cornua of that cartilage. The muscle walls-in the pericardium below and on both sides, it increases rapidly in bulk posteriorly, is interrupted twice by tendinous intersections just in front of the shoulder-girdle, and finally merges completely with the metamerically interrupted abdominal muscles, under cover of the shoulder-girdle.

The Genio-glossus muscle arises on each side from the mandible deep to the submentalis just to one side of the symphysis. It is composed of a narrow ribbon of fibres which pass directly caudad to be inserted on to the anterior edge of the posterior cornu of the basibranchial cartilage. These two cornua are so completely clothed by the coraco-branchialis that the genio-hyoideus appears to be inserted on to the ventral surface of this other muscle.

The Capiti-pectoral Muscles.

The Infraspinatus and Latissimus Dorsi muscles are included here in order to establish the position and relations of the Cucullaris and Attrahens Scapulae muscles.

The Cucullaris (Fig. 80, Cu.) arises from the lateral intermuscular septum and fascia dorsalis at the level of the septum immediately behind the last superficial dorsal constrictor, its anterior fasciculi being deep to the dorso-laryngeus muscle. The muscle is not very broad at its origin and the fibres converge to a fine tendon which is inserted into the scapula just above the glenoid cavity. This insertion is covered by the lower end of the infraspinatus.

The Attrahens Scapulae (Fig. 80, At.Sc.) arises by a fine tendon from the postero-ventral edge of the cranium just laterally to the origin of the lateral trunk muscles. The muscle expands into a thin narrow ribbon as it extends directly backwards, with a slight inclination ventrad, beneath the cucullaris and dorso-laryngeus to be inserted into the anterior margin of the suprascapula. At its insertion it is covered by the cucullaris.

The Infraspinatus (Fig. 80, S.sp.) arises from the suprascapula along its dorsal edge and passes down to be inserted into the outer side of the humerus near the head of the bone.

The Latissimus Dorsi (Fig. 80, L.D.) arises from the fascia dorsalis at the level of the lateral septum ventrally to the fifth, sixth, and seventh dorsal myomeres. From this relatively broad origin the fasciculi converge to a thin broad tendon which is inserted on to the inner side of the humerus opposite the infraspinatus.

COMPARISON WITH THE ANURAN TADPOLE.

The muscles of the mandibular segment.—The ventral superficial constrictors differ only in that the Csv.1b is more extensive in the urodele than in the anuran larva.

In the identification of the pterygoideus I have been guided by the relation of the muscle to the ramus mandibularis V. The muscle resembles that of the anuran tadpole in this relation, but differs in that it is inserted in front of the temporalis. This is a return to the more primitive situation of the two insertions relative to one another which was observed in the elasmobranch and many of the bony fishes.

It seems probable that we should be correct to regard the temporalis muscle of the urodele larva as containing in its posterior portion the fibres which form the masseter of the later anuran tadpoles. At no stage in the development of these muscles was a definite retractor anguli oris or depressor labii superioris observed in the urodele larva, though in sections of the 13 mm. larvae an antero-dorsal group of fibres of the temporalis have the appearance of being inserted into the tissues of the lip at the side of the mouth, but it is possible that this is only due to the forward bulging of the belly of the muscle above and in front of its insertion. On the whole it appears wiser to assume that the anterior portion of the temporalis which functions for a while as the depressor of the upper lip in the anuran larva is never so developed in the urodele.

The quadrato-mandibularis of the urodele must be accepted as representing the massetericus as well as the quadrato-mandibularis of the tadpole.

The superficial ventral constrictors in the hyoid segment present a partial return to the condition of these muscles in the fishes.

A typical Csv.2 is developed as in the elasmobranch fishes and Dipnoi. This forms a continuous sheet beneath the branchial arches just as in the Dipnoi, but is not interrupted by any skeletal structures on either side as it rises to its origin from the fascia dorsalis. In the older Axolotls the extent of its origin is reduced by the relative backward growth of the lower jaw.

Deep to this Csv.2, there is developed the muscle which has been designated the ceratohyoideus externus. Although the muscle fails to reach its fellow in a mid-ventral raphe, its development from the deeper and anterior portion of the hyoid muscle plate leaves no choice in the matter ; we are practically compelled to recognize this as homologous with the interhyoideus of the elasmobranchs and with part, at least, of the protractor hyoidei of the bony fishes.

4. Perennibranchiate Urodele.

Necturus (Figs. 83–84).

The following description is based on the dissections of *Necturus maculatus*. This dissection has been carried out with Wilder's account of the muscles of the head of *Siren lacertina* (1891) and Norris's account of the Cranial Nerves of the same species (1913) open beside me. It will be found that, in the main, the muscles of *Necturus* are similar to those of *Siren*, and the Axolotl.

MUSCLES OF THE MAXILLO-MANDIBULAR SEGMENT.

The Submentalis is, relatively, a smaller muscle than in the Axolotl.

The Intermandibularis is essentially the same.

Wilder has confused the posterior portion of this with anterior part of the Csv.2a. He describes an intermaxillaris anterior which includes the Csv.1a, Csv.1b and the Csv.2a. The gap which he describes between the fibres of his intermandibularis anterior laterally is quite obvious in both the Axolotl and *Necturus*, but it lies between the posterior margin of the Csv.1b and the anterior margin of Csv.2a.

The muscles of mastication are remarkably massive.

The Temporalis (Figs. 83–84) (Masseter of Wilder, and of Norris, who in the main adopts Wilder's nomenclature).—The three portions which Wilder describes are not recognizable in *Necturus*, nor is it possible to recognize any boundaries whereby one may determine the portion of this muscle which should be regarded as homologous with the quadrato-mandibularis of the Axolotl. The origin of the muscle is extensive ; it is from the whole of the lateral surface of the skull behind the foramen for the V-VII nerve trunks. This area comprises the anterior surface of the quadrate, where that lies upon the otocrane, the anterior otocranial wall medial to the quadrate, and the lateral one-half of the dorsum of the skull. Medial to the muscle lies the pterygoideus muscle, and between them a strong fascial partition which Wilder designated the ligamentum intermusculare anterius. The median fibres of the temporalis muscle arise from the outer surface of this fascia almost as far forward as the posterior boundary of the orbit. The fibres arising from the fascia form a small antero-median portion of the muscle which is separated from the rest by a cleavage plane which, however, does not extend the full depth of the muscle. The posterior, and main, mass of the muscle bulges backward and ventrally beyond the posterior limit of its insertion and this portion covers, almost completely, but is in no way attached to,

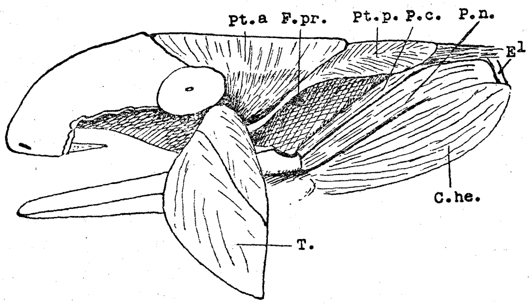

Fig. 83.—*Necturus.*—Lateral aspect of the more superficial muscles. The M. temporalis has been detached from its origin and turned down.

the depressor mandibulae. Deep within this part of the muscle there is a tendon, as described by Wilder, into which the fibres are inserted. The fibres of the antero-median portion of the muscle are attached to the median border of this central tendon towards its deep margin. The tendon emerges from the anterior edge of the muscle immediately below the orbit and is inserted into the tip of the low coronoid process of the mandible and then runs along the upper and outer edge of the mandible, becoming blended with the deep fascia of the lower lip and perichondrium of the jaw.

It is not found possible to define any clean or nearly clean cleavage plane in this muscle, which would indicate the possible boundary between components comparable with the temporalis and quadrato-mandibularis of the Axolotl.

Innervation.—The motor supply to this muscle leaves the main trunk of the Vth nerve actually before the various rami have separated. Doubtless, microscopic examination would reveal that it is a branch of the R. mandibularis.

The Pterygoideus.—This muscle was described by Wilder as the temporalis. As in *Siren*, two parts of the muscle can be recognized dorsally.

The Pars Posterior (Fig. 83, Pt.p.) is the smaller part. It arises from the dorsal median intermuscular septum (ligamentum intermusculare mediale, of Wilder), the fascia covering the anterior end of the dorsal trunk muscles and a small area of the dorsum of the skull just in front of the origin of these last muscles. The muscle has a central tendon into which the fibres are inserted. Those arising from the intermuscular septum are inserted into the median surface of the tendon, those from the other origins into its outer surface. The muscle tapers as it passes rostrad, laterad and ventrad ; from its anterior apex the tendon issues and continues in the same direction to become attached to the inner surface of the tendon of the temporalis muscle in front of all its fibres and just above and behind the insertion into the conoroid process of the jaw.

Innervation.—Just where the tendon issues from amongst the muscle fibres this muscle passes directly dorsad of the foramen prooticum from which the Vth and VIIth nerves issue. The motor twig to the muscle rises directly from the crowded branches of these nerves as they issue from the foramen. Doubtless it comes from the R. mandibularis V, but this could not be demonstrated by dissection.

Pars Anterior (Fig. 83, Pt.a.).—This is very much the larger part of the muscle and has an extensive origin. It arises from the dorsum of the skull from medial to the auditory capsule posteriorly, forward, till its anterior margin lies above and medial to the anterior boundary of the orbit ; also from the sloping lateral surface of the anterior process of the parietal bone, which extends forward laterally to the frontal to reach the low antorbital prominence. This latter, however, really lies a little posterior to the anterior boundary of the eye. A third area of origin is situated below the second and extends neither so far forward nor so far back. This area is the sulcus in front of the ophthalmicus profundus and optic foramina and the upper surface of the os transversum lateral to the sulcus.

The whole of the fibres are gathered to a short, relatively broad, tendon which is bound to the inner surface of the mandible for a short distance in front of the joint. The anterior fibres and anterior margin of the tendon pass below the eye to this insertion.

Innervation.—This also is by a nerve which was traced only to the closely packed branches of the V-VII complex in the opening of the foramen prooticum, again doubtless a branch of the R. mandibularis V.

The deep portion of this muscle, that arising from the sulcus in front of the ophthalmicus profundus foramen, is very certainly the muscle which Norris illustrates and identifies as the pterygoideus (Norris, *l.c.*, Figs. 10 and 11). Although it is separated from the rest of the muscle by a slight gap at its origin, along which the deep ophthalmic and optic nerves run, it is not possible to separate the fasciculi from those of the rest of the muscle without dividing the fasciculi. It is not possible to regard this portion as a separate muscle, but it is of particular interest as foreshadowing the division of the pterygoid into the partes internus and externus which will be found in the reptiles. It is probable that this is the muscle which Wilder describes as the pterygomaxillaris, although it is markedly different from the muscle in *Siren* as he describes it. It is very definitely not wrapped around the inferior surface of the mandible at its insertion to become subdermal as he describes. Norris depicts the ventral end of the muscle in *Siren* and shows it subdermal (Norris, l.c., Fig. 11).

The ramus mandibularis V, when it leaves the foramen prooticum, turns sharply laterad and slightly dorsad and then turns ventrad through the temporalis muscle, a good deal closer to the deep surface than to the superficial. It reaches the upper edge of the ramus of the lower jaw behind the insertion of the temporalis and then turns forward along the jaw. It follows from this that the whole of the pterygoid muscle lies medial to the nerve. The composite supraorbitalis and infraorbitalis trunks also issue from the foramen prooticum, they run directly forward with but a very slight inclination dorsad on the lateral surface of the pterygoid muscle medial to the ligamentum intermusculare anterior, the one turning laterally at the posterior boundary of the orbit, the other medially and dorsally, to pass one below and the other above the orbit.

MUSCLES OF THE HYOID SEGMENT.

The ventral constrictor sheet is essentially similar to that of the larger Axolotl. It will be remembered that in the smaller of those the Csv.2b could be traced dorsally to the upper end of the cerato-hyoideus externus, but that in the larger specimens this was not possible. In *Necturus* the origin of the Csv.2b is from the fascia covering the cerato-hyoideus externus, interhyoideus, along a line which runs horizontally caudad from the posterior end of the lower jaw to the root of the first external branchia, that is to say, which crosses the interhyoideus just where it turns dorsad behind the angle of the jaw. Wilder (1891) designates the Csv.2 " intermandibularis posterior ". Drüner (1903) terms the Csv.2a the " interhyoideus ", and the Csv.2b he calls the " cephalo-dorso-pectoralis " or sphincter colli.

Innervation.—Norris says that the branch of the R. mandibularis V which pierces the ramus of the jaw divides into anterior and posterior divisions after its emergence on the inferior and internal surface thereof. He further says that the posterior division innervates the posterior portion of the intermandibularis posterior and the anterior portion of the interhyoideus. That the interhyoideus should be innervated by a branch of the Vth nerve was quite unexpected and a very careful search was made for this posteriorly trending division. It was found, on both sides of my specimen, that the nerve divided, very soon after its emergence from the mandible, into anterior and posterior divisions, but the posterior division passed almost directly mediad, with but a slight trend caudad, and on both sides it was found to terminate before the very definite break between the anterior margin of the Csv.2 and posterior margin of Csv.1 was reached.

The ramus jugularis of the VIIth nerve was traced, just as Norris describes, on to the Csv.2 below the interhyoideus, cerato-hyoideus externus, and was found to send branches back to its posterior margin as well as forward nearly to the anterior margin.

The Depressor mandibulae (Digastricus, Wilder ; Cephalo-dorso-mandibularis, Drüner).—This muscle is more compact than is that of the Axolotl, the two parts are well defined.

Pars Cephalognathica (Fig. 83, P.c.).—This arises from the back of the suspensorium and the otocrane ; it is a narrow muscle deeper than it is broad. Insertion is by a short tendon, common to both parts of the muscle, into the posterior end of the mandible. The upper half of the deeper surface of this muscle is closely knit to the levator hyoidei. Wilder apparently failed to recognize this fact and describes the two together as the anterior portion of the digastricus.

Pars Notognathica (Fig. 83, P.n.).—The origin of this more massive part of the muscle is from the top of the first epibranchial cartilage and from a strong branchio-cephalic membrane which forms the roof of the anterior part of the branchial chamber. This membrane is attached in front to the postero-inferior edge of the suspensorium and otocrane medial to it and, extending horizontally backward, is bound to the upper half of the first epibranchial cartilage. The inferior surface of the skull immediately in front of its line of attachment forms the roof of the mouth, and this membrane carries the mucosa of that roof to the first branchial arch. The fibres of the muscle pass rostrad and ventrad to their insertion.

Innervation.—The pars cephalognathica is innervated by a branch from the hyomandibular trunk of the VIIth which divides to supply this muscle and the levator hyoidei. The nerve to the pars notognathica comes from the ramus jugularis. I only find one such ; Norris describes two in *Siren.*

The Levator Hyoidei (Fig. 83, L.hy.) is a small compact muscle which arises from the back of the otocrane and the branchiocephalic membrane deep to the upper end of the pars cephalognathica of the last muscle. The fibres are inserted into a thin tendon which is continued ventrad to be inserted on to the back of the ceratohyal just below the tip.

Innervation.—This is, as already described, by the same branch of the truncus hyomandibularis VII as innervates the muscle which covers it.

This muscle is of some interest on account of its presenting a partial fusion of the levator hyoidei and the pars cephalognathica of the depressor mandibulae. Although intimately knit to the more superficial muscle it may be separated, leaving clean cleavage surfaces. The tendon, however, is more closely bound to the deep margin of that of the depressor, though here also there was found a very definite narrow band of lighter texture between the two, indicating quite clearly the line of union.

Edgeworth describes and illustrates this muscle in 14½ mm. embryos of *Necturus*. He believed it to be a transient stage in the development of the depressor mandibulae (1911, p. 215). It is also present in *Siren* (Drüner and Norris).

The Interhyoideus (Fig. 83, C-H.e.) (Cerato-hyoideus externus, Wilder, Norris and Drüner).—This arises from the ventral surface of the ceratohyal, the area of origin extending from close to the inner, and anterior, end of the cartilage back to behind the posterior end of the mandible. The insertion is on to the spur of the first epibranchial cartilage just lateral to and below the origin of the pars notognathica of the depressor mandibulae and from the branchio-cephalic membrane just in front of the cartilage. The muscle is remarkably massive and bulges backward beyond its surface of origin. The deep surface of the muscle is clothed by a membranous tendon into which the fibres arising from the ceratohyal are inserted and which is itself inserted into the branchio-cephalic membrane. The fibres inserted into the epibranchial cartilage arise from a dense superficial aponeurosis.

Innervation.—By a branch from the ramus jugularis VII after that for the pars notognathica of the depressor mandibulae has been given off.

The cerato-hyoideus internus (cerato-branchialis) is not one of the hyoid muscles, it is described below as the subarcualis rectus I.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

These have been described by Drüner and by Wilder ; the synonymy is as follows :

This work.	Drüner.	Wilder.
Subarcualis rectus (I)	Ceratohyoideus internus	Ceratohyoideus internus
Subarcualia recti II-IV	Subarcualia recti	Constrictor arcuum branchialium
Superficial dorsal branchial constrictors	Levatores arcuum branchialium	Levatores arcuum
Subarcualia obliqui	Subarcualia obliqui	Protractor arcus ultimi
Interbranchiales.	Branchiales.	Depressores Branchialium.
Mm. marginales	Interbranchialis III	Hyo-trachealis
Constrictor pharyngei	Interbranchialis IV	Dorso-trachealis
Dorso-laryngeus	Dorso-laryngeus A and B	Dorso-laryngeus

The Subarcualis Rectus I (cerato-branchialis) arises from the posterior surface of the median end of the ceratohyal and from the basihyal alongside of it. The muscle is a small flattened spindle of fibres which pass almost directly caudad with a slight inclination laterad to be inserted into the distal end of the first ceratobranchial and median end of the first epibranchial.

Innervation (After Norris).—By a combined nerve formed by anastomosis of terminal motor twigs of the post-trematic rami of IX and of the second branchial nerve, this latter being a branch of the Xth.

The Superficial Dorsal Branchial Constrictor muscles are four in number; they arise from the fascia dorsalis along a curved line which commences in front at the postero-dorsal corner of the superficial surface of the pars cephalognathica and extends caudad with a convexity dorsad to the antero-dorsal corner of the suprascapula and infraspinatus muscle. The fibres of the first muscle pass nearly horizontally caudad to be inserted on to the tip of the first epibranchial above the origin of the pars notognathica.

Innervation.—This is apparently the muscle, of which Norris describes the innervation, under the designation second branchial levator. He describes the first levator as being innervated by the first branchial nerve, ramus post-trematicus IX. This holds true for the deep levator of the first arch. The first superficial dorsal constrictor is innervated by a branch of the second branchial nerve, Xth.

The Second Constrictor is inserted into the tip of the second epibranchial cartilage. Its fibres have a direction almost directly ventrad and laterad. Like the other three the muscle is wider at its origin than at its insertion.

Innervation.—A branch of the second branchial nerve.

The Third Constrictor is inserted into the tip of the third epibranchial. Its fibres have a general direction laterad, ventrad and caudad.

Innervation.—A branch of the second branchial nerve.

The Fourth Constrictor is inserted into the strong membrane which, attaching the third branchial arch to the body dorsally, forms the lateral part of the roof of the branchial chamber between the last arch and the trunk muscles. Its fibres have a general direction nearly horizontally rostrad.

Innervation.—This appears to be double. I find, as Norris describes, a twig from the second branchial nerve and also one from the large truncus intestio-accessorius as it curves ventrad beneath the muscle; Norris also describes this second motor twig.

The Levator Arcus Branchialium I (Fig. 84, L.a.b.).—So far as I can ascertain, the true character of this muscle has not previously been recognized. Apparently Wilder noted the muscle, for he writes that the first levator has a direction, in *Siren*, different from that of the rest, but that it had a much deeper origin and somewhat deeper insertion than the other muscles escaped his observation.

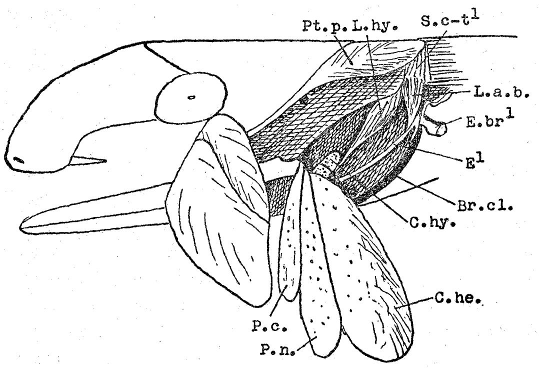

Fig. 84.—*Necturus.*—The same as Fig. 83, but with the Mm. depressor mandibulae and interhyoideus detached and turned down.

The muscle arises from the postero-internal and dorsal corner of the auditory capsule immediately medial to and above the uppermost corner of the origin of the pars cephalognathica, lateral to the posterior edge of the cranial origin of the first transverse spino-capitis muscle, under cover of the lateral margin of the first longitudinal dorsal myomere and the origin of the first superficial dorsal constrictor. The muscle is a relatively stout, short bundle of fibres roughly square in cross section; it arises by a very short flat tendon and swells very rapidly. The direction from its origin is caudad, laterad and ventrad deep to the upper end of the pars notognathica, and under this muscle it contracts again, its fibres being inserted into a narrow flat tendon which is inserted into the upper end of the anterior and external surface of the first epibranchial cartilage on a level with the top of the origin of the interhyoideus.

Innervation.—The ramus pre-trematicus of the IXth nerve passes laterad and ventrad deep to the muscle and sends several exceedingly fine fibrils into its deep surface; just where these end it was quite impossible to determine, they were much too fine to trace. The ramus post-trematicus winds caudad and laterad around its median and external surfaces and then passes ventrad across, superficial to the tendon of the muscle. The motor twigs to the muscle are given off as the nerve lies against the median surface.

The Interbranchial Muscles.—These are so essentially similar to those of the Axolotl that no further description is called for.

The several small muscles related to the outer ends of the epibranchial cartilages which were described by Wilder in *Siren* were not found in *Necturus*.

The subarcualia recti, including the first (cerato-hyoideus internus) are essentially similar to those of the Axolotl.

The Constrictor Pharyngei arises from the fascia dorsalis immediately behind, and in contact with, the fourth superficial dorsal constrictor, from the membrane into which that constrictor is inserted, immediately ventral to its line of insertion and from the third epibranchial cartilage.

There is little doubt that this extensive sheet represents the dorso-laryngeus and the third and fourth interbranchial muscles of Drüner. The insertion is into a mid-ventral raphe, and extends back so that the posterior fibres run directly transversely and ventrad from origin to insertion.

Innervation.—By twigs from the truncus intestio-accessorius of the Xth.

The Capiti Pectoral Muscles do not call for description; they are similar to those of the Axolotl.

5. Review of the Branchiate Amphibians.

Following the study of the anatomy and development of all the branchiate adult and larval amphibians except the Caecilians, a general survey seems desirable.

The next section of this paper will be devoted to the study of the adult anatomy of the Anura, Caducibranchiate Urodeles and the Caecilians. In these we shall have left behind most of those structures which, in tetrapods so far studied, have served us as identification marks whereby to determine homologies as between these and the fishes. So far we have been studying more or less fish-like animals, and in the Dipnoans and larval amphibians we believe we have identified, in much modified form, not a few of the primitive muscles of the elasmobranch fishes; most of these will later be found further modified in the abranchiate amphibians and the higher tetrapods.

Before passing to these more modified forms it is proposed to review again the muscles, and discuss the homologies adopted.

At the outset a general statement may be made, which applies to the arguments and evidence generally, in order to save repetition later.

Throughout the whole of this work it has been accepted as a fact that muscles which are innervated by the motor division of the same nerve are all of them to be regarded as having been developed from the primordial muscle plate of the segment to which that nerve belongs. There are, of course, exceptions to this generalization, and, where those exceptions are recognizable, they have been noted. In the great majority of instances the truth of the general proposition has been specifically demonstrated. So much is that so, that one has felt justified in assuming its truth in those instances where one met muscles whose homologies were to be determined, but whose development was not known in stages early enough to establish, beyond doubt, their segmental origin; the levator hyoidei of the anuran tadpole is an instance in illustration of this. In such cases, however, one has never had to rely only on the innervation of the muscle to determine its segmental origin. There has always been, in addition, the relation of the muscle to skeletal structures and/or a comparable muscle in one or more other forms to which one was able to appeal.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

On the ventrum of the head it has been found that the mandibular muscles of the primitive and larval amphibians are essentially similar to those of the fishes, and that there has been surprisingly little alteration in the muscles when compared, not with those of the bony fishes, but with the more primitive elasmobranchs. Already, in one or two of these, the ventral mandibular superficial constrictor showed a division into a submentalis and intermandibularis. It will be remembered that in not a few of the elasmobranchs this muscle, in its posterior portion, extended dorsally superficial to the ramus of the lower jaw. This condition was particularly noted by Lightoller, who designated it the Csv.1b or pars extramandibularis. There is no trace of any pars extramandibularis in the amphibians we have studied, nor, be it noted, was there in any one of the bony fishes.

Of the dorsal mandibular muscles of the elasmobranchs there apparently remain in the amphibians only derivatives of the mandibular adductors. The levator maxillae superior (L.1) and the first dorsal superficial constrictor (Csd.1) do not appear to have persisted in any form at all.* Lightoller is of the opinion that the L.1 persists as the pterygoideus muscle of tetrapods; this question has already been discussed, and it will be returned to after we have described the adult anatomy of the Amphibians.

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* It may, however, be suggested that, since the extrinsic muscles of the eye-ball, levator bulbae and palpebral muscles, etc., are innervated by the Vth nerve, and by the mandibular ramus thereof, this is evidence that they are derivatives of the mandibular muscle plate. So far the argument is probably sound, but it might be further argued that their dorsal situation indicates that they may be regarded as derivatives of the missing dorsal muscles. This suggestion is tempting, but the question is complicated by the presence of both extrinsic eye muscles, and the two dorsal muscles in certain of the Selachians.

Further discussion of the rest of the derivatives of the adductor muscles of the primitive fishes is also reserved till later.

The Muscles of the Hyoid Segment.

It will be remembered that in the elasmobranch fishes there were, in this segment, superficial dorsal and ventral constrictors, deep constrictors, dorsal (the interbranchial muscle, Csd.2a or pars quadrato-hyoidea of Lightoller) and ventral (the interhyoideus), and the levator hyoidei.

In the amphibians the hyoid muscles are depressor mandibulae, levator hyoidei, interhyoideus (the cerato-hyoideus externus) and the ventral superficial constrictor. In the Dipnoi there is, in addition, a dorsal superficial constrictor and a retractor mandibulae, the depressor mandibulae.

The Depressor Mandibulae.

This muscle is of particular interest because it has generally been regarded as the forerunner of portion of the digastricus of the higher vertebrates. Lightoller has recently expressed the opinion that it is to be regarded as a composite muscle developed from the pars quadrato-hyoidea and the levator hyoidei, the pars cephalognathica being derived from the levator hyoidei and the pars notognathica from the pars quadrato-hyoidea; a somewhat similar, but not so explicitly expressed, opinion was held by Drüner and by Gaupp.

It appears, however, that the pars cephalognathica may, itself, be a composite muscle.

Lightoller's conclusions were founded on a study of the muscles of the Axolotl and adult *Megalobatrachus,* in neither of which has any levator hyoidei been preserved. It would appear that he was unaware of the fact that a levator was present in some, at least, of the perennibranchiate urodeles, and, so far as I am aware, there had been at that time no record of its transient development in the anuran tadpole; I believe that my discovery of this muscle is a definite contribution to the subject; I can find no previous mention of the muscle.*

There appears no reason to doubt that I have correctly identified this little muscle, although I have not been able to trace it back to the stage where it is separated from a primordial hyoid muscle plate. It is very clearly innervated by the VIIth nerve and is attached on the one hand to the skull and on the other to the upper end of the ceratohyal. Further, there is a veritable levator hyoidei developed in *Siren* and in *Necturus.*

It can be stated quite confidently that the levator hyoidei of the anuran tadpole is a caducous muscle and that it takes no part in the formation of the depressor mandibulae in the Anura. I have been able to observe the development of the one and the gradual disappearance of the other, and at no time does the posterior margin of the depressor come into contact with any portion of the levator; there is always a considerable gap between the two muscles.

On the other hand, I have observed in the 13–14 mm. larva of the Axolotl (*Amblystoma tigrinum*) that a few of the deeper fibres of the pars cephalognathica of the depressor are inserted into the tip of the ceratohyal. These few fibres may be regarded as a very transient levator hyoidei, but the pars cephalognathica is at this stage a well developed muscle, and these few fibres form but a very small portion of the whole.

In *Necturus,* and presumably also in *Siren,* the levator hyoidei is related to the pars cephalognathica precisely as this little transient muscle is to the larger in the larval Axolotl, and the two muscles are innervated by twigs of the one branch of the VIIth nerve. In *Necturus,* however, the levator maintains its identity throughout life, its tendon being bound to that of the cephalic head of the depressor.

There is no levator hyoidei in the adult Anura, nor, so far as is known at present, in the adult caducibranchiate and cryptobranchiate urodeles.

But if the levator is not a contributor to the cephalic head of the depressor mandibulae in the Anura, whence comes the definite duality of the depressor?

Since the muscle is very evidently not developed from the levator in these amphibians it is to them one must look for the explanation of a duality of constitution which is exhibited in all amphibians, but which in some other forms appears conceivably due to the incorporation of the levators. Since the duality is clearly not due to the incorporation of the levator in the Anura it is probably not due to that factor in those other forms.

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* Edgeworth (1935, Figs. 417 and 419) reproduces two drawings from Luther in which this muscle is shown and designated Suspensorio-hyoideus.

It will be remembered that in the anuran tadpole the pars notognathica arises from the lateral end of the anterior edge of the ceratohyal and that this origin persists until, at metamorphosis, the ceratohyal becomes converted into the stylohyal.

Also it will be remembered that in the 13–14 mm. larvae of the Axolotl, this head of the depressor was very much smaller than the cephalic head and took its origin from the ceratohyal immediately behind the posterior end of Meckel's cartilage.

Now it will also be remembered that in the Dipneumona there is a retractor mandibulae which is formed from the middle portion of the hyoid muscle plate. Edgeworth's description of the development of this muscle has already been quoted. It is attached, in front of the dorsal portion of the constrictor sheet, to the auditory capsule.

Edgeworth quite definitely states that this retractor is not homologous with the depressor mandibulae of the amphibia. With this statement I find myself unable to agree, in view of the fact that in the Anura, at least, the depressor is certainly not homologous, as he states, with the levator hyoidei.

To my mind we have here the explanation we seek. To me it seems that the pars cephalognathica may be homologized with this retractor of the dipneumonous dipnoans, and perhaps with those lateral fibres of the interhyoideus of *Neoceratodus* which arise from the mandible.

It further seems probable that this muscle is homologous with the pars quadrato-hyoidea of the elasmobranchs. It was pointed out, when reviewing this muscle in the section describing the selachian muscles, that the anterior part of the dorsal superficial sheet in the hyoid segment was probably really the deep constrictor forced to the surface by changes in the visceral skeleton in its own segment and in that in front. In any case the pars quadrato-hyoidea is the most anterior portion of the hyoid sheet, and it is just this portion which gives rise to the retractor mandibulae of the dipnoans; the posterior portion forms an interrupted dorso-ventral sheet behind it.

This homology, however, in view of the evidence, cannot be regarded as excluding the possibility of the hyoid levator being a contributor to the cephalic head of the depressor in tetrapoda other than the Anura. It is possible that in these last the articulation of the ceratohyal to the meta-pterygoid, by divorcing the levator from the rest of the muscle, introduced a peculiarity into the history of these muscles which is not present in other tetrapods, in none of which does the articulation of the ceratohyal and the suspensorium occur.

The origin of the posterior part of the depressor from the ceratohyal in its early stages is of importance in determining its homology. It is noteworthy that in the youngest Axolotls which it was found possible to dissect, it was not possible to demonstrate the muscle at all; when first it appeared it was a very narrow muscle immediately behind the jaw. As the dorsal portion of the Csv.2b grew smaller and smaller, this muscle increased in bulk. One gained the definite opinion that this posterior head of the depressor was developed by the transfer of the dorsal fibres of the constrictor sheet to the mandible. Druner was of the opinion that the depressor could be divided into a deep layer derived from the hyoid levator and a more superficial layer which he derived from the cerato-hyoideus externus. It is possible that he observed the apparent decrease in size of this last muscle, which takes place as the dorsal fibres of the more superficial constrictor are transferred to the posterior end of the mandible, and concluded that it was an actual reduction of the cerato-hyoideus which he observed. In my experience the interhyoideus muscle of the amphibian is never caducous.

It is now suggested that the pars notognathica of the depressor mandibulae is derived from the remainder of the dorsal portion of the superficial hyoid constrictor, the partes interinscriptionalis and arcuata.

The phylogenetic history of the depressor mandibulae, under this interpretation, may be regarded as being presented in two stages in the amphibians.

Stage one is the dipnoan, in which the anterior, deeper, fibres of the dorsal constrictor, the pars quadrato-hyoidea, are modified to act as a retractor mandibulae, thus forming the primitive pars cephalognathica.

Stage two is the more advanced, amphibian, in which the remaining fibres of the dorsal constrictor are transferred inferiorly to an insertion on the end of the mandible and form the pars notognathica.

Finally, it is not improbable that the levator hyoidei, which appears to have been lost entirely by the abranchiate amphibians, may also be incorporated in the pars cephalognathica, in forms other than the Anura.

Edgeworth states that in certain Anura (and *Lepus*) the lower end of the hyoid myotome, after its separation from the interhyoideus, becomes separated from the part above to form a hyomaxillaris muscle which, later, gives rise to the inner portion (cephalic head ?) of the depressor mandibulae. He further states that in the urodeles, *Necturus* and *Triton*, a corresponding anlage develops into a hyomaxillaris ligament and that in the Selachii no hyomaxillaris anlage is formed (1911, pp. 213–220).

Clearly there is some confusion here ; to begin with, whereas there is a strong hyomaxillaris ligament in the Axolotl, such a ligament in *Necturus*, and presumably in *Siren*, is represented by the conjoined tendons of the levator hyoidei and of the pars cephalognathica and, moreover, there is a well-defined and relatively large levator hyoidei muscle developed in these two genera. One is compelled to assume that the levator in the Urodela was developed from a hyomaxillaris anlage, as in the Anura.

My own study of the development of the depressor leads to the belief that both parts are developed from anterior and dorsal portions of the hyoid myotome. At their first appearance in the youngest urodele larvae I have been able to recognize them in, there has been a well developed Csv.2b extending dorsally behind them. Further than this in these forms there has been a well developed Csv.2a ventral and medial to the two parts of the depressor.

The lower end of the hyoid myotome would be the mid-ventral portion, or the forerunner of this, and the presence of perfectly typical Csv.2a and b surely indicates that it was not this portion of the hyoid myotome which gave rise to the depressor in the amphibians.

Apparently that which Edgeworth describes was in reality the lower and anterior portion of the dorsal part of the hyoid myotome ; maybe Edgeworth refers to the Csv.2 under the name of "interhyoideus ".

Schultze describes five muscles in the upper part of the hyoid segment in anuran tadpoles which he studied.

Their synonymy is as follows :

Schultze.	This work.	
Orbito hyoideus	Dilator hyoidei	
Suspensorio-hyoideus	Levator hyoidei	
Cerato-hyo-angularis	Pars notognathica	Depressor mandibulae
Suspensorio-angularis	Pars notognathica	
Quadrato-angularis	Massetericus (tadpole)	
	Masseter major	Adult
	Masseter minor	
	Masseter minimus	

The Interhyoideus and the Superficial Ventral Constrictor.

The ventral superficial hyoid constrictor sheet in the amphibians has been designated interhyoideus, subhyoideus, cephalo-dorso-pectoralis, sphincter colli, posterior intermandibular, and posterior mylohyoid muscle by different writers. The interhyoideus has been fairly constantly designated cerato-hyoideus externus.

Lightoller has homologized the anterior portion of the Csv.2 with the interhyoideus of the selachians, and the posterior portion he regards as the homologue of the pars inscriptionalis of the hyoid superficial ventral constrictor, and there is no doubt that there is strong evidence in support of such a view.

The anterior part of the Csv.2 in the urodeles arises on each side from the ceratohyal and the fibres are inserted into a mid-ventral raphe deep to the Csv.1 precisely as is the interhyoideus in the selachians. Not only is this so, but in the Anura the only superficial ventral constrictor is certainly developed from a muscle which arises on each side from the ceratohyal and is inserted into a mid-ventral raphe, is in fact developed from a veritable interhyoideus.

These facts would seem to settle the question quite satisfactorily ; but doubt is introduced by the presence of the so-called cerato-hyoideus externus. This muscle is very definitely developed from the deep surface of the anterior portion of the ventral hyoid plate, as also is the interhyoideus, not only in the selachians, but also in the teleosts. There is little room for doubt that it is the interhyoideus which, in the teleosts, contributes the hyoid component to the protractor hyoidei. This lies deeply to the rest of the ventral constrictor derivatives and its fibres have a nearly longitudinal direction, similar to that of the cerato-hyoideus externus.

It is demonstrable, then, that the interhyoideus muscle of the selachians was capable of being modified so that its fibres have a nearly longitudinal direction, and its insertion transferred from the deep surface of the Csv.2 to deeper structures. These modifications have taken place in the teleosts.

It appears, therefore, that one must conclude that the cerato-hyoideus externus is homologous with the interhyoideus of the selachians.

The alternative is to regard this amphibian muscle as a quite new muscle, and to this one might be persuaded by the insertion of the anterior portion of the Csv.2a deep to the Csv.1b. In this connection it may be pointed out that the posterior portion of the Csv.1b (Csv.1b^2) is itself inserted deep to the anterior portion (Csv.1b^1) of the same muscle in the frogs.

In the Dipnoi there is an interhyoideus muscle deep to the superficial hyoid constrictor, but there is no cerato-hyoideus externus.

Having in mind the fact that the Csv.2 of the perennibranchiate urodeles extends right back to the posterior margin of the opercular fold, it seems that this extensive sheet may be regarded as homologous with the partes interinscriptionalis and arcuata of the selachians.

In the Anura there is no cerato-hyoideus externus. The interhyoideus has been modified to act as a Csv.2.

The Muscles of the Branchial Segments.

In the selachians the muscles of these segments were superficial dorsal and ventral constrictors, interbranchial muscles, levators, epibranchial spinal muscles, epiarcualia obliqui, adductores arcuum branchialium and coraco-branchiales.

In the amphibians generally, the following are seen : superficial dorsal constrictors, interbranchiales, subarcualia transversi, obliqui and recti ; in particular groups there are also one single branchial levator, a single coraco-branchialis, and possibly a ventral superficial constrictor sheet.

The Superficial Dorsal Constrictors and the Branchial Levator.

The discovery of a veritable branchial levator in *Necturus* may be regarded as providing partial confirmation of the identification of the so-called levators of the amphibians as the homologues of the superficial dorsal constrictors.

These muscles are four in number in every branchiate amphibian that has yet been studied. They arise from the fascia dorsalis and are inserted into the subcutaneous fascia close to the upper ends of the epibranchial arches. Both at their origin and at their insertion they are definitely more superficially placed than are musculi marginales, and these latter are, apparently beyond question, homologous with the deep constrictors of the branchial segments in the selachians. In the selachians the levators are more deeply placed than the deep constrictors. When to these facts is added the discovery of a branchial levator in just precisely the situation of the levators in the Dipnoi and in the teleosts it would appear that we must conclude that, except for this single levator, those muscles are not developed in any of the amphibians except the Dipnoi. In these latter all five levators are developed, and they are deeply placed, as in the teleosts and as in the elasmobranchs. It should be particularly noted that in the dipnoans the musculi marginales are continued dorsad to insertions on to the cartilaginous roof of the branchiopharynx, and that the levators are placed, each of them, deep to its own segmental M. marginalis.

The Ventral Branchial Muscles.

The various accounts which have been published describing the development of these muscles are conflicting, and none of them agree with my own findings, so that their development is still far from being properly understood.

It appears quite clear that the primordial branchial muscle plates divide into dorsal, middle and ventral portions in the amphibians as in the selachians. It is further clear that the dorsal portion gives rise only to the superficial constrictors (levators), that the middle portion gives rise only to the Mm. marginales, and that from the ventral portion there are developed the various ventral muscles.

The superficial constrictors in *Amblystoma* very certainly give rise, at metamorphosis, to an anterior portion of the cucullaris.

The Mm. marginales in all forms are completely caducous.

The fate of the superficial constrictors in the Anura is not so clear.

In the fourth branchial segment there is no M. marginalis developed in any of the amphibians which has yet been studied.

In well advanced tadpoles of various anuran species I find the following muscles : superficial dorsal branchial constrictors (the so-called levators), constrictor pharyngei, omo-hyoideus, cucullaris, dorso-laryngeus, cranio-hyoideus and cranio-laryngeus.

Of the superficial constrictors there are quite certainly three, and, it may be, four. There are no other muscles present which could possibly be interpreted as " levators ".

Edgeworth (1911, p. 247) says that on the atrophy of the cerato-branchialis (subarcualis rectus I of this work) and Mm. marginales, all four levators extend downwards, and their lower ends become attached to the body and processus posterior medius of the hyoid bar.

Now, in the anura which I have studied the four muscles which are attached below as just described are the constrictor pharyngei (petrohyoidei anterior), dorso-laryngeus, cranio-hyoideus and cranio-laryngeus (petrohyoidei posteriores), and these are fully developed whilst still three, at least, of the constrictors are short muscles, and are not in any way changed from their early form. Later these short muscles disappear without, apparently, contributing to the formation of any other muscles whatsoever.

Edgeworth (l.c.) further says that in the 12 mm. larva of *Rana* there is a downgrowth of the fourth levator forming the diaphragmato-branchialis lateralis of Schultze. Its upper end, he says, becomes attached to the fourth bar, its lower end to the diaphragm, and that the cucullaris is formed early in metamorphosis from cells proliferated from the outer surface of this levator.

I find the cucullaris quite extensively developed in tadpoles long before the development of the pectoral girdle or fore limbs, and in slightly later stages a muscle, which subsequently proves to be the omo-hyoideus, having just the attachments of the diaphragmato-branchialis lateralis of Schultze.

It is possible that both these muscles are derived from the upper end of the fourth branchial muscle plate.

The insertion of the constrictor pharyngei into the mid-ventral raphe and its situation immediately behind the fourth branchial arch leads one to identify it as the fourth subarcualis transversus with some confidence, notwithstanding the fact that one has been able to observe it to grow downward from above. It may be suggested that there is incorporated with it the missing fourth M. marginalis, and that there has been no splitting off of the ventral moiety, which in the other segments gave rise to the ventral muscles, so that in consequence the composite muscle had to grow down to reach the mid-ventral raphe.

There is no muscle reaching the mid-ventral line behind this in the Anura.

Drüner was of the opinion that in the Urodeles an atrophied fifth branchial segment is present, and represented by nerve rami and muscles, behind the fourth. One notes, in conformity with this suggestion, that in the urodeles, *Necturus*, and the Axolotl, the muscle sheet which occupies the situation of the constrictor pharyngei of the Anura is much more extensive.

It seems probable that the three posterior petrohyoid muscles of the Anura are modified derivatives of this fifth segment, and that one of them represents the dorso-laryngeus of the urodeles.

The history of the omo-hyoideus is of particular interest. There is little doubt that, in its anterior part, which appears first, it is a derivative of one of the branchial muscle plates. Its innervation in the adult by the first and/or second spinal nerve by way of the hypoglossal nerve, is therefore a definite instance of the capture of a Xth nerve muscle by one of the spinal nerves.

THE CEPHALIC MUSCLES OF THE ABRANCHIATE AMPHIBIANS.

It is now proposed to review the adult anatomy of the various groups of the Amphibia, excluding the perennibranchiate forms.

In all these the branchial skeleton has given place to the " hyoid " skeleton which, variously modified, acts as the support of the tongue throughout the higher vertebrata. This profound modification of the visceral skeleton has naturally been accompanied by equally profound modifications of the musculature, whose inception has already been studied in the branchiate larvae and adult amphibians.

Together with those which have just been studied, the further modifications which will be met with constitute the connecting links between the primitive musculature of the fishes and that of the tetrapods, and their comprehension is a necessary prelude to the proper understanding of the cephalic musculature of the reptiles and the mammals.

1. The Adult Caducibranciate Urodeles.

The Adult Amblystoma.

(Fig. 85.*)

MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a and b are similar to the muscles in the Axolotl as also are the muscles of mastication; so much is this so that no further description is called for.

MUSCLES OF THE HYOID SEGMENT.

The Csv.2a and b are essentially as in the Axolotl. The ceratohyal has lost its connection anteriorly and medially with the rest of the hyoid skeleton. It is now an elongated spathulate cartilage with a curved cylindrical posterior end. This cylindrical portion curves dorsad behind the end of the mandible and, at its tip, is attached to the hinder margin of the auditory capsule behind, and somewhat higher than, the mandible. The Csv.2a arises from the dorsal surface of this short posterior cylindrical section of the ceratohyal. The Csv.2b arises from the outer surface of the depressor mandibulae. Actually its origin is from a strong fascia, covering this muscle, which is bound in front to the fibrous capsule of the maxillo-mandibular joint and behind to the pectoral girdle. The greater part of the fibres of the Csv.2b converge to be inserted just behind the jaw joint.

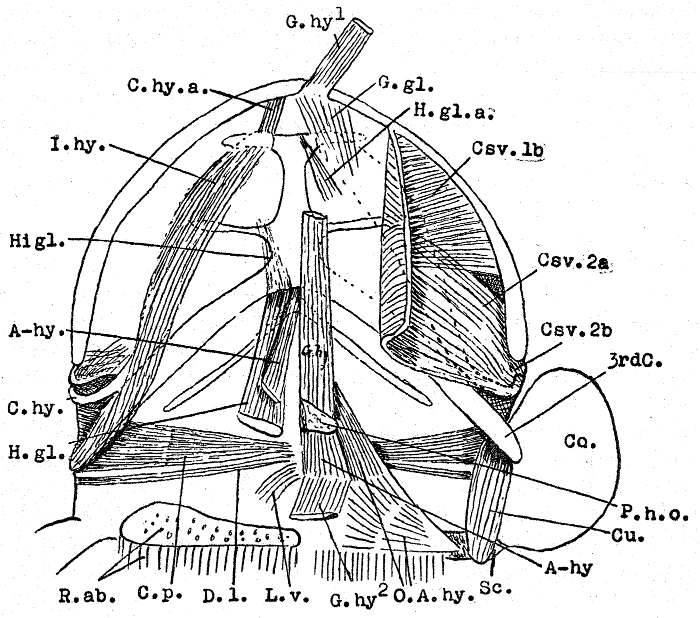

Fig. 85.—*Amblystoma.* The muscles of the ventrum of the head.

The Pars Cephalognathica of the depressor mandibulae is similar to that of the Axolotl. The Pars Notognathica is more extensive, and the two parts together now occupy most of the

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[*] Fig. 85 is a slightly schematic illustration of the ventral musculature of *Amblystoma*. Besides the muscles described in the text, the following structures are shown. The hyoid skeleton, 3rd C, its third cornu. The post-hyoid ossicle, P-h.o., the coracoid of the left side turned away outward, Co., the lower end of the scapula, Sc., the anterior end of the rectus abdominis muscles, R.ab., the dorsal end of the ceratohyal cartilage curling to its attachment to the back of the skull, C.hy. The anterior end of the hyo-glossus muscle is represented as seen through the hyoid plate and cornua; these latter are indicated, where they are dorsal to the muscles, by dotted outlines.

position of the superficially placed upper end of the interhyoideus and the superficial constrictors, arising from the fascia dorsalis. This statement, it should be understood, is relative for, to judge by the specimens at my disposal, there has been an actual condensation of structures in this area so that the posterior end of the jaw is brought actually nearer the pectoral girdle and there is much less dorsi-ventral depth.

The Interhyoideus (Fig. 85, I.hy.) now arises from the tip of the third process of the hyoid plate. This is the longest of the four lateral processes ; its dorsal end lies above and behind the point of attachment of the stylohyal to the skull. The origin of the interhyoideus is wrapped right around this cartilage, but the fibres curve so that they come to lie ventral to and in front of the cartilage between it and the upper end of the flattened portion of the ceratohyal. The muscle follows down the direction of the third process till it comes to lie a little distance medial to the posterior end of the jaw, where it turns more directly forward and gains the ventral surface of the ceratohyal at about the middle of its length. It is inserted on to the anterior one-third of the length of this surface. The ceratohyal lies dorsal to the third process behind the jaw above, and below this it lies anterior.

Whether the Cerato-hyoideus anterior (Fig. 85, C.hy.a.), a tiny muscle which joins the anterior tip of the ceratohyal to the ramus of the jaw just to one side of the submentalis, is a mandibular, hyoid or hypobranchial spinal muscle cannot be stated. Nothing is known of its innervation or development beyond the fact that, like the genioglossus of the Anura, it first makes its appearance independently of any muscle except for its proximity to the submentalis ; it may be a portion of the genio-glossus.

No levator hyoidei is to be found ; this was, of course, not expected to be found.

MUSCLES DERIVED FROM THE BRANCHIAL MUSCLE PLATES.

Drüner found in the adult *Amblystoma* a cerato-hyoideus internus, interbranchiales 4 and 5, dorso-laryngeus, levatores arcuum branchialium 1, 2, 3 and 4, and a laryngeus ventralis.

In the specimens at my disposal no muscle was found which could be identified as a cerato-hyoideus internus.

Interbranchiales 4 and 5 and the dorso-laryngeus have been, it is believed, identified, as also the " levatores arcuum branchialium ". Notwithstanding this agreement in the number of the muscles it will be found that my description is radically different from that of Drüner.

The superficial dorsal constrictors (levators of Drüner) are believed to have given rise to a cephalic head of the cucullaris. This muscle, it will be remembered, arose from the fascia dorsalis behind the dorso-laryngeus and with its anterior dorsal corner deep to that muscle ; this was the condition in the Axolotl. In *Necturus* the superficial dorsal constrictors were found to constitute an almost continuous sheet whose anterior part arises immediately above the pars cephalognathica of the depressor mandibulae, and whose posterior margin is so closely related to the anterior margin of the cucullaris that one has to dissect carefully to separate the two muscles. The dorso-laryngeus is situated superficially to this closely knit portion of both muscles. In both *Necturus* and the Axolotl the anterior boundary of the cucullaris is just at the posterior boundary of the superficial constrictors.

In the adult *Amblystoma*, the cucullaris (Fig. 85, Cu.) arises from a line which is precisely that of the origin of the superficial constrictors in the Axolotl and in *Necturus*, as well as from an origin which is similar to the origin of the cucullaris in those forms. It is nearly three times as wide at its origin as the muscle in the larva and in the other form.

This cucullaris of the adult *Amblystoma* separates itself into two portions as one liberates it from its insertion. The anterior portion is that which arises from the line of origin of the constrictors. This separation into anterior and posterior parts takes place, in every specimen dissected, at the same line and extends down almost to the insertion of the muscle.

It is concluded that as the branchial slit is closed and as the branchial arches are metamorphosed into the hyoid skeleton the constrictors grew down along the branchio-pectoral membrane to a new insertion on to the scapula along with the cucullaris.

Innervation.—Though I cannot state it as a fact, I believe that this interpretation of the origin of the cephalic head of the cucullaris is further supported by its innervation. I find three nerves entering the deep surface of the muscle. Two of these come from a nerve which is believed to join the ramus intestino-accessorius just after its emergence from among the other branches of the IX-X nerve complex. The nerve is very fine and I was unable to trace it in any dissection without breaking it.

The Dorso-laryngeus (Fig. 85, D.l.) and the Constrictor pharyngei (C.p.) present quite altered outlines. In the Axolotl these muscles together formed, on each side, a triangular sheet with its apex at the origin of the dorso-laryngeus and its base at the mid-line beneath the pharynx. In the adult this outline has been reversed, the apex now lies immediately ventral to the larynx, where the posterior boundary of the larval muscles was, and the base extends from the point of origin of the dorso-laryngeus forward, superficially to the cucullaris, along the same line of origin, but not extending quite so far forward.

Along this line of origin one finds a variable number, four to seven, of groups of fine strands of fasciculi which pass ventrad and mediad deep to the upper end of the interhyoideus. These reach the ventral surface of the pharyngeal mucosa behind the posterior cornua of the hyoid. Close to this point they are inserted into a transverse intersection, the posterior group alone not being interrupted by the intersection. Contracted to a narrow ribbon they then pass directly across to be inserted ventrally to the larynx.

The posterior, uninterrupted, group is constantly present ; it arises in the position of the M. dorso-laryngeus of the Axolotl. This strand, right from origin to insertion, is separated from the rest by a constant small interval ; it is believed to be the M. dorso-laryngeus.

The remainder of this narrow sheet of muscle fibres is homologized with the M. constrictor pharyngei of the Axolotl. The origin has been transferred from the last branchial cartilage to a higher fixed point. Whilst thus gaining in length, the muscle has lost in width.

Actually the transfer has not involved more than a short migration of the dorsal ends of the fibres. Quite a short forward rotation, with some dorsal movement, brings the point of origin in the Axolotl to the position of that in the adult.

The dorso-laryngeus is inserted on either side of the larynx, the constrictor pharyngei, just in front of it.

Immediately behind the insertion of the M. dorso-laryngeus there is a short laryngeus ventralis muscle (Fig. 85, L.v.). The fibres of this muscle arise from the submucosa behind the larynx and curve rostrad and mediad to an insertion on each side of the posterior half of the length of the slit-like closed larynx.

Innervation.—This is from the truncus intestino-accessorius X.

It seems possible that Drüner's description of the muscles of the adult *Amblystoma* really applies to some other amphibian. Naturally I have been puzzled by the marked differences in our two findings. To test the correctness of my own I have cleaned these muscles very completely, working under a relatively high power of the Greenough dissecting microscope ; I have then carefully liberated them from their origins on both sides and have cut away the whole thickness of the pharyngeal ventral floor, from in front of the larynx to behind the posterior limit of the laryngeus ventralis, removing the muscles and larynx intact. The preparation was then lightly stained with borax-carmine and studied after clearing in Spalteholz solution.

The above interpretation of the origin of the cephalic head of the cucullaris muscle and its situation deep to the origin of muscles which must be regarded as derivatives of muscle primordia more deeply placed than the superficial dorsal branchial constrictors once more raises the question as to whether, after all, it would not be better, and more correct, to regard these last as levators.

It is admitted that their situation in the adult, deep to the constrictor pharyngei and dorso-laryngeus, is contrary to that which should have been expected. On the other hand, in the larva the dorso-laryngeus lies superficially to the trapezius at its origin.

Now, according to Edgeworth, the cucullaris is developed from one or more primordia split off from the dorsal ends of the branchial muscle plates medial, that is deep, to the portions which give rise to the superficial muscles. Volker, according to Addens (1928), has shown that in *Larus ridibundus* the cucullaris is developed from split-off portions of the occipital myomeres. It may be remembered that Edgeworth has already been quoted as stating specifically that the cucullaris of *Rana* is developed early in metamorphosis from cells proliferated from the outer surface of the fourth levator.

All these descriptions of the development of the cucullaris ascribe its origin to primordia more superficially placed than that of the dorso-laryngeus, which, however, is found superficially to it. The dorso-laryngeus is unquestionably a deep constrictor.

Although the evidence is conflicting, and far from conclusive, I find, after my study of the structures themselves, that the so-called " levators " of the amphibians appear to me to be superficial muscles.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The genio-hyoideus muscle (Fig. 85, G.hy.) has increased in width and slightly in thickness, otherwise it is as in the Axolotl.

The claviculo-hyoideus is now quite clearly differentiated into three separate muscles, the hyo-abdominis, the hyoglossus, and the omo-abdomino-hyoideus.

Upon removal of the genio-hyoideus the last two muscles are brought into sight, the last being superficial to the lateral portion of the hyo-glossus.

The Omo-abdomino-hyoideus (Fig. 85, O.A.hy.) arises from the third hyoid cornu close to its attachment to the basihyal plate. At its origin it is a relatively thick muscle with an oval cross section. The medial fibres pass directly caudad to be inserted into the first tendinous inscription of the rectus abdominis, the lateral fibres swing laterally and caudad to be inserted into the scapula just laterally to the glenoid cavity. The intermediate fibres radiate between these two insertions. In similar manner the fibres which are attached to the scapula radiate widely, the most posterior pass directly mediad and ventrad to the first inscription, the rest having intermediate directions. When this muscle is dissected free and examined by transmitted light, a tendinous inscription is found running transversely across it just where the narrow anterior portion definitely commences to widen out, and another inscription, which passes obliquely from behind forward and laterad, commencing at the lower end of the inscription of the rectus abdominis and ending a short distance behind the lateral end of the first. Whilst these suggest a duality of origin for the muscle—cephalic and spinal, similar to that of the omo-hyoideus of the Anura—since nothing is known of the early history of the muscle, one can but mention this possibility. The muscle is fairly certainly homologous with part, at least, of the omo-hyoideus of the Frog.

The Hyo-glossus (Fig. 85, H.gl.) muscle arises actually as the anterior continuation of the rectus abdominis ; it comes forward on each side of the pericardium. As it reaches the anterior limit of the pericardium, its strands become gathered together to form a relatively stout rounded muscle. This continues forward under cover of the genio-glossus and medially to the omo-abdomino-hyoideus. Alongside of the origin of this last muscle, the hyoglossus passes forward dorsally to the inner end of the third cornu and ends by being inserted into the connective tissue of the tongue just above the second cornu.

The Abdomino-hyoideus (Fig. 85, A-hy.) arises as the forward continuation of the middle strip of the rectus abdominis. The two muscles lie side by side dorsally to the posterior end of the genio-hyoidei. They are short flattened muscles which are inserted into the posterior edge and ventral surface of the post-hyoid ossicle.*

The Genio-glossus (Fig. 86, G.gl.) is a very thin sheet of muscle fibres which arise from the inner surface of the mandible, close to the upper edge, for a short distance on each side of the symphysis and extend directly caudad, to end in the tissues of the tongue.

The Hyo-glossus Anterior (Fig. 86, H.gl.a.) arises by a very fine short tendon from the anterior edge of the hyoid plate. The two muscles arise almost together at the mid-line. The fibres pass caudad and laterad and terminate in the substance of the tongue.

Innervation.—All the hypobranchial spinal muscles are innervated by the hypobranchial nerve from the Ist and IInd spinal nerves.

Plethodon and *Diemyctylus.*

(Fig. 86.)

Of these genera I had for dissection two specimens each of *P. glutinosus* and *D. viridescens.* All four specimens were in an excellent state of preservation, and permitted the dissection of the muscles without difficulty. They were, however, all small and one was not able to determine the innervation of most of the muscles.

The two genera are described together because they are so essentially similar. *Plethodon* is one of the Lechriodont salamandrine urodeles and, therefore, closely allied to *Amblystoma* ; while *Diemyctylus* is one of the Mecodonta, also a salamandrine. It is therefore somewhat surprising to find that the former should so closely resemble the latter in its cephalic musculature, and differ in quite important details from the more closely allied *Amblystoma.*

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* The post-hyoid ossicle is a small triangular plate of bone developed from the posterior end and cornua of the basibranchial cartilage of the Axolotl. Into its two anterior edges the genio-hyoideus is inserted into its base, that posterior continuation of these muscles which is inserted into the tendinous inscription of the rectus abdominis. The ossicle is bound in its place only by the muscles which are attached to it.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Submentalis (Csv.1a).—Abnormal in both forms, this muscle is better developed in *Plethodon* than in the other genus. It is represented by two small flat sheets of fibres, one on each side of the symphysis menti. Each arises from the subdermal, inferior, surface of the mandible, and its fibres pass caudad and mediad to be inserted into a delicate membrane. This membrane is but ill differentiated from the deeper connective tissues anteriorly, but becomes quite definite between the median ends of the ventral superficial constrictor muscles behind the Csv.1a.

The Intermandibularis muscle (Csv.1b) is divided into anterior and posterior portions, in *Plethodon,* by a small triangular gap. This division is not present in *Diemyctylus.*

The muscle arises from the median surface of the mandible a short distance above the ventral edge. The line of origin commences a short distance posteriorly to the posterior margin of the submentalis and extends back to an equal distance anterior to the jaw joint. The anterior fibres are transverse in direction and, in *Plethodon,* a few of these are apparently araphic. In *Diemyctylus* none reaches the mid-line, all being inserted into a narrow median raphe. The posterior fibres are inclined caudad. In *Plethodon* the fibres are of varying length (see Fig. 86) and the very delicate raphe is so transparent that the genio-hyoid muscle is seen through it quite clearly. The membrane is, however, here quite unattached to the deeper structures. When the muscles of one side are detached from their origin it is found that one can reflect the other set, without rupturing any connections, by turning the freed set back across the mid-line.

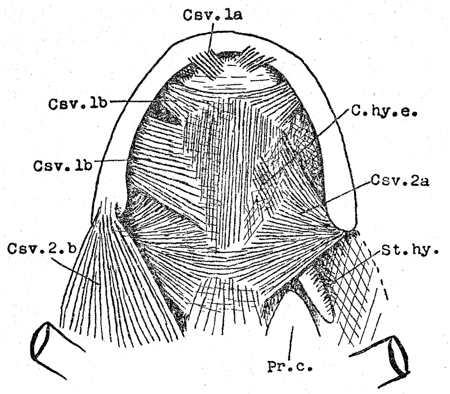


Fig. 86.—*Plethodon.* The muscles of the ventrum of the head.

It is to be particularly noted in this connection that the underlying anterior portion of the Csv.2a is not attached to this median raphe in either of the genera.

Innervation.—It is quite impossible to speak positively on this. One can only record that fibres of the Vth nerve alone were found related to the muscles.

Muscles of Mastication.

There are present here the same three muscles as in *Amblystoma.* Except that they are, relatively, smaller than in that genus no differences worthy of note were observed.

MUSCLES OF THE HYOID SEGMENT.

The Csv.2a arises from the posterior margin of the quadrate immediately beneath the depressor mandibulae muscle. From this origin the fibres pass mediad, radiating rostrad and caudad, with the middle fibres of the muscle directly transverse in direction. The most anterior fibres run forward nearly parallel with the ramus of the jaw and extend a long way forward beneath the Csv.1b. The most posterior fibres trend caudad some distance and, in *Plethodon,* lie deep to the Csv.2b at their origin and for a little part of their length.

The Csv.2b arises by a narrow, short and strong band of ligament from the lateral and inferior surface of the mandible at and behind the joint. From this origin the fibres radiate caudad. The most medial fibres pass caudad and mediad, the most lateral more directly caudad, in *Plethodon*. The muscle is better developed and larger than in the other genus and its thickened medial margin lies superficially to the posterior fibres of the Csv.2a, whilst its more lateral fibres have a direction directly caudad. In *Diemyctylus* the medial margin of the muscle lies posteriorly to the posterior fibres of the Csv.2a. Medially the two portions of the muscle form a continuous sheet of fibres. Laterally, near the origin of the two portions, there is a small gap between them. The most lateral fibres have a mediad trend so that their insertion lies medially to the shoulder joint, instead of, as in *Plethodon*, laterally thereto.

The insertion of the muscle is into a sheet of membrane which lies, subdermally, over the anterior portions of the shoulder girdle.

Innervation.—A twig of the VIIth was the only nerve observed related to either part of the muscle.

The resemblance of the Csv.2b to that of *Ichthyophis* is very close, whilst the condition in *Diemyctylus*, in which Csv.2a and b form a continuous sheet on either side of the mid-line, is intermediate between the condition of the muscle in *Plethodon*, *Amblystoma*, and *Notophthalamus*.

The Cerato-hyoideus externus (interhyoideus muscle) is present in both genera, and may be seen in *Plethodon*, through the membrane into which the Csv.2a is inserted, medial to the anterior part of the Csv.2a.

The Depressor mandibulae in both forms is a small muscle which arises from the squamosal and posterior superior area of the skull. Whilst no actual separation into partes cephalo- and noto-gnathica is visible, it was found that, in both forms, the muscle separated cleanly into a smaller, anterior and deep, and posterior, more superficial, portion. There appears no reason to doubt that these are the two " partes " of the muscle which have been found so well differentiated in other amphibians.

MUSCLES OF THE BRANCHIAL SEGMENTS AND THE HYPOBRANCHIAL SPINAL MUSCLES.

Whilst these present some departures from the types already described, they are not of a kind or degree to call for detailed description.

Molge. (s. *Notophthalamus.*)

Material.—A single specimen of *M. torosus*, excellently preserved, which was received from the American Museum of Natural History.

MUSCLES OF THE MANDIBULAR SEGMENT.

There is no M. submentalis.

The Intermandibularis muscle arises from the anterior half of the inner surface of each mandible and meets its fellow in the mid-ventral raphe. The fibres are directly transverse.

The muscles of mastication are sharply divided into pterygoideus and temporalis.

The Pterygoideus is very imperfectly divided into partes posterior, anterior, and internus. The pars posterior arises from the mid-dorsal intermuscular septum above the posterior end of the skull and for a little distance beyond it posteriorly. The extreme posterior tip of the muscle is very narrow and it lies medially to the anterior end of the longissimus dorsi muscle of its own side. Passing forward, the muscle gains in bulk and turns laterad to pass beneath the supratemporal bar ; as it does so its most anterior fibres have a nearly directly transverse direction, but with a slight caudad inclination from their origin. At this point there is a superficial division of the muscle, but the plane of separation does not extend deeply. In front of it the muscle arises from the intermuscular septum and dorsum and side of the skull as far forward as the middle of the orbit. The pars posterior has no attachment to the dorsum of the skull behind the supraorbital arch, but when freed from its origin lifts off the skull quite cleanly. When it is so detached and the free end carried forward and laterally, a deeper part of the muscle is found below it, and from which it separates quite cleanly for a little distance. These deeper fibres, however, merge with the deeper fibres of the pars anterior and the whole of the fibres converge to a short narrow tendon, which is inserted into the upper margin of the inner surface of the mandible a little way in front of the joint and deep to the insertion of the temporalis.

The M. Temporalis arises from the dorsum and anterior surface of the otic capsule and from the anterior surface of the parotic process and anterior edge of the quadrate, behind and lateral to the line of the supratemporal arch. The fibres pass laterad and ventrad to a relatively extensive insertion along the upper edge of the outer surface of the mandible for a short distance in front of the joint. Those fibres arising from the quadrate and parotic process close along side of it are partially separated from the rest in a manner suggestive of the massetericus minor of the frog.

The Relations of the Branches of the Vth Nerve.

The Foramen prooticum is placed below and to the inner side of the posterior root of the supratemporal arch.

The ramus mandibularis turns laterad and ventrad as soon as it separates from the other rami and passes down to enter the lower jaw just internal to the insertion of the temporalis. To reach this destination the muscle penetrates the M. temporalis, but does not divide it into superficial and deep portions. The Ramus maxillaris passes laterad and dorsad between the Mm. pterygoideus and temporalis. Lateral to the supratemporal arch, just at its posterior end, the nerve becomes superficial and runs ventrad and rostrad along the dividing plane between the muscles. Following the anterior margin of the temporalis when the other muscle passes back underneath it, the nerve next turns rostrad around the lower margin of the orbit.

The Ramus ophthalmicus profundus runs forward between the pterygoideus muscle and the side wall of the cranium.

THE MUSCLES OF THE HYOID SEGMENT.

The muscles of this segment present certain peculiarities which resemble the arrangement of these muscles in the Caecilians, and, being intermediate between the conditions there found and those of the Urodela, serve to assist in the comprehension of the caecilian muscles.

The Csv.2a presents two very definite portions which are here described as the partes superficialis and profunda.

Pars Superficialis.—This arises, under cover of the origin of the depressor mandibulae, from the inferior edge of the sulcus on the back of the parotic process and otic capsule. From this origin the fibres pass directly transversely and ventrally to an insertion into a mid-ventral raphe.

Pars Profunda.—This arises from the same edge below, i.e. lateral to, the superficial part of the muscle and from the tip of the cerato-hyal, which latter is placed immediately behind the upper end of the origin of the superficial part. At its origin this is a narrow thin ribbon and curves ventrad, laterad and rostrad deep to the posterior end of the mandible, passing first deep to the pars superficialis. Just medial to the mandible, a little way anterior to the joint, the fibres are gathered together to form a fine rounded cord and the muscle becomes bound to the lateral edge of the perimysium of the interhyoideus muscle which lies deep to it. The muscle fibres then diverge rather widely ; those most laterally placed run forward and mediad and reach almost to the symphysis, the median do not run forward so much. All the fibres are inserted into a median ventral raphe deep to the Csv.1.

The Csv.2b arises from the superficial fascia in the neighbourhood of the insertion of the depressor mandibulae. The fibres radiate widely. The anterior fibres have a direction nearly transverse but with an inclination caudad. The most posterior pass caudad with an inclination mediad. The former are inserted into a median raphe, the latter into the dense subcoracoid fascia, by which it is bound to the pectoral arch. The most posterior fibres are inserted well out from the mid-line, almost below the humero-scapular joint, and the line of insertion of the intermediate fibres curves from this point mediad and rostrad to the insertion of the anterior fibres.

The Depressor Mandibulae presents no indication of the pars notognathica. The muscle arises from the surface of the sulcus on the postero-dorsal area of the parotic process and the otic capsule. No trace of division into anterior and posterior parts can be found, and none of the fibres arise from the fascial structures behind the head. The fasciculi are gathered to a quite small area of insertion on the posterior end of the mandible, behind the joint.

The Interhyoideus is similar to that of *Amblystoma* but the anterior end of the ceratohyal is a good deal broader in this than in that genus, and in accord with this extra width of the available area insertion, the muscle is much more spread out anteriorly than in the other form, so much so that it appears to have an insertion into a mid-ventral raphe.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Constrictor Pharyngei arises from the dorsal fascia almost in common with the Dorso Laryngeus. The point of origin is immediately behind and above the postero-dorsal corner of the origin of the depressor mandibulae and under cover of the posterior continuation of the fascial covering of that muscle and the origin of the rhomboideus anterior muscle, but superficial to that of the M. cucullaris. The two muscles curve, alongside of each other, ventrad and caudad to be inserted at the mid-ventral line. The constrictor pharyngei is inserted into the medial raphe ventral to the larynx, the dorso-laryngeus curves dorsad to be inserted into the anterior end of the arytenoid cartilage at its dorsal edge.

The Hypobranchial Spinal Muscles.

The Genio-hyo-coracoideus arises, on each side of the symphysis, from the anterior end of the mandible. It is a narrow ribbon of fibres which extends straight back to be inserted on to the subcoracoid deep fascia, between the plane of insertion of the Csv.2b and the procoracoids. As the muscle passes the first arch of the hyoid it is bound thereto.

The Coraco-hyo-glossus arises as an anterior prolongation of the lateral portion of the rectus abdominis deep to the humero-scapular articulation. The more superficial fibres are inserted into the anterior arch of the hyoid alongside the hyoid plate. The deeper fibres are gathered to form a rounded muscle which passes forward above this arch and ends in a brush of fibres in the substance of the small tongue. The two portions of the muscle cannot be cleanly separated, except just as the glossal fibres dive above the cartilaginous arch.

The Capiti Pectoral Muscles.

The Cucullaris arises from the skull immediately behind, and deep to, the tip of the cerato-hyal. It has the upper end of the origin of the pars superficialis of the Csv.2a superficial to it and the origin of the attrahens scapulae muscle deep to it. The fibres pass laterad and ventrad to be inserted into the anterior edge of the scapula just above the joint cavity.

The origin of the Attrahens Scapulae has just been mentioned; the fibres of the muscle radiate from the point-like origin to be inserted along the anterior margin of the scapula and suprascapula.

Spelerpes. (s. *Pseudotriton.*)

I have had for dissection one specimen of the adult, received from the American Museum of Natural History.

This genus reproduces, in the anatomy of its cephalic musculature, features already described in other genera. To describe these in detail would serve no good purpose; therefore, only those features of particular interest will be described.

No submentalis muscle was found.

The Csv.2b has a much more extensive origin than in any other form studied. The line of origin commences at the anterior margin of the well developed pars notognathica of the depressor mandibulae and extends back almost to the transverse level of the shoulder joint; this line, moreover, is placed higher than is the origin of the muscle in other forms—it is placed mid-way between the mid-lateral and mid-dorsal lines. The fibres of the muscle pass directly ventrad to be inserted into a mid-ventral raphe. The muscle extends so far back as to cover the procoracoids and the anterior part of the coracoids.

The tiny muscle which was described in *Amblystoma* under the name of Cerato-hyoideus Anterior is in this genus very well developed. It arises from the mandible close beside the symphysis and passes caudad and slightly laterad along the lateral margin of the ceratohyal cartilage till it lies beneath the posterior end of the mandible. It is inserted along the lateral edge of the ceratohyal.

This muscle is of interest because that in *Amblystoma* is so small that one questioned the wisdom of recognizing it as a separate muscle; this establishes its individuality.

The Laryngeal muscles are essentially similar to those of the Axolotl; this is of interest, as it is the perpetuation of a larval condition.

The muscles of mastication are more differentiated than those of any other Urodele studied.

The Pterygoideus presents for description three parts.

The Pars Posterior arises as a fine point behind the posterior limit of the skull between the longissimus dorsi and the mid-dorsal intermuscular septum, and along the septum so far forward as to permit of the most anterior fibres passing laterad and ventrad with but a little inclination rostrad to the insertion. The lateral surface of the muscle is clothed by a strong fine tendinous perimysium into which the great majority of the fibres are inserted. This perimysium tapers and becomes thicker as it extends forward and finally, as a narrow tendon, is inserted into the apex of the coronoid process of the mandible.

The Pars Anterior arises from the dorsum of the skull in front of the last part. The muscle tapers to a short tendon which is inserted into the coronoid process just behind and medial to the other tendon. The most posterior fibres arise a little way posterior to the orbit, and these have a direction rostrad, laterad and ventrad. The most anterior fibres arise medial to the centre of the orbit and their direction to their insertion is caudad, laterad and ventrad.

The Pars Interna arises from the side wall of the skull beneath the pars anterior. There is a very definite cleavage plane between the two muscles and the fibres of the pars interna run caudad and laterad nearly horizontally, but with a slight inclination ventrad, converging to a short tendon by which they are inserted on to the upper edge of the inner surface of the mandible deep to all the other muscles of mastication just in front of the joint.

The Temporalis muscle arises from the anterodorsal surface of the otic capsule, parotic process and quadrate. Its fibres pass ventrad and slightly laterad to be inserted along a short length of the upper edge of the outer surface of the mandible behind the coronoid process.

The Quadrato-mandibularis is a small muscle which arises from the lower end of the quadrate and the skull under cover of the temporalis. Its fibres converge to be inserted into the upper edge of the inner surface of the mandible behind the tendons of the pterygoideus partes anterior and posterior. The general direction of the muscle is, from its insertion, laterad and rostrad and very slightly ventrad. This muscle passes dorsally to the tapered thin posterior end of the pars interna of the pterygoideus, the two crossing almost at right angles close to their insertions.

THE RELATIONS OF THE RAMI OF THE VTH NERVE.

The three rami of the nerve issue from the cranium under cover of the origin of the temporalis. The R. mandibularis turns at once laterad and ventrad between the temporalis and the quadrato-mandibularis; the main nerve plunges between Meckel's cartilage and the dentary, but just before so doing it gives off a branch which runs forward along the outer surface of the mandible. Where it enters the mandible the nerve lies between the temporal and quadrato-mandibularis insertions.

The Ramus Maxillaris passes forward against the wall of the skull till the anterior margin of the temporal muscle is reached; it at once turns laterad around the lower surface of the pars posterior of the pterygoid muscle, and then turns forward across the superficial face of that muscle.

The Ramus Ophthalmicus Profundus passes forward against the side wall of the cranium under cover of the origin of the pterygoideus muscle and the anterior portion of the origin of the quadrato-mandibularis.

2. Adult Anura.

The Frog. (Figs. 87–89.)

The following description of the muscles is based on a study of numerous specimens of *Hyla cerulea*, *H. aurea*, *Limnodynastes peronii* and *L. tasmaniensis*, and a single adult *Mixophyes fasciolatus*. The similarity of the muscles in all five forms was very close. Except in the depressor mandibulae of *Mixophyes*, no differences worthy of note were observed.

I have departed from the nomenclature of Gaupp's edition of Wiedersheim's "Anatomie des Froches", where it appeared desirable to reflect in the designations the homologies of the muscles with those of the fishes. This has only been done where it seemed reasonably certain that the homologies in question were correct.

The Submentalis, Csv.1a (Fig. 87).—This is a compact muscle whose fibres extend from one mandibular ramus to the other immediately behind the symphysis, without any tendinous intersection.

The Intermandibularis, Csv.1b.—This is the muscle which Gaupp terms the submaxillaris; it is, apparently beyond question, homologous with the intermandibularis of certain of the bony fishes and with the Csv.1b of the elasmobranchs. The simple Csv.1b of the younger tadpoles was found to give rise to a broad intermandibular sheet, in which a posterior portion, later developed, was differentiated from an anterior.

The Csv.1b[1] (Fig. 87) is the anterior portion of this sheet. The fibres arise from the inferior margin of the mandible, in its more transverse, anterior, part, on either side of the Csv.1a. They pass obliquely caudad and mediad and are inserted at the mid-line into a median raphe.

The Csv.1b[2] (Fig. 87) is the posterior portion. These fibres arise from the inner surface of the mandible close to the dorsal edge and pass towards the mid-line with a slight obliquity forwards, and are inserted into the median ventral tendinous intersection. The anterior limit of the origin of this portion is above the middle of the width of the last portion, the posterior limit is a little in front of the posterior end of the mandible. The greater part of the line of insertion lies deep to that of the last portion.

The Interhyoideus, Csv.2 (Fig. 87).—Gaupp designated this the " Subhyoideus ". Its development indicates that it is homologous with the interhyoideus of the fishes.

This muscle arises from the upper, posterior, end of the anterior cornu of the hyoid (stylohyal) close to its attachment to the otocrane. Where this muscle arises, the portion of the stylohyal is situated dorsally and medially to the posterior end of the lower jaw, so high up and far toward the mid-line that the muscle appears to be coming from the postero-medial and dorsal area of the otocrane lateral to the origins of the levator scapulae superior and the rhomboideus anterior muscles. From this, comparatively narrow, origin the muscle widens out and becomes folded on itself. The anterior fibres cross the posterior intermandibular area behind the Csv.1b[2] to be inserted, in series with that muscle, into the mid-ventral raphe. The line of contact is very clearly marked by a transverse branch of the submaxillary artery, and the two muscles are quite freely separable. The anterior fibres, moreover, are not parallel with those of the mandibular sheet. There is a tolerable gap between the two muscles at the posterior margin of the Csv.1b[2] close to the mandible, through which the artery makes its way. The posterior margin of the gap is formed by the anterior fibres of Csv.2 ; these come into view from above and lateral to the posterior fibres of Csv.1b and, therefore, have a slight inclination caudad, as though coming from an origin on the mandible beneath the Csv.1b.

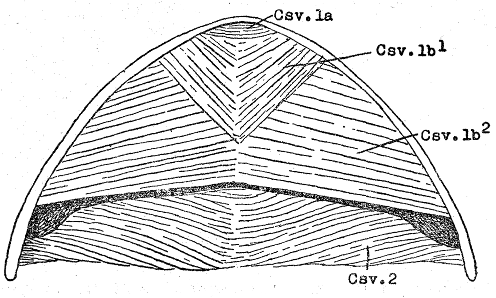


Fig. 87.—*Hyla*. The ventral constrictor muscles.

This definite break in the continuity between the mandibular and hyoid sheets is of interest. In a majority of the fishes and other amphibians which we have studied, these two ventral constrictor sheets become intimately blended along their contiguous margins. In those forms, however, the hyoid sheet is developed from a primitive superficial sheet and the interhyoideus lies dorsally to it. In the Frog there is, apparently, no primitive superficial hyoid sheet and the superficial constrictor of the adult is developed from the interhyoideus. This probably accounts for the definite break between the two, and the break provides evidence of the correctness of the interpretation here presented.

It has been stated above that the interhyoideus is folded on itself. Those fibres which arise from the highest point run obliquely forward toward the mid-line beneath those arising below and in front of them. They are not attached to the more superficial fibres. When the head is strongly dorsi-flexed the muscle becomes unfolded, and the posterior fibres are exposed. The posterior limit of the muscle can now be observed to extend from their origin to the mid-ventral line, passing dorsally to the posterior end of the mandible and slightly in front of it on each side.

This line corresponds very closely with the line of fusion of the posterior margins of the opercular folds to the ventrum of the throat at the metamorphosis of the Axolotl to the adult *Amblystoma.* In both the *Amblystoma* and the Frog there is a narrow membranous sheet connecting the perimysium and the skin along the posterior margin of the superficial hyoid constrictor. In the former it marks the line of closure of the branchial chamber. It may be designated the " post-opercular myo-integumental fascia ".

When the head of the frog is slightly ventri-flexed, the fold of the Csv.2 passes behind this fascia and the anterior margin of the muscle comes to lie almost directly beneath it.

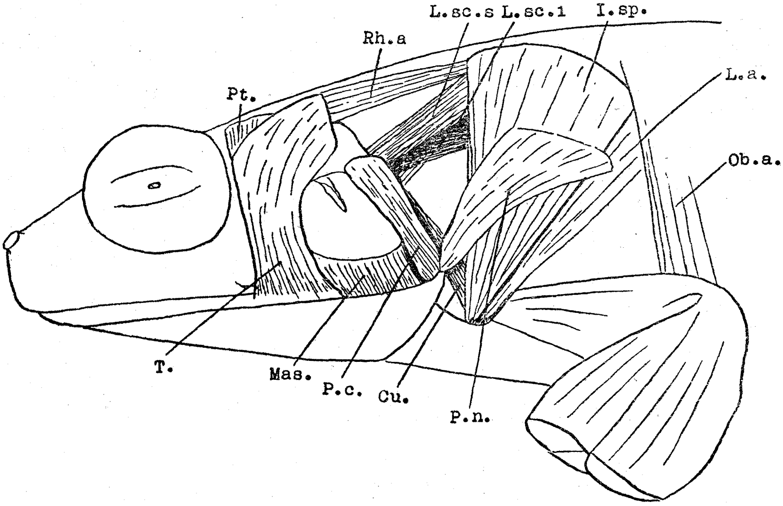


Fig. 88.—*Mixophyes.*

Innervation.—The break between the mandibular and hyoid ventral constrictor sheets enables one to state with the utmost confidence that the former is innervated by the Vth nerve alone, and that this nerve does not send any twigs backward across the interval. The communication between the VIIth and IXth nerves debars one from speaking with equal certainty about the innervation of any of the muscles innervated from the hyoid trunk of the VIIth. One can, however, assert with confidence that the Csv.2 is innervated only by twigs which are all traceable to the ramus jugularis of the hyomandibular trunk of VII.

THE DEPRESSOR MANDIBULAE.

The Pars Cephalognathica (Fig. 88, P.c.) arises from the postero-lateral and superior corner of the auditory capsule immediately above the centre of the tympanic annulus, and from the superficial perimysium of the pars lateralis of the temporalis muscle dorsally and medially to that point. From this origin the fibres pass ventrad, laterad and caudad, to be inserted on to the outer side of the mandible immediately behind the joint.

The Pars Notognathica (Fig. 88, P.n.) arises from the fascia dorsalis superficially to the suprascapula and the infraspinatus muscle, this origin extending from the anterior margin of the suprascapula back as far as the anterior margin of the superficial oblique abdominal muscle. By the fascia dorsalis the origin of the muscle is carried to the mid-dorsal line, but the dorsal margin of the muscle itself is nearly coincident with that of the suprascapula beneath it, except posteriorly, where it falls to a lower level between the fascia of origin of the abdominal muscle superficial to it and the latissimus dorsi muscle deep to it. From this wide origin the fibres converge to be inserted on to the posterior end of the mandible, behind the pars cephalognathica. A broad ribbon at its origin, this muscle becomes a narrow, and thicker, muscle at tis insertion.

Innervation.—Both parts of the depressor mandibulae are innervated by twigs from the ramus jugularis of the hyoid trunk of the VIIth nerve.

Edgeworth (1911, p. 217) states that in " Rana, at metamorphosis, the orbito-hyoideus extends upwards on the atrophy of the processus muscularis of the palato-quadrate, the lower end of the orbito-hyoideus gains a new insertion to the hind end of the lower jaw. The cerato-hyo-angularis, suspensorio-angularis and quadrato-angularis assume a more vertical position on rotation of the palato-quadrate, and form the inner portion, whilst the original orbitohyoideus forms the outer portion, of the depressor mandibulae ".

Edgeworth, apparently, bases the whole of his descriptions on the study of serial sections. I have found that such study, even when carried out on sections cut in all three planes, is liable to be most misleading. The closest study fails altogether, at times, to discover the cleavage planes between muscles whose component fibres are parallel or only slightly inclined to one another. It is, therefore, more than probable that the development of this muscle in *Rana* is similar to that in the frogs I have studied.

Edgeworth adopts the nomenclature of Schultze.

The synonymy is as follows :

Edgeworth-Schultze.	This work.
Orbito-hyoideus	Dilator hyoidei
Cerato-hyo-angularis	Pars notognathica
Suspensorio-angularis	Pars cephalognathica
Quadrato-angularis	Massetericus minimus

When it is remembered that the pars cephalognathica extends upward and backward across the surface of the processus muscularis under the dilator hyoidei and, in later stages, nearly parallel with it, it is readily understandable that the increasing bulk of this muscle should have been mistaken, in serial sections, for the other in a new situation and with new attachments. This description of the development of the depressor mandibulae by Edgeworth caused me to review again, and with added care, my own dissections. I am quite confident that the pars cephalognathica of the early tadpole gives rise to the main part of the same muscle in the adult. That some few fibres of the caducous dilator hyoidei may persist and contribute to the adult muscle is not impossible, but I can find no evidence of this.

If I have not correctly identified the quadrato-angularis, then the muscle is not present in any stage of the development of the several frogs I have studied. The error of regarding this as one of the components of the depressor series probably comes from the fact that it arises very low down on the quadrate and is inserted directly above the joint on to the superior edge of the mandible. When first found in my tadpoles it had a more vertical direction than it has in the adult.

The Muscles of Mastication.

The six muscles which were found in the later tadpoles are all recognizable in the adult.

The Pterygoideus (Fig. 88, P.t.) arises from the dorsum and side wall of the skull behind the orbit and in front of the temporalis muscle, it is for the most part covered by the latter muscle, but appears superficially between it and the orbit close to the mid-line dorsally. From its origin the muscle tapers rapidly as it passes ventrad, laterad and slightly caudad, beneath the temporalis and terminates in a fine ribbon-like tendon which continues the direction of the muscle as it lies against the lower edge of the anterior wall of the auditory capsule. It passes across the dorsal surface of the os transversum, pterygoid bone of authors, in contact with the anterior surface of the quadrate, and is inserted near the inferior margin, on the inner side of the mandible just in front of the joint.

The Temporalis muscle (Fig. 88, T.) must be described in two parts. The Pars lateralis is the depressor labii superioris longus of the early tadpoles, and it constitutes a superficial and lateral portion of the muscle. It arises from the whole of the dorsum of the otocrane, extending medially over the top of the curve and down a short distance on the posterior slope. From this origin the muscle passes cephalad, ventrad and laterad. Its outer margin lies in contact with the inner surface of the post-orbital descending limb of the squamosal and the quadrato-jugal. Its insertion is a fleshy one on to the outer and upper surface of the mandible in front of the tympanic annulus.

The Pars medialis is the temporalis of the tadpoles, the two portions are very easily separated and leave perfectly smooth surfaces after separation. The origin is from the antero-superior medial corner of the otocrane and from the dorsum of the skull medial thereto, between the last muscle behind and laterally and the pterygoideus in front and medially. It is a slightly smaller muscle than the other division of the temporalis ; its direction is parallel to the other. The insertion is, by a short ribbon of tendon, into the mandible medial to the lateral division.

The Masseter Major (Fig. 88, Mas.).—This is the masseter of the tadpoles. It arises from the inferior edge of the post-orbital bar and from the tympanic annulus. The muscle is a quite thin sheet of short fibres which descend almost vertically to be inserted on to the upper edge and outer surface of the mandible behind the temporalis. The anterior portion of the muscle, arising from the squamosal, is the thicker and there is here some convergence of the fibres into an arcuate insertion into the upper surface of the mandible immediately behind that of the temporalis. Behind this the muscle is thinner and the insertion is carried, by a short fascial sheet, down the outer surface of the mandible almost to the inferior margin.

The Masseter Minor, the quadrato-mandibularis of the tadpoles.—This is a short triangular muscle which arises from the edge of the quadrate below the quadrato-jugal and is inserted into the inner edge of the upper surface of the mandible. The most anterior fibres of this muscle pass ventrad nearly vertically, with a slight inclination cephalad. The posterior fibres pass cephalad with a slight inclination ventrad.

The Masseter Minima.—This muscle has not, so far as I am aware, been previously described in the adult frog ; it is apparently the quadrato-angularis of Schultze's description of tadpoles.

It is a small flattened narrow muscle, pointed at both ends, which arises from the tip of the quadrate and inner surface of the extreme posterior end of the quadrato-jugal and passes forward along the upper surface of the posterior end of the mandible, between the masseter muscles, to an insertion immediately behind that of the masseter major, on to the upper surface of the mandible.

Innervation.—All these six muscles of mastication are innervated by twigs which they receive from the ramus mandibularis V as that nerve passes among them on its way to the ventrum of the mouth.

The course of the ramus mandibularis V is as follows. When it leaves the common trunk it passes dorsad, laterad and cephalad between the temporalis on its outer side and the pterygoideus medial to it, and comes into view as a subcutaneous structure between these muscles some little distance behind the orbit. It turns more directly laterad and may cross the temporalis and pass out of sight again at its lateral margin by running beneath the descending limb of the squamosal, or it may reach the same position beneath this bone more directly by penetrating the pars lateralis of the temporal muscle. Beneath the squamosal it turns caudad and perforates the masseter major, and continues for a short distance between this muscle and the masseter minima. It next turns cephalad again, passes over the last muscle and turns ventrad external to the ramus of the mandible and the masseter minor. Finally it perforates the posterior fascial insertion of the masseter major and turns mediad and cephalad to reach the ventrum of the mouth.

Deep Constrictors, apparently Innervated only by the IXth and Xth Nerves.

The Constrictor pharyngei (Petro-hyoideus anterior, of Gaupp) (Fig. 89, C.ph.) arises on each side from the stylohyal cartilage high up behind the origin of the Csv.2, and from the otocrane above and medial to this. From this restricted area of origin the muscle courses round on the under side of the pharynx, beneath the pharyngeal mucosa. The muscle widens considerably as it passes toward the mid-ventral line, and is inserted on to the lateral edge of the hyoid plate, from the root of the posterior cornu forward to that of the anterior cornu.

The three muscles which Gaupp designated posterior petro-hyoid are, probably, together homologous with the dorso-laryngeal and last interbranchial of the Axolotl and perennibranchiate urodeles generally. It will be remembered that in the tadpole with the fully developed branchial arches there is but a single muscle and that all three of the muscles we have to describe here are developed later than that one.

The three muscles arise together from the back of the skull between the temporalis above, the otoscapularis laterally, and the rhomboideus anterior medially, but slightly ventral to all three. From this origin they pass caudad, mediad and ventrad, superficial to the cucullaris and levator scapulae inferior, but deep to the levator scapulae superior. For purposes of description I have designated two of them cranio-hyoideus and cranio-laryngeus respectively ; the third is the dorso-laryngeus.

The Cranio-hyoideus (Fig. 89, C.h.a.), having reached the ventrum of the pharynx, turns more directly transversely than the cranio-laryngeus behind it, leaving a triangular gap between their ventral ends. Nearly, but not quite, parallel to the hinder margin of the constrictor pharyngei, and a little way behind it, this muscle passes to the body of the hyoid just behind its middle cornu, and is inserted thereon.

The Cranio-hyoideus (Fig. 89, Cr.hy.) is inserted to the outer edge of the posterior cornu of the hyoid (the thyreohyoid) dorsally to the insertion of the hyoglossus, and near the posterior end of the cornu a little distance caudad to the point where the last muscle gains the dorsal surface of the body.

The Dorso-laryngeus (Fig. 89, D.l.) may, perhaps, be the homologue of the dorso-laryngis of Drüner's description of the Urodela ; if so, the other two muscles will be regarded as added muscles differentiated from the single primordium present in the tadpole. It lies almost in contact with the posterior margin of the last muscle, but is continued past the insertion of the other and is inserted on to the lateral cartilage of the larynx immediately posterior to the point where that is bound to the end of the posterior hyoid cornu.

Innervation.—It has been quite impossible to satisfy myself that I have successfully separated the components of the nerve tangle. I therefore content myself with the statement that I have found none other than branches from these nerves reaching any one of these four muscles. I believe that the constrictor pharyngei is innervated by the IXth and the others by the Xth nerve, but I cannot be certain. The question must be decided by the study of appropriately stained serial sections, or by stimulation of the nerves.

The Hypobranchial Spinal Muscles.

The Genio-hyoideus presents three very definitely defined portions. Gaupp illustrates these three portions, but fails to describe them separately.

The Genio-hyoideus pars lateralis (Fig. 89, G.h.l.) is a narrow ribbon which arises from the inner surface of the mandible towards its dorsal edge just lateral to the origin of the submentalis ; it passes thence directly caudad to be inserted on to the outer edge of the middle cornu of the hyoid. As it passes back it lies beneath the loop of the stylohyal. A large branch of the hypoglossal (1st spinal) nerve passes forward along its dorsal surface. At its insertion it has the dorsally folded lateral margin of the sterno-hyoideus medial to it.

The Genio-hyoideus pars intermedius (Fig. 89, G.h.i.) is a similar ribbon-like muscle which arises just medial to the last, but closer to the lower edge of the mandible under cover of the

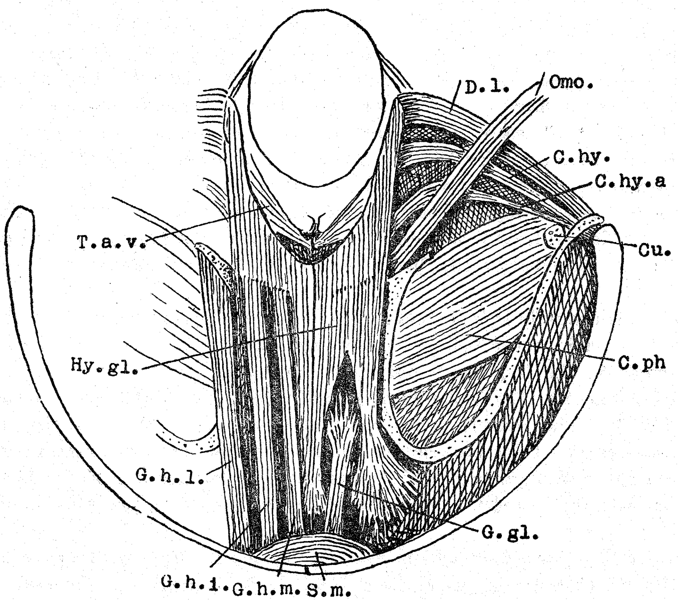


Fig. 89.—*Hyla*. Muscles of the ventrum of the head. C.hy., M. craniohyoideus ; C.hy.a., M. craniohyoideus anterior ; S.m., M. submentalis ; G.h.m., M. geniohyoideus medialis ; G.h.i., M. geniohyoideus intermedius ; G.h.l., M. geniohyoideus lateralis ; T.a.v., M. thyroarytenoideus ventralis.

submentalis. It passes caudad to be inserted on to the perimysium of the hyoglossal muscle, a small median bundle of fasciculi gaining an insertion on to the posterior margin of the hyoid.

The Genio-hyoideus pars medialis (Fig. 89, G.h.m.) is a third narrow ribbon which arises from the upper, inner edge of the mandible right alongside of the symphysis, separated from the origin of the pars intermedius by the origin of the genio-glossus. It passes back to be inserted in like manner to the last part, but superficial to it. By the perimysium of the hyo-glossus muscle, the insertion of these last two is carried back to the antero-lateral margin of the larynx.

The Genio-glossus muscle (Fig. 89, G.gl.) arises from the inner surface of the mandible between two genio-hyo-laryngeal muscles. It is a relatively short and stout muscle which passes caudad, dorsad and slightly mediad, to terminate in a brush of fibres which extend through the connective tissues of the tongue for two-thirds of its length from the anterior tip.

The Hyo-glossus (Fig. 89, Hy.gl.) is a surprisingly massive muscle which arises from the posterior cornu of the hyoid throughout its length and passes forward ventrally to the body of the hyoid, and then turns dorsad and breaks up into brushes of fasciculi. Three main divisions of these may be recognized, a median and two lateral. The median fasciculi are inserted in the tough submucous tissue along the mid-line of the tongue from close to the base, right forward almost to the tip, with those of the genio-glossus on either side. The fasciculi of the two lateral groups end in the same tissue along the margin and lateral area of the tongue outside the genio-glossus.

Since the antero-lateral corner of the larynx is bound to the posterior hyoid cornu, this muscle, when antagonized by the genio-glossus and genio-hyoideus, is capable of pulling the larynx forward and assisting in dilating it.

Innervation.—These muscles are innervated by the hypoglossal nerve. Whether the spinal II components of the trunk of this nerve reach these muscles or not, is impossible of determination by dissection.

THE CAPITI-PECTORAL MUSCLES.

Including the Omo-hyoideus, there are five of these to be described.

The Rhomboideus Anterior (Fig. 88, Rh.a.) arises from the posterior margin of the skull superficially, on either side of the mid-line and medial to the auditory capsule. The fibres pass directly backward to be inserted into the dorsal margin of the suprascapula. The longest fibres are medial, and are inserted farthest back along the dorsal edge of the suprascapula.

This muscle appears quite early in the development as a delamination of the first dorsal myomere which later grows backwards and gains an insertion on to the suprascapula.

Innervation.—The muscle is innervated by a twig which it was found impossible to trace back through the dorsal trunk muscle, from which it emerged beneath the muscle. It is probable that the twig came from the second spinal nerve, as in *Rana*.

The Levator Scapulae Superior (Fig. 88, L.sc.s.) arises from the back of the skull medial to the auditory capsule, ventrally to and behind the posterior limit of the origin of the temporalis. At its origin the muscle is fleshy and nearly cylindrical in section. From its origin it extends caudad, mediad and dorsad, and is inserted on to the anterior margin of the scapula just below the suprascapula. At its insertion the fibres are somewhat spread out, so that the muscle is here flattened.

Innervation.—This muscle is innervated by the second spinal nerve. The motor branch to this nerve leaves the main nerve before it combines with the first to form the ventral spinalis (Hypoglossal) trunk to the hypobranchial spinal muscles.

The Cucullaris (Fig. 88, Cu.) is the Trapezius of Edgeworth (1911) and the Capiti-scapularis of Furbringer (1875). The muscle arises from the postero-superior margin of the auditory capsule beneath the origin of the pars cephalognathica of the depressor mandibulae, behind the temporalis and lateral and slightly dorsal to the levator scapulae superior. It passes from its origin ventrad, laterad and caudad, to be inserted on to the scapula just above and lateral to the glenoid cavity.

Innervation.—This is by a twig which was traced back to the main trunk of the Xth nerve, distal to the point where the communications with the IXth nerve are effected.

The Levator Scapulae Inferior (Fig. 88, L.sc.i.) arises from the back of the skull beneath the superficial levator of the scapula. It extends backwards and slightly laterally to be inserted on to the deep surface of the scapula underneath the insertion of the same muscle, extending backwards across the deep surface of the scapula for a little distance.

The Omohyoideus (Fig. 89, Omo.) is included here because of its origin, at least in part, from a cephalic muscle, and because it is one of the muscles innervated by the hypoglossal nerve, formed by spinal nerves I and II.

It arises from the ventral surface of the body of the hyoid, medially to the middle cornu, and passes caudad, laterad and slightly dorsad. It crosses the dorsal surface of the scapula diagonally, above the glenoid cavity. At the posterior edge of the bone it curls round its posterior surface and becomes inserted, under the tendons of the infraspinatus and latissimus dorsi, on to the posterior surface of the scapula.

Innervation.—This is, as already stated, by the hypoglossal nerve.

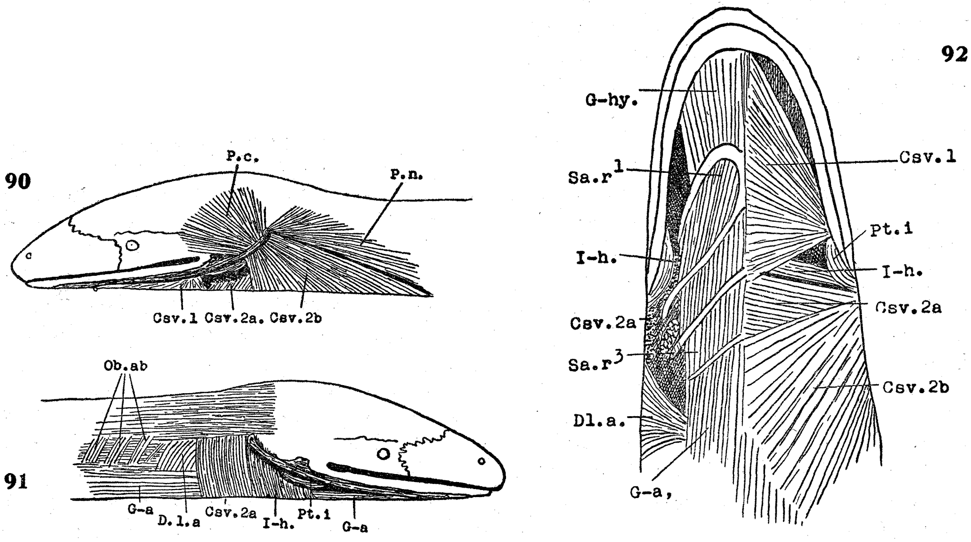
3. Adult Caecilians.

The Cephalic Muscles of Ichthyophis glutinosa.

(Figs. 90–92.)

Material.—This consisted of two very well preserved specimens of *I. glutinosa* which I received from Dr. J. Pearson, now Director of the Tasmanian Museum ; and a collection of sets of serial sections of several of the Caecilians from Prof. H. W. Norris, of Grinnel. I wish to tender my grateful thanks to these gentlemen for this assistance.

The serial sections originally formed part of the material on which the work of Norris and Hughes was based when they wrote their account of the Cranial and Anterior Spinal Nerves of the Caecilian Amphibians. Prepared and stained primarily for the study of the nerves, they were counterstained with a carmine preparation and are beautiful slides for general study.



Figs. 90-92.—*Ichthyophis.* G.a., M. genio-abdominis ; Pt.i., M. pterygoideus internus.

It may be of interest to record that, notwithstanding the perfection of these slides, it was not found possible to determine the details of the cephalic musculature by the study of them alone. I had the slides in my possession long before I received the complete specimen, and had, as I thought, made a complete description of the muscles. On receipt of the complete specimen, dissection was undertaken with a view to seeing the muscles actually in their relation one to another, and not with the intention of checking the description already prepared. It was with no little surprise that these relations were found to be different from those visualized from the sections. In several instances the boundaries of juxtaposed muscles had been wrongly located. This was in those instances where the direction of the fibres was nearly parallel.

A return to the sections, after the dissection, fully confirmed the later findings.

I may remark that, in the course of the study of the muscles in the serial sections, I very naturally also studied their innervation, and, as was to be expected, found it always to be as described by Norris and Hughes. Particularly have I studied the remarkable Csv.2b in this connection and find that there is certainly only the one motor supply to this muscle, namely, that described by Norris and Hughes from the ramus jugularis of the hyomandibular division of the VIIth nerve.

THE MUSCLES OF THE MANDIBULAR SEGMENT.*

Unfortunately I have not been able to consult the work on *Ichthyophis* by the brothers Sarasin. I give below the synonymy of the muscles from Wiedersheim (1879) and Norris and Hughes. These latter authors, for the most part, contented themselves with referring to the muscles in the course of their description of the nerves. I have been able to determine their synonymy with some certainty by actually identifying the muscles in the slides by comparison of their illustrations with the sections they illustrated.

Wiedersheim.	Norris and Hughes.	This work.
	Masseter	Masseter
Masseter	Temporalis	Pterygoideus
	Petrygoideus	Pterygoideus internus
Not described	Levator quadrati	Levator quadrati
Intermandibularis (anterior part only)	Intermandibularis	Intermandibularis

The Intermandibularis (Figs. 90, 91, Csv.1) muscle alone represents the superficial constrictor sheet of the mandibular segment, there being no submentalis. Each muscle is a triangular sheet which arises from the inner surface of the mandible well back towards the joint. The fibres diverge widely as they pass towards the mid-line to be inserted into the median raphe. The most anterior pass almost directly rostrad, reaching nearly to the symphysis, the posterior fibres nearly transversely but with an inclination caudad.

The Pterygoideus muscle arises from the lateral wall of the cranium and from its roof under cover of the temporal roofing bones. The anterior limit of the origin is placed medial to the orbit, the posterior lies to the inner side of the auditory capsule. It appears that none of the fibres arise from the deep surface of the temporal roof, but that the dorsal limit of the origin is the line along which the temporal squame of the parietal meets the descending limb of the bone. The inferior line of the origin of the muscle is but a little below this. The insertion is by short tendon, to which all the fibres converge, into the inner surface of the mandible towards its upper edge in front of the joint.

The Masseter arises from the ventral surface of the temporal roof and from the medial surface of the lateral ascending process of the quadrate. From this origin the fibres pass to be inserted into the upper edge of the mandible behind and slightly external to the insertion of the pterygoideus.

The Levator Quadrati lies deep to both of these muscles ; it is a narrow strip of short fibres which arise from the alisphenoid region of the side wall of the cranium beneath the origin of the pterygoideus anteriorly, and medial to the masseter posteriorly. The fibres pass ventrad and very slightly laterad to be inserted into the anterior process of the quadrate.

The Pterygoideus Internus (Fig. 92, Pt.i.) arises from the postero-median edge of the os transversum (pterygoid bone, of Wiedersheim and Sarasins). The area of origin is quite small, but the muscle expands very rapidly as it passes caudad and laterad, so that it is a relatively bulky muscle as it lies beneath the mandible at its insertion, on to the inferior surface thereof, below the joint.

THE RELATIONS OF THE RAMI OF THE VTH NERVE.

The Gasserian ganglion lies in a fossa above the posterior end of the origin of the levator quadrati, and the ramus mandibularis passes ventrad to the foramen in the gonial by which it gains the canal in the mandible so directly that one may trace the whole of this course of the nerve in one single transverse section 30μ thick. As it enters the gonial it has the insertion of the pterygoideus in front of it and to the inner side, and that of the masseter behind and external to it. As it passes down from the ganglion the posterior end of the pterygoid muscle lies deep to it and the masseter superficial to it.

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* Nothing is known of the development of any of the muscles of the Caecilians ; their segmental origin is therefore assumed from their innervation.

The Ramus ophthalmicus profundus and the ramus maxillaris run directly forward between the origin of the levator quadrati below them and that of the masseter above. The former maintains this position close against the cranial wall all the way to the orbit, the latter soon becomes separated from the former by passing superficially to the pterygoid. It continues forward between the pterygoid and the masseter to the anterior boundary of the muscles.

THE MUSCLES OF THE HYOID SEGMENT.

The synonymy is as follows :

Wiedersheim.	Norris and Hughes.	This work.
Intermaxillaris posterior part	Interhyoideus (of the urodeles)	Interhyoideus and Csv.2a.
Omo-humero-maxillaris	Omo-humero-maxillaris	Csv.2b
Cephalo-dorso-maxillaris	Depressor mandibulae	Depressor mandibulae
	Levator hyoidei	Not found
	Cerato-hyoideus-externus	,, ,,

The Ventral Constrictor sheet innervated by the VIIth nerve presents three divisions.

The Interhyoideus (Fig. 92, I-h.) is a relatively narrow band of fibres which arise high up along the ceratohyal, deeply placed beneath the post-articular projection of the mandible and its muscles, the pterygoideus internus and the Csv.2b. From that origin they pass ventrad, mediad and rostrad, to be inserted into the mid-ventral raphe deep to the posterior portion of the Csv.1b (the intermandibularis).

The Csv.2a (Fig. 92) is a broader sheet of fibres which arise from a fascia which covers the trunk muscles behind the origin of the interhyoideus. These Csv.2a fibres arise further dorsally than the interhyoideus fibres. At their origin they lie deep to the anterior end of the thyroid gland. For the greater part of their length the 2a fibres are hidden beneath the Csv.2b ; they pass mediad, parallel to the interhyoideus fibres to be inserted into the mid-ventral raphe behind them.

The Csv.2b (Fig. 92) arise from the outer edge and postero-ventral surface of the post-articular portion of the lower jaw. From this origin the fasciculi radiate widely. The most anterior have a direction mediad and ventrad with a slight inclination rostrad. The most posterior, those arising from near the tip of the gonial, have a direction almost directly caudad, with a slight inclination ventrad. These latter are inserted into the fascia dorsalis just below the mid-lateral line as far behind their origin as half the length of the head ; the anterior fibres are inserted into the abdominal fascia at the mid-ventral line superficially to the Csv.2a fibres. The intermediate fibres are inserted along a curved line joining these two extremes.

The Depressor mandibulae presents two clearly defined parts.

The Pars Cephalognathica (Fig. 90, P.c.) has an extensive origin from the dorsal surfaces of the squamosal and parietal bones. The insertion is into the anterior edge and surface of the post-articular portion of the gonial. The foremost fibres pass directly caudad from origin to insertion just above the joint, the most posterior pass ventrad and rostrad to their insertion at the top of the anterior edge of the gonial.

The Pars Notognathica (Fig. 90, P.n.) is a somewhat larger muscle than the last. It arises from the fascia dorsalis above the Csv.2b. In outline the muscle is triangular, the apex being at the insertion into the tip of the gonial. The inferior fibres of the muscle are the longest ; these run parallel with the dorsal fibres of the Csv.2b. The most anterior fibres arise almost at the mid-dorsal line and pass rostrad and ventrad to their insertion.

I have been unable to find a levator hyoidei in any of the caecilians which I have been able to study. Norris and Hughes illustrate a levator hyoidei in a late larval stage of *Ichthyophis*. Unfortunately I have not been able to study any larval stages of these amphibians. Apparently the levator hyoidei of the larva is either a caducous muscle or it becomes converted into the pars notognathica of the adult. I have been unable to find any other muscles than those just described, which are innervated by the VIIth nerve. The illustration given by Norris and Hughes (1920) leads me to believe that it is portion of the pterygoideus internus which they have so identified. This, of course, is innervated by the Vth nerve.

Discussion.—The same muscles that were found in the Urodela are present in the Caecilia in the hyoid segment, though not arranged in quite the same manner.

The situation of the interhyoideus and its insertion into the mid-ventral raphe is a more primitive arrangement than has been met in any other amphibian, and is, indeed, a return to the elasmobranchian condition.

The origin of the Csv.2a is rather more deeply placed than we have found it in other amphibians, but not sufficiently so to raise any doubt as to its correct identification. It will be remembered that in the urodeles this origin is carried deeply by the attachment of the stylohyal to the back of the cranium. In the caecilians there has been a remarkable elongation of the neck region, and one of the results (or causes) of this has been that continued backward trend of the dorsal ends of the branchial cartilages which we find correlated with the more posterior situation of the origin of the Csv.2a. One remarks that, in the urodeles the thyroid gland is placed just behind and superficially to the origin of the Csv.2a, as it is in the caecilians.

The innervation and the origin of the Csv.2b are the two features of this muscle in the caecilians which lead us directly to its identification. Here, as in other amphibians, the muscle arises from a superficial fascia by which it is bound to the posterior end of the superficial surface of the mandible immediately below the pars notognathica of the depressor mandibulae. Its wide insertion and long posterior extension must be regarded as resultants of the elongation of the neck region.

Although I have identified one of the muscles of *Ichthyophis* as the interhyoideus, attention should, perhaps, be drawn to the fact that this is not the muscle which Norris and Hughes identify as the cerato-hyoideus externus. This muscle they illustrate in a section of a larval *Ichthyophis*. That which they identify thus is placed more superficially than is the interhyoideus of my description. It is, of course, possible that the muscle may have been more superficially placed in the larva.

MUSCLES OF THE BRANCHIAL SEGMENTS.

The Subarcualis Rectus I (Fig. 92, Sa.r^1) (Cerato-hyoideus internus of Norris and Hughes).—This is a short muscle which arises, dorsally to the genio-abdominis, from the posterior edge of the ceratohyal cartilage for the greater part of its length. The fibres pass caudad and laterad to be inserted into the anterior edge of the first ceratobranchial cartilage. This muscle extends further out, laterally, than do the other straight subarcual muscles, and, moreover, its fibres have a definite obliquity.

Subarcuales Recti II and III (Fig. 92, Sa.r.2 and 3) are two short muscles placed between the first and second, and second and third ceratobranchial cartilages above the genio-abdominis ; they are inseparable from, and their fibres run absolutely parallel with, those of the larger muscle. The muscles were not noted by Norris and Hughes.

Subarcualis Rectus IV.—Behind the third ceratobranchial cartilage there is a thin layer of short longitudinal fibres which arise from the posterior edge of the inferior surface of the cartilage just as do the fibres of recti II and III from the other cartilages. These fibres are inserted irregularly into the rather dense connective tissue which lies between and below the laryngeal muscles. The commingling of these fibres and those of certain of the laryngeal muscles was remarked on by Norris and Hughes.

Innervation.—This is by a branch which continues forward that ramulus of the laryngeus recurrens which innervates the constrictor pharyngei.

The Constrictor Pharyngei (Hyopharyngeus internus of Norris and Hughes) is doubtless the homologue of the transversus ventralis 4 which gives rise to the constrictor pharyngei in the urodeles. It arises from the posterior margin of the greater part of the length of the third (the last) branchial arch on each side and its fibres pass directly mediad to be inserted into a mid-ventral raphe and, in part, into the trachea.

The Dorso-laryngeus is apparently represented by two portions.

The Pars Dorsalis (Figs. 91, 92, D.l.d.) (Levator Arcuum Branchialium of Norris and Hughes) arises from the fascia investing the trunk muscles deep to the inferior margin of the pars notognathica of the depressor mandibulae and the posterior origin of the Csv.2b. From this origin the fibres pass ventrad and caudad, converging to be inserted into a tendinous condensation of tissues by which it is bound to the extreme tips of the second and third branchial arches.

Pars Ventralis (Hyo-pharyngeus of Norris and Hughes) arises from the inferior surface of the posterior edge of the fourth arch, third branchial, and its fibres pass mediad and caudad to meet the other muscle in the mid-line dorsal to the larynx. The muscle is incompletely divided into a more median and a lateral portion at its origin.

Norris and Hughes also describe a Dilator laryngis, a Sphincter laryngis and a Laryngeus ventralis.

There is a little doubt as to whether I have identified the Dilator correctly. I find a very definite and quite separated bundle of fibres arising from the third branchial cartilage out near the most lateral limit of the pars ventralis of the dorso-laryngeus and passing across ventrally to the other muscles, and obliquely to their fibres, to an insertion into the arytenoid cartilage. Norris and Hughes depict the dilator between the constrictor pharyngei and the pars ventralis of the dorso-laryngeus.

The Sphincter forms an almost complete collar for the entrance to the larynx. Its fibres are inserted into a mid-dorsal raphe. Its weakest point is ventrally, where it is apparently fused with the tiny Laryngeus ventralis of the larva.

In addition to these, I find a muscle which appears to be the Interbranchialis 4 which these authors describe in *Herpele*. It is a narrow thin muscle which arises from the tip of the last two branchial arches by a fine tendon and, widening slightly as it passes caudad and mediad, is inserted a little distance behind the larynx into the tissue at the side of the trachea. The muscle is certainly not a fourth interbranchial ; it may perhaps be derived from a fifth arch, or it may be an anterior slip of the rectus abdominis.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The Genio-abdominis (Figs. 91, 92, G-d.) (Thoracicohyoideus of Wiedersheim and of Norris and Hughes) arises from the mandible just to one side of the symphysis. The fibres pass back to be inserted on to the anterior edge of the first ceratobranchial cartilage. From the posterior edge of this cartilage the muscle takes a second origin and continues caudad to an intersection placed below, and attached to, the third ceratobranchial. Behind this intersection the muscle is continued to become fused with the rectus abdominis.

The dorsal surface of the muscle is practically continuous with the interarcual muscles between the branchial cartilages.

The Genio-hyoideus (Fig. 92, G-hy.) muscle arises from the mandible dorsal to the genio-abdominis and, being wider than this last, may be seen lateral to it, before the more superficial muscle is removed. It is inserted into the anterior edge of the ceratohyal cartilage and to the central piece which connects this to its fellow.

4. **Review.**

The several short discussions which have been introduced in the course of the description of the cephalic musculature of the abranchiate amphibians renders a lengthy review of their features unnecessary.

THE PTERYGOIDEUS MUSCLE.

A final review of the evidence on which this muscle was identified as the pterygoideus in the Elasmobranch fishes is advisable before passing to the higher vertebrata.

The most recent discussion on the origin of the pterygoideus muscle with which I am acquainted is that in Dr. Lightoller's work on " Probable Homologues in other Vertebrates of some of the Elasmobranch Constrictors and Levators ".

I am deeply indebted to Dr. Lightoller, not merely for permission to read his typescript, but for the present of a copy of it, together with a set of his illustrations. I found his work exceedingly valuable, and I owe not a little to his stimulating criticisms of my own work as it progressed.

He and I have approached the same problems from rather different angles, and, after numerous discussions, have agreed to differ on certain questions. One of these is the origin (evolution) of the pterygoideus. That we should be unable to see eye to eye on this question may be regarded as one of those numerous instances which illustrates the importance of the personal factor in equations of this kind.

Now it is unquestionable that the levator maxillae superior of *Carcharinus* is very similar to the pterygoideus of the amphibians, but it is believed that this similarity is more apparent than real. This muscle is situated behind and lateral to the mandibular and maxillary rami of the fifth nerve, whilst the pterygoid of the amphibians is situated medial to and in front of these nerves.

It may also be pointed out that the levator maxillae superior could, apparently, only attain to its insertion on the lower jaw by means of the subdermal fascial layers, so that a mandibular adductor derived from this muscle should have its insertion superficial to that of the muscles derived from the elasmobranch adductors, whereas the insertion of the pterygoideus in the tetrapods is always deep to the other muscles of mastication.

Another line of comparison offers further support for the interpretation of the origin of the pterygoideus muscle which is here advanced.

In such bony fishes as *Amia, Polypterus, Girella* and *Platycephalus,* the more typical members of the Teleosts, the position, origin, insertion, and relation to the rami of the fifth nerve, of the muscle which I have identified as the pterygoideus are all such as to satisfy this identification completely.

In addition to this muscle there is, lying deep to it and also posterior and dorsal, one which a consensus of opinion, seemingly correctly, regards as the homologue of the elasmobranchian levator maxillae superior. The muscle in question is the levator arcus palatini. In the Chondrostei, the levator maxillae must be regarded as truly represented by the M. protractor hyomandibulae.

If these last identifications are correct then, clearly the pterygoideus muscle of the bony fishes cannot have been derived from the first levator also.

Still another objection to regarding the pterygoid as derived from the levator is the relation of the ramus maxillaris of the fifth nerve to the muscle in the amphibians. Always this nerve is superficial to the muscle. Since the levator maxillae superioris is placed entirely behind the fifth nerve in the elasmobranchs, it is difficult to understand how it can have found its way, not only in front of the nerve but deep to it, in its alteration to become the pterygoideus. It may be pointed out that the ramus maxillaris is entirely a sensory nerve, and, therefore, not subject to transportation by any muscle to which, otherwise, it would have supplied motor twigs.

On the other hand, the relation of the muscle which I have identified as the pterygoideus in the elasmobranchs, to the branches of the fifth nerve is the same as that of the pterygoideus in the amphibians and remains constantly so in all the changing forms that have been passed in review in the preceding pages.

The ramus ophthalmicus profundus may pass forward either superficially to the muscle, or in rare instances deep to it, both in the elasmobranchs and amphibians.

The ramus maxillaris in every instance passes forward superficially to the muscle.

The ramus mandibularis either passes behind the muscle or it crosses superficially to it between origin and point of insertion.

The diagram (Fig. 93) is intended to illustrate the relation of the pterygoideus muscle to the maxillary ramus of the fifth nerve as the muscle changes its situation. A, represents three elasmobranchian situations for the origin and insertion of the muscle ; the nerve passes forward superficially to the muscle. In B, we have the muscle arising behind the orbit, but in front of and above the exit of the nerve, as in several amphibians. In C, we have illustrated the condition in the Axolotls ; the nerve has to run backwards beneath the muscle to reach its posterior margin, around which it turns in order to pass forward. In D, we have the pterygoideus medius and internus of the reptiles illustrated. In E, the temporo-masseteric mass is illustrated, lying superficially to the nerves. In F, the temporo-masseteric muscles deep to the pterygoideus externus are shown by the dotted lines, and the ramus maxillaris is indicated as running forward to the anterior margin of these and then turning back so as to curve around the posterior margin of the pterygoid muscle, as in C. This last illustrates the fact that the more superficial muscle is really deep to the nerve which, itself, is deep to the more deeply placed muscle.

It is of interest to note in this connection that in the Axolotl the posterior extension of the pterygoideus muscle is correlated with a posterior transportation of the proximal portion of the ramus maxillaris. This, instead of coursing straight forward, as it does in those amphibians in which the M. pterygoideus does not extend its area of origin back to the otic capsule, passes from the foramen prooticum first dorsad and caudad and then turns forward over the posterior margin of the muscle. Actually this means that the nerve passes first backwards and then curls dorsad around the inferior margin of the muscle in order to pass forward to its destination.

The significance of the partial division of the pterygoideus muscle into partes internus and externus in *Necturus,* its division into three parts in *Pseudotriton,* and the presence of a pterygoideus internus muscle in *Ichthyophis* will be discussed after the muscles have been described in the Reptilia and the Aves.

THE MUSCLES OF THE HYOID SEGMENT.

The dorsal muscles of the segment have been sufficiently discussed, but some further consideration of my interpretation of the ventral muscles is desirable.

Lightoller, apparently misled by Drüner, regarded the interhyoideus—M. ceratohyoideus externus—of the amphibians as an interarcual caducous muscle and dismissed it completely from his discussion of the amphibian ventral constrictors. This resulted in his acceptance of Drüner's identification of the fore part of the superficial ventral hyoid constrictor as the interhyoideus.

I have shown that the " cerato-hyoideus externus " is a hyoid muscle, that it develops from the hyoid muscle plate, and has, in the 13 mm. larva of the Axolotl, no relation to any other than the hyoid segment. Norris and others have shown that the muscle is innervated only by the seventh nerve. The muscle is not caducous, but persists as a functional muscle in the adult of every amphibian in which it is developed.

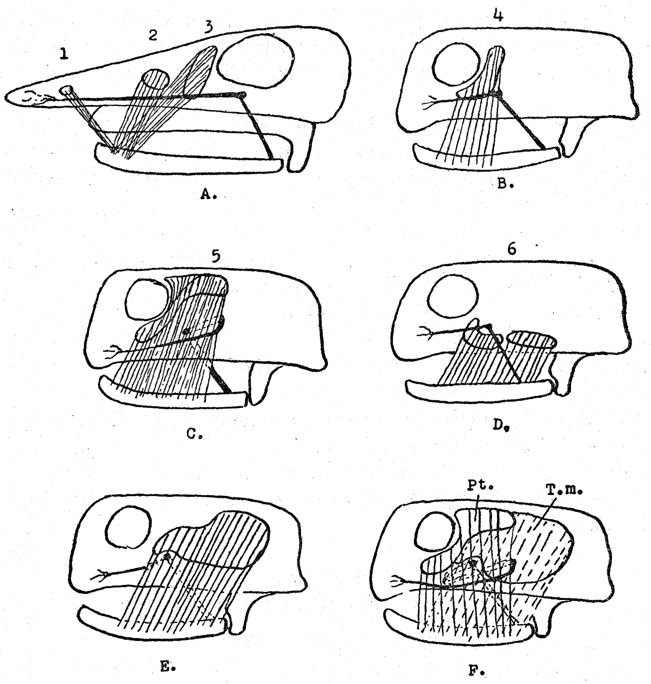

Fig. 93.—A diagrammatic presentation of the relation of the muscles of mastication to the branches of the fifth nerve.

I have found, further, that the primitive origin of the superficial constrictor of the hyoid segment is not in any part from the ceratohyoid, as in the adult, but entirely from the subcutaneous tissues dorsal to the upper end of that cartilage and along a line which commences in front of and ends well behind that upper end. The origin of the anterior part of the muscle from the ceratohyoid in the adult and older larvae is a secondary origin.

Unquestionably the appearance of the anterior part of the Csv.2, that which Lightoller and I designate Csv.2a, is very much, if not exactly, that of the interhyoideus of the elasmobranchs, but, it is believed, this resemblance is a parallelism and not a true homology.

In *Notophthalamus* the division of the Csv.2a into a pars superficialis and pars profunda, the latter arising in part from the cerato-hyoid cartilage, and running obliquely forward deep to the Csv.1, makes the resemblance to the elasmobranchian condition more perfect.

It is noteworthy that in the earliest stages no part of the ventral hyoid musculature arises from the ceratohyoid cartilage, that in this stage—the 13 mm. larva of the Axolotl—the superficial constrictor sheet is quite continuous, and the interhyoideus, deep to it, arises from the tissues close to the dorsal end of the ceratohyal. In all the adult urodeles studied one finds the anterior part of the constrictor sheet passing deep to the posterior end of the mandible to gain an attachment to the dorsal end of the ceratohyal, whilst the dorsal end of the interhyoideus has been forced, or has moved, back to gain an attachment to the dorsal end of the thyreoid cartilage, developed from the last branchial cartilage.

Comparison with the muscles in the Anura seems to lend further support to the identification of this anterior part of the superficial constrictor as the interhyoideus. In these forms the muscle which Gaupp designates the subhyoideus, and which is correctly identified as the interhyoideus by Lightoller, is developed from a muscle which, in early larval stages, arises from the ceratohyal cartilage on each side and meets its fellow in a mid-ventral raphe. There can be no question that this is a veritable interhyoideus.

But the position is complicated by the fact that there is no muscle developed in the Anura which may be identified as the superficial constrictor.

In these amphibians the Csv.1 presents three very definite parts, (1) a submentalis, and (2) an intermandibularis posterior, whose fibres are oblique to and underlie (3) a pars anterior, just as the anterior fibres of the Csv.2 underlie those of the Csv.1 in the urodeles. On the other hand, the fibres of the interhyoideus do not underlie the M. intermandibularis in the Anura.

The interhyoideus of the Anura, then, resembles the anterior part of the Csv.2 of the Urodela in its origin from the upper end of the stylohyal, but differs in that it does not gain an insertion deep to the Csv.1.

In the Anura there is no cerato-hyoideus externus.

It is surely only reasonable to conclude that there is no cerato-hyoideus externus, because the muscle deep to the constrictor which gives rise to it in the urodeles has here given rise to a superficial constrictor.

Again, in the Anura the superficial hyoid constrictor sheet is one muscle, and one only, whereas in the Urodela the constrictor sheet is always sharply divided into two, recalling the partes arcuata and inscriptionalis of the elasmobranchs.

Lightoller has suggested that the cerato-hyoideus externus may be, in part, a ventral extension of the pars quadrato-hyoidea of the Csd.2. Whilst the origin, dorsal to the mid-lateral line, supports this suggestion, it may be said that there is no evidence in its development to indicate a duality in its composition.

Finally, if the cerato-hyoideus externus be not homologous with the interhyoideus of the elasmobranchs and with portion of the protractor hyoidei of the bony fishes, then it must be regarded as an entirely new muscle. In view of its large size and importance functionally, this does not appear a reasonable interpretation. It seems more reasonable to regard it as a muscle inherited but modified.

APPENDIX.

The Laryngeal Muscles of the Amphibians.

Mixophyes Tadpole. (Fig. 94.)

The laryngeal muscles here described are those of a tadpole of full size, but before the formation of the pectoral limb girdle. It is the same as the youngest stage of which the cephalic musculature generally was described.

For the study of these muscles, the larva was cut transversely behind the branchial cavity and all the structures were carefully dissected off the posterior wall. The heart and pericardium were then removed. The whole branchial structure was then freed from the cranium dorsally, and opened along the mid-dorsal line. It was now found possible to cut free the posterior part of the basket and remove it completely. This portion was then stained and studied, after clearing and mounting in canada-balsam, spread right out flat.

The Dorso Laryngeus (D.l.) reaches the larynx, coming from above and laterally to it, behind the most posterior fibres of the constrictor pharyngei. Just before the muscle reaches the outer margin of the sphincter laryngei it turns on its edge so that the most anterior fibres reach the dense procartilaginous tissue surrounding the laryngeal aperture on the dorsal surface thereof and along the anterior half of the length of the slit-like closed aperture. To reach this insertion the fibres pass dorsally to and in front of the anterior half of the sphincter.

The Constrictor Pharyngei (C.ph.) apparently acts as a subsidiary dilator of the larynx. A posterior fasciculus of its fibres diverges from the rest of the muscle a little distance above and behind the larynx and passes to the anterior and deeper edge of the sphincter, and the fibres are inserted into the same raphe to which the fibres of that muscle are inserted. Actually, right at their termination these fibres are in series with those of the sphincter.

The Sphincter Laryngei (Sph.) would perhaps be better termed a laryngeus ventralis. The muscle is in two halves ; each arises in the mid-line behind the larynx and curves round it to be inserted into a raphe in the mid-line in front. The posterior raphe is exceedingly thin, so that it is only under higher magnification than one uses for dissection that one discovers the interruption in the continuity of the fibres. The anterior interruption, on the other hand, is quite an obvious gap between the two muscles. It is this division into two halves which suggests that this is really a laryngeus ventralis and not a true sphincter.

The division of the muscle strongly suggests that it is derived from two muscle plates, and, as it is a ventral muscle, the suggestion presents itself that it is a ventral " rest " of a fifth branchial segment.

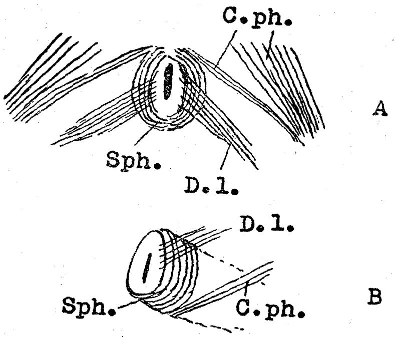

Fig. 94.—*Mixophyes* tadpole, stage C.—The laryngeal muscles.

Necturus.

The Dorso-laryngeus and the Constrictor pharyngei are as in the Axolotl, except that the latter lies entirely dorsally to the larynx and trachea, meeting its fellow in a median raphe above the trachea behind the larynx.

The Laryngeus Ventralis is a triangular little sheet of muscle which arises from the fascia behind the constrictor pharyngei and ventrally to the dorso-laryngeus. At its origin the muscle is very narrow, but as it passes mediad and rostrad towards the mid-line its fibres radiate and are attached to the dorsal edge of the arytenoid cartilage beneath the median end of the fibres of the dorso-laryngeus.

This last muscle is peculiar and unlike any other amongst the many forms studied.*

Its point of origin is quite a distance from the mid-line ; actually it is at about the junction of the middle and median thirds of the distance between the mid-line and the margin of the last branchial cartilage.

The Sphincter Laryngei is a very small muscle, just a few fasciculi which arise from a dorsal raphe at the anterior end of the arytenoid cartilages and pass round to be inserted beneath them, but not meeting in a median raphe ventrally.

Amphiuma.

I have not been able to dissect *Amphiuma* ; the following description is based upon a study of several excellent sets of serial sections. For these my grateful thanks are tendered to Professor H. W. Norris. These sections formed portion of the material Professor Norris worked on when he wrote his account of the cranial nerves of *Amphiuma means* (1908). There are several sets of transverse sections and one very fine set of sagittal sections. Whilst it was not found possible to determine the whole cephalic muscular anatomy with sufficient certainty that it was entirely correct, this want of certainty does not apply to the description of the laryngeal muscles except as to the origin of the two sheets which are inserted dorsal to the larynx.

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* This condition recalls that of the 7 mm. larva of *Limnodynastes peronii*. Here the posterior fibres of the sphincter appear to be inserted into the loose connective tissue on each side of the larynx a little distance from it; it also resembles somewhat the thyreo-arytenoideus ventralis of the adult *Hyla*.

The laryngeal muscles of *Pseudotriton* and *Siren* are essentially similar to those of the Axolotl except that, according to Wilder (1891), in *Siren* the laryngeus ventralis is a longitudinal muscle.

The structure of the arytenoid cartilage is more complex than in other amphibians.

The anterior tip of each cartilage lies alongside of the laryngeal fissure and is here a thin rod of fibro-cartilage ; a little further back it becomes flattened, and extends more deeply. This added depth is of hyaline cartilage. A ridge next appears on the outer side of the hyaline portion so that the cartilage comes to be triangular in cross section. The ridge rapidly subsides again posteriad, but almost at once the cartilage divides into a ventral and a dorsal arm. The ventral is the shorter and is formed entirely of hyaline cartilage, and tapers to a point rapidly. The dorsal, fibro-cartilaginous, arm is continued backwards and fuses with a succession of tracheal cartilages whose separate identity is manifested only by the fact that they project slightly both dorsally and ventrally around the trachea, but fail to meet in the mid-line either above or below.

In the 51 mm. larva the laryngeal muscles are very simple. A laryngeus dorsalis reaches the larynx from an origin high up on the fascia dorsalis and its fibres pass rostrad and ventrad to their insertion into the connective tissue condensation around the larynx close to the dorsal margin of the embryonic cartilaginous arytenoid. The Constrictor pharyngei has a dual origin : the more dorsal is from the deep, subdermal fascia immediately behind and lateral to the dorsal tip of the last branchial cartilage, the more ventral is from the dense connective tissue behind the tip of that cartilage. The fasciculi from these two origins meet behind and medially to the last cartilage and are continued mediad to be inserted into a mid-ventral raphe ventrally to the larynx and trachea.

The laryngeus ventralis and constrictor laryngei are both present ; neither extends more than half-way round the larynx.

In the adult the same muscles are present but they have been rearranged.

The Dorso-laryngeus arises from a connective tissue condensation which is situated a little higher than, and just behind, the tip of the last branchial arch. From above this point, there radiate dorsad the fibres of what is probably a pars dorsalis of this muscle, the appearance being very much that of the pars dorsalis of the muscle in *Ichthyophis*. From its origin behind the last branchial cartilage, the dorso-laryngeus passes rostrad and ventrad. The muscle is somewhat broader than that of *Ichthyophis* and also stouter. The more posterior fibres are inserted into the ridge of the arytenoid, but the great bulk of them are collected into a rounded muscle which courses forward alongside of the dorsal edge of the cartilage just above the ridge till the most prominent point of it is reached, when the muscle tapers suddenly and is inserted into that point.

In sagittal sections this muscle is very definitely divided into a dorsal and a ventral bundle of fibres between its origin and insertion, and it is believed that the more posterior fibres are those which, behind their insertion, are gathered together to form the ventral bundle. This suggests that there is here a dilator laryngei, as in *Ichthyophis*, but the fibres are so completely devoid of any dividing fascial or perimysial plane at both origin and insertion that it is not possible to assert the duality of the muscle.

The Constrictor Pharyngei is a thicker and broader muscle than the dorso-laryngeus. It arises behind and below the other from the connective tissue around the dorsal end of the last branchial cartilage. It is not nearly so broad a sheet of fibres as is the muscle in the Axolotl, being more like that of the adult *Amblystoma*, though relatively thicker. The insertion is into a mid-ventral raphe below the larynx and anterior end of the trachea. Its course is parallel and ventral to the dorso-laryngeus, but its anterior fibres reach forward only so far as the posterior margin of that muscle, whilst the posterior fibres are placed further back. I do not find any fibres of this muscle to have an insertion other than into the ventral raphe.

The Sphincter Laryngei.—The fibres of this muscle arise from a median raphe dorsal to the larynx, commencing immediately behind the apex of the lateral ridge of the arytenoid cartilage. They are placed between the longitudinal portion of the dorso-laryngeus and the cartilage as they pass around the larynx to be inserted into the mid-ventral raphe between the larynx and the constrictor pharyngei. These fibres have a slight inclination caudad from above down.

The Laryngeus Ventralis.—This name has been applied to a well differentiated muscle anterior to the sphincter. Its fibres arise from the mid-ventral raphe in front of the constrictor pharyngei. They pass dorsad with a slight inclination caudad to be inserted into the submucosa on each side of the larynx.

Amblystoma. (Fig. 95.)

The Arytenoid cartilages are simple, elongated plates of cartilage enlarged at the anterior end.

The Dorso-laryngeus (D.l.) and Constrictor Pharyngei (C.ph.) have already been described. Suffice it here to say that the dorso-laryngeus curls dorsad, just as it reaches the lateral margin of the sphincter, in order to reach the dorsal edge of the tip of the arytenoid cartilage in front of that muscle, where it is inserted.

The Sphincter Laryngei (Sph.) presents a relatively wide interval between its two halves dorsally ; ventrally they meet one another at the mid-ventral raphe.

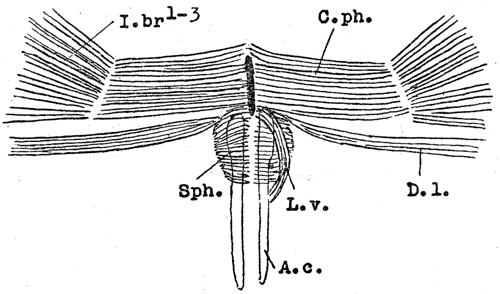


Fig. 95.—*Amblystoma.*—The laryngeal muscles.

The Laryngeus Ventralis (L.v.) arises from the mid-ventral line below the anterior margin of the sphincter and winds round the outer surface of that muscle from in front caudad and dorsad, to be inserted into the arytenoid cartilage behind the sphincter.

In this amphibian, as in *Hyla*, there is a deep slip of the rectus abdominis which takes its origin anteriorly from the submucosa a short distance posterior to where the dorso-laryngeus leaves the ventrum of the pharynx to pass dorsally and laterally beyond it. This slip recalls, strongly, the so-called interbranchialis 4 of the Caecilians.

In the 13 mm. larva it is not possible to recognize a laryngeus ventralis differentiated from the sphincter.

In the well-grown Axolotl the laryngeus dorsalis—dorso-laryngeus—is a wider sheet of fibres and it lies for the most part ventrally to the larynx and trachea. A few fibres, comparable in number to those present in the adult muscle, along the anterior border of the muscle only find their way to the dorsal edge of the arytenoid cartilage in front of the sphincter.

Molge.

The Constrictor Pharyngei (Fig. 96) is here reduced to an oval strand of muscle fibres which pass around the lateral fornix of the pharynx and across its floor to reach the ventrum of the larynx. Here the fibres are spread out just sufficiently to permit of the formation of a complete muscular layer below the larynx and are inserted into a mid-ventral raphe. Just where the muscle reaches the ventrum of the pharynx it is interrupted by a tendinous intersection, very similar to that which interrupts this muscle in *Amblystoma*. It is exceedingly fine and only visible when the dissected muscle is viewed by transmitted light after staining and clearing.

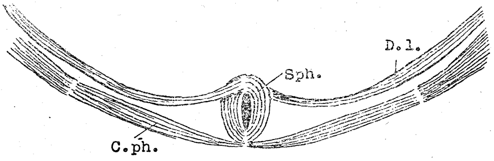


Fig. 96.—*Molge.*—The laryngeal muscles.

The Dorso-laryngeus passes from its origin alongside the last muscle till it has almost reached the larynx. It now leaves the other muscle, turning dorsad and very slightly rostrad, passing across the anterior face of the sphincter laryngei, and is inserted into the anterior end of the arytenoid cartilage near its dorsal edge.

The Sphincter Laryngei arises from the mid-ventral raphe below the larynx and curves round it with an inclination rostrad to be inserted into a mid-dorsal raphe above it. A bundle of these fibres appear to have a slightly more oblique direction than the others, to be inserted a little distance from the mid-line amongst the connective tissues beneath the mucosa. These perhaps represent a Laryngeus Ventralis muscle.

Ichthyophis. (Fig. 97.)

The muscles of the larynx in the adult *Ichthyophis* are slightly different from those of the larva, as described by Norris and Hughes. They have already been briefly described.

The Hyopharyngeus internus (C.ph.) has been already described as the homologue of the constrictor pharyngei (transversus ventralis 4). This muscle is perforated by the larynx. It arises from the median edge of the last branchial arch and its fibres are inserted into a median raphe, except where they are attached to the larynx or trachea as that passes through the muscle. The anterior fibres have a direction mediad and caudad at a sharp angle ; the most posterior pass almost directly mediad, with only a slight inclination caudad.

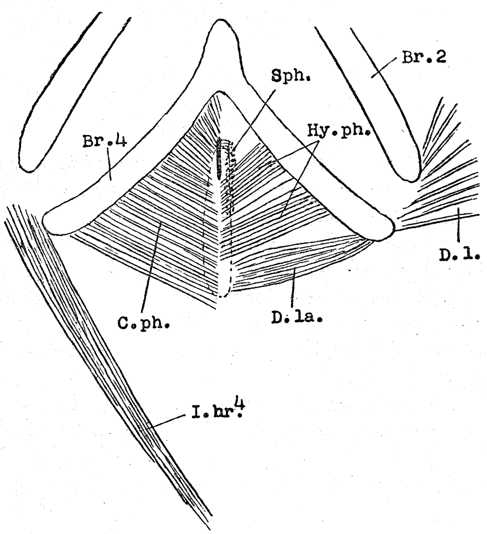


Fig. 97.—*Ichthyophis.*—The laryngeal muscles.

The most anterior fibres are in front of and ventral to the larynx ; those next to these are inserted into the arytenoid cartilages as they penetrate the muscle obliquely from in front caudad and ventrad, behind these the fibres are inserted into a median raphe dorsal to the trachea.

The Hyopharyngeus (Hy.ph.) has been identified as the pars ventralis of the dorso-laryngeus. The muscle lies entirely dorsally to the larynx and trachea. Its fibres arise from the same edge of the last branchial cartilage as the last muscle and pass obliquely caudad and mediad to be inserted into a mid-ventral raphe dorsal to the trachea and larynx. These fibres are imperfectly divided into posterior and anterior portions, the latter arising from the more central, or ventral, the former from the more lateral, or dorsal, portion of the branchial arch.

The Dilator Laryngis (D.la.) arises from the tip of the last branchial arch and pass mediad with a slight inclination rostrad to be inserted into the arytenoid cartilage towards its posterior end. In the adult, this muscle lies posterior to, and is not overlapped by, the hyopharyngeus ventrally, but it would appear that such an overlap is present in the larva. It is possible that this is a specialized portion of the Dorso-laryngeus pars ventralis.

The Sphincter Laryngei (Sph.).—I have adopted this name rather than increase the synonymy of these muscles, but as it is not a continuous circular muscle the name is probably incorrect. Constrictor laryngei would be more appropriate.

The muscle is in two halves ; each half arises from the strong connective tissue ventral to the larynx and curls round it to reach its fellow in a mid-dorsal raphe. The ventral gap between the two muscles is, as in *Mixophyes,* quite appreciable.

The Laryngeus Ventralis, which Norris and Hughes describe in the larva, is not distinguishable in the adult. This has been determined, like all the other features of *Ichthyophis*, by careful comparison of the entire specimen and the serial sections.

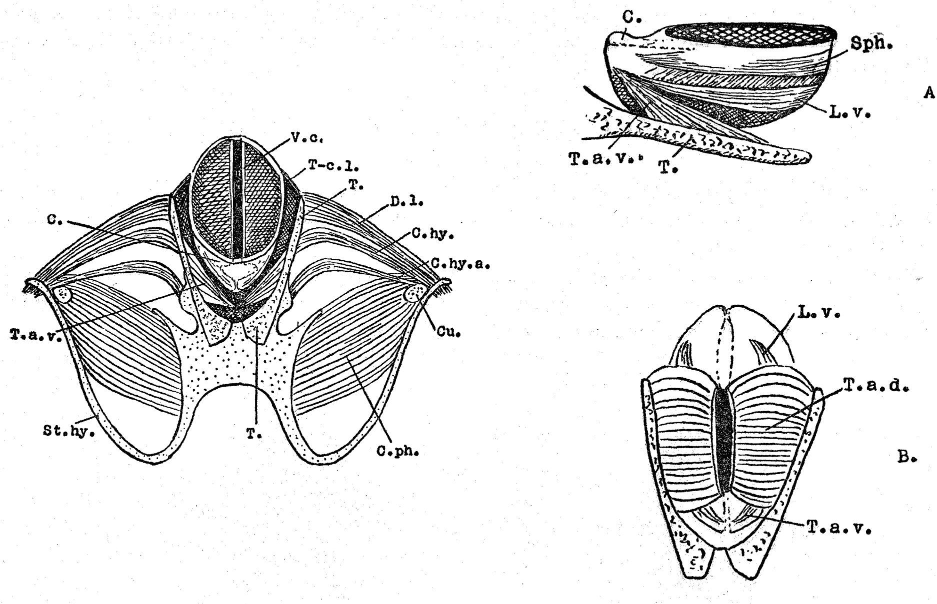
Whilst it proved possible to dissect all the muscles described, the dissection was further checked by separating the whole of the muscles, together with the larynx and anterior part of the trachea and ventral laryngeal mucosa, and then, after staining and clearing, studying them again.

The " Interbranchialis 4 " (I.br.) which Norris and Hughes describe in *Herpele* is present in the adult *Ichthyophis.*

Hyla. (Figs. 98, 99.)

The three ptery-hyoid muscles and the Constrictor Pharyngei have already been sufficiently described (p. 184).

The arrangement of the remaining muscles is quite unlike any that have been previously described, and the identification of the muscles of those simpler forms in this complex laryngeal mechanism is by no means a simple matter.



Figs. 98-99.—*Hyla.*—Laryngeal muscles. C., Cricoid cartilage; T.a.d. & T.a.v., Mm. thyreo-arytenoideus dorsalis and ventralis; T-c.l., Thyreo-cricoid ligament; V.c., Vocal cords.

The Sphincter Laryngei (Sph.).—This name is applied to a muscle which almost completely surrounds the larynx towards the ventral edge. The muscle arises from the perichondrium of the arytenoid cartilage a little behind the anterior end thereof, and is inserted into a median raphe posteriorly. The muscle is incompletely divided into two portions; some of the dorsal fibres arising anteriorly are inserted into the perichondrium a short distance from their origin, whilst some of those inserted into the posterior raphe do not extend quite half-way towards the anterior origin of the muscle, but are inserted like the short anterior fibres.

The Laryngeus Ventralis (L.v.) arises from a median raphe anterior to the larynx and passes around it dorsally to the Sphincter to be inserted into the median posterior raphe.

The Thyreo-arytenoideus Ventralis (T.a.v.) arises in common with the laryngeus ventralis. Its fibres pass caudad and dorsad to be inserted along the median and ventral margin of the ossified thyreoid cartilage.

The Thyreo-arytenoideus Dorsalis (T.a.d.) arises from the median and dorsal edge of the thyreoid bone and passes dorsad and mediad to be inserted on to the lateral surface of the arytenoid cartilage above the laryngeus ventralis.

To attempt the identification of these muscles without detailed knowledge of their development is to some extent speculation, but there is evidence which justifies the speculation, and seems to indicate that the nomenclature adopted is probably correct.

It is necessary, first of all, to recognize that the anterior end of this larynx is the ventral end of the more simple larval larynx, and that the dorsal surface is the posterior end.

With this recognized, one cannot but remark that the dorso-laryngeus of the branchiate amphibians is inserted on to the arytenoid cartilage in front of the constrictor laryngei. We further recall that we have had reason to believe that the dorso-laryngeus is interrupted at the tips of the branchial cartilages in the caecilians.

With these facts in mind, one suggests that the dorso-laryngeus in *Hyla* has been interrupted at the thyreoid cartilage and that its pars ventralis is the muscle which has been designated the thyreoarytenoideus dorsalis, its pars dorsalis being that which has been designated the dorso-laryngeus.

The laryngeus ventralis is here thought to have been divided into laryngeus ventralis and thyreo-arytenoideus ventralis.

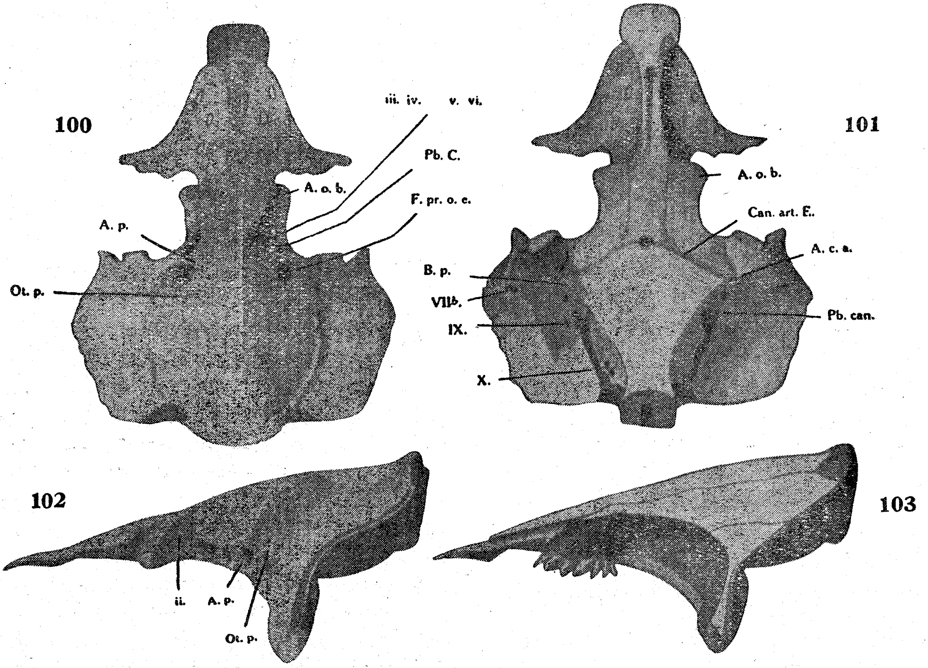
In view of the fact that in the tadpole, prior to metamorphosis, a few of the posterior fibres of the constrictor pharyngei are intimately related to the antero-ventral portion of the larynx, there is justification for suggesting that the cranio-hyoideus and cranio-hyoideus anterior are portions of the constrictor pharyngei.

THE SKULLS OF THE AMPHIBIANS.

1. The Dipnoi.

The skull of the dipnoans is peculiar by reason of the very complete retention of the cartilaginous case in the adult, more complete than, and more massive than, even any elasmobranch presents us with.

That of *Neoceratodus* was very fully described by myself in 1931, and that of *Lepidosiren* by Bridge in 1893. It is believed that the reproduction of the illustrations which accompanied those descriptions is sufficient for the present purposes (Figs. 100–109).



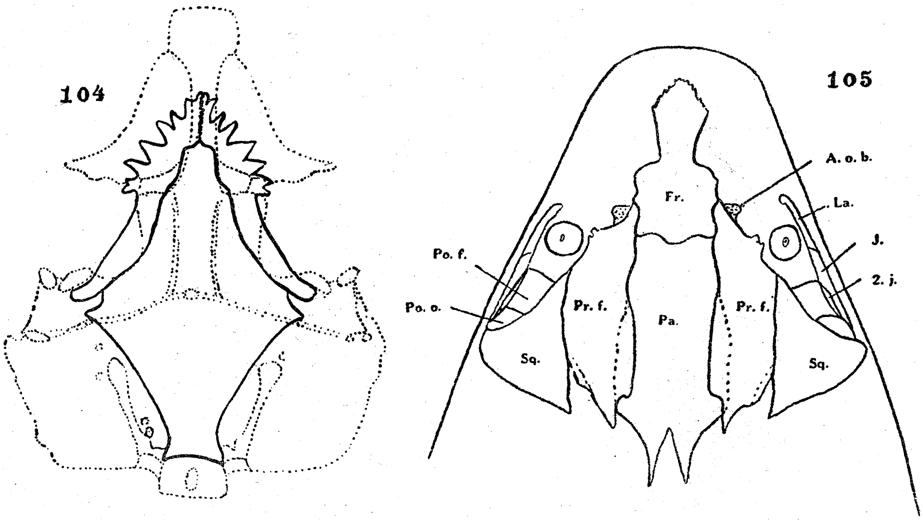
Figs. 100-103.—*Neoceratodus*. Figs. 100-102. Three views of the chondrocranium. Fig. 103. Side view with the dermal bones in place.

Before proceeding further, however, it will be convenient, with these illustrations before us, to discuss the significance of the three big bones on the base of the skull and that on the side of the skull which I identified as the squamosal bone.

The parasphenoid, lying upon the base of the skull in the middle, is at once recognizable. As compared with that of the fishes, it is markedly reduced. The lateral wings, which are of almost universal occurrence in the fish skull, are missing.

On either side of the parasphenoid is the bone which has been designated pterygo-palatine. These occupy essentially the position of the pterygoid bones of such reptiles as the chelonians and cotylosaurians. When compared with the fishes, the three bones together will be observed to occupy almost the position of the parasphenoid.

The designation pterygo-palatine is either one of convenience, a cloak to cover ignorance, or it is an implication that we have here a bone which is a combined palatine and pterygoid. Whilst the evidence in favour of a palatine component is far from convincing, its situation and its manner of development, as a membrane bone applied to the base of the skull, are, it is believed, sufficient to satisfy all the demands of an identification as the pterygoid bone, homologous with that of the *reptiles* and embolomeran amphibians. The so-called pterygoid bone of all other *amphibians* develops as a membrane bone in relation to the palato-pterygoid arch, and may or may not make contact with the side of the base of the skull and the edge of the parasphenoid bone which covers that base.



Figs. 104-105.—*Neoceratodus*. Outlines of the bones, seen from above and from below.

Now, the dipnoan amphibians resemble the rest of the group in that the pterygoid bones make contact with the parasphenoid medially. This is a particularly interesting relation, because it at once suggests that the pterygoid bones are homologous in the two divisions of the group. The appearances here are entirely deceptive. There is, in the dipnoans, no palato-pterygoid arch or process, and the bones are developed quite differently. I would not willingly lay myself open to a charge of dogmatizing and, therefore, explain that the appearances are regarded as being "entirely" deceptive because, for me, the evidence of development outweighs mere adult topographical relations ; since the pterygoid bone of the dipnoan amphibians develops differently from that of the remainder of the amphibians, it is deemed to be a different bone in the two groups.

This belief is further supported by the resemblance of the dipnoan bone to the pterygoid of many reptiles, both in the manner of its development and in the topographical relations in the adult. The topographical relations of the adult bone in the Embolomeri are much more nearly those of the reptiles than those of the amphibians, and in them the parasphenoid is probably entirely absent.

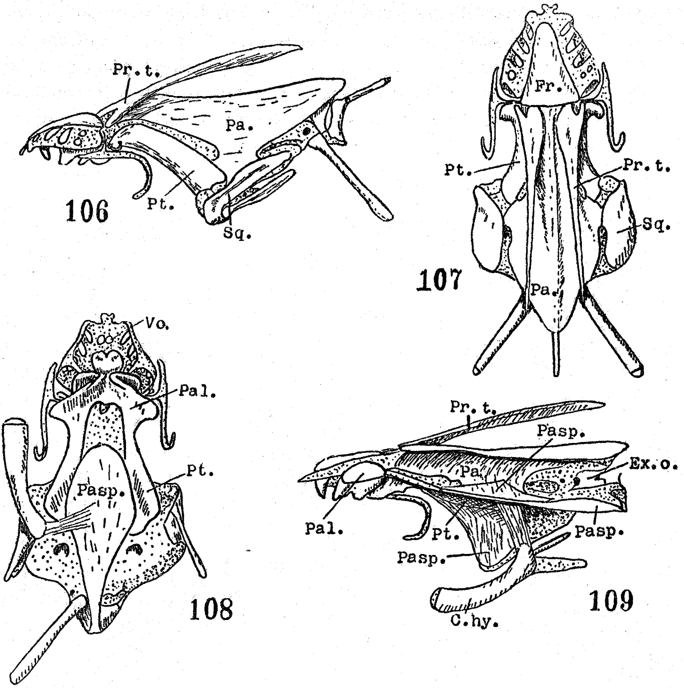
In the fishes, one seeks in vain for any bones which may be compared with the pterygoids of the dipnoans. One is, once again, struck by the fact that the parasphenoid of the fishes occupies the position of all three, so that one could readily reproduce the dipnoan condition by cracking free the lateral wings of the parasphenoid. Unquestionably, the lateral portions of the parasphenoid as seen in the fish have, in the dipnoans, been replaced by the pterygoids.

The question now arises : Is this a replacement by some other element, or is it the result of the failure to fuse of three centres of ossification of the complete bone ?

The latter seems the more probable explanation ; it is simple and calls for none of the complicated series of changes which must have preceded replacement by some other element.

What were those complicated changes ?

Firstly, it could be assumed that the replacement was by an entirely new centre of ossification. The possibility of this is at once admitted, but if this new centre developed on an already fully encased skull, it is difficult to understand why it should have arisen. On the other hand, if it appeared at the lateral edge of the parasphenoid on a largely cartilaginous skull, why should it have invaded an area already adequately protected by the parasphenoid, and in doing so surely introduce instability into an area of bone to which important muscles of mastication were almost certainly attached ?



Figs. 106-109.—*Lepidosiren* (from Bridge, 1898).

Before passing to consider another possible method of replacement it should be noted that a " new centre " hypothesis must imply a homology with the pterygoids of the remainder of the amphibians.

A second possibility is to assume that one of the bones of the palatal arch has come to occupy this situation.

In the fishes, with the exception of the Holocephali, the palate is hung to the skull by the hyomandibular bone or cartilage.

The Holocephali themselves, in a number of features, provide the evidence that the inception of the monimostylic suspension, characteristic of the amphibians, antedated the development of the piscine bony palate, possibly without any stage of hyoid suspension. If we grant that the evidence under this head is inconclusive, it is still difficult to accept the theory that one of the bones of the palatal arch has migrated back and taken up this position on the base of the skull, as against the more simple explanation of the origin of the bone by the splitting of the parasphenoid.

There are no recognizable transitional stages in the progression of the palatal element. Therefore, if we adopt this hypothesis, it is left to our imagination to decide whether we prefer to believe that the palatal element became attached to the base of the skull anteriorly and grew backwards, or that it, in effect, crawled up the mandibular arch and became attached posteriorly and then grew forward.

If the bone is to continue to be regarded as the homologue of the pterygoid of the remainder of the amphibians, except the Embolomeri, one or other of these hypotheses must be accepted. Some workers may elect to make the choice, but for me it appears a useless and fruitless exercise of the imagination.

There is, in my mind, little room for doubt that the pterygoid bone of the dipnoans is homologous with that of the embolomeran amphibians and with that of the reptiles, and in these we can see the reduction of the median remnant of the parasphenoid.

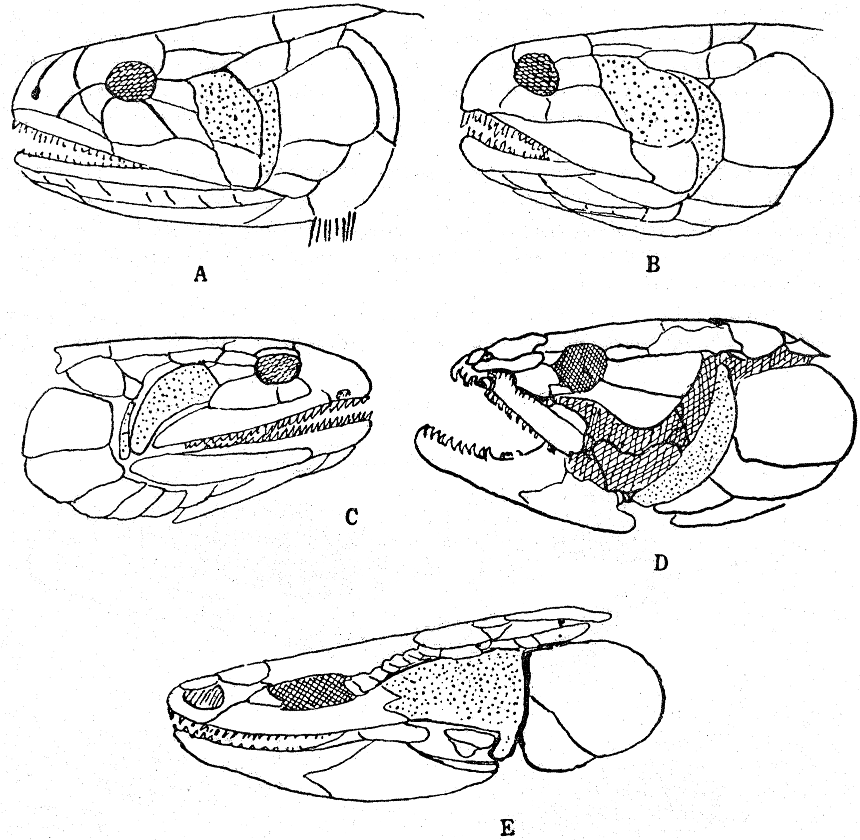


Fig. 110.—A, *Megalichthys*. B, *Rhizodopsis*. C, *Osteolepis*. D, *Amia*. E, *Polypterus* (from Wellburn and Gregory, Traquair, Gregory and Allis).

Entering the realms of pure speculation, one could offer a possible mechanical explanation of the gradual extinction of the central portion of the parasphenoid bone by the mediad growth of the lateral portions, once the bone had been split, and indeed this may also explain why it was so split.

The deeper portions of certain of the muscles of mastication are, and probably were, attached to the lateral area of the ventral surface of the parasphenoid. It is at least possible that, by early attachment to the perichondrium, these muscles penetrated the ossific membrane and determined a line which was not so readily ossified, and in time split the bone into three parts. Once the bone was split it is, at least, not unreasonable to suppose that, with increasing strain on the origin resulting from increasing size and strength of the muscles of mastication, there would have been increased need of strong attachment of the bone of origin to the skull. This need could have been met by increased area of attachment of the bone to the skull.

In conclusion, it is believed that the pterygoid bones of the dipnoan and embolomeran amphibians are homologous, on the one hand with the lateral wings of the parasphenoid bone of the fishes, and on the other with the pterygoid bone of the reptiles, and that the so-called pterygoid bone of the remainder of the amphibians is not homologous with these.

The squamosal bone of the dipnoans is of interest as an important link in the probable evolution of the tetrapod bone from one of the bones of the cheek armature of the fishes.

In *Neoceratodus* the bone presents a dorsal squame, which is in series with the other subdermal bones that form the roof of the temporal fossa, and a descending limb which is fitted to the upper surface of the quadrate cartilage. The homology of this bone with those of the higher vertebrata was, it is believed, sufficiently established in the communication of 1931. At that time it was not known that the bone in *Neoceratodus* resembles completely that of such anuran forms as *Bufo* and *Calyptocephalus*.

Before proceeding further, I would stress again a point of view stated previously (1931, p. 256) : " Any attempt to homologize the cranial elements of the fishes, dipnoans and [other] amphibians can only be made under the assumption . . . that, having evolved from a common ancestor, the same inherited [evolutionary] potential produced the same cranial elements in all."

This attitude permits one to discuss and suggest homologies in various forms without, of necessity, implying that any of the elements are derived directly from any other.

It appears probable that the squamosal of the tetrapods has been evolved by the modification of a bone comparable to the preoperculum of the fishes, with, perhaps, the addition of one or two of the cheek plates in front of it.

In Figs. 110 and 111, I have arranged a series of side views of skulls to convey my ideas in this connection. The squamosal and its assumed homologues have been stippled in each drawing.

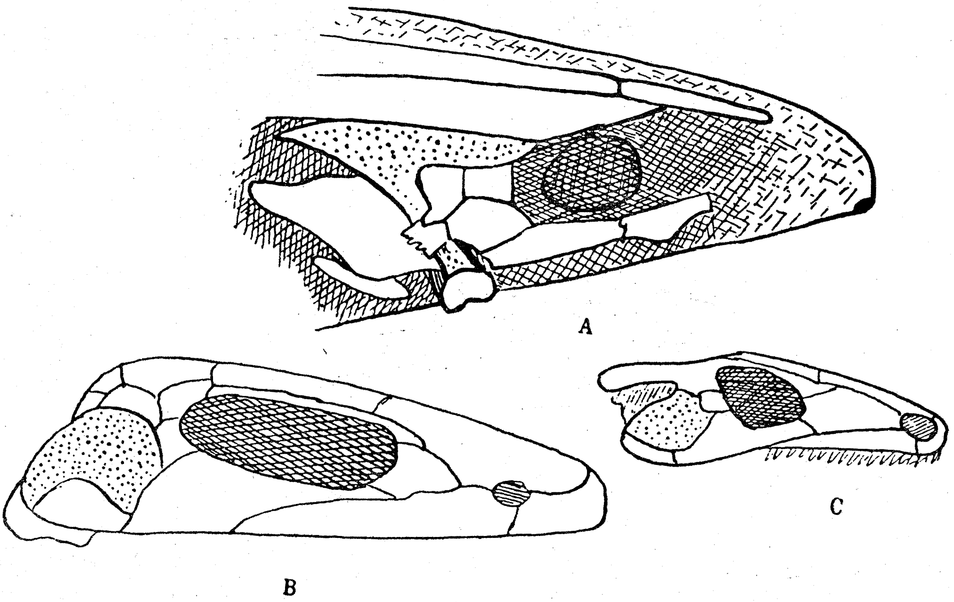


Fig. 111.—A, *Neoceratodus*. B, *Loxomma*. C, *Seymouria*. (B and C from Embleton and Atthey, and Gregory.)

The fish bone from which the squamosal is deemed to have been derived is that one of the cheek plates which was attached to the quadrate and hyomandibular. So long as the hyomandibular remained this bone gained only fibrous or no attachment to the skull. Any attachment other than fibrous would have impeded the mobility of the hyo-cranial joint. When the hyomandibular was absent and the quadrate was firmly attached to the skull, the squamosal also gained attachment to the skull, whilst still retaining its relation to the quadrate. Both its position in the roof of the temporal fossa and its attachment to the quadrate are, then, primitive features and are preserved in *Neoceratodus*, some anurans, and a large number of fossil amphibians. Whether the subdermal roofing flange of the bone which is present in some chelonians and other primitive reptiles is a secondary growth or a persistent primitive feature it is not possible to say. In the great majority of the higher vertebrata, the quadrate-attached is the only primitive portion persisting, and to this have been added various expanded flanges which may or may not contribute to the completion of the cranial wall and roof.

Thyng (1906) demonstrated the close association of the squamosal bone and the quadrate cartilage in the embryonic mammal, a relationship which is explained by the foregoing suggestions.

2. The Skulls of the Euamphibia.*

The Skull in the Anura.†

(Figs. 112–114.)

In several features the skull of the Anura is more primitive than that of any other amphibian type. Of these, two are outstanding: the platybasic "elasmobranchian" form of the cavum cranii and the form of the synpterygoid (parasphenoid) covering of the basis of the cranium.

The uniformity of the skull throughout the Anura is such that it were largely a waste of time to describe any one of them in detail; all are essentially similar to the much figured and described skull of *Rana.*

There is an extreme simplification of the ossific pattern of this skull as compared with that of the bony fishes. There are but two ossifications of the primordial cartilage on each side in the parachordal region, the prootic and the exoccipital, and in the trabecular region only one.

In the young skulls the two ossifications of the parachordal region are separate, not only from those of opposite sides but also from one another.

In the adult skull these four ossifications are completely fused and have in their extension encased the auditory capsule in one continuous mass of bone, in which no sutures are recognizable. Not only is this so, but the anterior, prootic, ossification has invaded the side wall of the cavum cranii in front of the incisura prootica, giving rise to a veritable alisphenoid lamina.

The ossification of the primordial cartilage in the trabecula region is more diffuse at its inception, so that it is hardly possible to regard it as a paired process. In the ultimate result there emerges a relatively extensive bone which encircles the cavum cranii. The antero-posterior extent of this area of ossification, the sphenethmoid bone, is subject to fairly wide variation. It may extend back sufficiently far to articulate with the anterior margin of the alisphenoid lamina of the parachordal ossification, the prootic, and it may extend so far forward as to contribute to the formation of the posterior walls of the nasal capsule. The full range of these variations is presented within the single genus *Hyla,* and cannot be regarded as being of any phylogenetic significance.

Of the covering bones, commencing with those on the ventral surface, the extensive synpterygoid, parasphenoid, is one of the most striking features of the skull. This large single covering bone of the basis cranii is found, elsewhere than in the amphibians, only in the fishes. Its presence is one of the primitive features of the amphibian skull.

The palatine bones are developed along the posterior margin of the inferior surface of the lateral expansion of the ethmoidal cartilage behind the nasal capsules. Usually these are but narrow splints and are devoid of any palatal extension, but at times, and notably in *Pelobates,* they extend well over the palatal surface of the ethmoid cartilage and may even reach anteriorly to the internal nares. In no anuran skull do these bones articulate with one another at the mid-line, nor are they found between the nares.

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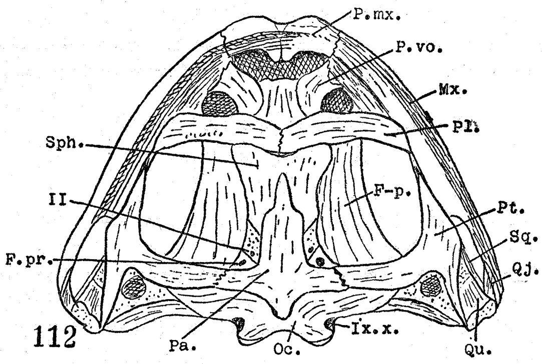
* The term Euamphibia is used here, in a different sense from that in which it has been used in the past, to include the Anura, Urodela, Apodes and Stegocephalians, except the Embolomeri. A justification for this procedure is offered in section 3 of "Phylogeny of the Amphibia", pp. 232-236.

† It might have been thought advisable to deal first with those very ancient amphibians, the "Embolomerus" forms from the Lower Carboniferous rocks. They are, however, reserved till the end of the section, when it will be found that their peculiar specializations are such that they form a very fitting introduction to the section of the work dealing with the Skulls of the Reptiles. Not only is this so, but any discussion of the fossil forms must rest upon a knowledge of the recent, which, alone, we are able to dissect and to disarticulate and thereby determine beyond doubt the relations of the bones to one another and to the soft structures. For this reason none of the fossil forms will be discussed till the recent have been passed in review.

The Prevomers are of variable extent. Typically they are situated medially to the internal nares, supplying the medial and a large part of both anterior and posterior margins to those apertures. They may or may not articulate with palatine laminae of the maxilla. Occasionally these two bones articulate at the mid-line, and commonly they are articulated to the anterior margin or inferior surface of the anterior portion of the ethmoid; exceptionally, as in *Calyptocephalus gayi* (Parker, 1881) they articulate with the fore-end of the synpterygoid.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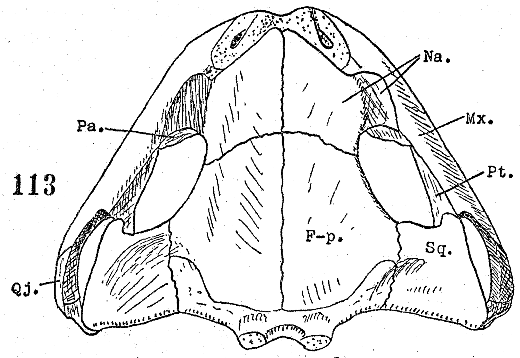
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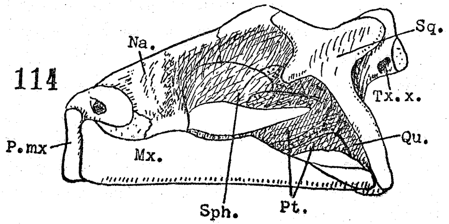
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Figs. 112-114.—*Bufo* (from Parker, 1881).

The dorsum of the skull is more or less completely covered by two pairs of bones which have been designated fronto-parietals and nasals. In *Pelobates fuscus* (Parker, 1881) the four bones are fused to form a remarkable solid cuirasse, but in the great majority of instances the bones are quite separate and distinct.

The Fronto-parietals cover more or less completely the occipital and sphenoidal regions but may meet at the mid-line only over the former region, and in front thereof may diverge, leaving an area devoid of bony covering between their divergent ends and the posterior boundary of the sphenoid bone. The area in question is that of the dorsal fontanelle, and here the cavum cranii is enroofed by membrane only.

The Nasal bones are variable in their relation to the other pair of roofing bones and in their extent. Most typically they are developed around the anterior margin of the incomplete cartilaginous tectum nasi and spread forward over the nasal capsules. In this typical form the nasals are not in contact with any other bones. Extending further back, they come to lie in contact with the anterior portion of the sphenethmoid, and further backward extension leads to sutural contact with the anterior margin of the fronto-parietal. In, e.g. *Calyptocephalus gayi* and *Bufo* (Parker, 1881) the nasal bones are particularly extensive ; they extend forward almost to the margin of the external nares and backward, covering the sphenethmoid bone completely, to suture with the fronto-parietal, and then, expanding laterally, they make sutural contact with the ascending lamina of the maxilla. In *Bufo agua* the nasal bones extend back so far as to give the impression that in this form the skull is roofed by paired parietals and frontals and that, as in the Chelonia, the nasal bones are absent.

Actually the designation of the nasal bones is rather a matter of mutual agreement than of definite identification. There are no relations to any structures which permit one to assert that the bones would not be as correctly designated prefrontals as similar bones are designated in the Chelonians. The fronto-parietals occupy the area which the frontals and parietals in the reptiles occupy, but since we have no evidence of two centres of ossification, one only of those bones is really present. The decision as to whether the single bone is a parietal which has grown forward or a frontal which has invaded the region of the parietal is simply evaded in the designation adopted. It seems probable that, of the two alternatives, the former is the more likely. The nasal bones certainly appear to be placed too far forward to be regarded as frontals, but actually they do not, in the Anura, extend so far forward as the prefrontals of the Chelonia.

The Septomaxillary bone ossifies in membrane in relation to the dorsal surface of the solum nasi. There is some variation in its situation, but in the generality of instances it is placed at the posterior and lateral margin of the external naris. The bone is in all probability a true dermal roofing bone of the dorsal series and the homologue of one or other of the several present in the roof of more primitive vertebrates. It is not, however, possible to indicate which of those it does represent.

The so-called Pterygoid bone, which I would regard as the Os transversum, is a triradiate bone related to the inner surface of the posterior end of the cartilaginous maxillary arch, the ramus of the quadrate, and the antero-inferior surface of the auditory capsule. The homologies of this bone will be discussed at some length in a later section. For the present it will suffice to draw attention to the fact that it develops first as a membrane bone in relation to the posterior end of the cartilaginous maxillary arch (pterygoid process) and later grows backward to attain the adult relations. It is in sutural contact anteriorly with the posterior end of the maxilla, and, finally, it forms the anterior and median boundary to the space through which the muscles of mastication pass from their origin to reach the lower jaw. This space may be conveniently designated the via masticatoria, and in the Anura it is bounded medially by the " pterygoid ", laterally by the quadrato-jugal, and posteriorly by the quadrate and its encasing bones, the postero-lateral ramus of the " pterygoid " and the descending ramus of the squamosal, when that is present.

The Squamosal bone is particularly well developed in the genus *Bufo* (Parker, 1881), and in these forms it is strikingly similar to that of *Neoceratodus*. There is the same splint-like descending ramus on the antero-lateral surface of the quadrate, and an expanded dorsal body, which sutures with the fronto-parietal and contributes to the formation of an incomplete roof to the temporal fossa. The squamosal also, in the great majority of the Anura, contributes to the boundary of the tympanum dorsally.

The quadrato-jugal bone, probably more correctly designated quadrato-maxillaris, since no jugal bone is present, sutures only with the quadrate and the maxilla.

The prootic and alisphenoidal regions of the skull of *Hyla* will be found described with greater detail in a later section of this work dealing with the serial homologies of the Alisphenoid bone.

The facial and trigeminal ganglia lie partly within the cranial cavity on a depression on the floor of the cavity with the prominence of the anterior semi-circular canal behind and above the recess. Portion of the ganglia, however, protrudes through the foramen prooticum. In front of the foramen there is an alisphenoidal extension of the prootic ossification. This has arisen by extension of the ossification into the crista trabeculae from the otic centre, and is very definitely not contributed to in any way by an ascending process of the quadrate.

The alisphenoidal lamina is perforated by the foramen for the internal carotid artery. It will be observed that in the Urodeles and in the Apoda this carotid foramen is placed further back.

There is no bony or cartilaginous bar between the branches of the fifth nerve as they pass away from the incisura prootica.

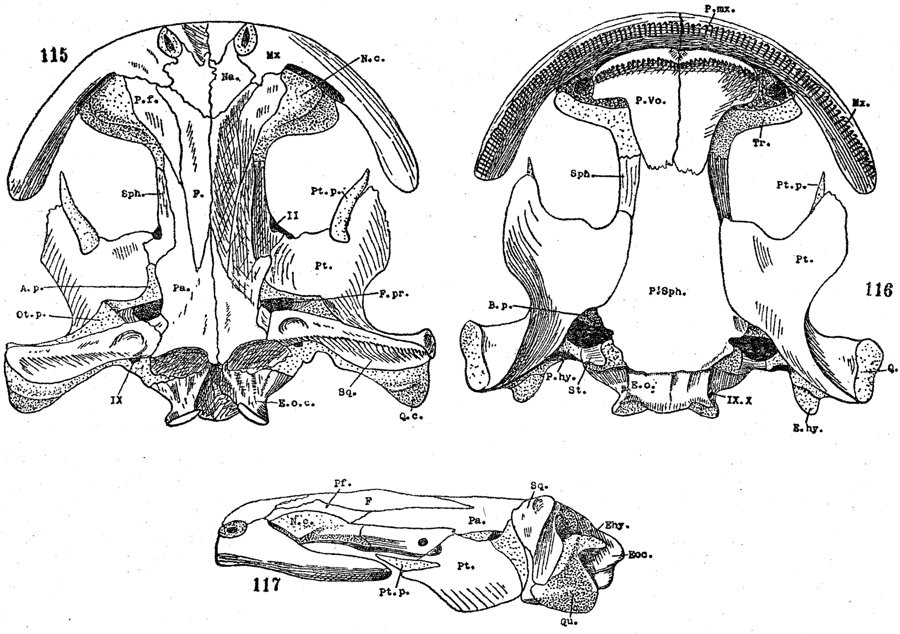
The Skull in the Urodela.

(Figs. 115–117.)

The endochondral ossifications of this skull are essentially similar to those of the Anura. The two ossifications, however, are less extensive, and the sphenethmoid is usually represented by paired bones which do not meet one another at the mid-line. They have been designated orbitosphenoids by some writers.

There are four pairs of dermal roofing bones, parietals, frontals, prefrontals and nasals.

The squamosal bone in the great majority of the genera is a simple splint applied to the lateral and dorsal surface of the quadrate ramus, but in exceptional instances is expended in the temporal roof and may make sutural contact with the parietal and with the frontal.



Figs. 115-117.—*Sieboldia* (from Parker, 1882).

The quadrato-jugal is absent, and, except in a few instances, in which the maxilla is extended far back, there is discontinuity in the maxillary arcade between the posterior end of the maxilla and the quadrate. In some forms the maxilla is reduced almost to complete extinction. The premaxilla commonly presents ascending processes which suture with the nasals between the external nares. The maxilla, when well developed, may suture with nasal, prefrontal and frontal, laterally to the external nares.

On the ventral surface of the skull the most extensive bone is the synpterygoid. This is not " T "-shaped as in the Anura, but tapers forward from its broadest point, below the auditory capsules, to its truncated anterior end. Actually the width of the bone is subject to greater variation than in the Anura ; it is widest in such forms as *Cryptobranchus* and *Menopoma* and narrowest in the English Newt (*Molge*).

The Prevomers are very extensive bones. Developed at first in the same situation as those of the Anura, they, in late stages of larval and early adult life, grow backwards on either side of the mid-line, lying below the anterior portion of the synpterygoid.

The Palatine bone is evanescent. It appears in early stages of development in the situation of the palatine in the Anura but disappears later.

The " Pterygoid " bones are subject to very wide variation in their size. Again *Cryptobranchus* may be taken as one extreme and *Molge* as the other. In the former genus the bone bears resemblance to that of the Anura, but with the wide angle between the two anterior rami filled in and the bone extended forward to form an extensive floor to the temporal fossa. As in the Frogs the via masticatoria is bounded medially and anteriorly by this bone. In *Molge* the pterygoid is reduced to a short splint with an expanded base which lies upon the ventral surface of the pterygoid process of the quadrate. In the former genus the pterygoid sutures with the lateral edge of the synpterygoid for some distance, in the latter genus it sutures with no bone at all.

The development of the " pterygoid " is a matter of importance, as its homology with the similarly-named bone in the Embolomeri and Reptiles will be questioned later.

It may be stated that throughout the recent Amphibia the so-called pterygoid develops as an epichondral ossification in membrane in relation to the pterygoid process of the quadrate ; later it extends so as to cover part of the ventral surface of the auditory capsule and to suture with the synpterygoid. Parker, very significantly, wrote of *Siren* (1882), " The suspensorium, having no pterygoid outgrowth, and no correlated pterygoid bone, is naked below ", emphasizing this constant relation.

With but rare exceptions, the quadrate presents well developed ascending, otic and basal processes by which it is articulated to the otic and prootic region of the cavum cranii. The ascending process* rises in front of and lateral to the prootic foramen and fuses with the crista trabeculae. In the great majority of the genera the greater part, if not the whole, of the quadrate remains unossified, as also does the prootic portion of the crista.

The otic process* may or may not fuse with the upper part of the otic capsule ; in the majority of genera the fusion is very complete.

The basal process is attached to the anteroventral and lateral corner of the otic capsule and is confluent with the ototrabecular bar in this position.

Immediately behind, and slightly above, the articular surface of the quadrate there is commonly a posteriorly projecting stapedial process with which the outer end of the stapes articulates.

Opposite the stapedial process there arises a pterygoid process of very variable length, absent altogether in some forms ; in most it is continued forward close to the trabeculae, but lateral and ventral to them, to fuse with the antorbital cartilage.

The foramina for the exit of the fifth and seventh nerves are found on the inner side of the cranial cavity near the anterior end of the otic capsule.

The Gasserian ganglion lies entirely within the cavum cranii in a recess bounded by the otic capsule behind, the crista trabeculae in front, and the auditory and ascending processes of the quadrate laterally. Its three branches leave the cranium through the foramen prooticum. The maxillary and mandibular rami pass on their way posteriorly to the ascending process, whilst the ophthalmic division insinuates itself between the ascending process and the crista trabeculae, passing forward to the inner side of the process.

The geniculate ganglion lies, for the most part, within the cranial cavity though portion of it may be insinuated along the facial canal. This latter perforates the fore-end of the otic capsule, and through it the ramus hyomandibularis reaches the outer surface of the otic capsule behind the stapedial process of the quadrate. The ophthalmic branch of the nerve passes through the foramen prooticum along with the maxillary division of the fifth. The palatine division penetrates the floor of the cranium, passing close to or through the carotid foramen to reach the anterior division of that canal along which the palatine terminal branch of the vessel travels.

The Skull of the Caecilians.

(Fig. 118.)

In their cranial characters the Caecilians present the same similarity one to the other that was observed in the Anura. In the complete cranial roof they present striking similarity to certain of the Stegocephali, and this similarity is also present in the palatal architecture, though not so markedly, and yet, perhaps, it is more genuine.

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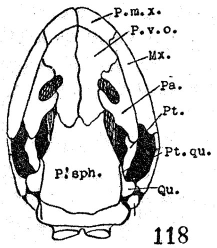
* Watson has confused these two processes ; for he writes of the Upper Triassic Stereospondyls that they have " an otic process of the palatoquadrate cartilage, which articulates with the prootic region of the skull " (1919, p. 58). It is the ascending process of the Urodeles which articulates with the prootic region of the skull.

Apparently the endochondral ossifications are similar to those of other Amphibia, but their development is not so well known, so that it is not possible to speak confidently here.

As in the Urodela there are paired parietal, frontal, prefrontal and nasal bones, but they are of somewhat different proportions. The parietals and frontals are similar, but the prefrontals are smaller and the nasals larger. A closer examination, however, discovers that the parietal and frontal bones extend laterally beyond the cavum cranii and contribute to the formation of a temporal roof which is completed by an extensive squamosal. Except in one species of *Caecilia* the squamosal bone sutures with the frontal and the parietal, though in several the suture with the latter bone is interrupted by a narrow fissure posteriorly. The squamosal bone does not extend down the short quadrate ramus as it does in the Urodeles and Anura but reaches only the otic (?) root of the quadrate.



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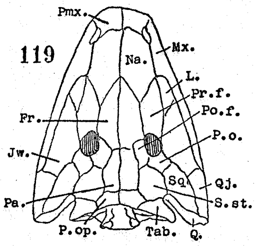

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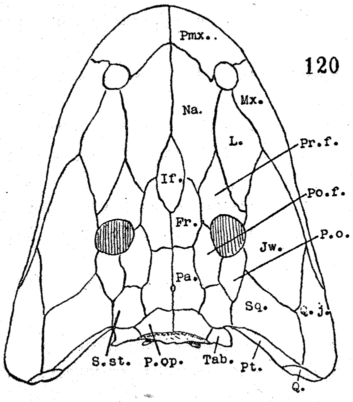

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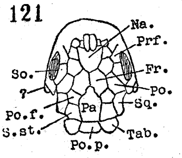


Fig. 118.—*Ichthyophis* (from Wiedersheim, but slightly modified to show more clearly the true relation of the os transversum to the pterygoid bone.)

Fig. 119.—*Capitosaurus* (from Zittel).

Fig. 120.—*Eryops* (from Broom).

Fig. 121.—*Dipterus* (from Watson).

There is some variety in the bones of the skull roof anterior to the orbit. The prefrontal may be replaced by a process of the maxilla which extends upward behind the nasal to reach the frontal bone. In *Ichthyophis* this process is present as well as the prefrontal bone. *Ichthyophis* is also peculiar in having an adnasal between the nasal and the premaxilla and in the possession of a circum-orbital bone.

Whilst this skull roof presents a stegocephalian "completeness", it is possibly only a parallelism, and comparable with the occasional complete roof found in certain genera of both Urodeles and Anura.

The stegocephalian similitude of the palatal aspect of the skull is due largely, if not entirely, to the double arch of teeth. These are situated, as to the external set, on the premaxilla and maxilla, and as to the internal set, on the prevomers and the palatine. This arrangement of the teeth is almost characteristic of the Labyrinthodont stegocephalians; it is found in Embolomerous, Rachitomous and Stereospondylous forms.

Not only is this so, but such an arrangement of the teeth in two complete arcades is not found elsewhere.

The Prevomers are large, resembling those bones in the Urodela.

The Palatine bones are extensive and form the anterior, lateral and posterior boundaries of the choanae. These apertures are placed relatively farther back than in either Anura or Urodela and are bounded medially by the prevomers.

An extensive palatine bone comparable with that of the Gymnophiones is found elsewhere amongst the amphibians only in certain of the Stegocephalia, e.g. *Eryops, Orthosaurus,* and *Capitosaurus.*

An Os Transversum has not been recognized in the palate of the Gymnophiones.

The so-called Pterygoid is a short, narrow, flat bone which extends from the pterygoid process of the quadrate to the posterior extremity of the palatine ; it lies in the floor of the temporal fossa, and forms the antero-median boundary to the via masticatoria. It is the homologue of the anterior arm only of the " pterygoid " of the Anura and the Urodela.

The quadrate is completely ossified and consists of a compact body which bears the articular surface on its lower face, and a glenoid cavity, on its posterior surface, into which the head of the stapes fits. Attached to the upper edge of the lateral surface of the body is a tympanic flange, of variable extent, which extends upwards, and both backwards and forwards, and sutures anteriorly with the lower edge of the squamosal bone. To the lower and inner corner of the body there is attached a tapering pterygoid process of variable length. The bone is attached by fibrous tissue only to the outer edge and upper surface of that part of the parasphenoid which extends laterally beyond the basis of the cavum cranii. The line of attachment extends from almost the postero-lateral corner of the parasphenoid to about the middle of the length of the orbit, and is along the medial surface of the body of the quadrate and the ventral surface of its pterygoid process. There is no trace of the basal and otic processes, nor of the ascending process. The ascending process was expected, for it is well developed in the chondrocranium of early embryonic stages.

The parachordal cartilages are to be seen imbedded in bone at the infero-lateral angle of the cavum cranii, but it is quite impossible in the youngest specimens at my disposal to find, in the transverse sections, any line of demarcation between the very extensive parasphenoid and the ectochondral bone which this encasement of the parachordals indicates must be present. Nor can one find, either in adult specimens of the prepared skull or in transverse sections, any indication of suture or duality of origin in the side walls of the cranium. These arise almost at right angles from the basis and are interrupted only by the vascular and nerve foramina. Immediately at the anterior boundary of the otic capsule, on the under surface of the floor of the cranial cavity, there is the carotid foramen ; this enters the cavum just behind the pituitary body, as determined by study of sections, there being no trace of pituitary fossa in the adult skull. Just as this canal reaches the cranial surface of the floor it gives off a branch which turns forward and laterad. The palatine branch of the facial nerve and the abducent nerve both enter this canal at the point of departure of the anterior branch, reaching this situation by passing caudad through a small canal which perforates the anterior margin of the prootic foramen. The fifth and seventh roots leave the cranial cavity together through the prootic foramen ; both their ganglion and that of the ophthalmicus profundus lie entirely external to the cranial wall in a recess which is bounded, as described by Norris and Hughes (1918), behind, by the body of the quadrate medially and posteriorly, and by the tympanic lamina of the bone laterally, with the prootic ossification above the ganglia. In front, the recess is bounded by the muscles of mastication, the parietal and prootic bone superiorly and the lateral flange of the parasphenoid and the pterygoid process of the pterygoid bone inferiorly. The various branches of the two nerves depart from this recess without any bony or cartilaginous structure intervening between them, excepting only the palatine whose course in this immediate neighbourhood has just been described.

In the sphenoid region my younger sections show the trabeculae and taenia marginata both encased in bone without sutures or other indication of any interruption in the ossification below the suture with the dermal roofing bones.

The Skull in the Stegocephalia.

(Figs. 119–124.)

The most completely known portion of the skulls of the Stegocephalia is the outer surface of the roof. The dermal bones are more numerous than in any of the recent groups. Besides parietals, frontals, prefrontals and nasals there are commonly present more or fewer of the following : post-parietals, tabulars, supratemporals, intertemporals, postfrontals, postorbitals and lachrymals as well as jugal, quadrato-jugal and squamosal bones.

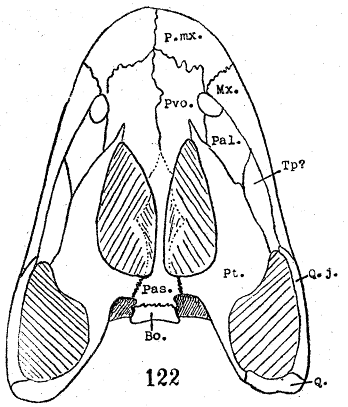
The general shape and position of these bones will be sufficiently gathered from the illustrations.

The illustration of the Dipnoan skull has been added for comparison. It is worthy of note that except for the fact that the parietal is undivided, this primitive amphibian presents all the bones of the dermal shield of the stegocephalian skull except the jugal and quadrato-jugal. Comparison with the dermal pattern of the embolomerous skull (p. 213) reveals an equally close resemblance.

Maxilla and premaxilla are always present and well developed.

The ossification of the oto-occipital segment of the primordial cranium appears to have been as variable as in the Anura and Urodela combined.

A separate " epipterygoid " bone has been described in isolated specimens of both rachitomous and stereospondylous skulls. It is, however, very probable that further investigation will show that the fragments so identified are but portions of the prootic ossification. There is little doubt that the epipterygoid bone of the reptiles is an ossification of the ascending process of the quadrate, and is essentially a reptilian feature. The complete absence of reptilian characters from the stegocephalian skull, and the retention of the ascending process in its primitive form in all the recent amphibians, renders it highly improbable that the bone should bave been present in members of a group which must have been ancestral to the recent forms.



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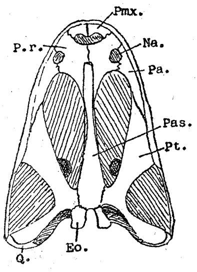

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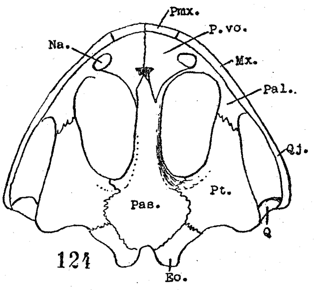

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Fig. 122.—*Eryops* (from Broom). Tp. Os transversum.

Fig. 123.—*Cyclotosaurus* (from Fraas, after Goodrich).

Fig. 124.—*Batrachosuchus* (from Watson).

The ventral surfaces of three typical stegocephalian skulls are illustrated here, and from them a general idea of the relation and extent of the bones will be gathered.

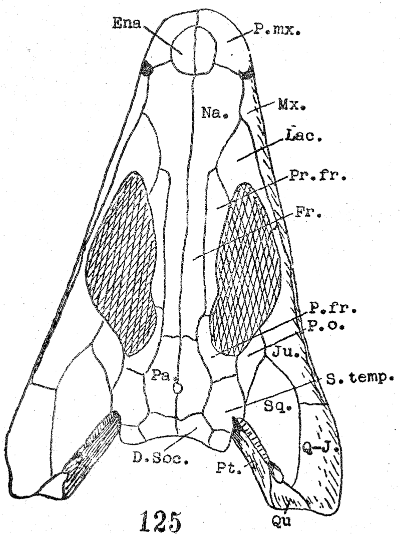
It remains to remark that the quadrate ramus of the pterygoid bone, in a number of genera, is folded around the posterior surface of the quadrate, rising towards the skull roof, and, apparently, contributing to the posterior wall of part of the tympanic recess. This dorsal extension of the pterygoid bone never rises so high as in the Embolomeri, and Cotylosaurian reptiles.

3. The Skull in the Embolomeri.

(Figs. 125–129.)

The following description is taken from Watson (1926). I have, however, been unable to accept the whole of his identifications of the bones he describes.

In its general facies this skull is essentially reptilian, the neurocranium is tropibasic, and, as in the reptiles, there results a compact cavum cranii with a narrower sphenoidal cavity lifted on to the dorsal edge of an interorbital septum. That essentially amphibian bone the large, primitive, synpterygoid, is not present on the base of this skull. The two most outstanding of the characteristics of the amphibian skull are therefore missing from this, and in their place reptilian characteristics are found.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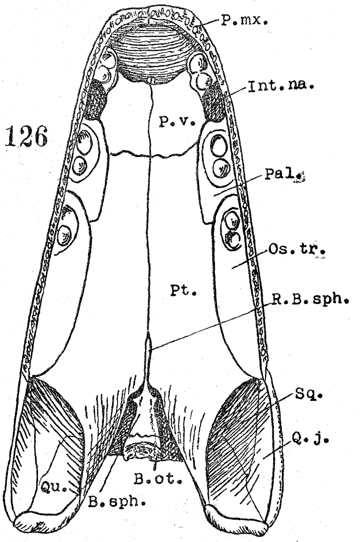
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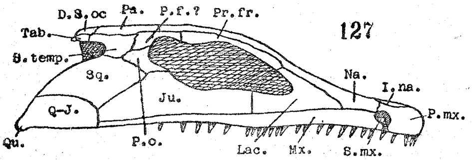
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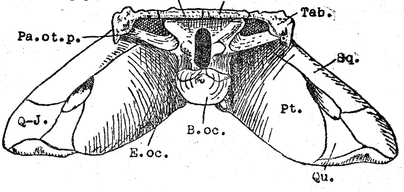
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Figs. 125-128.—*Orthosaurus* (from Watson, 1926). Pa.ot.p., Parotic process.

The oto-occipital portion of the neural cranium is laterally compressed, and is provided on each side with a parotic process of typically reptilian form. Entering into the composition of this part of the cranium there are distinct exoccipitals, basi-occipital, supraoccipital, basisphenoidal, and prootic ossifications. Watson claims to be able to distinguish between the basi-sphenoid and a covering parasphenoidal ossification by slight differences in their texture in *Palaeogyrinus*, but says the bones are indistinguishable in *Orthosaurus*. He describes the " parasphenoid " as covering " the greater part of the lower surface of the basi-occipital, overlapping the sides of that bone nearly to its articulation with the otic bones ". He continues, " In front of the otic region the joint bone bears a pair of well formed basi-pterygoid processes which project laterally and somewhat downwards. The lower surface of each process at its root has a groove passing from the posterior round on to the anterior surface ; this housed the internal carotid artery."

There is some confusion here. Watson depicts, in *Palaeogyrinus*, a well marked suture between the basi-occipital and the bone in front of it on the base of the cranium. This suture meets the exoccipital above, so that the basi-occipital does not reach the prootic bone. Apparently it is the basisphenoid which the parasphenoid is believed to overlap.

In view of the other striking reptilian features, it is not advisable to accept the slender evidence of " slight differences in texture ", as conclusive evidence that there is any membrane-derived bone covering the inferior surface of the basisphenoid. It appears more probable that the bone is a typical reptilian basisphenoid.

The groove on the inferior surface of the basitrabecular* process probably did not house the internal carotid artery. That vessel runs dorsally to the basitrabecular process in the reptiles, and dorsally to the plane of the parasphenoid bone in the Amphibia.

Anterior to the oto-occipital segment of the neuro-cranium there is an ossified interorbital septum which has been designated " sphenethmoid ". The sphenoidal cavity is an excavation along the thickened dorsal part of this septum. The two olfactory canals leave the fore-end of the cavity, and tunnel the portion of the bone in front. Posteriorly the sphenethmoid articulates with the anterior end of the roof of the neuro-cranium behind the posterior end of the sphenoidal cavity. Below this articulation the posterior margin of the bone bears, about the middle of its depth, two processes which suture with the prootic. Below this again, the posterior edge meets the anterior end of the rostrum basisphenoidei and in front of this its ventral edge bears the splint-like " parasphenoid ",† so characteristic of many reptiles. Two apertures are present between the posterior end of the sphenethmoid and the neuro-cranium. The upper of these was believed by Watson to have transmitted the Vth nerve only, the lower to have transmitted the optic and eye-muscle nerves and the internal carotid artery.

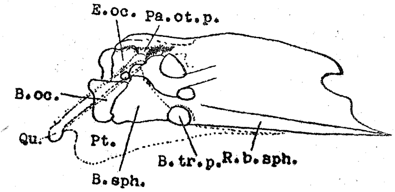

Fig. 129.—*Palaeogyrinus* (from Watson, 1926, but with the quadrate and pterygoid bones " restored " in dotted lines).

In view of the fact that it is quite unusual in the amphibians and the reptiles for the incisura prootica to be separated from the sphenoptic fissure by any cranio-mural ossification, it is more probable that the upper aperture transmitted all the nerves anterior to the VIIIth, except the olfactory, and the ophthalmic vessels, whilst the lower will have been the foramen of entry of the cerebral branch of the internal carotid artery.

So far as may be decided from Watson's figures and description, the pituitary fossa was situated immediately above and behind the planes of the basitrabecular process, and it would appear that the anterior part of the cavum cranii was sharply tilted upward immediately in front of the fossa. The floor apparently rose on the sloping posterior face of the sphenethmoid, between the two processes which separate the arterial from the other foramen, to reach the sphenoidal cavity, formed in the posterior end of the thickened dorsal part of the sphenethmoid bone.

The dermal roofing pattern is relatively simple, as compared with that of other labyrinthodont amphibian skulls, though more complex and primitive than that of any recent amphibian.

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* The designation " basitrabecular ", which Goodrich wisely adopts for the basipterygoid process, will be used instead of the older name. This course appears advisable because there is a distinct tendency on the part of a number of morphologists to disregard the fact that the process is an ossification of a process of the trabecula related to the fenestra hypophysios. In the result these careless thinkers find a " basipterygoid " developed as a process of the parasphenoid or situated far from the fenestra. The term basitrabecular should act as a corrective. One of the most surprising instances of disregard of the site of the trabecular origin of the basitrabecular process is the identification of the process in *Eusthenopteron* by Watson (1926). Clearly, if the bone identified as the basisphenoid is an endochondral ossification of the basi-trabecular plate it can be none other than a presphenoidal ossification; it is obviously too far forward to be regarded as a basisphenoidal ossification.

† It has recently been demonstrated that this " parasphenoidal splint " is an endoperichondral ossification and a presphenoidal not parasphenoidal bone (Kesteven, 1940*b*, 1941*a*).

In the mid-line the parietals cover the greater part of the oto-occipital segment of the cranium and extend forward over the posterior end of the sphenoidal cavity. Their common suture is interrupted by a pineal foramen. Behind the parietals a pair of dermo-supraoccipital bones are present. In front of the parietals the frontals may or may not be fused with the nasals, and in front of the last a pair of internasal ossicles may or may not be present. Tabular, supratemporal, postfrontal and prefrontal bones are present. In front of the prefrontal a typical reptilian "lachrymal" bounds the orbit anteriorly and extends, in some forms, right forward to the external nares, as in primitive reptiles. A postorbital bounds the orbit posteriorly. The squamosal makes sutural contact with the supratemporal, postorbital, quadrato-jugal, quadrate and pterygoid bones. The premaxilla sutures with the maxilla at the transverse plane of the external nares, and the latter bone extends back well behind the orbit, from which it is separated by the jugal.

The palate of the Embolomeri is, perhaps, the most characteristic feature of the skull, and is very dissimilar to that of any other amphibian.

The synpterygoid (parasphenoid or vomer) is reduced to a narrow splint lying along the ventral edge of the interorbital septum.

The pterygoid bones are very extensive and contribute the greater part of the bony palate. They meet in a common median suture which extends from that between the prevomers back almost to the posterior end of the palate. The parasphenoid appears between them posteriorly. Laterally they suture with the palatine and os transversum. There is no suborbital or subtemporal deficiency in the palate. At the transverse plane of the anterior margin of the via masticatoria, the lateral margin of the pterygoid swings mediad and caudad, forming the whole of the median boundary of the "via". Also, at this transverse level, the inner portion of each pterygoid turns dorsad, rising in close relation to the side wall of the auditory capsule, apparently in the manner indicated by the dotted line in Fig. 129, till it meets the inner margin of the squamosal just behind its suture with the supratemporal. The inner margin of the pterygoid, here better termed its dorsal margin, now continues caudad in sutural contact with the postero-medial margin of the squamosal till the tympanic notch is reached. The posterior limit of the bone is indicated in Fig. 127, where it was shown as it lies in contact with the inner and posterior surface of the quadrate just proximal to the articular surface.

The os transversum, palatine, and prevomer are simple bones whose form and relations are sufficiently indicated in the figure of the palatal aspect of the skull.

The quadrate is largely encased by the quadrato-jugal, squamosal and pterygoid bones, but is exposed in the roof of the via masticatoria, and probably articulated with the lateral end of the parotic process as in many reptiles.

In the extended description of the Embolomeri which Watson gave in the Croonian lecture (1926) he fails altogether to describe the relation of the quadrate to the skull. In an earlier paper (1913) he describes the quadrate as being exposed on its under surface and as "passing upward on the under surface of the roof of the skull until it is received into a slit in the squamosal, which thus covers it both dorsally and ventrally".

On a later page he wrote, "Examination of these primitive and extremely well preserved skulls seems to show that the ordinary idea of the autostylism of the tetrapoda is incorrect in postulating a connection between the pterygo-quadrate cartilage and the otic region. It is, I think, quite certain that there never was such a connection in primitive forms, except through the dermal bones of the temporal region."

Although not so stated, it would appear that his later examination of embolomerous material has caused him to regard the above description as incorrect. The squamosal of *Palaeogyrinus* is described as terminating behind "by overlapping the dorsal surface of the quadrate". Apparently, then, there is no support at all for the suggestions relative to the autostylism of the Tetrapoda.

The epipterygoid has been identified in *Palaeogyrinus*. It is a short ossicle which, lying against the anterior edge of the ascending posterior lamina of the pterygoid, articulated below with the basitrabecular process and had an expanded free upper extremity.

The tympanic notch mentioned above is a pit situated on the postero-dorsal surface of the quadrate and under cover of the squamosal laterally and the upper margin of the ascending lamina of the pterygoid medially. Watson writes of the notch, "There is, in all the members of that group of Embolomeri which includes *Loxomma*, a curious pit on the quadrate, so placed that it faces toward the otic capsule, which must have lodged some structure. This can only have been a process from the cartilaginous stapes, representing the lower part of the hyomandibular ".

The tympanic cavity in both amphibians and reptiles lies behind the quadrate and below the parotic process. In the embolomerous amphibians, the remarkable ascending lamina of the pterygoid has obviously walled in the tympanic space between itself and the quadrate, whilst the squamosal completes the walling-in dorsally. Only the distal aperture of the cavity remains. This is the tympanic notch.

Watson has designated a certain pit on the outer wall of the otic region the " pseudo-fenestra ovalis ", and he rightly says that the pit, in *Palaeogyrinus,* is situated in the position that the fenestra ovalis might have been expected to occupy. The situation of the pit in *Eogyrinus,* in front of the parotic process, is, however, not one in which the fenestra ovalis would be sought. It is probable that when material has been found which exhibits the true relation of the head of the quadrate to the skull, the fenestrae of the ear will also be located.

Appendix.

The " Sauramphibia ".

It has been claimed that the Embolomeri are the most primitive amphibians known, " and those which most nearly resemble the fish ancestors of that class " (Watson, 1926).

To the present writer this appears to be an untenable position, and to rest very largely upon a fundamentally wrong concept.

It is quite apparent that the view can only be based on the assumption that the primitive pterygoids were large expanded bones meeting, or nearly meeting, in the mid-line of the palate, and that the primitive " parasphenoid " was a narrow splint.

It is believed, here, that it is not possible to place any but quite secondary values upon the similarity or dissimilarity of dermal roof patterns, as evidence of phyletic relationships.* It is so readily demonstrable that closely allied forms in most, if not all, vertebrate groups have, at times, very dissimilar roof patterns, whilst widely unrelated forms in different groups may present essentially, and even actually, similar roof patterns.

It is therefore, to the more stable endochondral ossifications and the bones of the palate that one must turn for reliable evidence in phylogenetic question.

Goodrich (1930, p. 318) accepts Watson's view and states the position relative to the history of the parasphenoid more explicitly : " The parasphenoid in the Embolomeri was comparatively small, closely connected with the basisphenoid posteriorly, and extending forward below the sphenethmoid as a narrow grooved blade. In the more advanced types (Rhachitomi, Stereospondyli) the interpterygoid palatal vacuities become progressively enlarged, the parasphenoid expands behind and becomes immovably sutured to the pterygoid."

The discussion of this question may well be introduced by a brief statement of facts of particular relevance :

(1) The basisphenoid bone is an endochondral ossification of the primordial chondrocranium in the region of the hypophysis cerebri, and is either perforated by the hypophysial fenestra or forms the floor of the pituitary fossa, and is usually perforated by the canal for the internal cerebral branch of the internal carotid artery.

(2) It is therefore possible to recognize a basisphenoidal segment of the basis cranii, and in the Amniota this segment lies immediately in front of the basioccipital segment ; its position is determined by that of the hypophysis cerebri in all vertebrates.

(3) In the Anamniota as a group, the basisphenoidal segment of the cranial floor is either (*a*) not ossified at all, (*b*) incompletely ossified, or (*c*) ossified in complete continuity with the ossification of the occipital segment and the auditory capsule.

(*a*) Not Ossified at all.—Omitting the typical Elasmobranchii, which, in the complete absence of ossification, shed no light on the present question, this condition is found in a majority of the Chondrostei, Urodela and Anura, and in all the Dipnoi. There was also complete absence of ossification of the basisphenoidal, pituitary region in the Osteolepida.

(*b*) Incompletely Ossified.—This condition is characteristic of the whole of the bony fishes excepting only those mentioned above. In fishes with a myodome, the little bone which has been identified as the basisphenoid lies entirely in front of the pituitary body and, on that account,

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* It has, however, already been noted that there is nothing in the dermal roof pattern of early Dipnoans to contraindicate community of origin of Dipnoans, Embolomeri and Euamphibia.

its homology with the basisphenoid of the Tetrapoda has been questioned and it has been proposed to designate it " suprasphenoid ". On the other hand, the horizontal transverse arm of the bone in such fishes certainly occupies the position of the anterior portion of the pituitary fossa, and that is basisphenoidal in the Tetrapoda. It would seem that it is certainly homologous with, at least, the anterior portion of the bone. In this respect the Palaeoniscid skull resembles the majority of the bony fishes. In the absence of the myodome the basisphenoid, if present at all, is exceedingly thin and is so intimately fused with the underlying " parasphenoid " that it is quite impossible, in adult skulls at least, to recognize the composite nature of the bone.

In the apode amphibians it is questionable whether any basisphenoidal ossification is present at all. In none of the adult or young specimens examined, in serial sections, is there any indication of a dual contribution to the bony floor of the pituitary region. Apparently a very extensive basicranial fontanelle is floored by the synpterygoid only, though there may be a small contributing basisphenoidal element completely fused with it, as in the fishes without a myodome.

(*c*) Ossified in complete continuity with the occipital segment and auditory capsule.— This condition is found in some of those amphibians in which the cartilaginous chondrocranium is extensive in this region. Endochondral ossification commences in definite occipital and auditory centres and extends uninterruptedly forward along both the floor and sidewalls of the cavum cranii, and ultimately a continuous bony case results, in which no sutures are visible.

(4) In the Anamniota the synpterygoid is an extensive bone on the basis cranii. It commences at, or behind, the occipital segment and, extending forward beneath the pituitary, sphenoid and (in some forms) ethmoid regions, supplies the strength which the absence of endochondral ossifications calls for. In both the fishes and the amphibians this bone is characteristically expanded below the auditory capsules and, when the skull is laterally compressed in the auditory region, this lateral auditory wing of the bone rises on the lateral wall of the capsule.

(5) In the Amniota the " parasphenoid " takes the form of a narrow splint applied to the lower surface of the rostrum basisphenoidei and the membranous cartilaginous or bony interorbital septum, and is really a presphenoid ossification, not a membrane bone.

(6) Excepting only in the Dipnoi, in the presence of a well, or moderately well, developed parasphenoid, the pterygoid bones never meet at the mid-line. It is only when the " parasphenoid " takes the form of a prepituitary splint, which we now identify as the vomer, that the pterygoids meet one another medially.

(7) The divergent pterygoids are characteristic of the Anamniota, the convergent of the Amniota.

Features such as these, which may be described as being characteristic of the whole of the Anamniota, must assuredly be regarded as having resulted from a community of inheritance.

The Anamniota are undoubtedly more primitive than the Amniota, and the Fishes than the Amphibians.

Therefore features characteristic of the Anamniota must be regarded as more primitive than those characteristic of the Amniota.

The unossified or poorly ossified pituitary region of the basis cranii, strengthened and supported by an extensive parasphenoid which had also lateral auditory wings, is to be regarded as being more primitive than a well-ossified basisphenoid bone and a parasphenoid reduced to the vomerine splint.

The separated and divergent pterygoids are to be regarded as being more primitive than the contiguous convergent pterygoids.

It follows that Amphibians of the type of the Rhachitomi, Stereospondyli, the Anura, Urodela and Apoda, which possess these primitive features, must be regarded as being more primitive than the Embolomeri, and this would still hold good even were there no representatives of those (regarded as the more primitive) of equal geological antiquity with the others.

On the other hand, there can be no doubt whatever that the Embolomeri are so essentially reptilian in their cranial characters that they may be regarded as the most advanced of all the amphibians, " advanced " being taken to mean more nearly like to a group of vertebrates which we are all agreed to regard as standing higher in the evolutionary scale than the amphibians.

Comparison of the embolomerous skulls with those of the anapsid cotylosaurian reptile, *Seymouria*, and its allies will discover for the investigator that, bone for bone, and area for area, there is a similarity so complete that one is forced to inquire further in order to satisfy oneself that the one is an amphibian and the other a reptile.

Since it is beyond question that the features wherein the Embolomeri differ from the remainder of the Amphibia are essentially reptilian, it follows that such resemblances as they present to the fishes must be either only apparent, due to wrong interpretation of the component structures in the crushed and distorted skulls, or due to inheritance from some common ancestor of all.

When it is remembered that the Cotylosauria date right back to middle Carboniferous times it becomes clear that, already, that advance in structure which was to give rise to the reptiles must have taken place in early Carboniferous times. It would appear that once the tetrapod structure had been evolved, the early members of the group were exceedingly plastic and that differentiation into the various divisions took place very rapidly. The result of this rapid differentiation was that, side by side, chronologically, we find the fishes, dipnoans, amphibians and reptiles, and between these last two the embolomerous amphibians, which alone of their class may be regarded as having stood in the direct current of evolution which produced the reptiles and Amniota generally. The rest of the Amphibia are, therefore, to be regarded as constituting a specialized end-group, or a branch on the genealogical tree of the animal kingdom.

Since the parasphenoid of all the fishes, with the possible, but improbable, exception of certain of the Osteolepida, was an expanded bone with lateral auditory wings, the view that would regard the primitive amphibians as having the vomerine type of parasphenoid and the later, more specialized forms, as having a parasphenoid which has become expanded as a result of, or as one of the features of, that specialization, surely runs contra to the circumstantial evidence available and to probability. The view necessarily assumes that the peculiar narrow parasphenoid of the osteolepid* fish was the primitive form of the bone and that the expanded form found in all other anamniotes, except the Embolomeri, was, and is, a modification of the unique forms. Since both are parasphenoid bones the inference that one is a modification of the other is inescapable.

If this be not the assumption on which the view is based, then another equally untenable position must be taken. It being granted that the, slmost universal, expanded parasphenoid is the primitive, it is assumed that in the Osteolepida it has been reduced to the narrow vomerine type, and through them handed on to the primitive amphibians. At this point evolution has taken two divergent directions. On the one hand the reduced parasphenoid is retained, and the reptiles result; on the other the expanded primitive form is once more developed and the rest of the amphibia are evolved.

The position is untenable because it also involves an acceptance of a belief in the possibility of a reduction in the progress of endochondral ossification of the basis cranii, and a loss of the basisphenoid ossification which is so successfully achieved by the Embolomeri.

Actually the belief that the Embolomeri are the most primitive amphibians rests upon the further belief that in their cranial structure they resemble the Osteolepida, and that aspect of the question has already been dealt with.

The reptilian characters of the embolomerous palate will be discussed again in a later section; suffice it here to remark that they are very real and indicate a not distant alliance with the Reptiles. On this account it is now proposed that they be separated in our classification from the rest of the Amphibia under the significant title of "Sauramphibia".

THE PHYLOGENY OF THE AMPHIBIA.

1. General Considerations.

In his remarks on the affinities of the Arthrodires which form the concluding section of his work on the Head of the Macropetalichthyids, Stensio (1925) expresses the opinion that they are to be considered as an offshoot of the Elasmobranchian stem of fishes. The evidence which he advances in support of this view is as convincing as, in the nature of the problem, appears possible, and there will be few who will disagree with the conclusion he arrived at.

In the course of his discussion he points out that "close relationship between the Arthrodires and the Elasmobranchs of course implies either that bone has arisen independently in different

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* It should be remembered that the Osteolepida which present the peculiar narrow parasphenoid are known only from imperfect crushed specimens, so that it may be that the lateral wing has not been described because it has not yet been found, and not because it was not present in the complete skull.

groups of vertebrates or that it is a very old sort of tissue that was present already among the most primitive vertebrates and from these was bequeathed to the common ancestors of the Arthrodires and Elasmobranchs ".

In support of the second alternative he points out that in the earliest Holocephali known there were related to the cranium, bone-like, or perhaps true bony, plates. He also draws attention to the Cephalaspids, Ostracoderms and the Acanthodei, all provided with bony shields and plates, and remarks of *Menaspis*, one of the Cochliodontids, there is evidence of " armour on the head and anterior part of the trunk ".

Whilst it is a fact that the palaeozoic and early mesozoic Elasmobranchs were more generally equipped with bony head-plates or relatively large bony scales, and that this is definitely evidence of their derivation from an ancestor provided with bony shields, it is not evidence that the bony structures are more primitive than the cartilaginous basis on or in which these bony shields are developed, nor, indeed, is that implied by Stensio.

On the other hand, if there be truth in the suggestion that the common ancestor of the Arthrodires and Elasmobranchs was already provided with the power to develop bone, both endochondral or at least ectochondral, and membrane-derived, we may reasonably ascribe all these bony features, wherein the bony fishes and the Dipnoi resemble one another, to that common ancestor.

It is no longer necessary to postulate an ancestor common to these animals and not to the Elasmobranchs. In other words it becomes possible to visualize the separation of the three groups from the one stem.

It may be suggested that already amongst the palaeozoic fishes which, heretofore, we have agreed to regard as Elasmobranchs, it is possible to recognize the beginning of the three groups.

The Acanthodei may well be regarded as presenting an approximation to the primitive Teleostome, whilst the recent Chondrostei would be regarded as presenting a persistent and more advanced remnant of that group.

The Holocephali would be regarded as the most primitive form of the dipnoan stem, the modern representatives of the group being regarded as degenerates in relation to the formation of bone. A parallel case of degeneration in this respect is presented by the Acipenserids on the one hand and the Polyodontids on the other, amongst recent fishes.

Whilst their general morphology indicate that the Holocephali are unequivocably Elasmobranchs, it is still not without significance, especially in view of the geological antiquity of the group, that they possess a quadrato-maxillary arch which is firmly ankylosed to the cranium, for, otherwise, the existence of Elasmobranchs of great antiquity which had autostylic and monimostylic fixation of the arch, indicates that this modification of the manner of attachment of the upper jaw is of still greater antiquity and was initiated and brought almost to the dipno-amphibian condition amongst the elasmobranch fishes.

The concept that the Elasmobranchii, Teleostomi and Dipnoi all arose independently from a more primitive group, at about the same time, explains both the similarities and dissimilarities which these three present amongst themselves, and also their almost equal antiquity.

It may be remarked that not only these three groups but, maybe, also the Arthrodires, Anaspida, Antiarchi and Cephalaspids arose from the same primitive generalized vertebrate group. The Ostracoderms perhaps represent a more primitive form of fish than any of the rest.

The most significant features common to the Dipnoi and the Holocephali, and those which give rise to the suggestion that it is from a form similar to the latter that the former have been evolved, are those features of the muscular anatomy which have already been discussed in this connection, particularly the form of the muscles of mastication and the Csd.2 pars quadrate-hyoidea, and the autostylism of the maxillary arcade.

The fact that the Holocephali are archiprosencephalic, whilst the Dipnoi are neoprosencephalic is a complete barrier to any suggestion that the Dipnoi are directly descended from the Holocephali. It is, however, not without significance that those Elasmobranchs which are regarded as the most primitive of the recent forms, the Notidanidae and the Holocephali, have elongated and slender forebrains, which in their form and simplicity may well have been the " raw material " from which the neoprosencephalon was evolved.

Any dogmatic statement on the subject were little short of foolishness, for the whole subject is almost pure speculation, but it may be said that speculating on the interpretation of the very meagre evidence available leads one to the impression that the Dipnoi are descended from elasmobranchian ancestors which probably presented similarities, if they were not actually allied, to the Holocephali.

The evidence of the cephalic musculature and of the cranial structure, in its bearing on the "dipnoid" ancestry of the Amphibia has already been discussed.

In a recent communication on the problems of vertebrate morphology Professor Graham Kerr (1932, p. 420) writes, "It may be accepted as one of the canons of morphological science that the reliability of its conclusions bears a distinct relation to the breadth of their foundations. Conclusions as to the systematic position of particular vertebrates in the scheme of natural classification, and conclusions as to the evolutionary path along which their bodily structure has progressed towards its present-day condition, must, in order to be reliable, conform to the above mentioned canon. In particular it is essential that due regard be paid to all the available data whether these are provided by the anatomist, the palaeontologist or the embryologist . . . Conclusions resting on evidence provided by a single organ-system should be given only a cautious and provisional acceptance. And if that particular system be the skeletal—which in the case of extinct animals is as a rule alone available—the need for caution is greatly intensified."

Of the systematic position of the Dipnoi he writes (p. 421), "The study of Dipnoan structure during its various stages up to that of the adult leads to two certain conclusions: (1) that the existing Dipnoi constitute a self-contained group quite independent of the Teleostomi, and (2) that the closest affinities of the Dipnoi are with the Amphibia."

This statement is followed by a long list of the evidence on which the conclusions are based.

The present writer had previously (1931) reviewed as completely as was then possible to him those features of the development and adult anatomy of the Dipnoi and Amphibia which yielded evidence of the close affinity of the two groups. The conclusion then arrived at has been further confirmed by the work done on the development and adult condition of the musculature. For that reason the Dipnoi are here treated as primitive amphibians.

In order that this conclusion may have that breadth of foundation which Kerr very justly demands for such, I quote the list he gives and refer to my own list and comments of 1931.

Kerr (1932, p. 421) wrote, "As regards general form of body a young Lepidosiren presents all the general appearance of a Urodele, even showing a slight narrowing of the neck region, practically the only conspicuous distinguishing feature being the limbs, although in the case of Lepidosiren this has become less marked owing to the limb having lost its paddle form and assumed, or, as I would say, reverted to a styliform condition, differing from a pentadactyle limb mainly in the absence of a terminal expansion to form a foot and the absence of concentration of flexibility into localised joints. The lung of the young Dipnoan, with its ventrally placed glottis, the protostylic attachment of the lower jaw to the cranium, the presence of an atrial septum, the tendency of the pocket valves of the conus to revert to the condition of continuous endocardiac ridges, the splitting of the ventral aorta by a horizontal septum into pulmonary and systemic cavities, the presence of a posterior vena cava, the high development of the pallium of the cerebral hemisphere with its incipient cortex, the presence of choanae opening into the buccal cavity, the development of outgrowths from the endolymphatic duct of the otocyst, the development of the external gills agreeing exactly with those of the urodeles, in the larvae of two out of the three genera, and the fact that the cement organs where they are present arise from the ectoderm without any participation by the endoderm, constitute together an assemblage of features which demonstrates irrefutably the close relationship with and the distinctness from the other fishes. There is another feature which would be by itself almost convincing to anyone experienced in Dipnoan study, namely the general agreement in histological structure of the tissues with those of the Urodele Amphibia."

Kesteven wrote (1931, pp. 183–196):

"There are a large number of characters wherein the dipnoans resemble the amphibians more than other fishes do, and, though the contrary has been argued, not one of them is devoid of phylogenetic significance. I give a list of the characters in question and discuss the more important of them.

Adult Features.

The mode of swimming.
Autostylic and monimostylic suspension of the maxillo-mandibular arch.
The fenestration of the nasal roof.
The homology of the supra-orbital bone with the amphibian prefrontal.

The form of the brain.
The possession of internal nares.
The division of the auricle into right and left halves.
Certain features of the arterial system.
Certain features of the venous system.
The possession of true external gills.
The form of the air-bladder and its function.
The structure and position of the glottis.
The possession of an epiglottis.
The possession of a true pelvic girdle.
The mating call.

Embryological and Larval Characters.

The general course of the development.
The development of the external form.
The mode of development of the two-chambered auricle.
The origin of the amphibian characters in the arterial system.
The origin of the amphibian characters in the venous system.
The mode of origin of the cerebral hemispheres.
The early form of the chondrocranium.
The development of the buccal cavity.
The form of the pituitary involution.
The development of the flask glands.
The development of the cement organs.
The history of the palato-quadrate.
The history of certain cranial myotomes and their derived muscles.

" *The mode of swimming.*—' When we consider the *clumsy movements* of the only existing fish retaining this type of fin (*Ceratodus*) . . . ' (Kerr). This is the only reference I can find in literature to the peculiarity of the mode of progression of *Neoceratodus* through the water. Whereas the great majority of fish appear to strike the water with the tail, a few of weak muscular development in the caudal region, and practically all fish when sick and exhausted, appear to undulate through the water much as a snake travels over the ground. In these cases the body flexures are, so far as my observations serve me, but two in number, producing a very wide open S-curve. Now the swimming motions of *Neoceratodus* recall these undulations ; there is a complete absence of the tail ' stroke ', but more than that, the undulations follow one another so that there appears to be a sequence of them, and they recall in a most striking manner the wagging of the ' tadpole's ' tail.

" It is a fact not without significance that this is the mode of swimming of practically all fish larvae. Again I speak from personal observation, for I can find nothing in literature on the matter. The opportunities of a single individual for making such observations are of necessity limited as to the variety of forms observed. The youngest pelagic fish larvae ' wiggle ' through the water ; as they increase in size the number of flexures of the body become less. Growing a little older, the youngster will, when frightened, start off with a jump, wiggle rapidly for a little space and then seem to be propelled through the water with the body held rigid ; closer observation discovers the tail striking the water with a lateral and oblique stroke. The adult starts off with a similar jump, the result of a powerful lateral sweep of the tail, and then continues with a rigid body.

" Since it is characteristic of larval forms, ' wiggling ' or undulatory progression may be regarded as having been the primitive mode of swimming, and there is ample confirmation of this inference in the metameric arrangement of the longitudinal musculature. The interest of these phenomena to our present problem lies in the fact that alone among the compact vertebrata, the adult dipnoans and the amphibians retain an archaic mode of swimming. Is this evidence that in their common ancestry there was none which had developed the tail as *the* organ of swimming ?

" *The autostylic and monimostylic suspension of the maxillo-mandibular arch.*—The mode of attachment of the quadrate to the neurocranium in the dipnoans is essentially and in *Neoceratodus* identically the same as in the amphibians, excepting only the aberrant *Ichthyophis* and *Siphonops*.

Herein the lung-fishes differ, it may be said, fundamentally from the rest of the fishes and resemble the frogs. As this matter will be returned to in the next section it may be left for fuller discussion there.

" *The fenestration of the nasal roof.*—The similarity noted here and the fact that it did not extend to other fish was noted by Bridge. Having described the fenestration, in a footnote he remarks : ' With the exception of the Dipnoi, this curious fenestration of the nasal roof occurs in no other vertebrates except certain Urodele Amphibia, and affords another instance of the many homoplastic modifications which are to be noted in the two groups.' It is a fact that, as he further notes, this fenestration has been observed, but hardly more than indicated, in certain selachians.

" Like several of the other features, which are here passed in review, wherein the lung-fishes resemble the amphibians more than any other of the fishes, this is not advanced as being in itself of phylogenetic significance, but considered in conjunction with all the others it lends weight, and receives weight. It is certainly significant that so ' many homoplastic modifications ' are found in the Dipnoi, whilst none are found in the ganoids which lived side by side with them. Why, one cannot but ask, are the resemblances between the crossopterygians and amphibians regarded as of phylogenetic import, while those between Dipnoi and amphibians must be deemed merely homoplastic ?

" *The homology of the supra-orbital bone with the amphibian prefrontal.*—This is a homology maintained by Bridge, but Kesteven has maintained the homology of the teleostean ectethmoid and the amphibian prefrontal ; if he be correct, this feature is not a peculiarity of the dipnoans.

" *The form of the brain.*—Herein we have a feature which is unquestionably of phylogenetic import. Here, in the Dipnoi, we have the inception of those modifications of the cerebral hemispheres which culminate in the mammalian neopallium. It is quite beyond question that, whereas there is a fundamental similarity in the brains of all other fishes, there is an equally fundamental departure from that type in the dipnoan brain, and that we must turn to the amphibians for a similar brain, and, further, that having so turned, we find the similarity between dipnoan and amphibian brains as complete as that between the rest of the fishes among themselves.

" *The possession of internal nares* may be merely a homoplastic variation, but equally it may have been derived from an ancestor common to the gnathostomes possessing them. As far as my reading serves me, it would appear that the dipnoi are the only animals below the Amphibia so endowed.

" *The division of the auricle into right and left halves.*—That this does not occur in other fish is, of course, not in need of telling, but, together with the form of the lung and the related modifications of the arterial and venous systems, it has been regarded as the result of parallel modification under the drive of similar environment. On the other hand, it is equally well known that in certain of the ganoids, especially *Polpyterus,* the air-bladder acts as a subsidiary respiratory organ (Budgett). There is not wanting evidence that in the Teleostei also the air-bladder acts as a subsidiary respiratory organ (Jobert). Although this is so, it is also a fact that in neither *Amia, Lepidosteus, Polypterus* nor the teleosts investigated by Jobert is there any indication of those modifications of the heart and vascular system which, in the dipnoans, resemble the amphibian arrangement. We have here, then, circumstantial evidence that there was nothing in the mere assumption of a respiratory function by the air-bladder to condition variations in the vascular system after the amphibian pattern ; some other circumstance or factor must be invoked. Since it *did* work in the same manner on both dipnoans and amphibians, it is at least not unreasonable to postulate ' inherited potential '.

" *The arterial system.*—Bridge briefly reviews the arterial systems of the dipnoans as follows : ' As in so many other features of its anatomy, *Neoceratodus* exhibits in its arterial system abundant evidence of the widespreading affinities of the group to which it belongs. In its branchial arterial system *Neoceratodus* presents a singular combination of features which, individually, are characteristic of Amphibia and Elasmobranchs. Special amphibian features may be noted in the origin of the afferent branchial arteries almost simultaneously from the anterior end of the conus arteriosus ; in the origin of a lingual artery from the efferent vessel of the first arch ; and in the derivation on either side of a pulmonary artery from the fourth epibranchial artery. Agreement with Elasmobranchs is to be found in the presence of two efferent branchial vessels in each branchial arch, although the relations of these vessels are more primitive than in most adult Elasmobranchs, inasmuch as the two efferent vessels of the *same* arch unite to form an epibranchial artery; and also in the origin and distribution of the anterior and posterior carotids. Lastly may be mentioned the fact that *Neoceratodus* agrees not only with the Amphibia, but also with those generalized Teleostomi, *Polypterus* and *Amia*, in the mode of origin of the great arteries for the air-bladder' (from the fourth pair of efferent branchial vessels). This last is described as a 'significant resemblance' (p. 338).

" 'Of the two remaining Dipnoi, the arterial system of *Protopterus* is better known than that of *Lepidosiren*, but in both cases further research is needed before a satisfactory comparison can be made with *Neoceratodus* and other Vertebrates. It is evident, nevertheless, that both genera differ from *Neoceratodus* in approximating more closely to the Amphibia than the lower fishes, in so far as the branchial part of the arterial system is concerned.' [*Lepidosteus* in its arterial system is said to offer 'a singularly interesting transition from the Elasmobranch to the Teleost' (*l.c.*, p. 334).]

" In this comparative review Bridge was struck by the dual nature of the similitudes of the arterial system, those wherein it resembled the amphibian on the one hand and those wherein it resembled the elasmobranch on the other; characters new and characters archaic.

" Of the new characters, conceivably, the origin of pulmonary arteries from the fourth pair of efferent branchial vessels may be causally 'post hoc' to the assumption of respiratory function by the air-bladder, but not so the peculiar origin of the lingual artery or the bunching together of the afferent branchial vessels at the anterior end of the conus arteriosus; else why has it not happened in *Polypterus* and *Amia*? In both of these the air-bladder functions as a respiratory organ supplied by pulmonary arteries similar to those of *Neoceratodus*.

" *The venous system.*—Features of this system which may be regarded as pointing to a common ancestor for the dipnoans and the Amphibia are the renal-portal vein, the inferior vena cava and the anterior abdominal vein. Bridge writes: 'Less is known of the venous system of *Protopterus* [than of that of *Neoceratodus*], but it is certain, nevertheless, that it presents a more advanced grade of evolution . . ., and, except for the doubt as to the existence of the anterior abdominal vein, it is essentially similar to that of a Urodele Amphibian in which the right posterior cardinal vein has aborted.' There is no evidence that any of these features is merely a homoplastic variation.

" *The external gills.*—Herein the Dipnoi share a distinction with the Crossopterygii as well as the Amphibia, and we are to assume that the feature was present in their common ancestor, but it is not evidence that the ancestor in question was more crossopterygian than dipnoan in character.

" *The form of the air-bladder and its function.*—Although the air-bladder of *Polypterus* is more complex than that of other ganoids, and to that extent it stands as an intermediate stage between the dipnoans and other fishes, it is not of great phylogenetic significance because it has not associated with it those other modifications of the respiratory and vascular systems which in their totality bring about the striking resemblance between the dipnoans and the amphibians. In the case of *Polypterus* the increase in the complexity of the walls of the air-bladder is a single isolated modification, and, moreover, one that may with justice be regarded as resulting from the influence of the environment; although the resemblance is marked, it well may be an analogous modification and not a homologous one. The development of a glottis might also be regarded as but another part of the same modification. On the other hand, the ventral position of the glottis cannot be so regarded; there are forms with air-bladder almost as complex and a dorsal glottis. It is believed that this position of the glottis is evidence of the existence of closer relationship between the Crossopterygii and the dipnoans than between the former and other ganoids. There is other evidence in support of this belief.

" *The possession of a fibro-cartilaginous epiglottis* by two of the dipnoans is not, in itself, significant, but being superadded to the glottis it is; unless we assume that it was evolved *pari passu* with the glottis, it surely pushes the origin of the glottis further back in time. Does it not indicate that the respiratory function of the air-bladder in the dipnoan ancestry was so well established that already there was diversity in the superadded structure amongst the members of the group?

" *The mating call* of *Neoceratodus* is essentially similar to that of the frogs. I know of no fish with a mating call.

" *The development of the cerebral hemispheres.*—Kerr (1902), when describing the development of the brain of *Lepidosiren*, describes the hemispheres as arising as 'two separate lateral bulgings of the wall of the thalamencephalon' and notes that herein the development of the brain of

Lepidosiren presents features of fundamental importance to a proper understanding of the morphology of the vertebrate brain generally. Professor Kerr returns to this question in his account of the development of *Polypterus* (1907), and his remarks are worthy of quotation in full.

" ' As has been pointed out elsewhere, I hold the view of von Baer, Reichert, Goette and Studnička that the true cerebral hemispheres *as seen in Vertebrata from Dipnoi upwards,* are to be looked upon as primitively paired structures—as lateral evaginations of the wall of the primitive fore-brain, developed doubtless in order to give space for the great increase in the mass of nerve matter in this region correlated with the increasing development of the olfactory organ. I find it difficult to realize how anyone can fail to be convinced that this is the correct view to take of the morphology of the hemispheres, *looking at their mode of development in the Dipnoi and Amphibia* and to their adult relations in the higher forms where that potent disturbing factor—the yolk sac—is present. In *Polypterus* a quite similar increase takes place in the mass of nervous matter forming the sides of the primitive fore-brain, but in this case there is no evagination of the brain wall to form hemispheres, beyond the small pair of olfactory lobes. Room is found for the nervous mass in other ways : (1) the side wall becomes greatly thickened to form the so-called " basal ganglia " ; (2) the thalamencephalon increases much in length and (3) the thickened portion becomes slightly invaginated instead of being evaginated. The nervous material which corresponds with the whole of the hemisphere in the higher forms—including the pallium or mantle—lies in the thickened wall of the thalamencephalon. What is ordinarily termed the pallium in the Crossopterygians is nothing more nor less than the roof of the thalamencephalon, which is of course epithelial here as elsewhere. The conditions in Actinopterygian Ganoids and Teleosts are obviously similar to those in *Polypterus* : what is ordinarily called the pallium in these forms is simply the epithelial roof of the primitive fore-brain, while the so-called basal ganglia are thickened walls including what corresponds to the whole of the hemispheres in higher forms.' Kerr concludes by pointing out that Studnička has already given utterance to exactly the same views '.

" Clearly we are compelled to conclude that the form and mode of development of the cerebral hemispheres are features wherein the Dipnoi differ fundamentally from the fishes and resemble the amphibians.

" Gregory finds that the Dipnoi and Crossopterygii were derived from a common ancestor, and concludes his paragraph thus : ' Nor should the difference in brain structure of these modern forms outweigh the abovementioned resemblance, for there is no evidence that the brains of the Devonian Crossopterygii were any more divergent from each other than were the other parts of the body.'

" With this conclusion I am unable to agree. If our knowledge of the recent dipnoans were confined to fossil skeletal structures only, we would unhesitatingly classify them along with the rest of the dipnoans, and we should find that they all differed from the crossopterygians in one fundamental respect—they are autostylic, while the Crossopterygii are without exception neohyostylic. In the very nature of the problem we can have no direct evidence as to the form of the Devonian brains, but it is surely more likely that the Devonian dipnoans resembled the recent in this respect, having inherited this brain form from an earlier ancestor, from whom also the Amphibia inherited it. If this view be not accepted, we must accept one of two alternatives : (1) the dipnoans and amphibians independently developed this type of brain ; (2) this type of brain was possessed by the common ancestor of the crossopterygians, dipnoans and amphibians, but the crossopterygians reverted to the ichthyic type.

" Neither of these alternatives is acceptable.

" With a view to emphasizing the character of the fore-brain, it is proposed to designate the whole of the fishes ' *Archiprosencephalica* ' and the rest of the Anamniota and the Amniota ' *Neopresencephalica* [*sic*] '.

" *The history of the palato-pterygo-quadrate.*—The significance of the autostylic condition of the Amphibia and of the Dipnoi was discussed by Huxley, Bridge, Dollo, Goodrich, and Luther (1909, 1913, 1914), all of whom agreed that the autostylism was a secondary character. According to Edgeworth, Fürbringer was the first to cast doubts on the correctness of this view. He was ' of the opinion that the primitive condition was one in which the mandibular and hyoid bars articulated separately with the cranium ' (Edgeworth).

" Edgeworth's opinion on the question is as follows : ' The sum of these skeletal phenomena suggests that Selachii, Batoidei and Teleostomi are descended from autostylic and monimostylic ancestors in which there was a pterygo-quadrate united to the chondrocranium at three points. The anterior end was probably fused with the ethmoid region. The middle region was probably fused with the trabecula by a basal process. The otic process was probably fused with the auditory capsule. This condition was lost and a streptostylic one was developed. *Heptanchus* is autostylic, the others amphistylic or hyostylic, whilst various traces are left in developmental phenomena or in adult anatomy of what existed in the past ' (*loc. cit.*, p. 257).

" In the main I find myself in agreement with Fürbringer and Edgeworth, though I cannot agree with the latter that any of the hyostylic elasmobranchs or teleosteans have descended from autostylic ancestors. I would point out that he has himself collected and produced evidence that, with the exception of *Lepidosteus*, *Petromyzon*, and two of the dipnoans, every anamniote, not excluding the Holocephali, sufficiently studied has an originally quite free palato-pterygo-quadrate cartilage (see Kesteven, 1931, Table I, p. 172). This should surely be interpreted to indicate that the primitive condition was a streptostylic condition. I cannot agree, however, that this primitive streptostylism was a hyostylism.

" Dollo wrote of the autostylism of the Dipnoi : ' c'est un pure conséquence de l'adaptation à un régime triturateur très accentué (mylodont), dans un but de consolidation de l'appareil masticatoir.

" ' 1. En premier lieu, la morphologie démontre, certainement, sans réplique, que les Vertébrés autostyliques dérivent de Vertébrés hyostyliques.

" ' Et l'Embryologie confirm cette conclusion.'

" This statement is supported by a quotation from Cope wherein Huxley is stated to have shown that the Batrachia are hyostylic in early stages and become autostylic in later stages of development.

" I have sought in vain for the embryological evidence that gives confirmation to the statement that autostylic vertebrata are derived from hyostylic forms.

" Kerr, too, is among those who believe that the primitive condition was one in which there was an attachment of the mandibular arch posteriorly.

" He states that ' the usually accepted idea of the mandibular arch is to regard it as a half-hoop shaped cartilage resembling the other arches, to which is added a forwardly projecting outgrowth—the palato-pterygoid bar—which forms the primitive upper jaw skeleton.'

" I have not met elsewhere this idea of an *added* palato-quadrate, nor can I find justification for the suggestion in the facts.

" There is, of course, growth in length of the maxillary segment of the first arch as there is growth in length of the mandibular, or as there is growth from the centre both ways in length of the branchial and hyoid arches, but this growth in length of the dorsal segment of the first arch is not fundamentally greater than in the other arches and does not suggest the addition of anything not added in the growth of the other arches.

" In its most primitive form, in the early embryos of elasmobranchs, the dorsal and anterior end of the first arch is almost in contact with the trabecula behind the rudiment of the nasal sac, lying close to the edge of the future mouth. With increase in size of the individual and the increasing gape, the upper and lower segments of the arch are lengthened proportionately, becoming segmented one from the other in the middle of the length of the arch just as do the other arches.

" As the upper segment grows forward it retains its close relation to the trabecula, and in some cases becomes temporarily continuous therewith, but it should be noted that this point of temporary continuity, or articulation, is not back close to the posterior end of the trabecula near the otic capsule, but anteriorly near the nasal capsule, either in front of, beneath, or behind it.

" The hinder end of the upper segment of this first arch does not become approximated to the skull base, but becomes attached to the lower end of the upper half of the second arch, hyomandibular.

" Turning now to the amphibians, it is clearly the forward end of the arch which so commonly becomes attached to and continuous with the lateral expansion from the forward end of the trabecula immediately behind the nasal capsule, whilst it is from the hinder end that are produced those processes, ascending, otic, and basal, whereby the posterior end of the bar becomes knit to, and continuous with, the trabecula, otic capsule, and parachordal cartilages.

" This hinder end is the morphological centre of the original arch, and is the point of fission into upper and lower segments ; it is not, as stated by Kerr, ' the dorsal portion of the original arch ' (*loc. cit.*, p. 320).

" Now, of all the points of cartilaginous continuity, temporary or permanent, which have been noted between the rudiment of the mandibular arch and the neurocranium, this anterior one between it and the trabecula in the neighbourhood of the nasal capsule is the only one which has been found to occur in every one of the major divisions of the Anamniota, hence I have been led to believe that it is the most primitive.

" In 1884 Cope described the structure of the skull of *Didymodus* and in the general discussion arising out of this study he expressed it as his opinion that the Holocephali were the most primitive of the elasmobranchs and traces thence the evolution of all the other fishes, the dipnoans and the amphibians. In the course of this discussion he quite plainly indicates that he regards the fixed upper jaw of the Holocephali as the primitive condition, for he says that these forms have not yet ' differentiated a suspensorium '.

" Portion of Kingsley's comment hereon is as follows : ' In this there are several important errors. In the first place the assumption that the monimostylic condition is the more primitive is at variance with every known fact relating to the comparative anatomy and embryology of the visceral arches.'

" I believe that there is no room for doubt that the maxillo-mandibular apparatus has been evolved from a visceral arch essentially similar to the arches behind it, and similar to the branchial arches as we see them to-day. If this be so it is surely unreasonable to assume that the primitive jaw was one in which the mandibular segment was in structural continuity fore and aft with the neural cranium. There must have been transitional stages between the original arch and the attached arch ; there was surely the slightly modified, the more modified, and the completely metamorphosed arch.

" If an originally ' floating ' visceral arch has become structurally continuous with the cranium at two points, it is not unreasonable to assume that the nearest point of contact was the first to be converted to the continuous state ; undoubtedly the dorsal end was the nearest. Thus far I have the support of Kerr, but we differ as to what shall be interpreted as representing the original dorsal end of the arch in the amphibians.

" Again, if the maxillo-mandibular apparatus has evolved from a visceral arch by the development and improvement of a joint at the point of division into dorsal and ventral halves, as a first or early step, then surely, as the first arch must have been attached to the second by muscular and fibrous tissue, the evolution of the protohyostylic condition should have been possible directly, without the intervention of a preliminary autostylic condition. Indeed had we but a few more examples of the incorporation of a portion of the hyoid arch into the basal attachment of the mandibular arch, as in *Neoceratodus*, we should have to assume that this was the primitive method of suspension. It is only the complete absence of any indication of the inclusion of any separate cartilages in the processes of attachment of the autostylic forms that justifies the assumption that this type of suspension has also been evolved directly from a primitive gnathostome as one of the original modes of fixation of the upper jaw posteriorly.

" In the Teleostei we see the development of a metapterygoid process that may well be regarded as an incomplete attempt at autostylism, and, indeed, we have no evidence that it was not in this way, without any structural continuity between the maxillary and hyomandibular segments, that autostylism was developed.

" In the present state of our knowledge, the final decision as to whether the greater probability is that the autostylic is an original or secondary mode of fixation of the maxillo-mandibular joint, must be by the personal equation. I am of the opinion that it has been evolved from a primitive suspension from the second arch, without that arch becoming modified to act as the suspensorium of the first.

" However, whatever be the decision on this point, Edgeworth has left us little room for doubt that the autostylism of the Dipnoi and amphibians is a feature of fundamental importance in which these creatures differ from the fishes. This he has proven not only by his clear demonstration of the essential similarity and identity of the three processes of attachment, but also by his demonstration of the modification in the mode of development of the muscles of mastication in the amphibians and dipnoans on the one hand and the fishes on the other. His conclusion quoted above (p. 181) is fully justified by his evidence.

" Though his main contention, as just stated, appears completely justified by his evidence, it is not so clear that he is correct in regarding the basal attachment as the most primitive, and the *processus ascendens* as being ' probably a later phylogenetic development '.

" It must be pointed out that throughout the Amphibia, the *processus ascendens* is the first to develop, and that, with the exception of *Siphonops* and *Ichthyophis,* it presents identical relations throughout the class. On the other hand the basal process develops later, becomes attached later and presents varying relations to the neural cranium, as to its point of attachment, and to the nerves, and finally these variations show absolutely no relation, in their occurrence, to the natural grouping of the creatures themselves. (See Tables II, III and IV, Kesteven, 1931.)

" Our knowledge of the development of the processes of attachment in the Dipnoi is incomplete ; unless the development in *Lepidosiren* is similar to that of *Ceratodus* it would seem that there are three different modes of development. Edgeworth states that in *Neoceratodus* the palato-pterygoid arises as an independent structure, and subsequently becomes attached by the same three processes as are found throughout the Amphibia. Agar has shown that in *Protopterus* the first chondrified portion is found as a spur from the trabecula behind the floor of the gasserian recess. His description and illustration of his findings in *Lepidosiren* indicate that it develops quite otherwise in this form, for, although he speaks of a basal attachment, it appears quite certain that in the earliest stage he illustrates the only attachment is by the *processus oticus,* and that a *processus ascendens* is present in the next stage.

" The condition in *Protopterus* is closely paralleled in *Petromyzon,* and, although I now think that one can place but little confidence in phylogenetic deductions based on the conditions in the cyclostomes, it is not entirely without significance that, as I have previously pointed out, the so-called basal attachment of *Petromyzon* is in truth by a *processus ascendens,* as judged by its position and relation to the nerves.

" Turning now to the evidence for an attachment by a *processus basalis* in the fishes, this evidence is very scanty, and fails to convince that it was of general occurrence in ancestral forms.

" In *Acanthias* Sewertzoff discovered that, prior to the establishment of the basal joint, there was continuity of the so-called basal process with the trabecula. This basal joint is, however, so far forward that it can hardly be homologized with the basal joint of the amphibians and the dipnoans.

" In *Lepidosteus* Veit found that the articulation of the maxillary rudiment with the basipterygoid process is preceded by a continuity in embryonic cartilage. In this case there appears no reason to cavil at the identification of the joint with that in the Amphibia.

" Unless the basal contact in *Gymnarchus* described by Assheton—and probably present in others of the Mormyridae (if one may judge from their adult structure as described by Ridewood) and in the Symbranchidae—can be regarded as homologous with the basal attachment of the amphibians, we have but one single instance of such a continuity among the fishes.

" The evidence for the homology of the spiracular cartilage and the otic process is more convincing. Personally, I incline to the opinion that the metapterygoid process of the Teleostei is also homologous with the spiracular cartilage, and therefore with the *processus oticus* of the dipnoans and the amphibians.

" It would seem that W. K. Parker and Bettany had the same inclination, for in the figures illustrating the chapters on the development of the Elasmobranch skull they consistently indicate the spiracular cartilage with the letters ' M.Pt.', and in the interpretation of the lettering these letters are translated ' metapterygoid ' (Parker and Bettany).

" It therefore appears that either the attachment by the ascending process, or that by the *processus oticus,* is the most primitive of the three attachments of the amphibian autostylism posteriorly, but the evidence does not permit us to decide in favour of either.

" It would be of interest to learn whether the evidence of Edgeworth's wonderful series of *Neoceratodus* is such that his oto-quadrate cannot be regarded as a spiracular cartilage. Neither he, Allis, de Beer nor Schmalhausen appear to have considered the little pellicle of cartilage in this light.

" *The development of the vascular and respiratory systems.*—Since writing the earlier part of this section—the Dipnoi and the Amphibia—I have received a copy of Kellicott's paper. From that I learn that both he and Semon have expressed views relative to the evolution of the Dipnoi similar to my own, though they did not regard the Dipnoi as primitive amphibians.

" To my mind Kellicott's thorough and detailed work should have established the views of himself and Semon, and the scant attention bestowed upon his work by subsequent writers on the evolution of the Tetrapods, is a distinct reflection upon their ability to appreciate work in other branches of comparative anatomy and embryology than their own specialties.

" This review, of the features of anatomy and phenomena of development in the Anamniota which bear upon the evolution of the various groups, would be incomplete without a summary of the features of importance under the above heading, but for me to undertake such a review when Kellicott has presented the facts so well and briefly in his ' General Conclusions ' would be foolishness. I therefore quote that section from his work almost at length.

" ' It was stated in the Introduction that the immediate object of this investigation was to test embryologically the evidence, based upon anatomical considerations, for certain supposedly Elasmobranch and Amphibian characters seen in the adult vascular system of *Ceratodus*. Throughout the course of this paper, as the development of the vascular and respiratory systems has been reviewed, the embryological evidence has necessitated continual subtraction from the list of real Elasmobranch resemblances and continual addition to the list of Amphibian characters. For instance, the Elasmobranch similarities seen in the arrangement and distribution of the carotid arteries and the connection between the anterior carotid artery and the vessels of the hyoid arch, the double efferent branchial artery, the hyoidean gill, all prove to be in the nature of parallelisms and are preceded by Ganoid or Amphibian arrangements ; the arrangement of the veins of the head and of the lateral cutaneous veins resembles as closely the Amphibian as the Elasmobranch. On the other hand the Amphibian resemblances in the adult system all have been confirmed—the origin of the afferent branchial arteries, the arrangement of the epibranchial arteries, the relations of the lingual artery, the abdominal vein, the renal-portal vein, are typically Amphibian, and, excepting in the Cyclostomes, it is only in the Amphibian group (*Necturus*) that there is a continuity between the cardinal veins and the branches of the caudal vein, comparable with the arrangement in *Ceratodus*.

" ' Furthermore, embryologically the similarities to the Elasmobranchs were only in such characters as are common also to the Amphibia, for instance, the method of formation of the primitive aortic arch and the arrangement of the lateral cutaneous veins. But the Amphibian resemblances are extremely numerous—the method of mesoblast formation, the hypoblastic nature of the cardiac endothelium and the details of its formation, the development of the thyroid body, nearly all of the numerous details of the formation and development of the heart, the arrangement of the visceral arches, the nature of the gill-pouches and gills, the presence of elongate " larval gills ", the arrangement of the afferent branchial arteries and their relations to the conus, the early development of the branchial arteries, the formation and relations of the hyomandibular artery, the development of the lingual artery, the formation and relations of the carotid arteries throughout a long period, the relations between the posterior cardinal veins and the pronephros, the later condition of the posterior trunk veins, the development of the inferior jugular veins, the development of the abdominal vein, the arrangement of the vitello-intestinal vein and the formation from it of the hepatic and subintestinal veins, the formation of the hepatic-portal vein and its relations with the subintestinal vein, the development of the lung—in all of these respects, to enumerate only the more important, there is close, usually exact correspondence between *Ceratodus* and the Amphibia.

" ' Characters more or less intermediate between Elasmobranch and Amphibian arrangements are the number of gill pouches, the development of the efferent branchial arteries which resembles the Ganoid rather than the Amphibian, the arrangement of the interrenal veins, and the frequent anastomoses between the posterior cardinal veins . . .

" ' The immediate object of this investigation as stated above is, of course, really a part of the larger question of the relationships of the Dipnoi. It is unwise to attempt exact or complete statements in the entire absence of knowledge concerning the development of the Crossopterygii, especially since such knowledge is soon to be expected, but it is absolutely impossible to believe that the Amphibian resemblances seen in *Ceratodus* in the development of the vascular, respiratory and urinogenital systems, as well as throughout the early processes of development, are in the nature of parallelisms. In the light of their embryology, it is impossible to believe that the Dipnoi and the Amphibia are not closely related and that they have not travelled for a time along the same path at some period during their history.'

" When to this striking evidence are added the facts that these two groups are eupulmonate, autostylic, and neoprosencephalic, differing in all three respects fundamentally from the rest of the Anamniota, it may be fairly claimed that Kellicott's conclusion is as completely proven as circumstantial evidence *can* prove it.

" Finally, it is also contended that all the recent work on the development of the Crossopterygii and Dipnoi has indicated that the latter are more nearly akin to the Amphibia than to the former, and that this fact should be admitted in classifications by assigning the Dipnoi a place among the Amphibia.*

"The Evolution of the Cheiropterygium.

" The evolution of the cheiropterygium is so wrapped in obscurity that Kingsley's summary—' No known facts of either embryology or palaeontology throw any certain light on the matter '—is still very true. The latest survey of the question that I am acquainted with is that of Gregory, who briefly reviews the previous work.

" It must be admitted that Gregory is correct in his statement that : ' The endoskeleton of the pectoral limb of the Rhipidistian offers the only remote approach to the tetrapod type hitherto known among recent or fossil types ' ; and whilst one notes that he is in agreement with Patten, Broom, and Watson as to which elements shall be regarded as homologous with humerus, radius, and ulna, one also notes his choice of the word ' remote ' and feels that therein he was wise.

" Gregory further expresses the opinion that the basal and central line of pieces in the fin of *Eusthenopteron* are probably homologous with the mesaxial series of *Neoceratodus*, and no reason is apparent why one should not agree with this suggestion.

" There is other evidence that the dipnoan fin was the starting point for the evolution of the tetrapod limbs, which, so far as I am aware, has not heretofore been advanced. I find that among the large number of fins which I have been able to dissect, the dipnoan fin alone is provided with a segmented musculature, the segments of which are placed along the length of the fin, on both sides thereof, so that the segments can be flexed independently.

" This extension of the muscle along the length of the fin was probably the first step in the development of the effectually jointed limb ; certainly such an extension must have preceded the modification of the skeleton, and in all probability it caused the modifications. This excursion of the muscles along the axis of the fin was a more important factor in the evolution of the limb than the mere development of a fleshy muscular lobe at its place of origin from the body. The muscles of this basal lobe could but actuate the fin as a whole, and condition the more perfect development of the single joint. The fleshy lobe of the rhipidistian fishes was no greater than, if indeed it was as large as those of such typical forms as *Parascyllium collare* amongst the sharks and *Periophthalmus barbatus* amongst the Teleostei.

" The evidence is, indeed, so scanty that theorizing on the evolution of the tetrapod limbs amounts to little more than speculation, but the following summary is at least not unreasonable.

" The primitive limb was probably an archipterygium as defined by Gegenbauer, and it may have been derived from an external gill as postulated by Kerr. The concentration of muscle fibres at the base of the archipterygium caused the shortening and broadening of the structure with the ultimate development of the various types of ichthyopterygia. The development of muscular tissue along the length of the archipterygium and its segmental arrangement led to the improvement of the joints between the skeletal units, and to the development of the cheiropterygium.

" Though it may be that the homologies of the proximal pieces of the fin of *Eusthenopteron* are as suggested by Gregory and others, it is equally probable that the fin presents an early stage in the transition from the form with a single piece next the proximal element and those with three or more which are typical of the recent fishes."

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* Three other features may now be added to this review.

The Squamosal bone of the Dipnoi, and in particular that of *Neoceratodus*, is so essentially similar, in all its relations to the chondrocranium and to the muscles of mastication, to that of such anuran forms as *Bufo* and *Calyptocephalus* that it is quite impossible to deny their complete homology.

Recently Dakin has shown that the osmotic index of the body fluids of *Neoceratodus* is that of an amphibian, and, moreover, that the striking difference between this index and that of the fishes is due to the concentration of urea in the fishes and its absence from the body fluids of the Dipnoans and of the Amphibians (Dakin, 1931).

Finally Dr. Bancroft has demonstrated that the young of *Neoceratodus* cannot be persuaded to live unless they be grown in an aquarium in which a shelving sandy " beach " is provided for them, so that they may rest with the mouth out of water just as the frog tadpole does.

2. The Evidence of their Cephalic Muscles on the Phylogeny of the Amphibia.

Since there are two conflicting views as to the origin of the Amphibia, it will be necessary to compare their musculature with that of the Teleosts and with that of the Dipnoi.

At the outset we cannot fail to observe that there is a very great difference in the ventral constrictors of the mandibular and hyoid segments of the amphibians and teleosts. True, in both there are Mm. submentalis and intermandibularis, but here the resemblance ceases. In the teleosts the posterior portion of the mandibular constrictor sheet has coalesced with the anterior portion of the hyoid sheet to form a protractor hyoidei, a muscle which is not developed in the amphibians.

It is a fact that in such a form as Pseudorriton the cerato-hyoideus externus and cerato-hyoideus anterior together simulate the protractor hyoidei of the teleosts, and that even the former muscle alone bears some resemblance to it, and it may be suggested with some justification that what we see is the protractor hyoidei derived from that anterior portion which, in the teleosts, is derived from the mandibular constrictor.

This resemblance is probably a parallelism superimposed on a partial homology. The essential fact to realize is that there is no evidence in the amphibian ontogeny of the suppression of a portion of the Csv.1. In the Selachians the Csv.1 develops as a continuous sheet. In the teleosts the sheet is divided to develop a submentalis, an intermandibularis and a portion of the protractor hyoidei (see p. 76-77).

In the Amphibians the sheet divides to develop a submentalis and an intermandibularis. Such a differentiation of the mandibular sheet into an anterior part, composed of fibres continuous from side to side—the submentalis—and a posterior part, composed of fibres which extend to the mid-line only—the intermandibularis—is already initiated in certain of the selachians and this division of the sheet is the only division found throughout the whole of the vertebrata, excepting only in the teleosts. It should be understood that the treatment of the mandibular sheet of the Selachians earlier in this work (p. 21), as consisting of a pars intermandibularis and a pars extramandibularis, is not based upon its development, but only on its adult relation to the mandible.

Therefore, to regard the cerato-hyoideus externus of the amphibians as being derived from the protractor hyoidei of the teleosts by the loss of the mandibular component, is to assume a return to a more primitive condition, whereas there is no reason to believe it could not have evolved directly.

This becomes the more apparent when we study and compare the ventral hyoid muscles in the two groups.

It will be remembered that the hyoid constrictor sheet in the teleosts is highly modified to form the complex hyohyoideus and that in this complex muscle it was not possible even to suggest what might be the boundaries between the superficial and deep constrictors which had contributed to its make-up.

In the Amphibians the superficial and deep constrictors are quite clearly differentiated, completely separate muscles, and it is probable that one is able to recognize the derivatives of the partes arcuata and interinscriptionalis of the elasmobranch sheet. Once more it is necessary to insist that the division of the Csv.2 of the elasmobranch into these parts was an anatomical convenience and not a developmental necessity, so that when we recognize the Csv.2 in an almost unaltered condition in the amphibians that is, perhaps, more than might have been expected, and surely indicates that its form in the Amphibia has been derived direct from the elasmobranch type without the intervention of a teleost stage.

The antero-posterior and laterad obliquity of the cerato-hyoideus externus which is responsible for the similarity of the muscle to the hyohyoideus of the teleosts, is really characteristic of the elasmobranch interhyoideus, and its attachment to the mandible close to the symphysis (per medium of the cerato-hyoideus anterior) is foreshadowed by the interhyoideus in the Holocephali. Here again there is no reason to suppose that the muscle as we find it in the amphibians could not have evolved direct from the Elasmobranchian condition.

Actually there is, then, no shadow of any teleostean influence to be found in the anatomy and/or development of these ventral constrictors.

Examination of the same muscles in the Dipnoi shows that they differ from those of the amphibians only in being more primitive. To argue that the muscles in the dipnoans are degenerate would also involve one in the assumption that their degeneration had taken the form of a return to the primitive elasmobranchian condition ; the resemblance to that simple form is undeniable and inescapable and, moreover, there is here even less indication of any teleostean influence.

Having dissected, and otherwise studied, the several forms, I have to record that the arrangement of these muscles in the Dipnoi appeals to me as being very definitely the connecting link between the amphibians and the Holocephali.

The mandibular adductor muscles of *Neoceratodus* bear a striking resemblance to those of the Holocephali. It seems to be beyond question that these were, in both cases, derived directly from the elasmobranchian condition. There is little trace of that division and specialization of these muscles so characteristic of the teleosts.

It is not impossible that the little retractores anguli oris, which have been described in the two dipneumonous forms, are comparable with that portion of the temporalis which acts as a retractor anguli oris in the teleosts.

In the amphibians the depressor labii superioris of the anuran tadpole appears very certainly to be homologous with that portion of the temporalis which, in the teleosts, acts in like manner to depress the labial bones.

This, however, is not evidence of a teleost influence, but rather that the utilization of the labial cartilages as a framework in connection with oral prehension had already taken place in the common ancestor of both groups. Clearly they are so used in the Holocephali.

Apart from this similarity, there is no trace of any evidence that the muscles of mastication of the amphibians have evolved from a teleostoman type. Their specialization is sui generis and not moulded on the teleostoman.

The depressor mandibulae is very definitely foreshadowed in the Holocephali, where its origin from the dorsal part of the hyoid superficial constrictor is beyond question. Here again we find no trace of any teleostean influence in the evolution of the muscle. There is nothing comparable to the depressor mandibulae in any teleost that has as yet been described.

Amongst the intrinsic branchial muscles we certainly find that the ventral branchial muscles—subarcualia obliqui, transversi and recti—are essentially similar to these muscles in the teleosts and have no parallel amongst the muscles of the branchial segments in the elasmobranchs. On the other hand, the musculi marginales of the Dipnoi and Amphibia are derived from the interbranchial muscles of the elasmobranchs, and these muscles are not developed in any teleost. It is difficult to understand how these muscles could have reappeared in the amphibians if they are descended from teleost ancestors, for the muscles are very completely discharged from the whole of the developmental history of the teleosts. It will be remembered that in these forms the branchial muscle plates split into dorsal and ventral portions and that there remains no connecting strand between the two halves. To assume that in the descendants of such forms this splitting should have been abandoned and the older method of developing a muscle from the middle segment returned to, is an assumption that evolutionary roads may be travelled backwards as well as forward, an assumption entirely contrary to the great mass of the evidence available ; so much so that it is almost repugnant to the modern morphologist. Moreover, the assumption would be invoked on behalf of relatively unimportant evanescent muscles.

The amphibians also differ from the teleosts in the complete absence of the epiarcual muscles ; herein, of course, they also differ from the elasmobranchs.

The conflicting evidence of the branchial muscles is probably to be explained by the fact that both the teleosts and amphibians are descendants of a form in which the dorsal branchial muscles, the interbranchial muscles, and the ventral branchial muscles were all developed. The teleosts lost both the dorsal and interbranchial, the amphibians lost only the dorsal.

If my identification of the superficial dorsal constrictors of the amphibians is correct, then this is a further point in which they differ from the teleosts ; if, however, these should prove to be in reality the levatores arcuum branchialium, as has been said in the past, then the resemblance here is to both the teleosts and the elasmobranchs.

Generally the conclusion that seems forced upon us by a comparative study of the cephalic muscles of the teleosts, dipnoans and amphibians is that there is no evidence either in their development or adult anatomy to indicate a teleostean ancestor for the Amphibia.

On the evidence before us, we are therefore justified in stating that the Dipnoi were probably derived directly from some elasmobranchian, or pre-elasmobranchian ancestor without any direct inheritance of teleostome characters, except such as were present in a more ancient common ancestor. And we may further state that the evidence points to the Dipnoi as presenting the most primitive definitely Amphibian form known, and that it probably approximates to the direct ancestor of the known Amphibia.

These conclusions, however, do not complete a review of the probable origin of the Amphibia, for the Embolomerous skull is so different from that of the rest of the class that one is practically forced to the conclusion that there are, amongst the fossil and recent forms, representatives of three very distinct tribes—the Embolomeri, the Dipnoi, and the remainder of the class.

Unfortunately, we are denied any knowledge of the Embolomeri except of their skeleton. The skull, however, presents differences which are here believed to be fundamental, and these we proceed to discuss.

3. The Serial Homology of Certain Bones in the Skulls of Amphibia and their Bearing on the Evolution of the Class.

The Amphibian skull presents itself in two very distinct forms. On the one hand, there are the skulls with expanded pterygoid bones related to the basis cranii, and, in all probability, developed in that relation in all the forms in which they are found, certainly as developed in the Dipnoi. Skulls of this type are found in the Embolomeri and the Dipnoi.

On the other hand, there are the skulls with a pterygoid bone completely, or almost completely, divorced from the basis cranii, and in all the recent forms, if not also in all the fossil forms, developed in relation to the pterygoid process of the quadrate, and only gaining such relation to the basis cranii as it possesses by later, secondary, growth.

It is significant that the Embolomeri, which present the former type of palate in its highest development, are remarkably similar to the Cotylosaurian Reptiles, and have been regarded by all who have studied them as probably presenting the amphibian type from which the Reptilia generally have evolved.

It is submitted that the two very distinct types of amphibian skulls are at once understandable if they be regarded as being derived by two different lines of evolution from a condition such as is presented by the Dipnoi.

On the one hand, there evolved the primitive " fish " type of palate with (1) a broad parasphenoid, (2) poor ossification of the basisphenoid region of the basis cranii, (3) a so-called pterygoid which presents three rami, bounds the via masticatoria medially and anteriorly, is developed in relation to the pterygoid process of the quadrate and gains such relation to the basis cranii as it presents by later, secondary, growth.

On the other hand, there evolved the more advanced " tetrapod " type of palate with (1) the parasphenoid reduced to a " vomerine " splint, (2) good ossification of the basisphenoid region of the basis cranii, (3) the pterygoid bone, expanded and contributing largely to the formation of the palate, occupying much of the situation of the broad parasphenoid of the more primitive type of palate, meeting its fellow in a more or less lengthy median suture, suturing with the median edges of the palatine and os transversum, bounding the via masticatoria medially and developed, in all probability, in relation to the basis cranii.

These two types of amphibian palate are represented by the Embolomeri on the one hand and the rest of the Amphibia on the other, with the Dipnoi as a connecting link between them.

It must be quite obvious that certain statements as to the situation, relations, and development of the " pterygoid " bone in the two types of palate suggest that they are not homologous.

At the outset one may say with confidence that the bone which has been designated pterygoid in the whole of the Amphibians, excepting the Dipnoi and the Embolomeri, is the same, and that the bone is homologous throughout. Its development has been observed in a sufficiently representative range of genera to permit one to assert this with confidence.

Comparison of the bones in a representative range of fossil palates serves to confirm the homology throughout the fossil forms.

On the other hand, one is also unable to deny the complete homology, one with the other, of the pterygoid bones of the Embolomeri and the Dipnoi.

When, however, the pterygoid bones of these last are compared with those of the other amphibian palates it becomes almost obvious that the bone in the two groups is not the same. The development of that of the Dipnoi has already been discussed (p. 201) and it appears entirely reasonable to assume that the pterygoid of the Embolomeri is developed in similar manner in relation to the ethmoid and sphenoid regions of the basis cranii. It is probable that the meeting of the pterygoids ventral to the " vomerine " parasphenoid is the result of secondary growth, and that like those of the Dipnoi they appeared first on each side of the much reduced parasphenoid.

To the present writer it seems probable that these median pterygoids of the " tetrapod " type have arisen by the division of the primitive parasphenoid into three parts. The Dipnoi are believed to represent a primitive condition in this division. The subotic wings of the bone are believed to have developed from their own centres of ossification, whilst the median portion has been developed from a third centre. It is for this reason that the parasphenoid has been so constantly designated the synpterygoid throughout this work.

It is further believed that the so-called pterygoids of the great majority of the amphibian palates are not homologous with these but are homologous with the os transversum of the reptilia. But, it will be at once asked, are not those bones already present in the palates of certain of the Stegocephalians, and if so how can it be that these forms possess two ossa transversa ?

An examination of the stegocephalian palates in question, and a comparison of them with other closely related palates discovers that this os transversum is only present in quite a few of the stegocephalians. The bone is said to be present in *Eryops, Capitosaurus* and *Metoposaurus*, may be present in *Rhinesuchus* and *Trematosaurus*, and is certainly absent in *Batrachosuchus, Cyclotosaurus* and *Branchiosaurus*. It is apparently also absent from the palate of *Archegosaurus*. The os transversum is apparently present in *Orthosaurus*, but its shape has been differently determined in each of the three descriptions available to me. Watson says that in the closely allied *Pteroplax* there is no os transversum, " the palatine extending back to the end of the maxilla ".

Clearly, if there be a bone in the lateral portion of the palate behind the palatine in any of the stegocephalian palates, it cannot be regarded as an established component of the palate, but as an adventitious element. Watson has suggested that there is evidence that in *Orthosaurus* this variability is carried still further by the division of the bone into two.

In order that a proper understanding of the os transversum be arrived at, it becomes necessary at this stage to anticipate later work and examine the bone in the reptilian palate.

At the outset it is found that the bone is certainly absent from most of these most primitive reptiles, the Cotylosauria. It is " possibly " present in *Seymouria* and *Pareiasaurus* alone amongst the members of this group.

The bone is also absent from the palate of the Testudinata and from that of the Ichthyosauria.

It is present in all other reptilian palates.

Though at first sight the transpalatine bone of such a reptile as *Thaumatosaurus* or *Amphistraena* bears a close resemblance to the bone so named in some of the Stegocephalians, a closer examination reveals that here, as in the great majority of the reptiles, the os transversum sutures with the lateral edge of the pterygoid well behind its anterior end, whereas in all the stegocephalians the os transversum lies in contact with the anterior end of the pterygoid and, further, it will be observed that the pterygoid lies to the inner side of the subocular palatal vacuity where it sutures with the os transversum in the reptilian palate, but to its outer side in the Stegocephalians.

It is, of course, quite impossible to prove this contention, but it is believed that the explanation of the seeming discontinuity and apparent variability lies in the fact that the os transversum of the reptilian palate is really the homologue of the anterior portion of the pterygoid bone of the generality of the Amphibia.

The so-called os transversum of the Stegocephalians might be designated post-palatine, if this belief be correct.

The evidence on which this belief rests may be briefly reviewed :

(1) The primitive condition of the covering of the basis cranii was by an expanded parasphenoid, which covered the whole of the basis of the cavum cranii and extended forward below the sphenoid and ethmoid regions.

(2) The development of endochondral ossification in the basisphenoid region was accompanied by a reduction of the parasphenoid bone ; probably this was a causal correlation.

(3) The reduction of the parasphenoid is associated with the development of pterygoid bones which, in all the most primitive reptiles, the Embolomeri and the Dipnoi, occupy the situation of the lateral portions of the primitive parasphenoid posteriorly and the whole of the anterior portion, excepting only the narrow vomerine splint-like remnant.

(4) The primitive form of the pterygoid bone is an expanded lamina which meets its fellow in the mid-line.

(5) Throughout the Amphibia, excluding only Embolomeri and Dipnoi, the so-called pterygoid articulates with the subotic region of the basis cranii, in the neighbourhood of the basal root of the quadrate.

(6) Throughout the Reptilia and in the Embolomeri the pterygoid articulates with the basisphenoid and commonly also with the subotic portion of the base of the cranium. The articulation with the basisphenoid is the only relation to the basis cranii which is constant.

(7) Throughout the whole of the Amphibia, excepting only the Embolomeri, the so-called pterygoids are widely separated anteriorly and lie laterally to the subocular palatal vacuity.

(8) Throughout the whole of the Reptilia and in the Embolomeri the pterygoid bones meet at, or are very closely approximated to, the mid-line anteriorly and lie medially to the subocular palatal vacuity or are so extensive as to close that vacuity.

(9) The primitive pterygoid bone exhibited by the Dipnoi is developed, like the parasphenoid bone, as a membrane bone on the ventral surface of the cavum cranii.

When to these facts there is added the sum of those many features which indicate that the Dipnoi are primitive, the most primitive Amphibians known, and that they probably approximate very closely to the common ancestor of the whole of the Amphibia, it appears reasonable to conclude that the final total justifies the belief that the pterygoid bones of the Reptilia are derived from the primitive parasphenoid and are not homologous with the pterygoid bones of the Amphibia, excepting only those of the Dipnoi and the Embolomeri.

The recognition of the os transversum of the reptilian palate as the homologue of the pterygoid of the amphibian rests largely on the acceptance of the last belief.

If the reptilian pterygoid really represents, and is to that extent homologous with, the lateral part of the parasphenoid of the amphibian palate, then the os transversum is at once recognizable as the anterior arm of the typical amphibian pterygoid. Throughout the whole of the Amphibia, excepting only the Embolomeri and the Dipnoi, this pterygoid bone acts as the bony boundary of the via masticatoria on its inner and anterior margins, and serves also as a strut maintaining in place the maxillary arcade at the anterior limit of that space. It will be at once granted that such a limitation of the " via " and such a strut to the arcade are mechanical necessities, and that, once developed, the structure would be maintained. The anterior boundary of the via masticatoria is the posterior boundary of the orbit. In the absence of a rigid bar between the two, contraction of the anterior muscles of mastication would result in their displacing the structures in the orbit forward or compressing them against the anterior boundary of the orbit.

In the apode Amphibia we observe the so-called pterygoid bone reduced to the reptilian (os transversum) condition, a short bar extending from the posterior end of the palatine mediad and caudad to articulate with the lateral edge of the parasphenoid and closing the via masticatoria anteriorly. In this form the articulation with the basis cranii in the region of the basal root of the quadrate has been lost by reason of the fact that the parasphenoid has extended laterally beyond the limit of the basis of the cavum, and the relation to the basal root of the quadrate has also been lost. On the other hand, the bone is closely related to a persistent, ossified, pterygoid process of the quadrate, which lies above its posterior end articulating with the same narrow subocular flange of the parasphenoid.

It is unquestionable that, were the parasphenoid of the Apoda divided into right and left halves we would quite unanimously agree that the so-called pterygoid should be regarded as an os transversum ; all its relations to bony and soft structures would be as in the reptiles.

It would appear that the strong development of the muscles of mastication had necessitated greater space, and that this had been obtained by the forward transportation of the anterior boundary of the via masticatoria, whilst the development of a lateral subocular flange of the parasphenoid had divorced the inner end of that bar from the basis cranii.

In similar manner, it is believed, the splitting of the parasphenoid bone into right and left halves and their separation from the basis cranii has determined the lateral migration of the os transversum in the reptilia, whilst the development of massive muscles of mastication has forced the bone forward.

It is submitted on behalf of the arguments just advanced, that they do not run contra to any evidence of palaeontology, embryology, osteology, or myology, and that they provide an explanation quite in harmony with both phylogeny and teleology.

Since, however, it is not contended that the homologies here suggested are proven beyond question by the facts adduced in evidence, it is desirable to examine briefly those facts which would appear to contradict the conclusions arrived at.

Probably the, apparently, most contradictory fact is that in some reptiles the pterygoid bone develops in relation to the pterygoid process of the quadrate in a manner similar to the development of the pterygoid of the Amphibia.

A critical examination of the conditions of this relation throughout the Sauropsida reveals that the resemblance is probably more apparent than real. As a matter of fact, the association of the pterygoid process and the pterygoid bone is not of general occurrence in the group ; it is actually the exception and not the rule. There is no such association in any of the Aves at all, and there is no doubt as to the complete homology of the bone in the two subclasses.

In the Crocodilia the pterygoid bones are developed in relation to the lateral edge of the basis cranii, exactly as postulated for the lateral portion of the parasphenoid, nor does it present any relation to any part of the quadrate.

In the Chelonia the relation to the pterygoid process of the quadrate is one of juxtaposition only, there is no actual ectochondral ossification.

In the Lacertilia, though there is, in some genera, a close association of the posterior end of the pterygoid bone and the pterygoid process in the neighbourhood of the epipterygoid cartilage, the complete absence of any such association in other genera, by reason of the complete absence of the pterygoid process itself, may be taken as evidence that there is no ectochondral ossification of the process even in those cases in which the process is present and closely placed to the pterygoid bone.

In the Ophidia the pterygoid bone is developed quite independently of any cartilage at all.

In *Sphenodon*, the only recent Rhynchocephalian, Howe and Swinnerton have very clearly demonstrated the first appearance of the pterygoid bone as an ectochondral ossification of the median and lower surface of the pterygoid process.

There is room for doubt that the pterygoid process of the Reptilia is the same thing as the process in the Amphibia, but assuming for the purposes of the present discussion that there is no doubt about the homology of the processes in the two classes, it must be admitted that the variation observable in the relation of the bone to the process within the Sauropsida at least suggests that the relation is not genetic, but is spatial only.

It may be pointed out that, if the pterygoid bone is, as here suggested, derived from the lateral portion of the parasphenoid and has been moved laterally, it must have become approximated to the quadrate, and may well have acquired secondary relation to the portion of the quadrate it came in contact with.

A critical examination of the facts of the development of the pterygoid bones in the Sauropsida reveals that in the great majority of the members of the class there is no genetic relation between the pterygoid bone and the pterygoid process.

If the facts be viewed with the idea that the pterygoid bone of the Sauropsida is homologous with that of the Amphibia, then, since the pterygoid bone is always developed as an ectochondral ossification of the process throughout the Amphibia, the occasional occurrence of this relation amongst the Sauropsida will be regarded as significant, and as the primary relation. If, on the other hand, one is able to view the facts without this bias, it has to be admitted that the weight of evidence of the known ontogeny of the bone amongst the Sauropsida indicates that the occasional occurrence is a secondary relation.

Actually the relation only appears in *Sphenodon* and in some Lacertilians.

It may be pointed out, as contradicting the homology here suggested, that, whereas the amphibian pterygoid bone is always developed in genetic relation to the pterygoid process, the reptilian os transversum never is.

Whilst this is quite true, it seems that it may be quite simply explained by consideration of the changes which have taken place in its situation, and of the forces which may be assumed to have been responsible for those changes. In its transposition from its posterior to its anterior situation, the bone has been divorced from the much reduced pterygoid process. The need for the rigid support and limitation to the muscles of mastication is assumed to have conditioned the retention of the anterior arm of the pterygoid as the muscle mass increased in size, to meet the demands of more active modes of living and greater strength for mastication. The cartilaginous process was reduced, as we know from the evidence available, but the bone was retained.

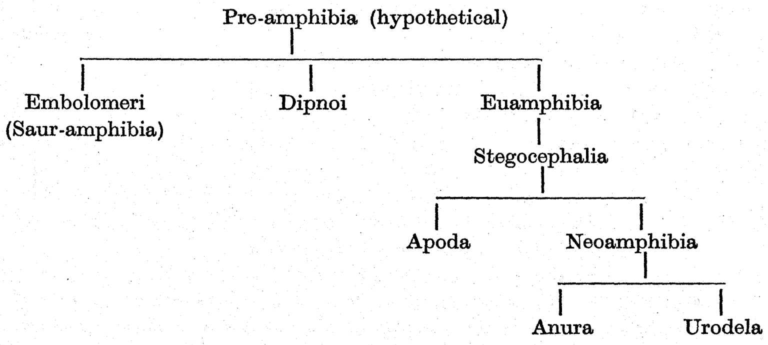
Finally, it may be remarked that it is not without significance that in the only Amphibians in which the basal and otic processes of the quadrate are not developed, the so-called pterygoid bone has lost its relation to the basis cranii in the region where the basal process would have been attached, and has been transported forward. The reference here is, of course, to the Apoda. Is this not an indication that the loss of these attachments of the quadrate is causally related to the changed position of the os transversum ? The processes in question are never present as part of the quadrate in any of the Sauropsida. Did the liberation of the quadrate condition the liberation of the os transversum also ?

Finally, it may be argued that the rachitomous palate as exemplified by *Eryops* presents a connecting link between the typical amphibian and the cotylosaurian condition as exemplified by *Seymouria*. At first sight it would appear that the only modification of the latter skull needed to bring about the condition in the former is that the admedian portions of the pterygoids should disappear between the lines joining the spicule of the bones between the palatine and prevomer and the basitrabecular process. This, however, is not so ; such a view would entirely overlook the fact that the parasphenoid in the cotylosaurian skull has been reduced to a vomerine splint, a fundamental difference between the two skulls, and it would also overlook the fact that, whereas the pterygoid of *Eryops* articulates with the parasphenoid and subotic portion of the skull, in the cotylosaurian, the articulation is with the basitrabecular process* lying anterior to the otic capsule.

As a matter of fact, *Eryops* presents a typical rachitomous palate ; its apparent resemblance to that of the Cotylosaurians is due only to the extension of the pterygoid bones anteriorly. Were it to lose that little piece of the bones which extends anteriorly to the palato-prevomerine suture it would lose entirely its apparent resemblance to the Cotylosauria.

There is, then, evidence of two distinct lines of descent presented by the Embolomeri on the one hand and the remainder of the Amphibia on the other.

The evidence of their cranial osteology, musculature and development suggests the following broad classification of the Amphibia.



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* It is a fact that a basitrabecular process has been stated to be present in the skull of *Eryops*, but the statement is based on a confused idea of the true nature of the process. It is obvious that the process so designated lies too far back to be a true basitrabecular process, and, moreover, the process is parasphenoidal with a lateral expansion of the basisphenoid above it.

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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 spheno-pterygoideus anterior read pterygoideus anterior.