ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

By F. H. EDGEWORTH, M.D.

Though the genealogies and affinities of Dipnoi and Amphibia have been much discussed, the particular problem of the derivation and possible genetic relationship of their autostylism and more or less marked monimostylism has received little attention.

The subject has been discussed from two points of view, firstly as a problem which affects each group separately, and secondly as one which is common to both groups.

The autostylic and monimostylic condition of the jaw-apparatus of Dipnoi was considered to be secondary by Huxley, Dollo, Bridge, Goodrich, and Luther. On the other hand, K. Fürbringer stated that it was not proven that their autostylism was derived from a hyostylism, and was of opinion that the primitive condition was one in which the mandibular and hyoid bars articulated separately with the cranium.

Of these authors only Luther took account of the mandibular muscles, and he suggested that a Levator maxillae superioris s. Constrictor i. dorsalis disappears.

The autostylic and mostly monimostylic condition of Amphibia was not considered by Semon, Assheton, and Kerr; it was thought to be secondary by Huxley, Dollo, Pollard, and Luther; and was held to be primary by K. Fürbringer.

The majority of these observers did not take the mandibular muscles into consideration, but Pollard thought that a Levator maxillae superioris disappears, and Luther put forward the theory stated below.

According to Dollo and Bridge the conditions were separately acquired in Dipnoi and Amphibia. Dollo thought that the condition in Dipnoi was an adaptation to a "régime tritateur," but in criticism of this opinion Bridge stated that such an explanation would not apply to Amphibia, and he also pointed out some resemblances between the larval Anuran condition and that of Marsipobranchii.

Huxley, Semon, Assheton, Kerr, and Boas did not discuss the problem.

Sewertzoff stated that the early stages of Ceratodus and Amphibia (especially Urodela) are very similar, whilst the later stages diverge. K. Fürbringer considered that the Amphibian condition was derived from a Dipnoan one. Versluys, who discovered the Levator quadrati of Gymnophiona, held that their streptostylic condition is primitive. This theory was developed by Luther, who stated that the semi-streptostylic condition of some Urodela, e.g. *Hynobius, Salamandrella,* is also a primitive one. He therefore rejected the theory of K. Fürbringer and held that, in any discussion of the relations of Amphibia and Dipnoi, features which are related to their autostylism must be left out of account.

In a paper published in 1911 I stated that the primordium of the masticatory muscles of *Scyllium, Acipenser, Lepidosteus, Amia* and *Salmo,* separated into an upper portion—the Constrictor i. dorsalis or its homologues—above the palatopterygoid process of the Quadrate, and a lower portion—the Adductor mandibulae or its derivatives—extending from that process to the Mandible. I also stated that the Levator bulbi of *Rana* is given off from the upper surface of the Levator mandibulae anterior, and did not regard it as homologous with the Constrictor i. dorsalis of Selachii and Teleostomi; nor did I recognise a Constrictor i. dorsalis in *Triton, Necturus* and *Ceratodus,* and regarded its absence as a primitive feature. I consequently looked upon the monimostylic condition of Amphibia and Dipnoi as primary, and the streptostylic condition of Selachii and Teleostomi as secondary, developed in correlation with a division of the primordium of the masticatory muscles into upper and lower portions, above and below the palato-pterygoid process of the Quadrate.

The primordia of the Obliquus superior and Rectus externus in Selachian embryos were looked upon as merely anterior projections from the upper ends of the mandibular and hyoid muscle-plates to form these muscles, i.e. I doubted the v. Wijhe doctrine, and it was considered that the ocular musculature was primarily formed solely from the premandibular somite.

These views have not passed unchallenged. Luther, in 1914, gave a full account of the mandibular muscles of Amphibia. In this valuable paper he came to the conclusion that the Levator quadrati and Compressor glandulae orbitalis of Gymnophiona, and the Levator bulbi of Urodela and Anura are the homologues of the Constrictor i dorsalis of Selachii and Teleostomi, and that the other masticatory muscles of Amphibia are (collectively) the homologues of the Adductor mandibulae of Selachii and Teleostomi.

In support of these conclusions he advanced the following arguments. The Levator quadrati of Gymnophiona closely resembles the Constrictor i. dorsalis in origin and insertion, only differing in that its origin is rostral (anterior) to the trigeminal foramen whereas that of the Constrictor i. dorsalis is caudal (posterior) to it. This difference is due to a forward shifting of the origin of the muscles in Gymnophiona. The Levator quadrati of Gymnophiona also, as Versluys recognised, corresponds with the Protractor pterygoidei of Saurii in position and derivation, and is certainly homologous with it. Further, there is a similarity in the proximal nerve supply of the Levator quadrati and Constrictor i. dorsalis—the nerve of the former coming from the Ganglion Gasseri in *Siphonops,* that of the latter coming from V_3 very high up. Among Salamandridae are forms, e.g. *Hynobius* and *Salamandrella* which possess a very moveable Quadrate and in which a part of the lateral fibres of the Portio sagittalis of the Levator bulbi shows many similarities to and is homologous with the Levator quadrati of Gymnophiona.

Ontogenetically, in *Rana* and *Pelobates*, all parts of the Levator bulbi are derived from a single Blastema, indicating a single genesis of the whole muscle. This Blastema is differentiated from the tissue lying dorsal to the Adductor, and there is no connection between it and the Adductor. The statements of Edgeworth in regard to the origin of the Levator bulbi of *Rana* might be explained by the lateness of development, for the muscle only functions after metamorphosis, and the whole difference between Selachii, Ganoids, Teleostei, and Sauropsida, on the one hand, and Amphibia on the other, be a mere matter of the time of division.

The nerve-supply of the Levator bulbi is derived in some cases from V_1, in others (Anura) from V_1 and V_2, in others again (Amphiumidae) from the N. pterygoideus V_3. This variation in the course of the nerve-fibres does not militate against the theory.

In view of this diversity of opinion the subject has been reinvestigated with the results described below. I may perhaps anticipate the conclusions by saying that all the additional evidence I have been able to collect supports the opinion I previously published. It is sub-divided as follows:

1. The skeletal evidence.
2. The evidence derived from the development of the masticatory muscles.
3. Relationship of the Quadrate and masticatory muscles of Elasmobranchii and Teleostomi to those of Dipnoi and Amphibia.

SKELETAL EVIDENCE

Dipnoi. The development of the Quadrate of *Ceratodus* has been described by Sewertzoff (1902), Greil (1913), and myself (1923). It is developed as an independent mass, which becomes fixed to the Chondrocranium by ascending, otic, and basal processes. The development of the Quadrate of *Lepidosiren* was described by Agar, who stated that the rudiment of the Quadrate is from the first continuous with the Trabecula by the Processus basalis. A strand of dense connective tissue connecting the distal end of the rudiment of the Quadrate with that of the palatine tooth probably represents the vestige of the pterygoid process. The otic process fuses with a shelf which is formed as an anterior continuation of the side wall of the auditory capsule. It is not possible to speak of a Processus ascendens as distinct from the basalis.

Urodela. In a 11 mm. larva of *Amblystoma punctatum*, according to Winslow, the ascending process of the Quadrate is fused with the trabecular crest, and the otic process has begun to develop. This process is longer in a larva of 12 mm. In a larva of 39 mm. the otic process has fused with the otic capsule, whilst the pterygoid process passes forward from the point where the ascending process joins the body of the Quadrate and ends free, just below the ventro-median surface of the eye. The basal process is formed by fusion of the dorso-median surface of the body of the Quadrate with the margin of the basilar plate. In a young animal of 69 mm.—in which the gills have atrophied—the condition is similar except that the pterygoid process passes forwards and outwards.

I find that in a larva of 13·5 mm. (fig. 41) the ascending and otic processes have fused with the trabecular crest and the auditory capsule respectively. The chondrified base of the pterygoid process is continued forwards as a thin column of cells the anterior end of which is continuous with the Trabecula. In a larva of 18 mm. the anterior cellular part of the pterygoid process has atrophied and the front end of the posterior part lies above the pterygoid part of the (as yet undivided) pterygoid-palatine bone. In a larva of 27 mm. the basal process is united with the margin of the basilar plate—as described by Winslow in the 39 mm. larva.

Larvae of *Amblystoma tigrinum* show similar conditions.

In *Triton* larvae, according to Gaupp, the Quadrate is formed independently of the Chondrocranium and fuses with it by ascending, otic, and basal processes. The basal process fuses with the ventral surface of the auditory capsule just where this unites with the basal plate. The pterygoid process, developed last, lies on the earlier-formed pterygoid bone, and has a pointed free extremity.

Peters (1910) stated that the basal and otic processes do not fuse, cartilaginously, with the auditory capsule, nor in *Siredon*, as far as his observations went—greatest length of larvae investigated 25 mm.—nor in *Necturus*.

In a larval *Triton cristatus*, however, of 33 mm. I find a complete cartilaginous continuity of the otic and basal processes with the auditory capsule.

The Quadrate in *Salamandra atra* is very similar to that of *Triton cristatus*.

In the adult state of *Desmognathus fuscus*, according to Wiedersheim, the Quadrate has two cartilaginous ends, "welche die prootische Gegend von unten und aussen umgreift." He also depicted a pterygoid process with a free anterior extremity.

I find that in a larva of 19 mm. (fig. 42) the Quadrate, which is oblique in position, has four processes. The pterygoid process is wholly cellular, and passes from the Quadrate to the Trabecula; the ascending process is continuous with the trabecular wall, the otic process is continuous with the outer wall of the auditory capsule, and the basal process is continuous with the inner part of the floor of the auditory capsule. There is only a short larval stage. In an adult of 35 mm. the conditions are similar except in regard to the pterygoid process, the anterior part of which has disappeared, and the now chondrified posterior part ends free, ventro-lateral to the eye.

The Quadrate of *Spelerpes* was not described by Wiedersheim. In a 25 mm. larva the Quadrate has pterygoid, ascending, and otic processes, but as yet no basal process. The pterygoid process is wholly cellular, its anterior end is continuous with the Trabecula. The cartilaginous ascending process is continuous with the trabecular wall, and the cartilaginous otic process is continuous with the outer wall of the auditory capsule. In a larva of 36 mm. the Quadrate has become oblique in position, sloping downwards and forwards. Chondrification has spread a little way along the pterygoid process. A basal process has developed and connects the Quadrate with the inner part of the floor of the auditory capsule. In an adult, of 49 mm., the conditions are similar, except that the anterior part of the pterygoid process has disappeared.

In the adult stage of *Plethodon glutinosus*, according to Wiedersheim, the pterygoid process of the Quadrate ends free, there is a basal joint, and the otic process is continuous with the auditory capsule. No statement was made in regard to the ascending process.

Plethodon cinereus is hatched in the adult state, measuring about 20 mm. There is no free-living larval stage. In a specimen measuring 25 mm. (fig. 43) the Quadrate is in an oblique position, sloping downwards and forwards, its pterygoid process ends free, the ascending process is continuous with the trabecular wall, the otic process is continuous with the auditory capsule, and the basal process is continuous with the floor of the auditory capsule. In a specimen of 49 mm. (fig. 44) the conditions are similar except that there is a band of closely aggregated cells across the basal process—the commencement of the basal joint.

In the first larval stage of *Amphiuma tridactylum* investigated by Winslow the Quadrate has an ascending process which joins the trabecular crest and a slender stapedial process which passes backwards and joins the small stapes; whilst in the second stage there are, additionally, otic and basal processes which are continuous with the otic capsule. The pterygoid process passes forwards from the ventral surface of the ascending process in close proximity to the ventral margin of the Trabecula; towards its anterior end it curves laterally and broadens into an oval plate which lies a short distance posterolaterally from the base of the antorbital process. In the adult, according to Wiedersheim, the Quadrate is continuous with the basilar plate and otic capsule by basal and otic processes, whilst the pterygoid process ends above the hinder end of the maxilla.

Comparison with *Cryptobranchus* and *Menopoma* suggests that the stapedial process is to be regarded as a forward process of the stapes which has fused with the Quadrate rather than as a backward process of the Quadrate. Investigation of earlier stages would decide this question.

Descriptions of the Quadrate in *Hynobius*, *Megalobatrachus* and *Menopoma* were published in this *Journal* in 1922.

The Quadrate of the adult stage of *Salamandrella Keyserlingii* was not described by Wiedersheim. Luther stated, though without giving any details, that the skull is semistreptostylic.

I find that in a 13·5 mm. larva (fig. 45) the Quadrate has pterygoid, ascending, and otic processes. The pterygoid process is continuous anteriorly with the Trabecula, its posterior part is cartilaginous and its anterior part cellular. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule.

In a 17 mm. larva (figs. 46–48) the basal process of the Quadrate has developed and chondrified, it extends to the floor of the auditory capsule. The other processes are as in the earlier larva, except that comparison of figs. 45 and 46 shows that chondrification has extended further forwards in the pterygoid process. In figs. 46 and 47 the anterior cellular part of the pterygoid process is not shown. The model only represents cartilage.

In a 22·5 mm. larva (fig. 49) the anterior cellular portion of the pterygoid process has disappeared. Cells have accumulated in the basal process.

In a 34 mm. larva (fig. 50) the Quadrate has become oblique in position, sloping from above downwards and forwards. A syndesmotic joint has developed in the basal process, and the monimostylic condition of earlier stages has become a semistreptostylic one.

In an adult of 105 mm. the pterygoid process of the Quadrate passes forwards and outwards and ends free beneath the outer border of the eye. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule. In the synchrondotic basal joint, on one side, a slightly curved slit-like cavity has developed.

Wiedersheim stated that in the adult form of *Ranodon sibiricus* the pterygoid process of the Quadrate is continuous with the outer posterior extremity of the nasal capsule. He did not describe the other connections of the Quadrate, but his figure 69 shows, I think, an ascending process continuous with the trabecular wall and an otic process continuous with the auditory capsule.

I find that in a larva of 21 mm. the Quadrate has pterygoid, ascending and otic processes, but as yet no basal process. The pterygoid process is continuous anteriorly with the Trabecula, just behind the antorbital process, its posterior part is chondrified, its anterior part a cellular strand. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule. The larva is very similar to the 13·5 mm. larva of *Salamandrella.*

In a larva of 25 mm. (figs. 51, 52) the anterior cellular portion of the pterygoid process has disappeared. The anterior end of the persisting posterior chondrified portion ends at a little distance behind the antorbital process, and is not continuous with it. A basal process has developed and connects the Quadrate with the inner part of the floor of the auditory capsule.

In a young adult 85 mm. long the ascending and otic processes of the Quadrate are continuous with the trabecular wall and auditory capsule respectively. A synchondrotic joint with a slight slit-like central cavity has developed in the basal process. The pterygoid process passes forwards and slightly outwards, but does not reach the posterior margin of the nasal capsule—there being a gap of ·86 mm. Its continuity with the nasal capsule described by Wiedersheim is thus developed during adult life.

Miss Platt (1897) stated that in a 19 mm. embryo of *Necturus* the Quadrate is fused only with the Crista trabeculae (= ascending process). In a 46 mm.

embryo a cartilaginous process, extending backwards from the ascending process, is fused with the auditory capsule (= otic process). Winslow (1898) described the otic process as being present and fused with the auditory capsule in a 21 mm. embryo. Neither observer mentioned the existence of a basal process.

I find that in a 25 mm. embryo (figs. 64, 65) the Quadrate has ascending, basal, and otic processes. The ascending process is continuous with the Crista trabeculae, the basal process is continuous with the prefacial commissure by a cellular bridge, and the otic process similarly with the auditory capsule. In a 30 mm. embryo (fig. 66) these connections have chondrified.

In *Siren*, according to Wiedersheim, the Quadrate has a slender ascending process continuous with the Ala magna, and otic and basal processes both articulating with the prootic territory. From the ascending process projects forwards a finger-like process, the extremity of which bends downwards into the orbit. The size of the specimen was not stated.

Wiedersheim doubted the homology of the above-mentioned process with the pterygoid process of other Urodeles, and suggested that it is homologous with the post-orbital process of the Quadrate of some Selachians.

Winslow, however, found in *Amphiuma* and *Amblystoma* that the pterygoid process projects forwards from the base of the ascending process and not from the body of the Quadrate. I found the same condition in larvae of *Megalobatrachus* and *Menopoma.* Secondly, the post-orbital process of the Quadrate in Notidanidae is almost certainly the homologue of the otic process of Amphibia. It is thus fairly certain that the anterior process of the Quadrate of *Siren* is a pterygoid process.

A very different account of *Siren* was subsequently given by Parker, who stated that in a specimen of 13½ inches (= 34 cm.) the dorsal end of the Quadrate is "bifurcate; and both the forks are confluent with the endocranium (the trabecula and its alisphenoidal crest). The part confluent with the base is the pedicle (= basal process); that which passes into the wall is the ascending process; outside these, above, we have the otic process which is confluent with the auditory capsule and the preauditory horn." The Quadrate has "no pterygoid outgrowth and no correlated pterygoid bone." The anterior margin of the Epihyal is confluent with the Quadrate.

In a specimen from Florida 67 cm. long (about the greatest length reached by this Urodele) I find that the Quadrate is similar to that of the younger specimen described by Parker with the exception that a short pterygoid process projects downwards and forwards from the ascending process. There is no joint in the otic or basal process. The latter process is continuous with the basal plate.

Anura. In *Rana*, according to Gaupp, the Palato-quadrate develops independently of the Chondrocranium, and fuses with it by the ascending process and the Commissura quadrato-cranialis anterior. Later on, in 21 mm. larvae, an otic process is formed and fuses with the auditory capsule, and then a pterygoid process is developed from the commissure and unites with the Processus maxillaris posterior of the Planum antorbitale. At metamorphosis the ascending and otic processes disappear, and the Palato-quadrate fuses with the Crista parotica by a new otic process. A basal process develops, abuts against, and then fuses with the floor of the auditory capsule, and a joint develops in it.

Gaupp was of opinion that the ascending and basal processes are homologous with the similarly named structures of Urodela. The otic process develops twice; of these the later one is probably homologous with that of Urodela, the earlier one being only a special provisional structure. His opinion concerning the Commissura quadrato-cranialis anterior is discussed later.

Gymnophiona. The development and adult anatomy of the Quadrate have been the object of researches by Wiedersheim (1879), P. and F. Sarasin (1890), Winslow (1898), Peter (1898), Marcus (1909), Versluys (1910 and 1912), and Luther (1914). The following is a summary of their statements. The Quadrate of *Ichthyophis* is formed as a triangular cartilage, with ascending, pterygoid, and otic processes. The ascending process becomes connected with the Taenia marginata—by cartilage according to Winslow, by connective tissue according to Peter. The otic process is only slightly marked and does not become united to the auditory capsule. The pterygoid process consists of a posterior part continuous with the Quadrate, and of an anterior part in two portions; these parts are united by cellular tissue. The Quadrate has no basal process; it has a jugal process. No mention of any process of the basal plate is made by either Winslow or Peter. On ossification, the Pterygo-quadrate is first surrounded and then replaced by bone except at its articular surfaces for the lower jaw and columella, and the upper end of the ascending process. The pterygoid process degenerates into connective tissue at the end of larval life.

In the adult the ascending process of the Quadrate passes upwards and slightly forwards along the posterior edge of the paraquadrate bone. The jugal process fills up the space between the ascending and pterygoid processes. The pterygoid process is continuous with either the pterygoid bone—in *Ichthyophis*, or with the maxillo-palatine bone—in *Caecilia* and *Siphonops* (Luther). A well-marked joint exists between the Quadrate and the basal bone in *Hypogeophis* larvae and in adult *Siphonops* (Versluys), and in *Caecilia* (Luther); whilst in adult *Ichthyophis* there is only a syndesmotic union (Luther).

In a 70 mm. larva of *Siphonops* (figs. 84–89) I find that the Quadrate has ascending, pterygoid, and jugal processes, but no otic or basal processes. There is a well-marked joint between the dorsal end of the ascending process and the upper of the two bars by which the Taenia marginata is continuous with the auditory capsule. A partially ossified process projects from the basal plate antero-laterally and then forwards, and its anterior end is continuous with the base of the pterygoid process of the Quadrate. In front of this cartilaginous continuity the now wholly ossified pterygoid process extends further forwards, and is continuous with a bone (probably the pterygoid bone) which expands into a plate lying on the upper surface of the maxillo-palatine bone. The jugal process is the ossified anterior edge of the Quadrate and of its ascending process—not merely of the former as in *Ichthyophis*. The Columella auris abuts against the posterior surface of the Quadrate. Younger larvae were not available. Two changes take place between this late larval condition and the adult state. The joint between the ascending process and the Taenia marginata is replaced by fibrous tissue, and a joint develops between the base of the pterygoid process of the Quadrate and the process of the basal plate.

In a 28·5 mm. larva of *Ichthyophis*—rather younger than the one modelled by Peter—both the Chondrocranium and Quadrate are in a precartilaginous condition (figs. 90, 91). The Quadrate has a long pterygoid process the anterior end of which is close to but does not actually touch the Trabecula. The ascending process is continuous with the Taenia marginata. Neither otic nor basal process is present. A short process projects laterally from the basal plate, turns back, and then inwards, to join the basal plate again. (This is also shown, in transverse sections of the 35 mm. larva, figs. 100–102.) The anterior end of the Columella auris is close to the posterior end of the Quadrate.

In a 35 mm. larva (figs. 98–102) the Chondrocranium and the Quadrate with its two processes are chondrified. The changes from the earlier stages are as follows. The anterior end of the, still continuous, long pterygoid process of the Quadrate is in contact with the Trabecula (fig. 98). The upper end of the ascending process is connected with the Taenia marginata by fibrous tissue. The process of the basal plate is tied to the Quadrate by fibrous tissue (figs. 100–102). The pterygoid bone has developed; its hind end is close to the medial surface of the Quadrate.

In a larva of 59 mm. (fig. 103) the middle portion of the pterygoid process has disappeared. The anterior end of the persisting front portion no longer touches though it is close to the Trabecula; it lies on the palato-maxillary bone. The anterior end of the persisting hinder portion of the pterygoid process is ossified. The basal plate with its process, and the posterior parts of the Taenia marginata and Trabecula, have degenerated. A fibrous ligament binds the basal bone to the body of the Quadrate, its pterygoid process, and the pterygoid bone.

On comparison of the above-described phenomena it is seen that:

(1) The anterior end of the pterygoid process of the Quadrate becomes continuous with the Trabecula in *Amblystoma*, *Desmognathus*, *Spelerpes*, *Hynobius*, *Menopoma*, *Salamandrella*, and *Ranodon*. In *Hynobius* and *Menopoma* on the subsequent development of the antorbital process, the pterygoid process is found to be continuous with its inner end. This latter condition is present in the youngest available larvae of *Megalobatrachus*. In *Amblystoma*, *Desmognathus*, *Spelerpes*, *Salamandrella* and *Ranodon*, the anterior part of the pterygoid process does not develop beyond the stage of a cellular strand, whereas in *Hynobius*, *Megalobatrachus* and *Menopoma* it becomes cartilaginous throughout its whole length. The anterior part of the pterygoid process disappears in the later larval stages of all these Urodeles. The continuity of the pterygoid process with the outer posterior part of the nasal capsule in *Ranodon* is of later

development, during adult life, and is not due to a persistence of an original connection with the antorbital process.

The pterygoid process ends free in *Triton*, *Salamandra*, *Plethodon*, *Amphiuma* and *Siren*. It is not developed in *Necturus*.

These phenomena indicate an ancestral Urodelan condition in which the pterygoid process was continuous anteriorly with the Trabecula, i.e. one in which there was a Pterygo-quadrate.

Gaupp held that the Commissura quadrato-cranialis anterior of the larval stage of *Rana* has no "analogue" in Urodela, but the new information above mentioned shows that it is homologous with the pterygoid process of Urodela, and should be similarly named[1]. The later-developed "pterygoid process" of Gaupp might have a new name.

In a 35 mm. larva of *Ichthyophis* the anterior end of the pterygoid process is in contact with the Trabecula. The only available larva of *Siphonops* was too far advanced in development for this—if present in younger stages—to be seen.

In *Ceratodus* there is no pterygoid process, or but (according to Greil) a transitory rudiment of one. In *Lepidosiren*, according to Agar, it is represented by a strand of dense connective tissue passing to a palatine tooth.

(2) The ascending process of the Quadrate is not present in *Lepidosiren* and *Protopterus* (Agar). It is present in *Ceratodus*, the larval stage of Urodela and Anura, and *Ichthyophis*, and is fused with either the trabecular wall or Taenia marginata. In *Siphonops* larvae, of which only a late stage was available, there is a joint. The cartilaginous continuity persists except in adult Gymnophiona, in which there is a fibrous union.

(3) The site of the union of the Quadrate with the base of the Chondrocranium varies. In *Lepidosiren* and *Protopterus* the basal process of the Quadrate fuses with the Trabecula, in Ceratodus with the junction of the Trabecula and Parachordal. In *Menopoma* and *Megalobatrachus* the basal process grows from the base of the pterygoid process, and not from the body, of the Quadrate. In the former it fuses with the basal plate, in the latter with a lateral process of the basal plate. In Amblystoma it fuses with the basal plate In *Necturus* it fuses with the praefacial commissure. In other Urodela and in Anura it fuses with the inner part of the floor of the auditory capsule. A syndesmotic joint subsequently develops in the basal bridge in *Plethodon*, *Hynobius*, *Salamandrella* and *Ranodon*. In *Siphonops* and *Ichthyophis* a lateral process of the basal plate develops—similar to that of *Megalobatrachus*. This in *Siphonops* fuses with the base of the pterygoid process. A diarthrodal joint develops in it subsequently. In *Ichthyophis* the process, which has only a transitory existence, does not fuse with the Quadrate, but is tied to it by fibrous tissue.

Comparison of the above series of forms with *Acanthias*, *Notidanus* and *Lepidosteus* (*vide infra*) suggests that the original site of basal union is with the Trabecula. This is also present in *Lepidosiren* and *Protopterus*. The other situations are due to various degrees of backward displacement. *Menopoma*,

---

[1] I have done so in figs. 71–73.

Megalobatrachus, *Siren*, *Amblystoma* and Gymnophiona are, in this, more primitive than other Urodela or Anura.

Versluys was of opinion that the basal s. basipterygoid joint of Amphibia is a very old phylogenetic feature, and in support of this theory adduced the observations of Veit on *Lepidosteus*. Such an opinion, however, does not account for the fact that—as Veit stated, though not referred to by Versluys—the development of a basal joint in *Lepidosteus* is preceded by a complete fusion of the Quadrate with the Chondrocranium at this point. A similar fusion preceding the formation of a joint takes place in *Acanthias*, *Siphonops*, *Plethodon*, *Hynobius* and *Salamandrella*. The developmental phenomena in all these cases can be explained by the theory of descent from forms possessing a fixed Quadrate. The Secondary feature of a joint may have been independently acquired. Further, the varying sites of such a joint support the theory that its development occurred at various phylogenetic stages in the backward shifting of the basal connection of the Quadrate with the Chondrocranium and, so, independently.

The above phenomena come out most clearly in a tabular statement:

The basal process fuses with	Trabecula	Junction of Trabecula and Parachordal	Basal plate	Praefacial commissure	Floor of auditory capsule
Protopterus	+	.	.	.	.
Lepidosiren	+	.	.	.	.
Acanthias	+*	.	.	.	.
Notidanus	? +*	.	.	.	.
Lepidosteus	+*	.	.	.	.
Ceratodus	.	+	.	.	.
Menopoma	.	.	+	.	.
Megalobatrachus	.	.	+	.	.
Siren	.	.	+	.	.
Siphonops	.	.	+*	.	.
Ichthyophis	.	.	A joint	.	.
Necturus	.	.	.	+	.
Amblystoma	.	.	+	.	.
Triton	.	.	.	.	+
Salamandra	.	.	.	.	+
Desmognathus	.	.	.	.	+
Spelerpes	.	.	.	.	+
Plethodon	.	.	.	.	+*
Amphiuma	.	.	.	.	+
Hynobius	.	.	.	.	+
Salamandrella	.	.	.	.	+*
Ranodon	.	.	.	.	+*
Anura	.	.	.	.	+*

* Subsequently a joint.

(4) The otic process of the Quadrate fuses with the outer wall of the auditory capsule in *Ceratodus*, Urodela and Anura. In *Lepidosiren* and *Protopterus* it fuses with an anterior process of the outer wall of the auditory capsule. In *Ichthyophis*, according to Marcus, it is present as a transitory process which does not fuse with the auditory capsule. This was not present in my larvae of *Ichthyophis* or *Siphonops*.

The above phenomena are summarised in the following tabular statement.

Dipnoi	Monimostylic	Streptostylic
Ceratodus	+	.
Protopterus	+	.
Lepidosiren	+	.

Amphibia		Larva		Adult	
Urodela*		Monimostylic	Semi-streptostylic	Monimostylic	Semi-streptostylic
Amblystomidae.	Amblystoma punctatum tigrinum	+	.	+	.
Salamandridae.	Triton cristatus	+	.	+	.
	Salamandra atra	+	.	+	.
Plethodontidae.	Desmognathus fuscus	+	.	+	.
	Spelerpes bislineatus	+	.	+	.
	Plethodon cinereus	.	.	Early adult +	Older adult +
Amphiumidae.	Amphiuma tridactylum	+	.	+	.
Hynobidae.	Hynobius nebulosus	Earlier +	Later +	.	+
	Salamandrella Keyserlingii†	Earlier +	Later +	.	+
	Ranodon sibiricus	+	.	.	+
Cryptobranchidae.	Megalobatrachus maximus	+	.	+	.
	Menopoma alleghaniense	+	.	+	.
Proteidae.	Necturus maculatus	+	.	+	.
Sirenidae.	Siren lacertina	+	.	.	.
Anura.	Rana	+	.	.	+
Gymnophiona.	Ichthyophis glutinosus	.	+	.	Streptostylic +
	Siphonops braziliensis	.	+	.	+

* I follow the classification of Dunn.

† s. Hynobius Keyserlingii (Dunn).

It would appear from the above that *Amblystoma*, *Triton*, *Salamandra*, *Desmognathus*, *Spelerpes*, *Amphiuma*, *Megalobatrachus* and *Menopoma*, are monimostylic in both the larval and adult states, and that *Necturus* and *Siren* are also monimostylic. The semistreptostylic condition of *Plethodon*, *Hynobius*, *Salamandrella* and *Ranodon* is preceded by an earlier monimostylic one.

It is, further, observable that the distribution of a long pterygoid process continuous anteriorly with the Trabecula, and of a basal joint, is not identical. The former occurs among Amblystomidae, Hynobidae, and Cryptobranchidae, whereas a basal joint occurs among Plethodontidae and Hynobidae, and in the former group not as a familial but only as a generic feature. Thus a joint develops in *Plethodon* but not in *Desmognathus* or *Spelerpes*. These occurrences do not harmonise with the theory of Versluys and Luther that the joint is an old phylogenetic feature.

The phenomena indicate, I think, that Urodela are descended from a monimostylic stock.

A pterygoid process may fail to be developed, e.g. *Necturus*, or not reach the Trabecula, e.g. *Triton*, or subsequently separate from it, e.g. *Amblystoma*, *Menopoma*, without the occurrence of any other skeletal change. On the other hand, the development of a basal joint does not occur as an isolated feature in *Ranodon*, *Plethodon*, *Hynobius* and *Salamandrella*. The anterior part of the pterygoid process either atrophies or fails to be developed. In *Ranodon* the continuity of the pterygoid process with the nasal capsule is a subsequent event.

Anura are monimostylic in the larval, semi-streptostylic in the adult, state. In Gymnophiona no larva is known in which the Quadrate is fixed to the

Chondrocranium by four processes. In larvae of *Ichthyophis*, however, the ascending process is at one period continuous with the Taenia marginata, and the extremity of the pterygoid process in contact with the Trabecula, and there is a (subsequently atrophying) lateral process of the basal plate which is tied to the Quadrate by fibrous tissue. Peter also described an incomplete otic process. Further, in an advanced larva of *Siphonops* there is a cartilaginous continuity between the Quadrate and the lateral process of the basal plate. The Quadrate in Gymnophiona larvae may thus be continuous with the Chondrocranium at three points.

These phenomena suggest that the streptostylic condition of adult Gymnophiona is not primary, but secondary to an original monimostylic one. The contrary opinion fails to explain the above-described structures.

The skeletal evidence thus suggests that Amphibia, like Dipnoi, are descended from autostylic and monimostylic ancestors. Further, the resemblance between the connections of the Quadrate with the Chondrocranium in Dipnoi and Amphibia is so close that, unlike Luther, I think it improbable that they have been separately acquired. This probability is rendered greater by consideration of the masticatory muscles—*vide infra.*

It is not without interest in regard to these speculations to note that in *Stegocephalia* and in *Lysorophus*—a member of the ancestral Urodeles from the Pennsylvanian deposits—the Quadrate was fixed (Case, Williston, Stromer, Luther, Sollas) though whether this monimostylic condition was of chondrogenetic origin, as in the Amphibia described above, cannot of course be determined.

DEVELOPMENT OF THE MASTICATORY MUSCLES

Elasmobranchs. Marshall (1881) described the mandibular head-cavity of *Scyllium*, in stages K–M, as consisting of a dorsal dilated portion continuous with a laterally compressed ventral portion extending down the whole length of the mandibular arch. The main branch of the vth nerve lies wedged in between the mandibular and hyoid head-cavities. By the middle of stage M the dorsal portion of the mandibular head-cavity has atrophied and disappeared. The walls of the ventral prolongation become converted into muscles.

v. Wijhe (1882) stated that in stage K of *Scyllium* the second somite is continuous with the lateral plate in the mandibular segment. The R. mandibular v. crosses the outer side of the position where the second somite is continuous with the lateral plate and then runs down on its anterior side. The second somite forms the superior oblique muscle whilst the lateral plate develops into the mandibular muscles.

Miss Platt (1891) stated that in 14 mm. embryos of *Acanthias vulgaris* there is a thickening of the inner wall of the base of the second somite—the primordium of "muscle E," and an out-pocketing of the dorsal end of the mandibular muscle plate, forming a rudimentary muscle which comes to occupy a position close to the inferior oblique muscle of the eye. She traced "muscle E" up to the 26 mm. stage.

Hoffmann (1896) stated that in *Acanthias vulgaris* the medial and antero-medial walls of the second somite thicken and proliferate cells which develop into mesenchyme. He did not describe any "muscle E." The Levator labi superioris develops from the upper part of the walls of the mandibular muscle-plate (Kieferbogenhöhle), whilst the ventral part develops into the Adductor mandibulae. No figures were given of this development of the mandibular muscle-plate.

Lamb (1901) confirmed the account given of *Acanthias* by Miss Platt. He stated, however, that by the 27 mm. stage there were only the very slightest remains both of "muscle E" and of the rudimentary muscle at the dorsal end of the mandibular muscle-plate (which he called "muscle F").

Dohrn (1904), confirmed by Neal (1909, 1914 and 1918), showed that muscle E persists and forms the mandibular component of the Rectus externus. He also stated that the Adductor mandibulae develops from the ventral part of the mandibular muscle-plate, but did not give any details.

Klinkhardt (1905) stated that in *Spinax* embryos, with head-lengths of 2·73 and 2·96 mm. the R. mandibularis v. runs down on the outer side of the mandibular cavity. Guthke, too, stated that in 11 mm. embryos of *Torpedo ocellata* the R. mandibularis v. lies close to the wall of the mandibular cavity.

No one of the above investigators made mention of the Constrictor i. dorsalis.

In a paper published in 1911 I stated that in *Scyllium canicula* the mandibular muscle-plate separates into three portions—from above downwards the Constrictor i. dorsalis, the Adductor mandibulae, and the lateral half of the Intermandibularis. The relations of the R. mandibularis v. to the mandibular muscle-plate and to the muscles developing from it were not described. To determine this further material was examined. In a 14 mm. embryo (figs. 1–5) the primordium of the Obliquus superior is continuous with the mandibular muscle-plate. Both consist of an epithelium enclosing a cavity which is continuous from the one structure to the other. The uppermost part of the mandibular muscle-plate is roundish in transverse section. ·05 mm. below the Gasserian ganglion it fairly suddenly broadens antero-posteriorly into a plate, and there is a little upward projection—a "shoulder"—·03 mm. high, from it, behind the R. mandibularis v. The mandibular muscle-plate extends to the mid-ventral line. The united Ri. maxillaris and mandibularis v., issuing from the Gasserian ganglion, pass down lateral to the mandibular muscle-plate for a short distance and then separate; the former passes downwards and forwards, whilst the latter passes down about midway between the anterior and posterior edges of the muscle-plate.

In a 17 mm. embryo (figs. 6, 7) the appearances are similar, except that the "shoulder" of the muscle-plate posterior to the R. mandibularis v. has grown upwards and measures ·06 mm. in height.

In a 20 mm. embryo (figs. 8–11) the primordia of the Obliquus superior and the mandibular muscle-plate have separated. The Obliquus superior is now solid; from it has separated a little flattened vesicle—the rudiment of muscle E—which is in contact with the anterior end of the Rectus externus. The cavity in the mandibular muscle-plate has disappeared owing to approximation of the medial and lateral walls. The muscle-plate consists of an upper part which is posterior to the R. mandibularis v. and broadens as it is traced downwards, a broad part with the nerve lying about its middle and a narrower ventral part. All these are in continuity.

In an embryo of 23 mm. (fig. 12) muscle E has fused with the Rectus externus. The primordium of the Palato-quadrate and Meckel's cartilage has developed. The mandibular muscle-plate is still a continuous strip, though one in which the future muscles are distinguishable. These are, from above downwards, the Constrictor i. dorsalis, the Adductor mandibulae and the lateral half of the Intermandibularis. The R. mandibularis v. is anterior to the upper part and crosses the lower part of the Constrictor i. dorsalis, i.e. this muscle is only in part formed by the upgrowing "shoulder" behind the nerve.

In an embryo of 29 mm. (fig. 13) the muscle-plate is fully separated into the muscles it forms. The upper end of the Constrictor i. dorsalis has grown up to the auditory capsule.

In an embryo of 35 mm. (figs. 14–17) the anterior end of the Adductor mandibulae has extended forwards to the roof of the nasal capsule.

In an embryo of 53 mm. a horizontal septum has developed in the Adductor mandibulae. There is as yet no definite separation of a Praeorbitalis from the anterior part of the upper portion of the Adductor.

The primordium of the masticatory muscles of *Scyllium* thus at first lies medial to the R. mandibularis v., with its upper end close to the Gasserian ganglion and continuous with the Obliquus superior. After separation of the latter, the mandibular muscle-plate becomes separated into the Constrictor i. dorsalis, Adductor mandibulae, and lateral half of the Intermandibularis. The upper end of the Constrictor i. dorsalis grows upwards and backwards behind the R. mandibularis v. to the auditory capsule. This upward growth begins to develop before the muscle-plate is separated from the Obliquus superior.

In 20, 21 and 22 mm. embryos of *Acanthias vulgaris* (figs. 21–23) the conditions are similar to those of the 20 mm. embryo of *Scyllium*. The primordium of the Obliquus superior has separated from the mandibular muscle-plate, and muscle E—relatively larger than in *Scyllium*—is confluent with the Rectus externus. The dorsal upgrowing end of the mandibular muscle-plate is posterior to the R. mandibularis v.; as it is traced down it is seen to broaden and the nerve to lie external to it about midway between the anterior and posterior edges.

In the various stages of *Scyllium* examined and in these embryos of *Acanthias* no "muscle F" was seen. It appears probable that it is identical with the upgrowing projection of the mandibular muscle-plate behind the nerve.

The description of the early stages of *Spinax* and *Torpedo* by Klinkhardt and Guthke, taken in conjunction with the position of the Constrictor i. dorsalis relative to the R. mandibularis v. in the adult forms of those fishes, suggests that a similar development takes place in them.

Luther was of the opinion that the Praeorbitalis had primitively a cranial origin and resembled the Adductor mandibulae in function. Subsequently, with increasing size of the eye and antero-posterior extension of the mouth, the Praeorbitalis separated from the Adductor and gained a more ventral origin.

Comparison of the developmental phenomena in *Scyllium* and *Heterodontus* does not support this view. In *Scyllium*, the Praeorbitalis is due to a forward growth of the Adductor and does not rise above the level of the Palato-quadrate, and even in a 53 mm. embryo cannot be distinguished from the upper portion of the Adductor (i.e. the part above the inscriptio) except by its origin from the nasal capsule. In a 47 mm. embryo of *Heterodontus* (fig. 25) the Praeorbitalis takes origin from a lateral projection of the nasal capsule and passes backwards nearly horizontally to join the Adductor. Its adult position with nearly vertical fibres (*vide* Luther's description and figure) is thus secondary.

Teleostomi. I stated that in embryos of *Acipenser*, *Amia* and *Lepidosteus*, the mandibular muscle-plate separates into the Constrictor i. dorsalis, Adductor mandibulae and Intermandibularis, but did not describe its relations to the Gasserian ganglion and the R. mandibularis v. To determine this further material was examined.

In a 6·5 mm. embryo of *Amia* (fig. 26) the mandibular muscle-plate is a vertical plate of cells, extending from the Gasserian ganglion downwards, its lower part curves inwards, but does not reach the mid-ventral line. It is medial to the R. mandibularis v. Its upper end diverges a little backward and is partly behind the Gasserian ganglion. (This position also holds true for the younger 5·5 mm. embryo.) The ventral end of the muscle-plate is continuous with that of the hyoid muscle-plate.

In a 7·5 mm. embryo (fig. 27) the mandibular muscle-plate is partially separated into the Constrictor i. dorsalis, Adductor mandibulae, and Intermandibularis. Its upper end diverges backward and outwards relative to the Gasserian ganglion. Its lower end is separated from that of the hyoid muscle-plate.

In an 8·5 mm. embryo (fig. 28) the Palato-quadrate and Meckel's cartilage have begun to develop. The Constrictor i. dorsalis, Adductor mandibulae, and Intermandibularis are fully separated from one another. Similar developmental phenomena occur in *Acipenser* and *Lepidosteus*.

Gregory (1905) stated that in a 9·0 mm. embryo of *Ceratodus* the 2nd (mandibular) head cavity is continuous ventrally with the central cavity in the mandibular arch. The musculature of the mandibular arch separates from it in later stages of development. The relation of these structures to the Gasserian ganglion is not depicted in this stage, but Gregory's figure 21 of the 10·9 mm. stage shows the mandibular muscles extending, median to the R. mandibularis v., up to the ganglion.

I stated (1911) that the primordium of the masticatory muscles does not separate into upper and lower portions as it does in *Scyllium*, but divides into two vertical strips—the Pterygoid and Temporal muscles (called in this paper Levator mandibulae anterior and Levator m. posterior).

Dipnoi

Terminology used in this paper		
Levator mandibulae anterior	*Ceratodus*	Pterygoideus. Jaquet, Edgeworth, 1911 Portio temporalis of the Adductor mandibulae. Luther, 1913 Pseudo-temporalis s. Adductor m. internus. Luther, 1914 Temporalis. Greil, 1913
	Protopterus	Pterygoideus. Jaquet Temporalis. Owen, Pinkus, Luther, 1913 Temporal muscle. Humphry Pseudo-temporalis s. Adductor m. internus. Luther, 1914
	Lepidosiren	Temporalis Hyrtl. Bridge, Luther, 1913 Pseudo-temporalis s. Adductor m. internus. Luther, 1914
Levator mandibulae posterior	*Ceratodus*	Adductor mandibulae s. Digastricus. Jaquet Temporalis. Edgeworth, 1913 Portio lateralis of the Adductor mandibulae. Luther, 1914 Portio lateralis s. Adductor m. posterior. Luther, 1914 Masseter. Greil
	Protopterus	Masseter. Humphry, Luther, 1913 Masseter s. part of Adductor m. externus. Luther, 1914 Muscle temporalis. Jaquet
	Lepidosiren	Masseter Hyrtl, Bridge, Luther, 1913 Masseter s. part of Adductor m. externus. Luther, 1914
Levator mandibulae externus	*Protopterus*	Retractor anguli oris and Buccinatorius. Humphry Muscle labialis superior. Jaquet Retractor anguli oris. Luther, 1913 Retractor anguli oris s. part of Adductor m. externus. Luther, 1914
	Lepidosiren	Retractor labiorum. Hyrtl Retractor anguli oris superficialis and profundus. Luther, 1913 Retractor anguli oris s. part of Adductor m. externus. Luther, 1914

Greil (1913) stated that in a 5·4 mm. embryo of *Ceratodus* (with three gill-clefts reaching the ectoderm) the upper end of the mesoblast of the mandibular arch is continuous with its fellow across the mid-ventral line, and with that of the hyoid arch above and below the 1st gill-cleft. It has a notch in its upper border, in which lies the G. maxillo-mandibulare v. and a slight projection from its anterior border—the "ciliary" mesoderm. On section it shows two cavities in its upper part—the 2nd and 3rd head-cavities. The walls of the 2nd develop into the Temporal muscle, and those of the 3rd into the Masseter muscle. There are rudiments of a praemandibular gill-cleft opposite the junction of the Temporal and Masseter muscles. These muscles are consequently praemandibular and mandibular formations. The G. ophthalmicum v. belongs originally to the praemandibular, and the G. maxillo-mandibulare v. to the mandibular arch. The Processus pterygoideus is the cartilage of the praemandibular, and the Quadrate that of the mandibular arch. In a 10·9 mm. embryo there is an anterior projection from the upper end of the Temporalis, which separates and forms the Obliquus superior. The notch in the upper end of the mesoblast deepens into a groove on its external surface. The N. maxillo-mandibularis v. runs in this groove, which deepens and separates the Temporalis from the Masseter. The primordia of the Temporalis and Masseter are continuous ventrally with that of the (lateral half of the) Intermandibularis until the stage of 11·6 mm. In an embryo of 13·9 mm. they are inserted into Meckel's cartilage. The Temporalis takes origin from the spheno-lateral cartilage and the cartilaginous bridge over the Incisura sphenotica, and the Masseter from the anterior surface of the Quadrate and its otic process. In an embryo of 17·8 mm. the origins of these muscles have spread to the antero-lateral surface of the auditory capsule.

Greil's theory that the Temporalis is a praemandibular, and the Masseter a mandibular, structure is open to many objections. (1) If, as Greil states, the G. ophthalmicum v. is a praemandibular, and the G. maxillo-mandibulare v. a mandibular structure, it might be expected that the Temporalis would be innervated by the former, and the Masseter by the latter. Now, both muscles (*vide* Luther) are innervated by the latter. (2) The Processus pterygoideus Quadrati is described by Greil as a small and transitory outgrowth from the Quadrate and not as an independent chondrification, as might be expected if, as he states, it is a praemandibular structure. I have however failed to find this pterygoid process in the embryos at my disposal. (3) The notch, deepening into an external groove for the N. maxillo-mandibularis v. separates an originally single undivided mass into two parts. Thus it is single in 6 and 9 mm. embryos (figs. 29–32), separated into two masses in a 11 mm. embryo (fig. 33). (4) If the outgrowth from the endoderm interpreted as the rudiment of a praemandibular gill-cleft is really such it should at least be constant in existence and position. Now, Greil represents it as a slight bulge of the endoderm opposite the anterior edge of the mesoderm mass in a 9·8 mm. embryo (fig. 278), and opposite the middle of the mesoderm mass in a 10·2 mm. embryo (fig. 287). Further, I have not been able to find any lateral bulge of the endoderm in front of the 1st gill-cleft in embryos of respectively 6 mm. (figs. 29 and 30), 7 mm., 8 mm., 9 mm. (figs. 31 and 32), and 11 mm. (fig. 33) in length. (5) If the theory were true it should be applicable to corresponding structures in Amphibia. But I have failed, in larvae of Urodela and *Rana*, to find any trace of what might be interpreted as a praemandibular gill-cleft, or of coalescence of two mesoderm masses into the primordium of the masticatory muscles, or of evidence of formation of the pterygoid process of the Quadrate from a separate centre.

These reasons, I think, justify rejection of Greil's theory, and it may be stated that the primordium of the masticatory muscles separates into a part in front of the N. mandibularis v.—the Levator mandibulae anterior, and a part behind the nerve—the Levator mandibulae posterior. His "ciliary mesoderm" becomes the praemandibular somite—homologous with the similarly named structure in other Vertebrates.

This praemandibular segment was stated by Greil to give rise to the Recti superior and externus by two dorsal processes, and to the Rectus inferior and Obliquus inferior by a ventral process. The Obliquus superior was said to be derived from an anterior projection of the Temporalis (i.e. my Levator mandibulae anterior), which grows out in a 10·9 mm. embryo. In the figures it is represented as continuous with the Temporalis in embryos up to a length of 13·9 mm.

I find, however, that the external ocular muscles are developed somewhat differently. In an 11 mm. embryo (figs. 34–36) the praemandibular somite is an epithelium lined cavity internal to the under half of the eye, i.e. behind the ii. nerve, with a concave external wall next the eye and a convex medial wall, and horns projecting above and below the eye. The Recti superior, internus and externus, are present as primordia—thickenings of the convex medial wall of the cavity, the Rectus superior of the upper horn, the Rectus externus of the junction of the floor and the posterior wall. The Obliquus superior is proliferated from, but still continuous with, the upper wall of the dorsal horn. From this point it projects forwards and inwards.

In a 12 mm. embryo (fig. 37) the Obliquus inferior is proliferated from the ventral horn.

In a 12·5 mm. embryo all the muscles are quite distinct and formed. Figs. 38 and 39 show their appearance as seen from above and below. The Rectus internus is the muscle called Rectus inferior by Greil. I hold it to be an Internus as it passes from the trabecular wall outwards and forwards below the ii. nerve to the Bulbus oculi, to which it is attached below the Obliquus inferior. It is opposite the Rectus externus and not opposite the Rectus superior.

I cannot find any evidence that the Obliquus superior is formed from an anterior projection of the Temporalis muscle as is stated by Greil to be the case in embryos from 10·9–13·9 mm. in length. Thus, in the 11 mm. embryo I have depicted there is a gap of ·08 mm. between the Obliquus superior and the anterior surface of the Levator mandibulae anterior, and, as stated above, the Obliquus superior at this stage is still continuous with the wall of the praemandibular somite.

All the ocular muscles are thus formed from the convex medial wall of the praemandibular somite—the Recti superior, internus, and externus, from thickenings of the wall, the two Obliqui from cells proliferated from it.

In Protopterus and Lepidosiren there are, a Levator mandibulae anterior, Levator mandibulae posterior, and Levator mandibulae externus, the last mentioned being represented in Protopterus by the Retractor anguli oris and in *Lepidosiren* by two muscles—the Retractor anguli oris superficialis and profundus. The development is not yet known for Agar's investigation did not extend to that of the individual muscles derived from the mandibular muscle plate. He stated that in stage 30 the future eye muscles are represented by a dense concentration of heavily yolked mesenchyme round the optic vesicle, which is continued by a narrow strand to the rudiment of the temporal muscle and can be traced further back curving in somewhat towards the middle line. There was no connection between this and the concentration of mesenchyme in the hyoid arch. No mention was made of a separate outgrowth from the dorsal end of the temporal muscle to form an Obliquus superior.

It would thus appear that in Dipnoi all the external ocular muscles are formed from the premandibular somite—an unexpected support of the theory I advanced in 1911 (*vide supra*, p. 226).

Luther was of opinion that the masticatory muscles of Dipnoi are collectively the homologue of the Adductor mandibulae of Selachii and Teleostomi. The above-cited observations of Gregory and Greil, however, show that the primordium of the masticatory muscles of *Ceratodus* has precisely the same relations to the R. mandibularis v. and the Gasserian ganglion as has the primordium of the Constrictor i. dorsalis l. Adductor mandibulae in *Scyllium* and *Amia*, i.e. it lies median to the nerve with its upper end close to the ganglion. Nor did these observers describe or depict the separation of any, subsequently atrophying, portion from the upper end of the primordium. I have, too, failed to discover it in embryos from the length of 6 mm. upwards.

It follows that the masticatory muscles of *Ceratodus*, and so probably of *Protopterus* and *Lepidosiren*, are collectively the homologue of the Constrictor i. dorsalis+Adductor mandibulae of *Scyllium* and *Amia*, and not solely of the Adductor.

Another terminology is therefore adopted, corresponding to the primitive position of the muscles relative to the R. mandibularis v.—Levatores mandibulae anterior and posterior.

Luther pointed out the homology in all three animals of the muscle here termed Levator m. anterior, but his opinion in regard to the other masticatory muscles differs from that adopted here. He thought that whilst in *Ceratodus* there is an Adductor m. posterior (here called Levator m. posterior), on the other hand in *Protopterus* and *Lepidosiren* there is no Adductor m. posterior but only an Adductor m. externus.

Comparison, however, of the developmental stages of *Ceratodus* with the figures given by Luther would make it probable that whereas in *Ceratodus* the Levator m. posterior lies in early stages posterior to the R. mandibularis v. and subsequently hypertrophies and bulges forward lateral to the nerve (cf. figs. 33 and 40); on the other hand, in *Protopterus* and *Lepidosiren*, the Levator m. posterior retains its primitive position posterior to the nerve.

Luther was of opinion that the Retractor anguli oris of *Protopterus* (and its homologues in *Lepidosiren*) is a part of (his) Adductor m. externus. He subsequently pointed out its homology with (his) Adductor m. externus of Urodela. Now the latter muscle (which I call Levator m. externus) is developed from the Levator m. anterior (*vide infra*), so that it is possible that a similar development will be found to occur in these Dipnoi.

No definite opinion, however, in regard to these matters is possible until the development is known.

Urodela. Luther[1] distinguished the following muscles, which he classified according to their relationship to the branches of the vth nerve.

Named employed in this paper	*Luther's names*
Levator bulbi	Levator bulbi
Levator m. anterior (anterior to V_3)	Adductor m. anterior (rostral or medial to V_2 and V_3)
Levator m. posterior (medial or caudal)	Adductor m. posterior (caudal to V_3)
Levator m. externus (lateral to V_3)	Adductor m. externus (lateral to V_2 and V_3)

The Adductor m. anterior was further subdivided by Luther into the Pseudotemporalis and Pterygoideus.

Scott and Osborn (1879) stated that in Triton the section of the pleuro-peritoneal cavity in front of the first gill-cleft becomes separated into two portions, each of which is lined by a columnar epithelium. The anterior portion lies close to the optic vesicle, whilst the posterior is enclosed entirely in the mandibular arch. The subsequent development was not followed.

Miss Platt (1897) stated that in 11 mm. embryo of *Necturus* (the first stage described) the mesothelial tissue of the mandibular arch is dorsally separate from that of the hyoid arch and passes directly into mesenchyme; ventrally it unites with that of the hyoid arch. The upper part divides into an external portion, the masseter (= A.m. externus, of Luther), and an internal portion, the temporalis (= A.m. internus posterior, of Luther), whilst the ventral part becomes the mylohyoid. The relations of these structures to the Gasserian ganglion and to V_3 were not described, nor was the development of the ocular muscles followed.

In a 15 mm. larva of *Menopoma* (figs. 53–55) the primordium of the masticatory and Intermandibularis muscles is a dorso-ventral strip of cells in front of the 1st gill-cleft. Its upper end is lateral to the Gasserian ganglion. It passes down internal to the R. mandibularis v. Its ventral end is continuous with that of the hyoid muscle-plate. The anterior edge of the upper part of the muscle-plate is continuous with the premandibular somite[2]. The cells of the latter are crowded with yolk-granules.

---

[1] Luther gave a complete list of the names employed by previous writers, which it is not necessary to quote.

[2] The development of the ocular muscles could not be followed owing to defective fixation of the younger larvae. I hope to do this later.

In a larva of 16 mm. (figs. 56–58) the muscle-plate has separated into the masticatory muscle-plate and the Intermandibularis. The premandibular somite has separated from the former. The relations of the muscle-plate to the R. mandibularis v are as in the previous stage.

In a larva of 20 mm. (figs. 59–61) the primordium of the masticatory muscles still forms a continuous whole. Its dorsal end extends up to the Crista trabeculae. The Levator bulbi is formed as an outgrowth from the anterior surface of the primordium—i.e. from the part which forms the Levator mandibulae anterior—at the level of the inferior border of the eye and slightly below the middle of the primordium. The outgrowth is ·03 mm. thick, it is ·36 mm. below the upper end and ·26 mm. above the lower end of the primordium. From the lower part of the primordium there is a backward outgrowth external to the R. mandibularis v. This is the Levator mandibulae externus. It extends upwards towards the otic process of the Quadrate which is beginning to form.

In a larva of 24 mm. (fig. 62) the Levatores m. anterior, posterior, and externus have separated from one another. The Levator m. anterior takes origin from the Crista trabeculae, the Levator m. posterior from the Quadrate, and the Levator m. externus from the otic process. The Levator bulbi has separated from the Levator m. anterior and forms a thin plate of cells below the eye.

In a larva of 28 mm. (fig. 63) the Levator bulbi has extended outwards, and also inwards towards the Trabecula.

There is a similar development of the Levator bulbi as an outgrowth of the anterior surface of the Levator m. anterior, in 16 mm. larvae of *Hynobius* and in 23 mm. larvae of *Triton cristatus.*

Anura. Luther distinguished the following muscles, which he classified according to their relationship to the R. mandibularis.

Names employed in this paper		*Luther's names*
Levator bulbi		Levator bulbi
Levator mandibulae anterior (anterior to V_3)		Pterygoideus s. Adductor m. internus (medial to V_2 and V_3)
Primordium of	Levator mandibulae externus (lateral to V_3)	Adductor m. externus (lateral to V_3)
	Levator mandibulae anterior subexternus	Adductor m. posterior subexternus
	Levator mandibulae anterior lateralis	Adductor m. posterior lateralis
	Levator mandibulae anterior articularis	Adductor m. posterior articularis
Levator mandibulae posterior (superficialis and profundus) (posterior to V_3)		Adductor m. posterior (superficialis and profundus)

Luther stated that in a 7-day *Bombinator* larva (? length) the precartilaginous Palato-quadrate is at right angles to the long axis of the body, with a Proc. muscularis, a Proc. ascendens, and a Commissura quadrato-cranialis anterior. The originally undivided primordium of the masticatory muscles has separated into a more superficial portion caudal to V_3—the Adductor mandibulae posterior, and an inner layer medial to V_3—medial to V_3 the Pterygoideus. The outer layer is a continuous one, being marked only by the different origins of the fibres—from the Pars metapterygoidea the Adductor posterior longus profundus and superficialis, and from the Processus muscularis the Adductor posterior subexternus, lateralis, and articularis. These muscle-primordia have, as already pointed out by Goette, an almost vertical position which closely resembles that of the adult. A rotation subsequently occurs so that they lie almost horizontally with the original upper ends posterior and the original lower ends anterior.

In an 8 mm. larva of *Rana temp.* (figs. 67, 68) the mandibular muscle-plate is in a vertical position, at right angles to the longitudinal axis of the body. Its upper end is medial to the lower end of the Gasserian ganglion. The R. mandibularis passes down lateral to the muscle-plate for a little distance.

In a 9 mm. larva (figs. 69, 70) the muscle-plate has separated into dorsal and ventral portions, the masticatory muscle-plate and the Intermandibularis. The upper end of the former is close to the Gasserian ganglion, as in the previous stage. It passes downwards and forwards below the eye, at about 45° to the longitudinal axis of the body. It is partially separated into the Levator mandibulae anterior and Levator m. posterior.

In a 9·5 mm. larva (figs. 71–75) the masticatory muscle-plate is nearly in a horizontal position so that what was anterior is now dorsal, and what was posterior is now ventral. It is fully separated into Levator m. anterior and Levator m. posterior. As these muscles are traced forwards it is seen that they have a mutual twist, so that in front the Levator m. anterior is below ("morphologically" posterior to) the Levator m. posterior. The R. mandibularis v. passes over the Levator m. posterior, obliquely forwards and downwards. The posterior ("morphologically" dorsal) part of the Levator m. posterior is partially separated into the Levator m. posterior superficialis and Levator m. p. profundus. Two outgrowths are given off from the lateral side of the front end of the Levator m. anterior—the primordium of the Levatores m. anterior subexternus, articularis, and lateralis below ("morphologically" posterior to) the R. mandibularis v. and the Levator m. externus above ("morphologically" anterior to) the nerve. These outgrowths occur from the lower part of the Levator m. anterior which is overlapped by the Levator m. posterior.

In a larva of 10 mm. (fig. 76) these outgrowths have separated. The primordium of the Levator bulbi is in process of being proliferated from the upper ("morphologically" anterior) surface of the Levator m. anterior. It extends over ·04 mm. and is situated under the eye, rather above the middle of the Levator m. anterior—this muscle extending ·2 mm. behind and ·33 mm. in front of the primordium.

In a larva of 11 mm. (fig. 77) the primordium of the Levator bulbi is separated from the Levator m. anterior. It can be seen in succeeding stages up to one of 20 mm. (fig. 78) in much the same condition. In a larva of 21 mm. (fig. 79) in which the hind legs are just visible externally, the Levator bulbi has greatly developed and spread, dorso-internally towards the side wall of the Chondrocranium, and externally under the eye.

As stated above, Goette and Luther showed that in *Bombinator* larvae the primordium of the masticatory muscles begins to separate into muscles before the forward movement of its lower end occurs. I find that in a larva of 8 mm. (figs. 80–83) the primordium is situated vertically and has separated into Levator m. anterior and Levator m. posterior, and the latter is beginning to divide into its superficialis and profundus portions. The dorsal end of the Levator m. anterior is anterior, and that of the Levator m. posterior is posterior, to the R. mandibularis v. As the muscles are traced down it is seen that they mutually twist round one another, so that ventrally the Levator m. anterior is posterior to the Levator m. posterior. In a larva of 9 mm. the shifting forwards of the lower ends of these muscles has taken place and the condition approximates to that of *Rana*.

Gymnophiona. Luther distinguished the following muscles:

Names employed in this paper	*Luther's names*
Compressor glandulae orbitalis	Compressor glandulae orbitalis
Levator mandibulae anterior	Pseudotemporalis Adductor externus
Levator quadrati	Levator quadrati
Levator mandibulae externus	Adductor m. externus minor
Levator mandibulae posterior	Pterygoideus

Marcus (1909 and 1910) stated that the primordium of the mandibular muscles in stages 20 and 24 of *Hypogeophis* is continuous dorsally with the 2nd or mandibular somite. Its upper end, in these stages, lies immediately beneath the G. maxillo-mandibulare v. In stage 28 the mandibular somite has separated from the primordium of the masticatory muscles. The former was said to develop into the Rectus superior, Rectus inferior, Obliquus inferior and perhaps the Rectus internus. The development of the primordium of the masticatory muscles was not followed.

The Obliquus superior was said to develop from the lateral plate of the premandibular somite. The 3rd somite was said to develop into the Rectus externus, Retractor tentaculi and perhaps the Rectus internus.

The development of the Compressor glandulae orbitalis was not followed.

Norris and Hughes (1913) stated that the Compressor glandulae orbitalis is innervated by a branch of the R. mandibularis v. in *Dermophis*, *Herpele* and *Geotrypetes*[1].

In a 28·5 mm. larva of *Ichthyophis*—the youngest available—(figs. 92–94) the primordia of the masticatory muscles consist of aggregates of round and spindle-shaped cells. There are as yet no muscle fibres. The R. mandibularis v. passes outwards above the pterygoid process of the Quadrate, and then downwards outside Meckel's cartilage. In front of this nerve is the Levator m.

---

[1] They further add that the statement of Marcus that this muscle is innervated by the iii. is obviously an error. I cannot find, however, that Marcus did make this statement.

anterior, behind it the Levator m. posterior. The Levator m. anterior is a triangular mass, the upper edge of which is just outside the Taenia marginata and, posteriorly, just beneath the upper part of the ascending process of the Quadrate. The posterior edge is vertical. The apex is close to Meckel's cartilage. The primordium of the Levator quadrati is present on the inner surface of the Levator m. anterior, from which it is not quite separated. It slopes downwards and backwards towards the pterygoid process of the Quadrate. The Levator m. posterior passes downwards from the ascending process towards Meckel's cartilage. It is far less in size than the Levator m. anterior.

In a larva of stage 2 (figs. 95–97) (a larva of which the tail was broken off and the length of which could not be determined but which in development was intermediate between the 28·5 and the 35 mm. larvae) the primordium of the Compressor glandulae orbitalis has developed. It is a column of cells which is posteriorly continuous with the anterior surface of the Levator m. anterior, and projects forwards for a little distance. The Levator quadrati is fully separated from the inner surface of the Levator m. anterior. The posterior end of the Levator m. anterior projects backwards external to the R. mandibularis v. and the Levator m. posterior. This is the primordium of the Levator m. externus. The Levator m. posterior has an additional head from the pterygoid process of the Quadrate and the pterygoid bone.

In a 35 mm. embryo (figs. 98, 99) the Levator quadrati has an additional insertion into the pterygoid bone. The Levator m. posterior is partially separated into two, corresponding to its primary and secondary heads of origin; the latter fibres pass downwards and backwards.

In a 59 mm. embryo (fig. 103) the Compressor glandulae orbitalis has separated from the Levator m. anterior. The upper end of the latter has spread backwards over the parietal bone. The Levator m. externus is a separate muscle. The lower, secondary, head of the Levator m. posterior, arising from the pterygoid process and the Pterygoid bone, passes backwards on the medial side of the jaw towards the extremity of the retroarticular process.

In the adult stage (*vide* Luther), the primary head of the Levator m. posterior from the ascending process has disappeared.

The masticatory muscles of a 70 mm. larva of *Siphonops* (figs. 84–89) resemble those of the 59 mm. larva of *Ichthyopis*, with the following exceptions. (1) The Levator m. anterior has no origin from the ascending process of the Quadrate. (2) The primary head of the Levator m. posterior from the ascending process of the Quadrate—presumably present in earlier stages—has disappeared, and only the secondary head of the muscle exists—taking origin from the pterygoid process of the Quadrate, the basipterygoid process and the os basale.

Discussion. Luther was of the opinion that the Levator bulbi of Urodela and Anura, and the Levator quadrati and Compressor glandulae orbitalis of Gymnophiona, are the homologues of the Constrictor i. dorsalis of Elasmobranchs and Teleostomi; whilst the jaw muscles of Amphibia are (collectively) the homologue of the Adductor mandibulae of these fishes.

Now, in *Menopoma, Hynobius, Triton cristatus,* and *Rana temp.* the Levator bulbi is formed from cells proliferated from the anterior surface of the Levator anterior, whilst in just earlier stages no trace of these cells is visible. On Luther's theory it should have been possible to detect a primordium becoming detached from the dorsal end of the primordium of the masticatory muscles and moving down to the position it occupies. This was not found. Further, if Luther's theory were true it should be found that the Levator quadrati and Compressor glandulae orbitalis of *Ichthyophis* are developed from a common primordium of the masticatory muscles and then separating into two—one passing to a position internal to the Levator anterior to form the Levator quadrati, and the other to a position in front of it to form the Compressor glandulae orbitalis. This was not found. The Levator quadrati is separated from the internal surface of the Levator anterior and the Compressor glandulae orbitalis is proliferated from its anterior surface. It is concluded that Luther's theory is not tenable.

Further, it is observable that the primordium of the masticatory muscles in *Menopoma, Hynobius, Rana,* and *Ichthyophis* extends from the Gasserian ganglion to the jaw just as does that of the Constrictor i. dorsalis + Adductor mandibulae in *Scyllium* and *Amia.*

The primordium of the masticatory muscles of these Amphibia is thus homologous with that of the Constrictor i. dorsalis + Adductor mandibulae, and not solely with the latter. The terms Levatores mandibulae are consequently employed instead of Adductores mandibulae. In this respect Amphibia are very like *Ceratodus.* The resemblance between the primordium of the masticatory muscles of Amphibia and *Ceratodus* extends to the muscles into which it develops. In Dipnoi the masticatory muscles can be classified according to their relationship to the R. mandibularis v. into Levatores m. anterior, posterior, and externus. The same thing is true of Amphibia—as was also pointed out by Luther. The developmental phenomena, however, suggest some modification of his opinions.

In early stages of *Menopoma* the primordium of the masticatory muscles is median to the R. mandibularis v., extending in front of and below the nerve. It separates into Levatores m. anterior and posterior. The Levator m. externus is formed by outward and backward growth from the Levator m. anterior external to the nerve. The Levator bulbi is proliferated from the anterior surface of the Levator m. anterior.

Determination of the homologies of the masticatory muscles of *Rana* with those of Urodela is rendered a little difficult by three facts: (1) Their primordium begins to separate into individual muscles during the forward movement of the lower end. (2) The lower parts of the Levator m. anterior and Levator m. posterior twist round one another so that the ventral end of the Levator m. anterior is below ("morphologically" posterior to) that of the Levator m. posterior. (3) The R. mandibularis v. crosses over the Levator m. posterior obliquely forwards and downwards.

In the larva of *Bombinator*, however, the primordium of the masticatory muscles separates into the Levator m. anterior and Levator m. posterior whilst the primordium is still in a vertical position, so that determination of their morphological value becomes possible. It is seen that the lower ends of the Levators twist round one another. The insertion of the Levator m. anterior, posterior to that of the Levator m. posterior, is thus not related to the secondary horizontal position of the muscles in the larva. It persists in the adult stage of Anura (*vide* the description and figure of Luther).

The Levator m. externus of *Rana* is proliferated from the lateral surface of the Levator m. anterior and grows backwards and outwards above (i.e. "morphologically" anterior to) the R. mandibular v. exactly as in *Menopoma*. The primordium of the Levatores m. subexternus, lateralis, and articularis is proliferated from the lateral surface of the Levator m. anterior below (i.e. "morphologically" posterior to) the R. mandibularis v.

Owing to the mutual twist of the lower ends of the Levatores m. anterior and posterior, the Levator m. externus and the primordium of the Levatores m. subexternus, lateralis, and articularis are proliferated from the Levator m. anterior below ("morphologically" posterior to) the Levator m. posterior.

These developmental phenomena show that the Levatores subexternus, lateralis, and articularis cannot be regarded as portions of the Levator m. posterior—as was thought by Luther (his terms being, of course, "Adductores").

The Levator bulbi is proliferated from the anterior surface of the Levator m. anterior, as in *Menopoma*, *Hynobius* and *Triton*.

As regards Gymnophiona, the muscle here called Levator m. anterior corresponds to Luther's Pseudo-temporalis + Adductor m. externus. He stated that his Adductor m. externus is homologous with the similarly named muscle of Urodela and Anura. But it is difficult to believe this, for—as he himself states—it lies anterior and not external to the R. mandibular v. Further, in transverse sections of these larvae of *Ichthyophis* and *Siphonops* I failed to find any separation of the muscle-mass in front of the R. mandibular v. into two portions. The Ri. maxillaris v. and buccalis pierce it from behind forwards, but the muscle-fibres are in apposition above and below those nerves. There is thus only one muscle, the Levator m. anterior, and the separation into medial and lateral parts described by Luther and by Norris and Hughes is of late development.

The Levator quadrati is separated from the inner surface of the Levator m. anterior. It is not formed dorsal to the Levator m. anterior and subsequently move down to its permanent position—as would be the case if it were homologous with the Constrictor i. dorsalis of Selachii and Teleostomi. It has no homologue in Urodela, not even in those Urodela which become semi-streptostylic.

The Compressor glandulae orbitalis is proliferated from the anterior surface of the Levator m. anterior, just as is the Levator bulbi of Anura and

Urodela. It has no genetic association with the Levator quadrati, as Luther supposed. The recent determination of its innervation by Norris and Hughes from the R. mandibularis v. in *Dermophis, Herpele,* and *Caecilia,* agrees with this.

Luther stated that there is no Adductor m. posterior in Gymnophiona, and that the "Pterygoideus" is homologous with the similarly named muscle of Urodela. Now the Pterygoideus of Urodela is one of the subdivisions of the Levator m. anterior, whilst the "Pterygoideus" of Gymnophiona is the Levator m. posterior, which acquires a secondary origin from the Pterygoid process and Pterygoid bone, whilst its insertion extends back to the end of the retroarticular process. I therefore regard the "Pterygoideus" of Luther as homologous with the Levator m. posterior of Urodela and Anura.

The muscle here termed Levator externus is identical with the Adductor externus minor of Luther. He stated that it is probably part of his Adductor externus, the separation being due to the passage of a couple of sensory nerves between the two portions. He added that it might be homologous, perhaps only analogous, with the Adductor posterior lateralis of Anura. I find that it is an outgrowth from the Levator anterior, lateral to the R. mandibularis v., just as in *Menopoma* and *Rana,* and consequently regard it as a Levator externus.

The above can be summed up in the following table:

	Levator mandibulae anterior	Levator mandibulae externus	Levator bulbi or Compressor glandulae orbitalis	Levator quadrati	Levator mandibulae posterior
Ceratodus	+	0	0	0	+
Protopterus	+	+	0	0	+
Lepidosiren	+	+	0	0	+
Urodela	+	+	+	0	+
Anura	+	+	+	0	+
Gymnophiona	+	+	+	+	+

Comparison of the masticatory muscles of Dipnoi and Amphibia brings out the following points:

The Levator m. anterior is large and simple in Dipnoi. It separates into the Pseudo-temporalis and Pterygoideus, of Luther, in Urodela. It gives off the primordium of the Levatores m. subexternus, lateralis, and articularis, in Anura. It separates into two parts at a late stage in Gymnophiona. This separation is not homologous with that which takes place in Urodela.

The Levator m. externus is absent in Ceratodus, and quite small in *Protopterus, Lepidosiren,* Anura and Gymnophiona. It is greatly developed in Urodela.

The Levator m. posterior is large in Dipnoi, especially in Ceratodus. It is much less developed in Urodela, Anura, and Gymnophiona. In the last-mentioned group the original head from the ascending process of the Quadrate is lost during development and a secondary one gained.

The Levator quadrati of *Ichthyophis* and *Siphonops* has no homologue in Dipnoi, Urodela or Anura. Its formation is related to the development of streptostylism. The development of semistreptostylism in some genera of Urodela is not associated with any change in the masticatory muscles[1] nor with the formation of a Levator quadrati—a fact which when taken into association with the scattered distribution of semistreptostylism in Urodela (*vide* table, p. 236) harmonises with the theory deduced from the skeletal evidence that the conditions of streptostylism in Gymnophiona and of semistreptostylism in Anura and some Urodela have been separately acquired in these families of Amphibia from an ancestral condition of monimostylism.

The argument in the above pages may be summed up as follows. In Selachii and Teleostomi the primordium of the masticatory muscles separates into dorsal and ventral parts—the Constrictor i. dorsalis and Adductor mandibulae. In Dipnoi and Amphibia it does not so divide into dorsal and ventral parts, but separates into dorso-ventral strips. The monimostylism which the skeletal evidence suggests as the primary condition in Dipnoi and Amphibia is related to this non-division of the primordium of the masticatory muscles into dorsal and ventral parts. The Levator bulbi of Urodela and Anura and the Compressor glandulae orbitalis of Gymnophiona are homologous structures, developed from cells proliferated from the anterior surface of the Levator mandibulae anterior. In Gymnophiona the secondary development of streptostylism is associated with the separation of a fasciculus from the medial surface of the Levator mandibulae anterior to form a Levator quadrati.

On the supposition, which is supported by the above-recorded phenomena, that Dipnoi and Amphibia have sprung from a common autostylic, monimostylic, stock, it is of interest to make comparison of the various cranial cartilages and muscles to ascertain in which groups the more primitive features occur.

Dipnoi are more primitive than Amphibia in:

1. The site of attachment of the basal process of the Quadrate.
2. The presence of an Epihyale (in *Ceratodus*).
3. The absence of a Fenestra vestibuli.
4. The condition of the hyoid muscles—consisting as they do of a Levator hyoidei), Interhyoideus, and Opercularis s. Constrictor hyoideus[2]. On the other hand, in Amphibia there is no Opercularis, and the Levator hyoidei

---

[1] It should be noted, however, that Luther states that in the adult condition of *Hynobius* and *Salamandrella* (which are semi-streptostylic) some fibres of the Levator bulbi are inserted into the pterygoid process of the Quadrate. This is of late development, e.g. it is not present in a 37 mm. larva of *Hynobius* in which the basal joint had already developed.

[2] According to Ruge the Levator hyoidei (C2 hd) is present in *Protopterus* but has almost entirely disappeared in *Ceratodus*—only the few bundles passing to the Hyomandibulare (the cartilage I call "Interhyale") can be regarded as its remains. I find, however, that it is in the adult a well-marked muscle passing, partially medial to the outer limb of the Interhyale, from the under surface of the auditory capsule to the apex and posterior edge of the Keratohyale. I do not find any fibres passing to the Interhyale. The condition is thus similar to that present in a 27 mm. embryo.

gains, in part or wholly, an insertion into the hind end of the lower jaw, forming a Depressor mandibulae.

5. The condition of the Constrictores branchiales (only known however in Ceratodus).
6. The number of Transversii ventrales.
7. The presence of a 5th branchial bar and musculature.
8. The condition of the laryngeal muscles.

Amphibia are more primitive than Dipnoi in:

1. The presence in some of a well-marked pterygoid process of the Quadrate, joining the Trabecula.
2. The number of the Subarcuales recti.
3. The absence of any backward extension of the hind end of the Genio-hyoideus (so that a Genio-coracoideus or Genio-thoracius is not formed).
4. The situation of the larynx, i.e. does not shift backwards.
5. The absence of a Constrictor oesophagi et laryngis.

Two features (1) the absence of a Levator mandibulae externus in Ceratodus, and (2) the absence of an ascending process of the Quadrate in *Lepidosiren* and *Protopterus*—are of doubtful phylogenetic significance. The first mentioned may perhaps be primary.

ON THE RELATIONSHIP OF THE QUADRATE AND MASTICATORY MUSCLE OF ELASMOBRANCHII AND TELEOSTOMI WITH THOSE OF DIPNOI AND AMPHIBIA.

Swinnerton (1902), from his observations on the development of the skull of *Gasterosteus* and other Teleostomi, suggested that Elasmobranchii and Teleostomi sprang from a common ancestral stock with a Quadrate "bearing dorsally two, possibly three, processes; an anterior one, parallel with its fellow, and not united with it, but with the ethmoid plate, so that a moveable upper jaw did not exist; a middle one articulating with the trabecula, in the region lying between the optic and trigeminal nerves; a posterior one articulating with the auditory capsule." He did not take the masticatory muscles into consideration, nor did he make any reference to Dipnoi or Amphibia.

In 1911 I suggested a similar theory based on comparison of the development of the masticatory muscles in Elasmobranchii, Teleostomi, Dipnoi, and Amphibia. It differed from Swinnerton's in that the middle and posterior connections were supposed to be continuous, so that the Palato-quadrate was fixed to the Chondrocranium at three points. I now restate the theory, with additions due to later work.

Scyllium is hyostylic. In a 23 mm. embryo (fig. 12) the Trabeculae are not yet developed, and the (continuous) primordium of the Palato-quadrate and Meckel's cartilage is not connected with any other structure. In a 29 mm. embryo (fig. 13) the Palato-quadrate is chondrified; the primordium of the spiracular cartilage is formed as a procartilaginous upgrowth of the hind end of the Palato-quadrate[1]. In a 35 mm. embryo (figs. 14–17) the antorbital process of the chondrocranium is formed; its antero-internal end is continuous with the Trabecula, and the roof of the nasal capsule. From this point it extends postero-externally. Its posterior end is continuous with the Palato-quadrate. The nasal roof itself has no relations with the Palato-quadrate, which at this stage does not extend so far forwards. The primordium of the spiracular cartilage is separated from the Palato-quadrate. In a 53 mm. embryo (figs. 18–20), in which the cartilages are more fully chondrified, the posterior end of the antorbital process has extended further backwards. Its antero-internal end is still continuous with the Trabecula and the roof of the nasal capsule. A ligament passes from the back of the nasal roof to the dorsal surface of the Palato-quadrate, and another from the lateral edge of the antorbital cartilage to the Palato-quadrate. The spiracular cartilage is chondrified. The anterior end of the Palato-quadrate has extended further forward and meets its fellow.

There is thus in early stages a cartilaginous continuity between the Palato-quadrate and the antorbital process of the chondrocranium. This degenerates into a ligament.

Acanthias is streptostylic and amphistylic. The basal process of the Palato-quadrate articulates with the Trabecula. Sewertzoff showed that this basal joint is preceded by a continuity of the basal process with the Trabecula.

Notidanus (*Heptanchus*) is autostylic and streptostylic. Gegenbaur stated that the otic process articulates with the postorbital process of the cranium and that the basal process articulates with the cranium by a "Palato-Basal-gelenk." Huxley subsequently stated that the basal process is attached to the cranium by a strong ligamentous band. The basal connection is thus variable in character.

I find that in a 58 mm. embryo the basal joint with the Trabecula is already formed. The otic process of the Palato-quadrate and the post-orbital process of the chondrocranium are separated by a small gap filled with mesenchyme. In a 70 mm. embryo the postorbital joint has developed[2].

The postorbital joint is thus not preceded by any cartilaginous continuity. The basal joint may be so preceded, but earlier stages were not available.

Heterodontus (*Cestracion*) is amphistylic. Huxley stated that the huge Palato-quadrate is united to the skull in the praeorbital region by a joint, and in the orbital region by fibrous tissue. "An otic process, or spiracular cartilage, is connected to the periotic cartilage above and to the quadrate below the ligament."

---

[1] Six embryos of *Scyllium* of 29–30 mm. were cut before finding this. The other embryos were not old enough or too old to show the continuity of the primordium of the spiracular cartilage with the Palato-quadrate. The process of formation and budding off probably takes but a short time. These occurrences are merely an illustration of the fact that size is not an exact criterion of stage of development. They may explain the failure of Dohrn to find that the spiracular cartilage is formed from the Palato-quadrate.

[2] It is well seen in a model of this chondrocranium lately made by my colleague Dr Henderson.

I find that in a 47 mm. embryo (figs. 24, 25) the anterior end of the Palato-quadrate is in contact with the Trabecula. The primordium of the spiracular cartilage is a dorsal procartilaginous process of the hinder end of the Palato-quadrate. The upper end of the Hyomandibula articulates with the lower surface of the auditory capsule, and its lower end with the Palato-quadrate and Meckel's cartilage. The chondrocranium is very immature, and the Trabecula is nearly at right angles to the Parachordal. Older embryos were not available.

Ganoids. Acipenser is hyostylic. Parker stated that this condition is developed at a very early stage (8·5–9·5 mm. embryos) and that there is no connection with the chondrocranium. My observations confirm this.

Polyodon is hyostylic. The development is not yet known. Bridge stated that the Palato-quadrate has no connection with the cranium either directly or by ligament, but is suspended by its posterior extremity from the distal end of the Symplectic, to which it is attached by two slender ligaments.

Polypterus is hyostylic. Budgett stated that in a 30 mm. embryo the anterior end of the Palato-quadrate articulates with a facet on the ventral side of the nasal capsule.

Amia is amphistylic. The Pars palatina of the Quadrate articulates with the Planum ethmoidale, is tied to the Trabecula by a basipterygoid ligament and to the hinder wall of the orbit by a ligament. In a 19 mm. embryo (Swinnerton) the Palato-quadrate has a large basal process projecting towards the Trabecula, and the latter has a slight lateral process. The anterior end abuts against the Planum ethmoidale. I can confirm these statements.

Lepidosteus is amphistylic. In development (Parker, Veit) the anterior end of the Palato-quadrate is united to the Cornu trabeculare by cartilage (Parker), or firm connective tissue (Veit). Further back, the Palato-quadrate is united to the Trabecula by embryonic cartilage in which a basal joint subsequently develops (Veit). Later on, an otic process is developed and projects towards but does not reach the auditory capsule (Parker).

Teleostei. In *Gymnarchus* (Assheton) the Pars palatina of the Palato-quadrate is continuous with the Trabecula by precartilaginous tissue, and the Pars quadrata articulates with the auditory capsule (= an otic process). In *Gasterosteus* (Swinnerton) the Pars palatina articulates, and in some stages is continuous, with the side of the ethmoid plate. In many Teleostei, e.g. *Belone, Zoarcia, Salmo*, there is a basal process projecting from the Quadrate towards the Trabecula (Swinnerton). The mode of suspension is hyostylic only posteriorly, but autostylic anteriorly.

It would appear, therefore, that the Palato-quadrate is continuous with the Chondrocranium in some genera of Selachii and Teleostomi at two points—anteriorly and in the middle, corresponding to the anterior and basal continuities of Amphibia. Further, there is an otic process in *Heptanchus, Lepidosteus*, and *Gymnarchus*. In *Heptanchus* it articulates with the postorbital process of the auditory capsule, in *Lepidosteus* it approaches but does not touch, or articulate with, the auditory capsule, in *Gymnarchus* it articulates with it[1].

Dohrn stated that the spiracular cartilage is of independent formation in *Scyllium*, *Pristiurus*, *Mustelus*, *Raja*, and *Torpedo*. But in *Scyllium*, as shown above, it is formed as a procartilaginous outgrowth of the hind end of the Palato-quadrate and subsequently separates and chondrifies. Similarly, in *Heterodontus* it is formed as a procartilaginous outgrowth of the Palato-quadrate. This evidence shows that, as Huxley suggested, the spiracular cartilage is homologous with the otic process.

Gegenbaur was of opinion that the articulation of the otic process of *Heptanchus* with the post-orbital process represents the primary articulation with the Chondrocranium, whilst the basal connection is secondary. Huxley was of the reverse opinion. Luther held that the post-orbital connection is not an ancestral feature. It only occurs in certain groups, "in which the independently preformed processes came into connection with one another." This theory evidently does not offer any explanation of the otic process—a process which is of ancient origin, for Luther states that there are many fossil forms as far back as the oldest Selachians known in which there is an apposition ("Anlegen") or union of the Quadrate with the post-orbital process.

Comparison of the whole series of forms—Amphibia, Dipnoi, *Gymnarchus*, *Lepidosteus*, *Heptanchus*—suggests the existence of an ancestral continuity of the otic process with the outer surface of the auditory capsule, and that the joint with the post-orbital process of the last named is a secondary phenomenon. In development the post-orbital process is formed at a later stage than the auditory capsule.

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 to the Trabecula by a basal process. The otic process was probably fused with the auditory capsule. This condition was lost and a streptostylic one 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.

The development of a moveable Pterygo-quadrate was probably correlated with the formation of a Constrictor i. dorsalis, i.e. with a division of the primordium of the masticatory muscles into dorsal and ventral portions —the Constrictor i. dorsalis and Adductor mandibulae. The ontogenetic phenomena in *Scyllium* and *Amia* have been described above.

There are certain skeletal and muscle differences between these various groups. (1) In *Amia*, *Polypterus*, *Lepidosteus*, and Teleostei, the anterior process of the Quadrate, just as in Amphibia, does not extend further forwards than its connection with the Chondrocranium; whereas in the majority of

---

[1] Assheton did not state whether the articulation was preceded by a continuity of tissue.

Selachii, in Batoidei, *Acipenser*, and *Polyodon*, it is prolonged anteriorly, nearly or quite meeting its fellow. To mark this difference the former condition—probably the primary one—might be called a Pterygo-quadrate, the latter a Palato-quadrate. In successive developmental stages of *Acanthias*, *Scyllium*, and *Acipenser*, the anterior end of the bar can be seen extending forwards until finally it meets its fellow. (2) No Processus ascendens has been described in Selachii, Batoidei, and Teleostomi, whereas one is developed in *Ceratodus* and Amphibia. The latter condition is probably a later phylogenetic development. (3) In Selachii and Teleostomi the primordium of the masticatory muscles lies in early stages median to the R. mandibularis v. and shows no trace of division either then or subsequently into parts in front of and behind the nerve. On the other hand, in Dipnoi and Amphibia, the primordium of the masticatory muscles separates into parts in front of and behind the nerve, i.e. Levator m. anterior and Levator m. posterior. This division is probably a later phylogenetic development.

Holocephali are monimostylic, the Palato-quadrate fusing with the Chondrocranium during development (Schauinsland, Dean). There is no Constrictor i. dorsalis. The masticatory muscles were described by Vetter and by Luther in terms of an Adductor mandibulae. If it could be shown that a Constrictor i. dorsalis exists in early developmental stages and subsequently atrophies, this would confirm their opinion, and also be evidence that the monimostylic condition is secondary and not primary. But the material for such an investigation was not available.

It is interesting to observe that the Pterygo-quadrate is fixed in Cyclostomata. In *Petromyzon* (Parker) the Pterygo-quadrate is continuous with the Chondrocranium by a basal process, and by one with the ethmoid region of the skull. In *Myxine* (Cole) the Pterygo-quadrate is continuous with the Trabecula by two bars, and its anterior continuation—the palatine—by a third bar. In *Bdellostoma* (Ayers and Jackson) the Pterygo-quadrate articulates with the auditory capsule, is continuous with the palatine, and from the junction, projects a process which is continuous with the Trabecula.

It would thus appear that, whatever the genealogical relationship of the Cyclostomata and Gnathostomata may be, the former have sprung from forms with a fixed Pterygo-quadrate.

I have the pleasure of thanking Dr Henderson for the loan of an embryo of *Scyllium* and a larva of *Amblystoma*; D. P. F. Murray, Esq. for embryos of *Heterodontus*; Dr Bancroft for embryos of *Ceratodus*; Prof. de Lange for larvae of *Bombinator* and *Ichthyophis*; Dr Dunn for larvae of *Desmognathus*, *Spelerpes* and *Plethodon*; Prof. Sewertzoff and Prof. Schmalhausen for larvae of *Salamandrella* and *Ranodon*, and the latter also for adult specimens of both these Urodeles.

I am also indebted to Mr Emery, laboratory steward, for efficient help in making the models, and to Miss Cross for the drawings of them. The expenses were met by a grant from the Colston Research Society.

April 7, 1924.

DESCRIPTION OF FIGURES

In any figures of sections of the same specimen the lowest number indicates the most anterior or the most dorsal section, as the case may be.

Scyllium canicula. Figs. 1–20.

Figs. 1–5. Embryo 14 mm. long, horizontal sections.
Figs. 6, 7. Embryo 17 mm. long; model fig. 6 seen from without; fig. 7 seen from within.
Figs. 8–11. Embryo 20 mm. long, horizontal sections.
Fig. 12. Embryo 23 mm. long, model seen from without.
Fig. 13. Embryo 29 mm. long, transverse section. The section is slightly oblique and cuts the primordium of the spiracular cartilage on the left side, whilst it is in front of it on the right.
Figs. 14–17. Embryo 35 mm. long, transverse sections.
Figs. 18–20. Embryo 53 mm. long, transverse sections.

Squalus acanthias. Figs. 21–23.

Figs. 21–23. Embryo 22 mm. long, horizontal sections; fig. 21 is the most dorsal.

Heterodontus. Figs. 24, 25.

Figs. 24, 25. Embryo 47 mm. long, drawings of model. Fig. 24 is of the left side; fig. 25 of the right side showing the mandibular muscles. Anteriorly the cartilage passes into procartilage at the dotted line, and this gradually into connective tissue. The anterior limit of the Chrondrocranium is thus indefinite. The primordium of the spiracular cartilage and the upper part of the auditory capsule is also procartilaginous. There is no post-orbital process.

Amia calva. Figs. 26–28.

Fig. 26. Embryo 6·5 mm. long, drawing of model showing the mandibular and hyoid muscles from the side.
Fig. 27. Embryo 7·5 mm. long, the same.
Fig. 28. Embryo 8·5 mm. long, transverse section.

Ceratodus forsteri. Figs. 29–40.

Figs. 29, 30. Embryo 6 mm. long, horizontal sections.
Figs. 31, 32. Embryo 9 mm. long, horizontal sections.
Fig. 33. Embryo 11 mm. long, horizontal sections.
Figs. 34–36. Embryo 11 mm. long, transverse section. There is a distance of ·08 mm. between figs. 34 and 35. Fig. 36 depicts the section next behind that in fig. 35.
Fig. 37. Embryo 12 mm. long, transverse section.
Figs. 38, 39. Embryo 12·5 mm. long, drawings of model of ocular muscles. Fig. 38 from above; fig. 39 from below.
Fig. 40. Embryo 19 mm. long, horizontal section. The section is slightly oblique, sloping from the middle line outwards and slightly downwards.

Amblystoma punctatum. Fig. 41.

Fig. 41. Larva 13·5 mm. long, horizontal section.

Desmognathus fuscus. Fig. 42.

Fig. 42. Larva 19 mm. long, transverse section.

Plethodon cinereus. Figs. 43, 44.

Fig. 43. Adult 25 mm. long, transverse section.
Fig. 44. Adult 49 mm. long, transverse section.

Salamandrella Keyserlingii. Figs. 45–50.

Fig. 45. Larva 13·5 mm. long, horizontal section.
Figs. 46, 47. Larva 17 mm. long, drawings of model of chondrocranium.
Fig. 48. Larva 17 mm. long, transverse section.
Fig. 49. Larva 22·5 mm. long, transverse section.
Fig. 50. Larva 34 mm. long, transverse section.

Ranodon sibiricus. Figs. 51, 52.

Figs. 51, 52. Larva 25 mm. long, drawings of model of chondrocranium.

Menopoma alleghaniense. Figs. 53–63.

Figs. 53–55. Larva 15 mm. long, horizontal sections; 53 is the most dorsal.
Figs. 56–58. Larva 16 mm. long, horizontal sections; 56 is the most dorsal.
Figs. 59, 60. Larva 20 mm. long, horizontal sections; 59 is the more dorsal.
Fig. 61. Larva 20 mm. long, drawing of model of masticatory muscles from the outside.
Fig. 62. Larva 24 mm. long, transverse section.
Fig. 63. Larva 28 mm. long, transverse section.

Necturus maculatus. Figs. 64–66.

Figs. 64, 65. Embryo 25 mm. long, transverse section; 64 is the more anterior.
Fig. 66. Embryo 30 mm. long, drawing of model of chondrocranium from below.

Rana temp. Figs. 67–79.

Figs. 67, 68. Larva 8 mm. long, horizontal sections; 67 is the more dorsal.
Figs. 69, 70. Larva 9 mm. long, sagittal sections; 69 is the more external.
Fig. 71–75. Larva 9½ mm. long, transverse sections; 71 is the most anterior.
Fig. 76. Larva 10 mm. long, transverse section.
Fig. 77. Larva 11 mm. long, transverse section.
Fig. 78. Larva 20 mm. long, transverse section.
Fig. 79. Larva 21 mm. long, transverse section.

Bombinator. Figs. 80–83.

Figs. 80–83. Larva 8 mm. long, horizontal sections; 80 is the most dorsal.

Siphonops braziliensis. Figs. 84–89.

Figs. 84–89. Larva 70 mm. long, transverse sections; 84 is the most anterior.

Ichthyophis glutinosus. Figs. 90–103.

Figs. 90, 91. Larva 28·5 mm. long, drawings of model of chondrocranium; 90 from below; 91 from outside.
Figs. 92, 93. Larva 28·5 mm. long, drawings of model of masticatory muscles; 92 from outside; 93 from inside.
Fig. 94. Larva 28·5 mm. long, transverse section.
Figs. 95–97. Larva stage 2 (of development intermediate between the 28·5 and 35 mm. larvae), transverse sections; 95 is the most anterior.
Figs. 98–102. Larva 35 mm. long, transverse sections; 98 is the most anterior: there is a distance of ·04 mm. between 100 and 101, and of ·05 mm. between 101 and 102.
Fig. 103. Larva 59 mm. long, transverse section.

ABBREVIATIONS

Add. mand.	Adductor mandibulae
ant. orb. proc.	antorbital process
asc. proc. Quad.	ascending process of Quadrate
aud. caps.	auditory capsule
basal proc. Quad.	basal process of Quadrate
Branch. i.	Branchiale i.
Col. auris	Columella auris
Comp. gl. orbit.	Compressor glandulae orbitalis
Constr. i. dors.	Constrictor i. dorsalis
Dep. mand.	Depressor mandibulae
Duct. endolymph.	Ductus endolymphaticus
g. max. mand. v.	ganglion maxillo-mandibulare v.
Gass. g.	Gasserian ganglion
genic. g. vii.	geniculate ganglion vii.
geniocorac.	Genio-coracoideus
hyoid m. pl.	hyoid muscle plate
Intermand.	Intermandibularis
Keratohy. c.	Keratohyal cartilage

lat. proc. basal pl.	lateral process of basal plate
Lev. bulbi	Levator bulbi
Lev. mand. ant.	Levator mandibulae anterior
Lev. mand. ext.	Levator mandibulae externus
Lev. m. ant. {subext. lat. art.} prim. of	primordium of Levatores mandibulae anterior subexternus lateralis and articularis
Lev. mand. post.	Levator mandibulae posterior
Lev. m. post. prof.	Levator mandibulae posterior profundus
Lev. m. post. superf.	Levator mandibulae posterior superficialis
Lev. quad.	Levator quadrati
ling. m.	lingual muscles
mand. gloss.	Mandibulo-glossus
mand. m. pl.	mandibular muscle plate
mast. m. pl.	masticatory muscle plate
max. pal. b.	maxillo-palatine bone
N. alv. v.	Nervus alveolaris v.
N. alv. vii.	Nervus alveolaris vii.
N. bucc. vii.	Nervus buccalis vii.
N. hypogloss.	Nervus hypoglossus
N. mand. v.	Nervus mandibularis v.
N. max. v.	Nervus maxillaris v.
Orbit. hyoid	Orbito-hyoideus
Obliq. inf.	Obliquus inferior
Obliq. sup.	Obliquus superior
Otic pr. Quad.	Otic process of Quadrate
Pal. quad.	Palato-quadrate
Paraquad. b.	Paraquadrate bone
Pariet. b.	Parietal bone
Plan. internus	Planum
Praeorb.	Praeorbitalis
praefacial com.	praefacial commissure
praemand. som.	praemandibular somite
proc. musc. Quad.	processus muscularis of Quadrate
ptery. b.	pterygoid bone
R. alv. v.	Ramus alveolaris v.
R. alv. vii.	Ramus alveolaris vii.
R. mand. v.	Ramus mandibularis v.
R. max. v.	Ramus maxillaris v.
R. max. mand. v.	Ramus maxillo-mandibularis v.
R. oph. prof. v.	Ramus ophthalmicus profundus v.
R. oph. superf. vii.	Ramus ophthalmicus superficialis vii.
R. post N. intermand. v.	Ramus posterior of Nervus intermandibularis v.
Spir. cart.	Spiracular cartilage
Sub. arc. R. i.	Subarcualis rectus i.
Suspens. ceratohy. and Quadang.	primordium of Suspensorio-ceratohyoideus and Quadrato-angularis
Suspen. hyoid.	Suspensorio-hyoideus
Taenia marg.	Taenia marginata
Trab.	Trabecula
R. max. ext. v.	Ramus maxillaris externus v.
Tr. hyomand. vii.	Truncus hyomandibularis vii.
Roman numerals	Cranial nerves

LITERATURE

Agar, W. E. (1905–6). "The development of the skull and visceral arches in Lepidosiren and Protopterus." *Trans. Roy. Soc. Edin.* vol. xlv.

—— (1907). "The development of the anterior mesoderm and paired fins with their nerves in Lepidosiren and Protopterus." *Ibid.* vol. xlv.

Assheton, R. (1907). "The development of Gymnarchus niloticus." *The work of John Samuel Budgett.* Cambridge.

Ayers, H. and Jackson, C. M. "Morphology of the Myxinoidei. 1. Skeleton and Musculature." *Univ. of Cincinnati Bulletin,* No. 1.

Bridge, T. W. (1878). "On the Osteology of Polyodon folium." *Phil. Trans. Roy. Soc.* vol. clxix.

—— (1898). "On the Morphology of the Skull in the Paraguayan Lepidosiren and in other Dipnoids." *Trans. Zool. Soc.* vol. xiv.

Budgett, J. S. (1902). "On the structure of the larval Polyterus." *Trans. Zool. Soc.* vol. xvi.

Cole, F. J. (1898). "A monograph on the general morphology of the Myxinoid fishes, based on a study of Myxine. Part I. The anatomy of the skeleton." *Trans. Roy. Soc. Edin.* vol. xi, part iii.

Dean, Bashford (1906). "Chimaeroid Fishes and their Development." *Carnegie Institution of Washington Publication,* No. 32.

Dohrn, A. (1885). "Entstehung und Differenzirung des Zungenbein- und Kiefer-Apparates der Selachier." *Mitt. a. d. Zool. Stat. zu Neapel,* Bd. vi, Hft. 1.

—— (1904 a). "Die Mandibularhöhle der Selachier." *Ibid.* Bd. xvii.

—— (1904 b). "Die Praemandibularhöhle." *Ibid.* Bd. xvii.

Dollo, L. (1895–6). "Sur la phylogénie des Dipneustes." *Bull. de la Société Belge de Géologie,* Tome ix.

Edgeworth, F. H. (1911). "On the morphology of the cranial muscles in some vertebrates." *Quart. Journ. Micros. Sc.* vol. lvi.

—— (1923). "On the Quadrate in Cryptobranchus, Menopoma and Hynobius." *Journ. of Anat.* vol. lvii, part iii.

—— (1923). "On the development of the Hypobranchial, Branchial and Laryngeal muscles of Ceratodus. With a note on the Quadrate and Epihyal." *Quart. Journ. Micr. Sc.* vol. lxvii, part iii.

Fürbringer, K. (1904). "Beiträge zur Morphologie des Skelets der Dipnoer nebst Bemerkungen über Pleuracanthiden, Holocephalen, und Squaliden." *Denkschr. Naturf. Ges. Jena.*

Gaupp, E. (1905). "Die Entwickelung des Kopfskelettes." *Hertwig's Handbuch.*

Gegenbaur, C. (1872). "Untersuchungen zur vergleichenden Anatomie der Wirbelthiere." Drittes Heft. *Das Kopfskelet der Selachier.* Leipzig.

Goodrich, E. S. (1909). *A treatise on Zoology.* Edited by Sir Ray Lankester. Part ix. Vertebrata craniata. (First fascicule. Cyclostomes and Fishes.)

Gregory, E. U. (1905). "Die Entwickelung der Kopfhöhlen und des Kopfmesoderm bei Ceratodus." *Semon's Forschungsr.* Liefg. v.

Greil, A. (1908). "Entwickelungsgeschichte des Kopfes und Blutgefäss-systeme von Ceratodus forsteri." Erster Theil. "Gesammtentwickelung bis zum Beginn der Blutcirculation." *Semon's Forschungsr.* Bd. i.

—— (1913). *Ibid.* Zweiter Theil. "Die epigenetischen Erwerbungen während der Stadien 39–48." *Ibid.* Bd. i.

Guthke, E. (1907). "Embryologische Studien über die Ganglien und Nerven des Kopfes von Torpedo ocellata." *Jen. Zeitschr. f. Naturw.* Bd. xlii.

Hoffmann, C. K. (1896). "Beiträge zur Entwickelungsgeschichte der Selachii." *Morph. Jahrb.* xxiv, 2.

Humphry, G. M. (1872). "The Muscles of Ceratodus." *Journ. of Anat. and Phys.* vol. vi.

—— (1872). "The Muscles of Lepidosiren annectens, with the cranial Nerves." *Ibid.*

Huxley, T. H. (1876). "Contributions to Morphology. Ichthyopsida. No. 1. On Ceratodus forsteri, with observations on the classification of Fishes." *Proc. Zool. Soc.*

Hyrtl, J. (1845). *Lepidosiren paradoxa.* Prag.

JAQUET, M. (1897–9). "Contribution à l'anatomie comparée des Systèmes squelettaire et musculaire de Chimaera collei, Callorhynchus antarcticus, Spinax niger, Protopterus annectens, Ceratodus forsteri, et Axolotl." *Archives méd. Bucarest,* Tomes II–V.

KERR, J. G. (1907). "The development of Polypterus senegalis Cuv." *The Work of John Samuel Budgett.* Cambridge.

KLINKHARDT, W. (1905). "Beiträge zur Entwickelungsgeschichte der Kopfganglien und Sinneslinien der Selachier." *Jen. Zeitschr. f. Naturw.* Bd. XL.

LAMB, A. B. (1901). "The development of the Eye-muscles in Acanthias." *Studies from the Biological Laboratories of Tuft's College,* No. XXIX.

LUTHER, A. (1909). "Untersuchungen über die vom N. trigeminus innervierte Muskulatur der Selachier." (Haie und Rochen.) *Acta Soc. Scient. fennicae,* Tome XXXV.

—— (1909). "Beiträge zur Kenntnis von Muskulatur und Skelett des Kopfes des Haies Stegostoma tigrinum gm. und der Holocephalen." *Ibid.* Tome XXXVII.

—— (1913). "Ueber die vom N. trigeminus versorgte Muskulatur der Ganoiden und Dipneusten." *Ibid.* Tome XLI, No. 9.

—— (1914). "Ueber die vom N. trigeminus versorgte Muskulatur der Amphibien mit einem vergleichenden Ausblick über den Adductor mandibulae der Gnathostomen und einem Beitrag zur Verständnis der Organisation der Anurenlarven." *Ibid.* Tome XLIV, No. 7.

MARCUS, H. (1909 and 1910). "Beiträge zur Kenntnis der Gymnophionen. III. Zur Entwickelunggeschichte des Kopfes." I Teil. *Morph. Jahrb.* Bd. XL, Heft I. II Teil. *Festschr. zum sechzigsten Geburtstag R. Hertwig,* Bd. II.

MARSHALL, M. (1881). "On the Head-cavities and associated nerves of Elasmobranchs." *Quart. Journ. Micr. Sc.* vol. XXI.

NEAL, H. V. (1909). "The morphology of the Eye-muscle nerves." *Proc. Intern. Cong. Boston* (1907). Separate pub. 1909.

—— (1914). "The morphology of the eye-muscle nerves." *Journ. Morph.* vol. XXV.

—— (1918). "The history of the eye-muscles." *Ibid.* vol. XXX.

NORRIS, H. W. and HUGHES, Miss S. P. (1918). "The Cranial and Anterior Spinal Nerves of the Caecilian Amphibians." *Journ. Morph.* vol. XXXI.

PARKER, W. K. (1882). "On the Structure and Development of the Skull in Sturgeons (Acipenser ruthenus and A. sturio)." *Phil. Trans. Roy. Soc.* vol. CLXXIII.

—— (1882). "On the Development of the Skull in Lepidosteus osseus." *Ibid.*

—— (1882). "On the structure and development of the skull in Urodeles." *Trans. Zool. Soc.* vol. XI.

—— (1883). "On the skeleton of the Marsipobranch Fishes." *Trans. Roy. Soc.* vol. CLXXIV.

PEETERS, J. L. E. (1910). *Over de Ontwikkeling van het Chondrocranium en de Kraakbeenige Wervelkolom van eenige Urodela en Anura.* Leiden.

PETER, K. (1898). "Die Entwicklung und funktionelle Gestaltung des Schädels von Ichthyophis glutinosus." *Morph. Jahrb.* XXV, 4.

PINKUS, F. (1895). "Die Hirnnerven des Protopterus annectens." *Schwalbe's Morph. Arbeiten,* Bd. IV.

PLATT, Miss J. B. (1897). "The development of the cartilaginous skull and of the branchial and hypoglossal musculature in Necturus." *Morph. Jahrb.* Bd. XXV.

—— (1901). "A contribution to the morphology of the vertebrate head based on a study of Acanthias vulgaris." *Journ. Morph.* vol. V.

POLLARD, H. B. (1892). "On the anatomy and phylogenetic position of Polypterus." *Zool. Jahrb. Abth. f. Anat. u. Ontog.* Bd. V.

SARASIN, P. and F. (1890). *Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon.* II. Wiesbaden.

SCHAUINSLAND, H. (1903). *Beiträge zur Entwickelungsgeschichte und Anatomie der Wirbeltiere.* I. Stuttgart.

SCOTT, W. B. and OSBORN, H. F. (1879). "On the early development of the common Newt." *Quart. Journ. Micr. Sc.* vol. XIX, New Ser.

SEWERTZOFF, H. (1899). "Die Entwicklung des Selachierschädels." *Festschr. f. Kuppfer.*

—— (1902). "Zur Entwickelungsgeschichte des Ceratodus Forsteri." *Anat. Anzeig.* Bd. XXI.

SOLLAS, W. J. (1920). "Structure of Lysorophus as exposed by serial sections." *Phil. Trans. Roy. Soc.* Ser. B, vol. CCIX.

SWINNERTON, H. H. (1902). "A study of the developing skull in the Three-spined Stickleback (Gasterosteus aculeatus)." *Quart. Journ. Micr. Sc.* vol. XLV.

VEIT, O. (1911). *Die Entwickelung des Primordialcranium von Lepidosteus osseus.* Wiesbaden.

VERSLUYS, J. (1912). "Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden." *Zool. Jahrb. Supplement,* XV, 2 Bd.

WIEDERSHEIM, R. (1877). "Das Kopfskelet der Urodelen." *Morph. Jahrb.* Bd. III.

v. WIJHE, J. W. (1882). "Ueber die Mesodermsegmente und die Entwickelung der Nerven des Selachierkopfes." *Verh. Kon. Akad.* Dl. XXII.

WINSLOW, G. M. (1898). "The Chondrocranium in the Ichthyopsida." *Tuft's College Studies,* No. 5. Reprinted from the *Bull. of the Essex Institute,* vol. XXVIII.

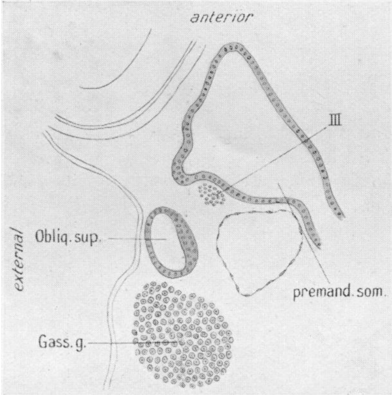

Fig. 1

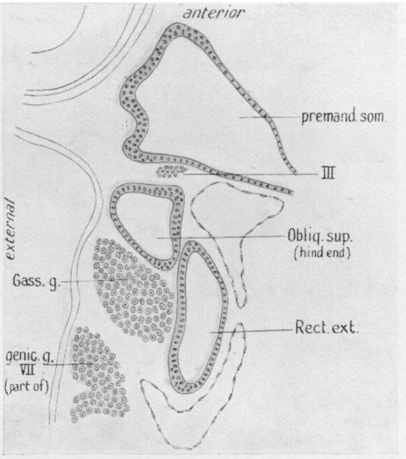

Fig. 2

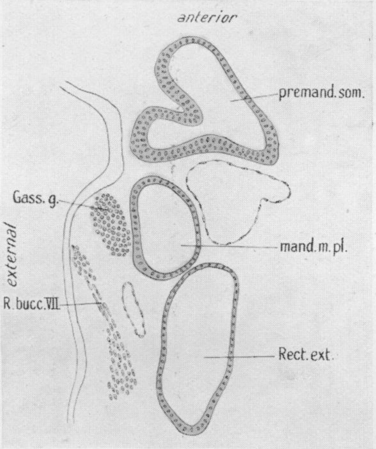

Fig. 3

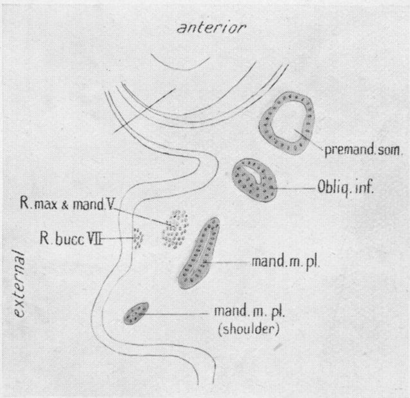

Fig. 4

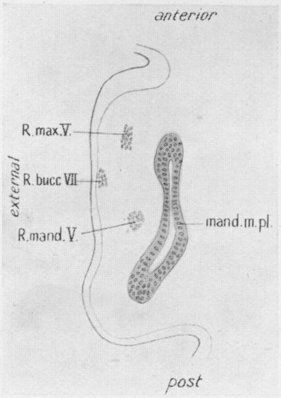

Fig. 5

EDGEWORTH—ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

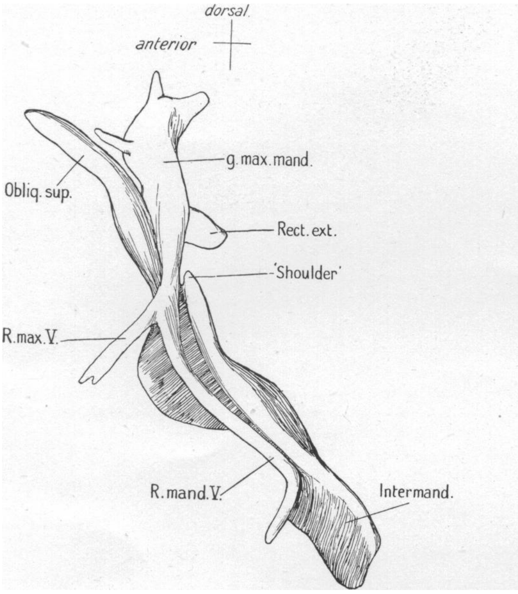

Fig. 6

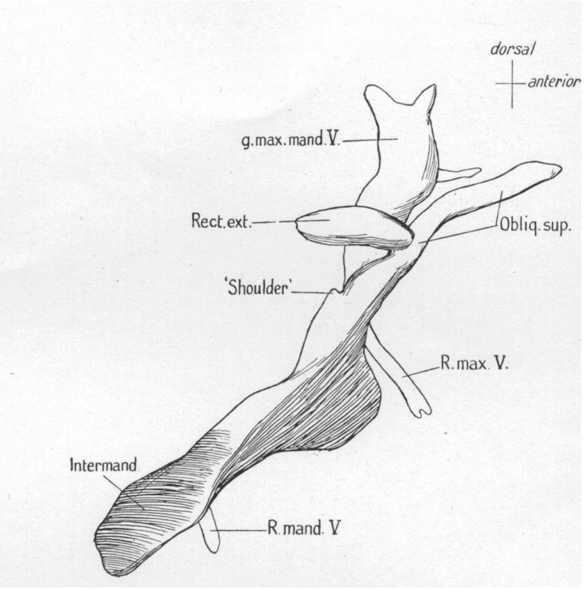

Fig. 7

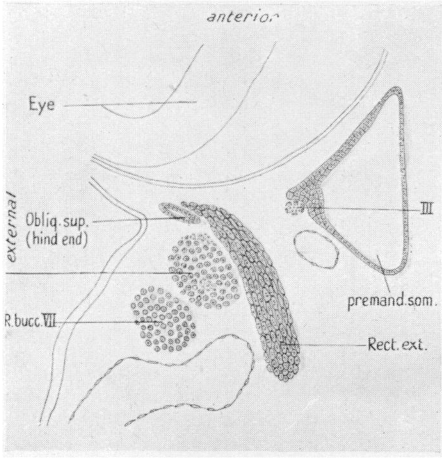

Fig. 8

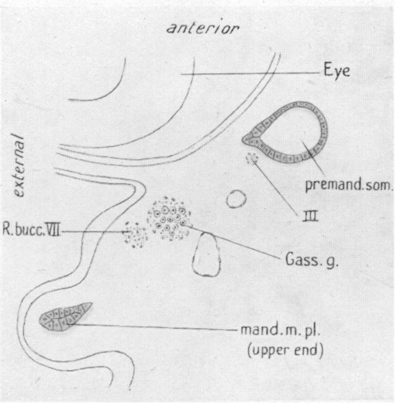

Fig. 9

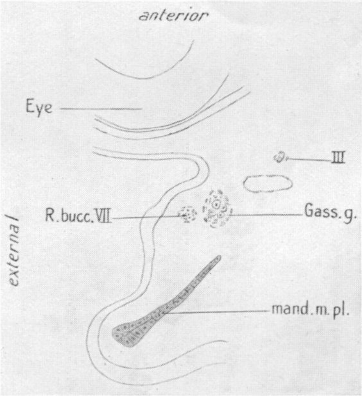

Fig. 10

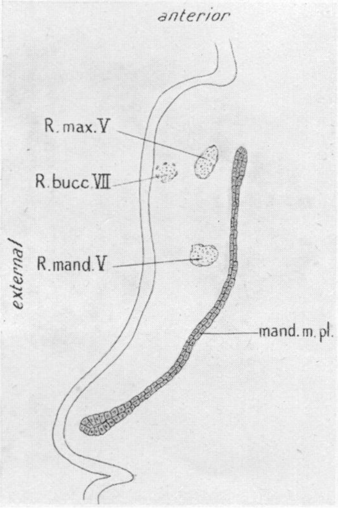

Fig. 11

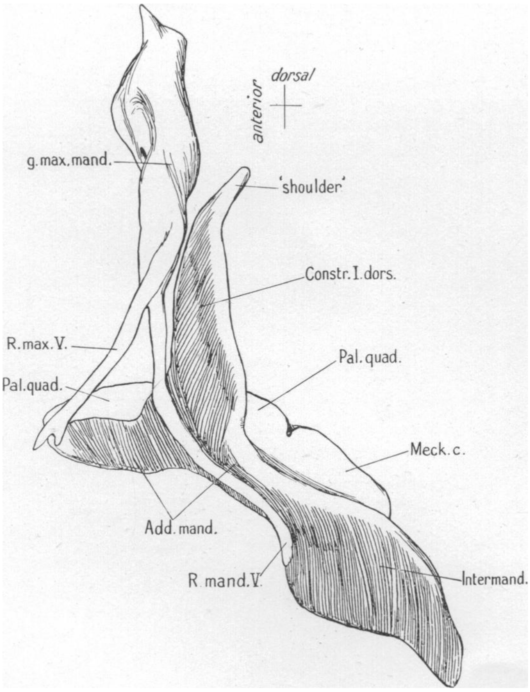

Fig. 12

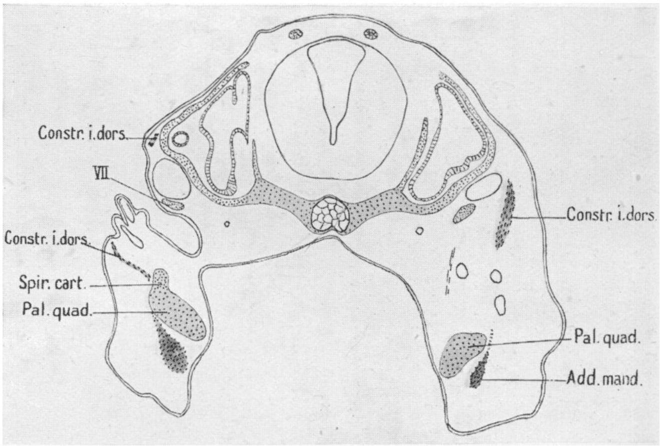

Fig. 13

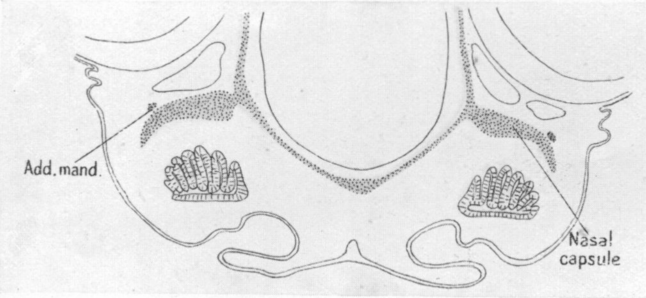

Fig. 14

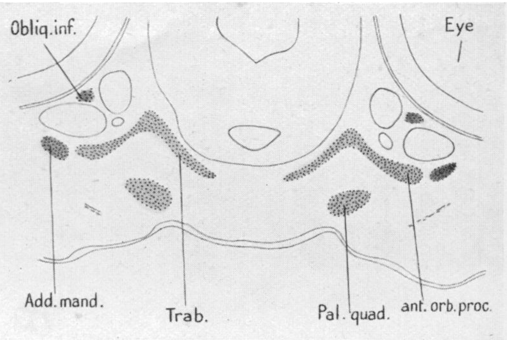

Fig. 15

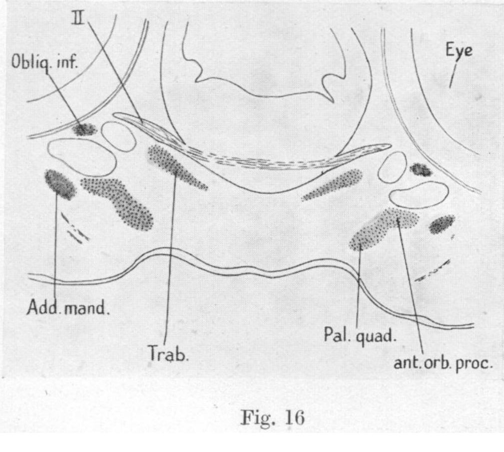

Fig. 16

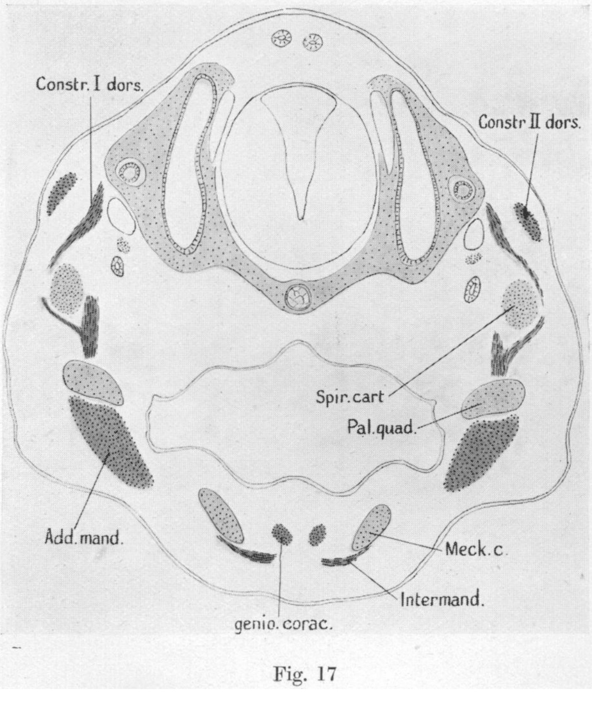

Fig. 17

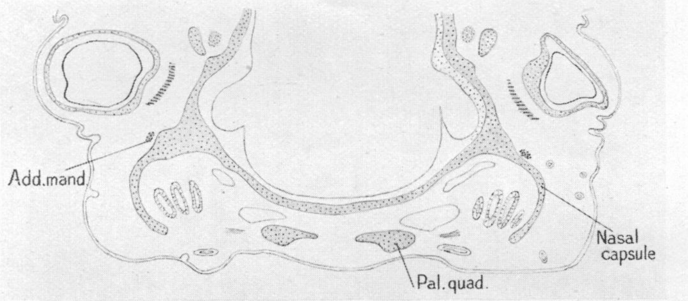

Fig. 18

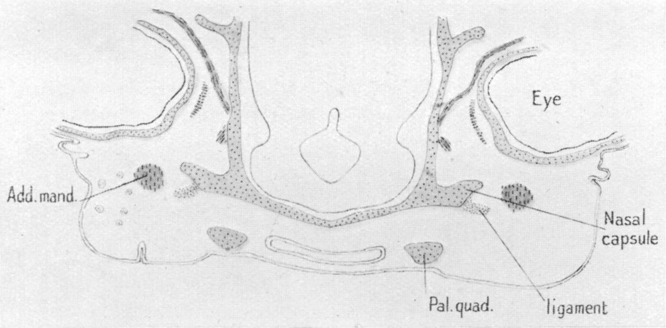

Fig. 19

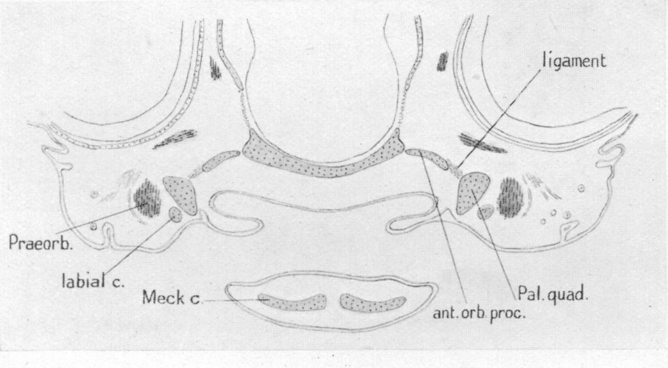

Fig. 20

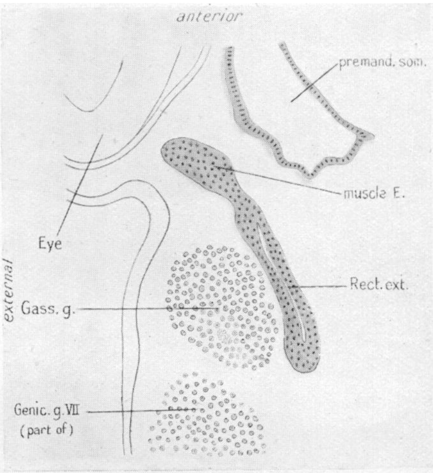

Fig. 21

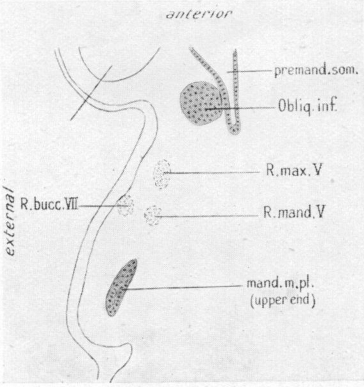

Fig. 22

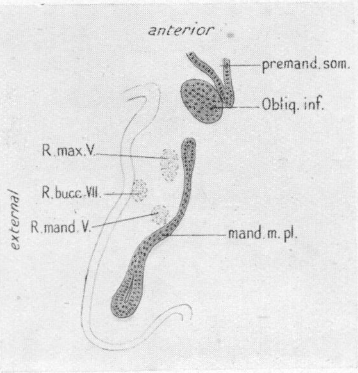

Fig. 23

EDGEWORTH—ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

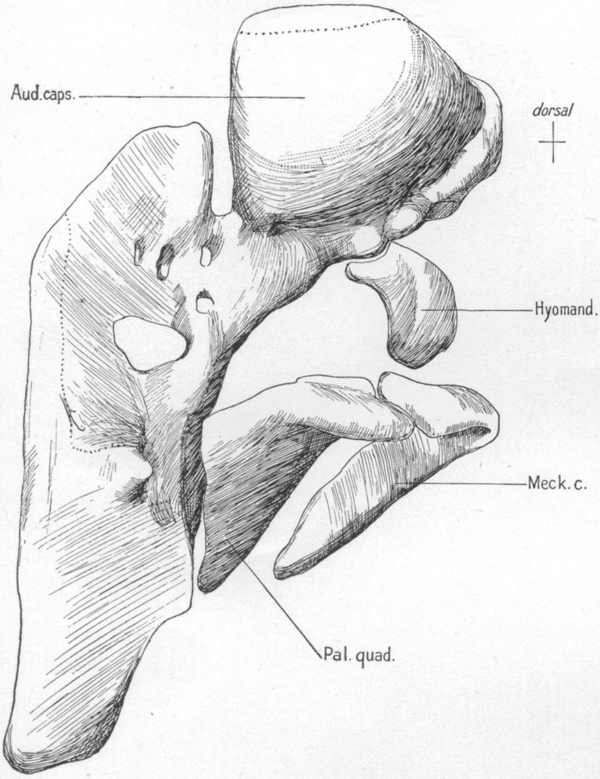

Fig. 24

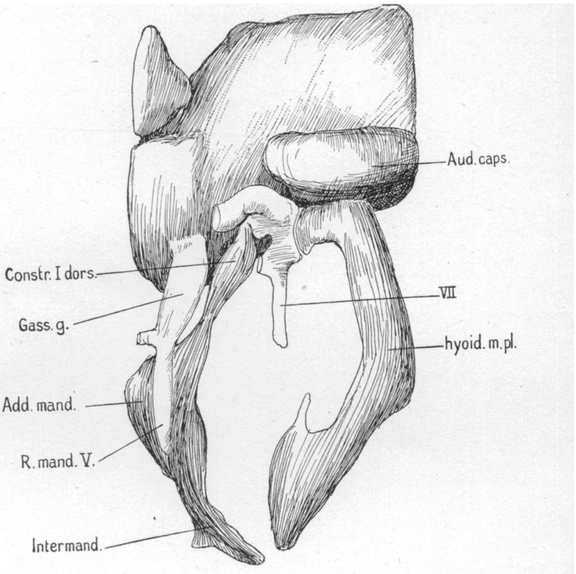

Fig. 26

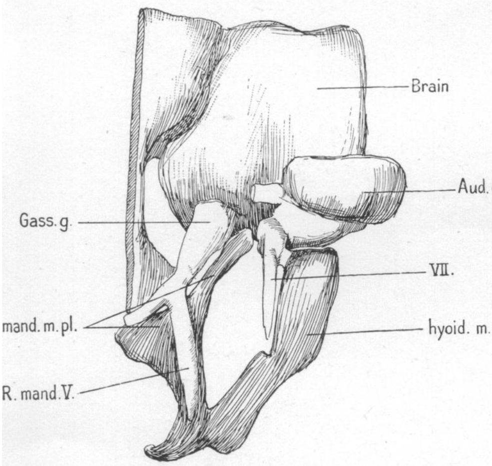

Fig. 27

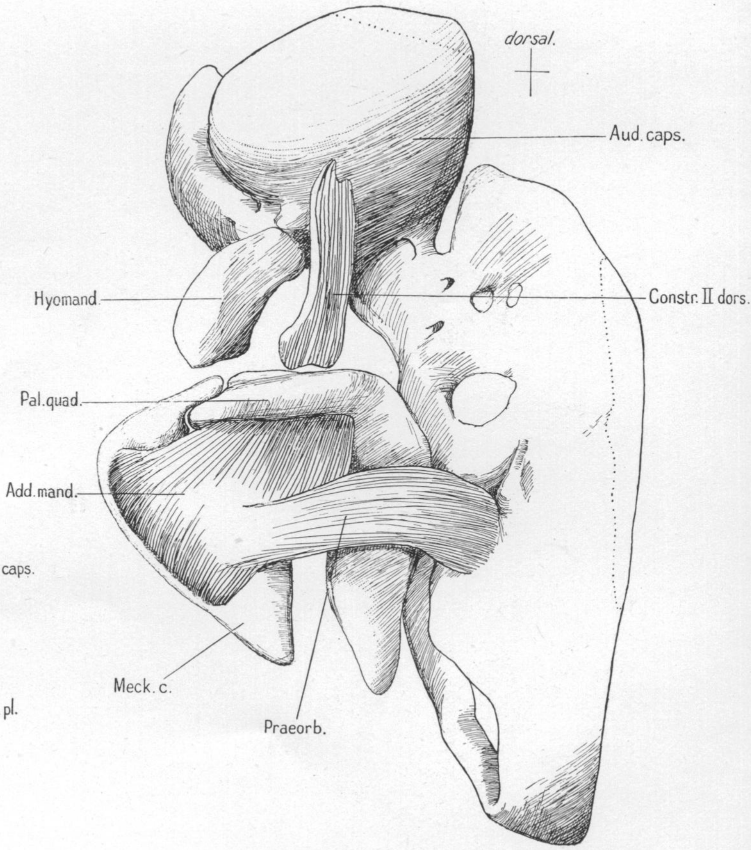

Fig. 25

EDGEWORTH—ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

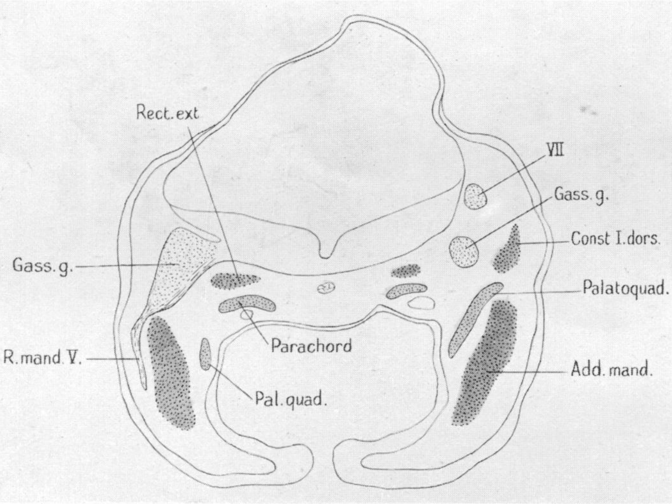

Fig. 28

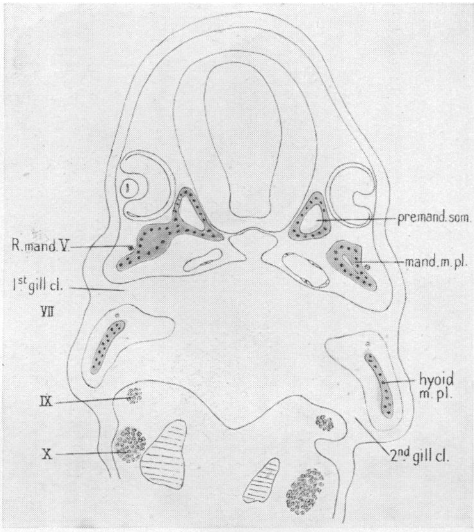

Fig. 31

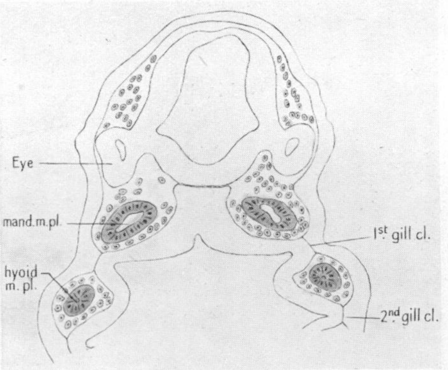

Fig. 29

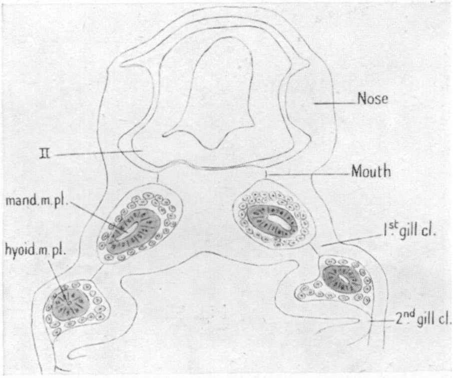

Fig. 30

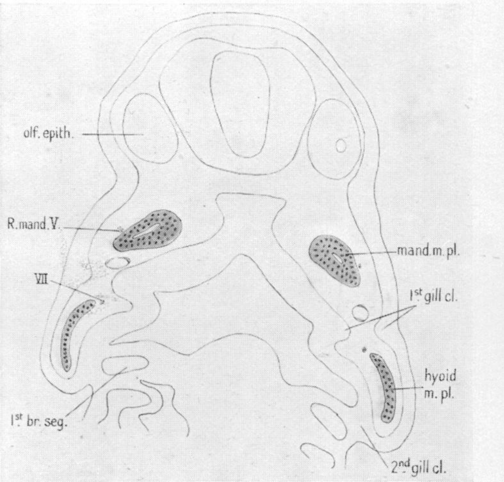

Fig. 32

EDGEWORTH—On the Autostylism of Dipnoi and Amphibia

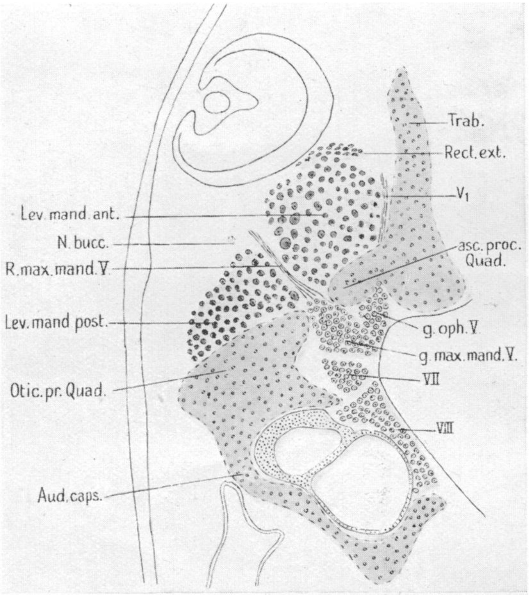

Fig. 33

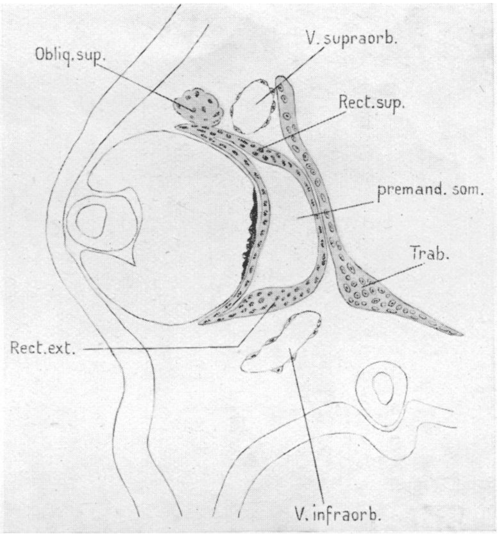

Fig. 34

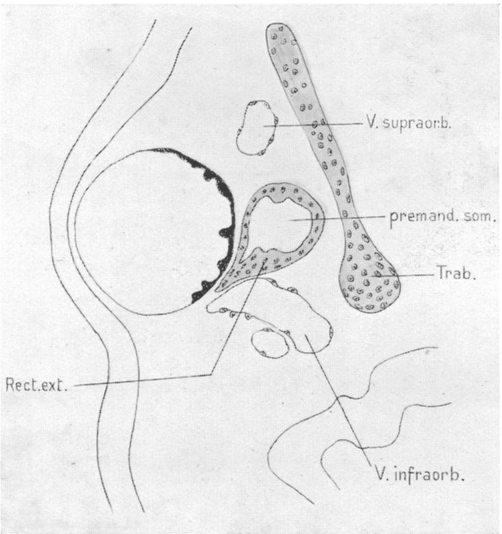

Fig. 35

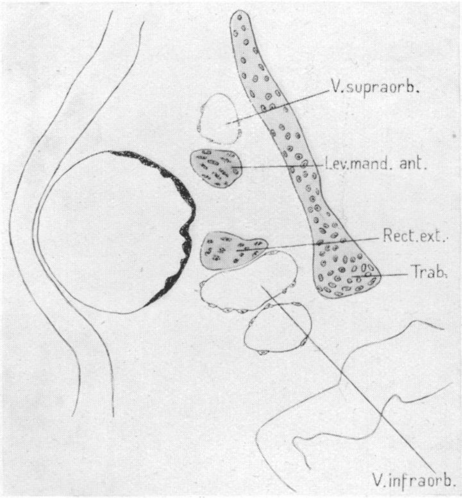

Fig. 36

EDGEWORTH—On the Autostylism of Dipnoi and Amphibia

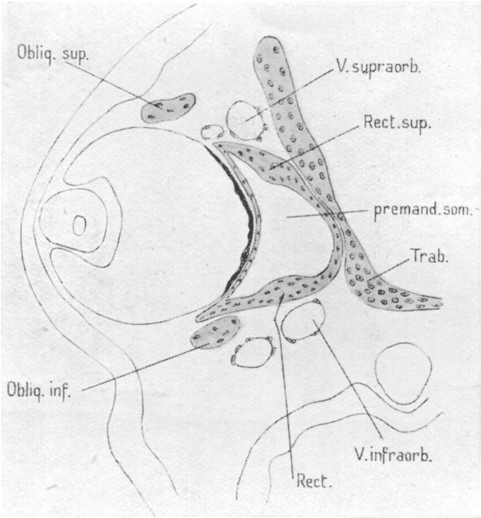

Fig. 37

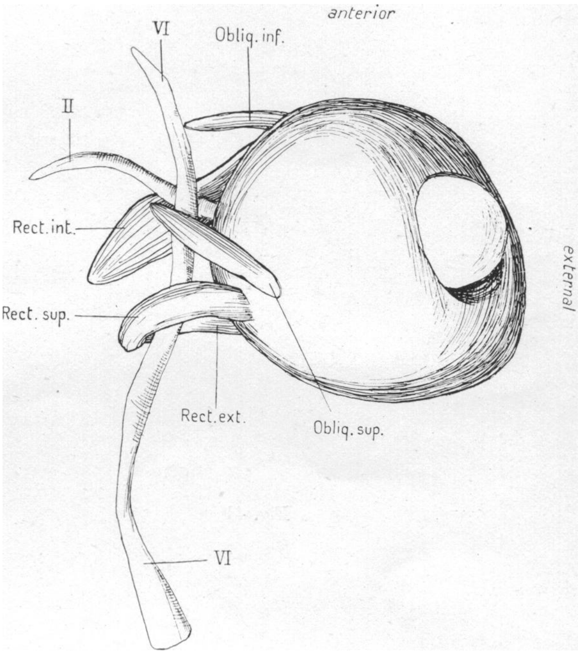

Fig. 38

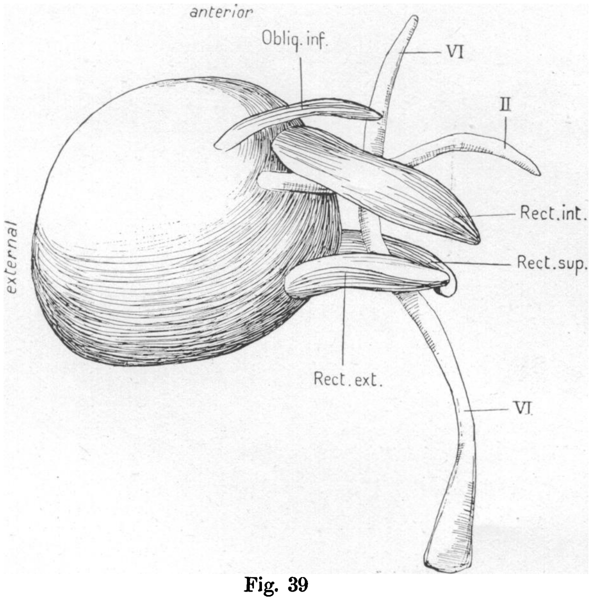

Fig. 39

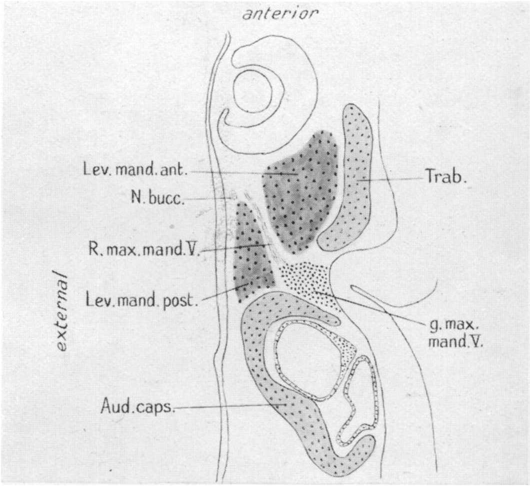

Fig. 40

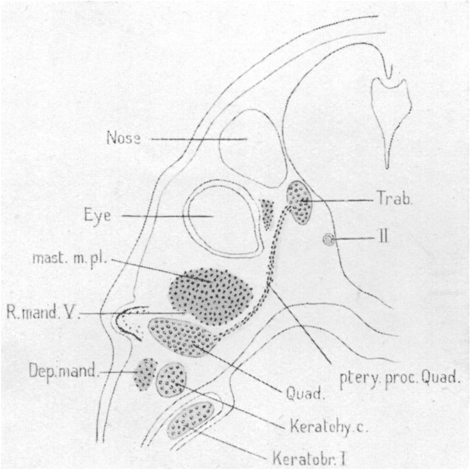

Fig. 41

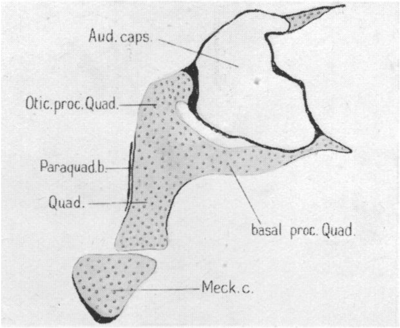

Fig. 43

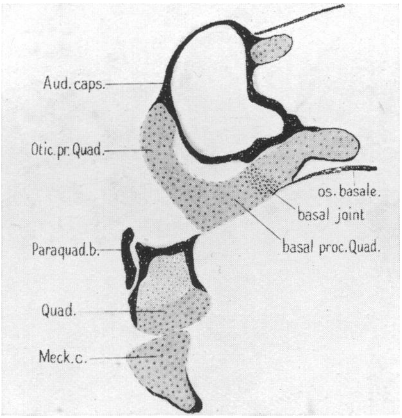

Fig. 44

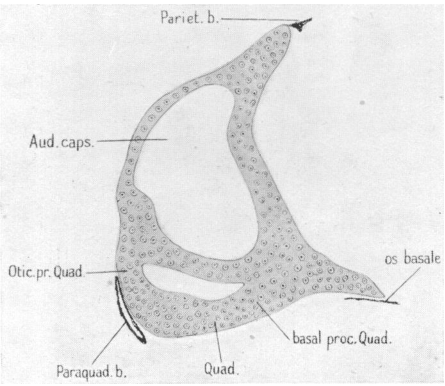

Fig. 42

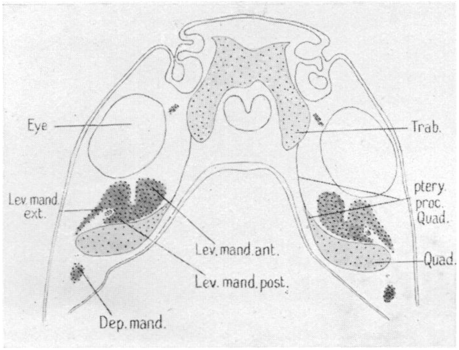

Fig. 45

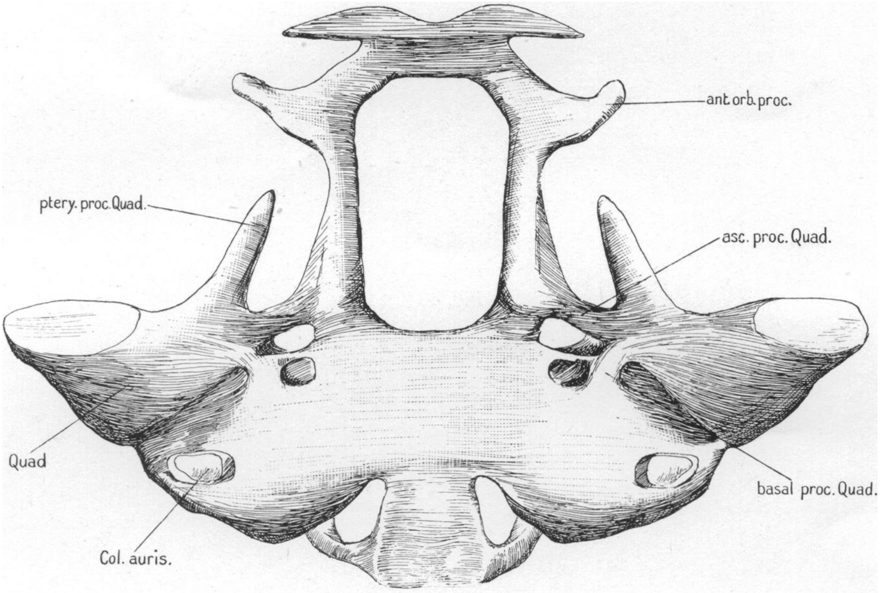
ant.orb.proc.
ptery.proc.Quad.
asc.proc.Quad.
Quad
basal proc.Quad.
Col.auris.

Fig. 46

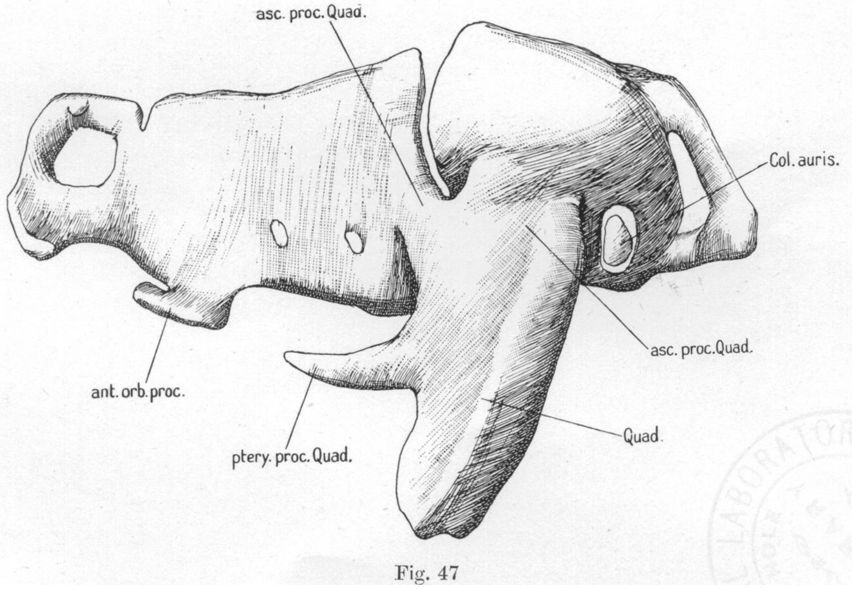
asc.proc.Quad.
Col.auris.
asc.proc.Quad.
ant.orb.proc.
Quad.
ptery.proc.Quad.

Fig. 47

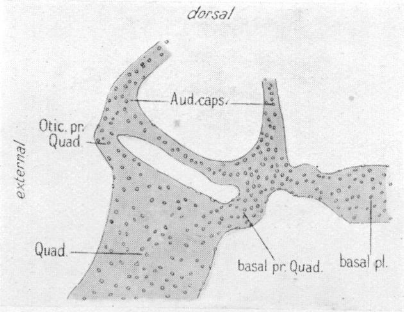

Fig. 48

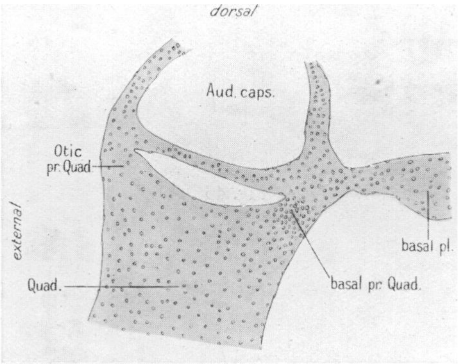

Fig. 49

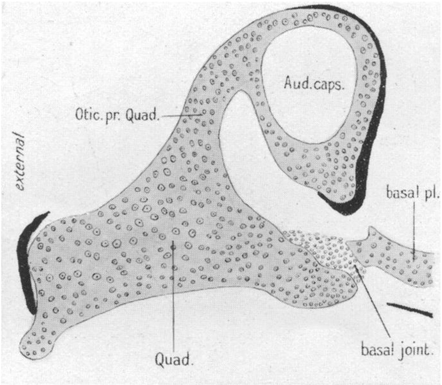

Fig. 50

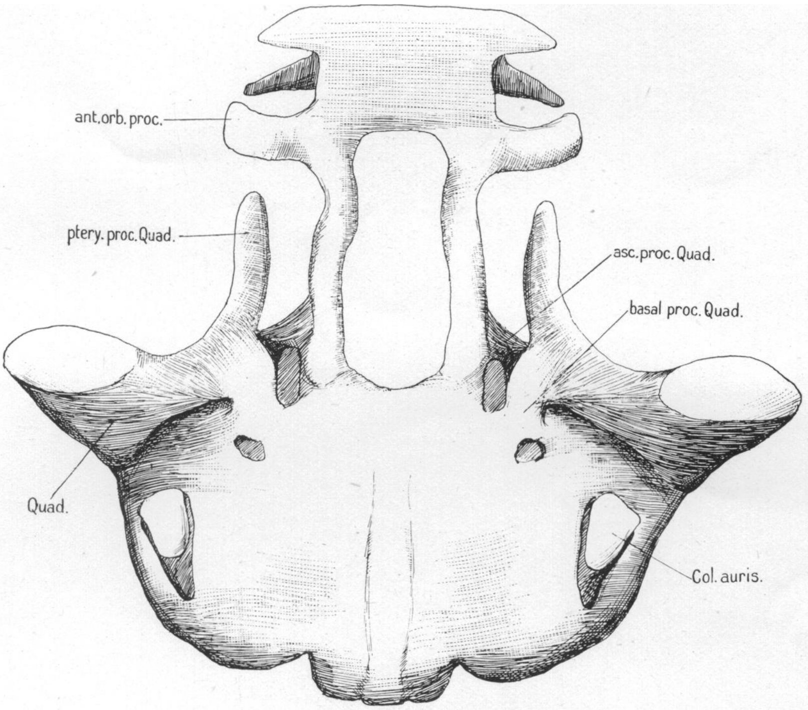
ant.orb.proc.
ptery.proc.Quad.
asc.proc.Quad.
basal proc.Quad.
Quad.
Col. auris.

Fig. 51

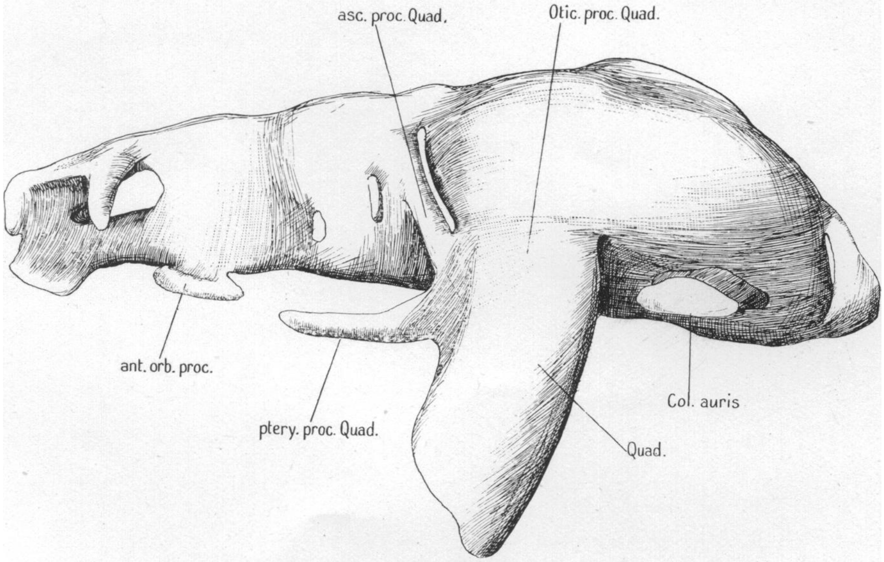
asc. proc. Quad.
Otic. proc. Quad.
ant. orb. proc.
ptery. proc. Quad.
Col. auris
Quad.

Fig. 52

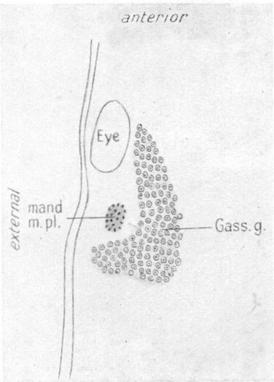

Fig. 53

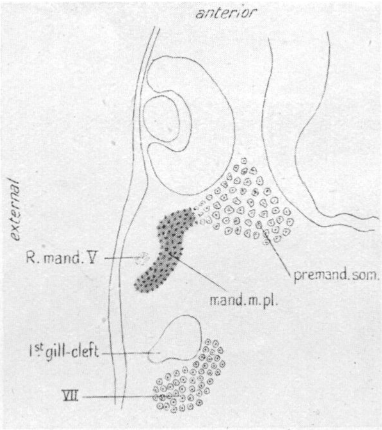

Fig. 54

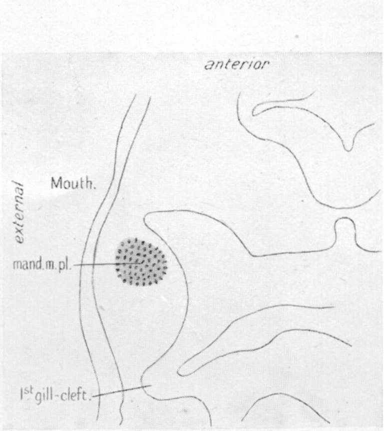

Fig. 55

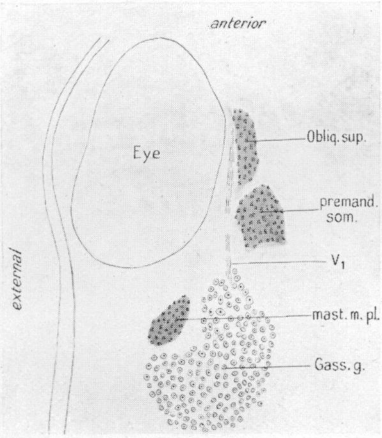

Fig. 56

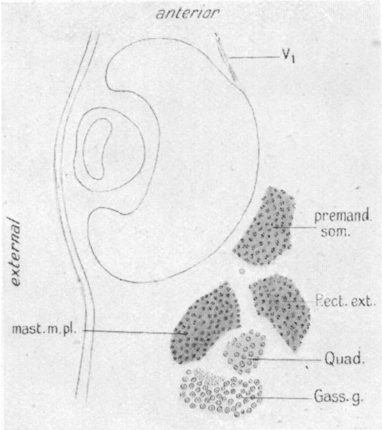

Fig. 57

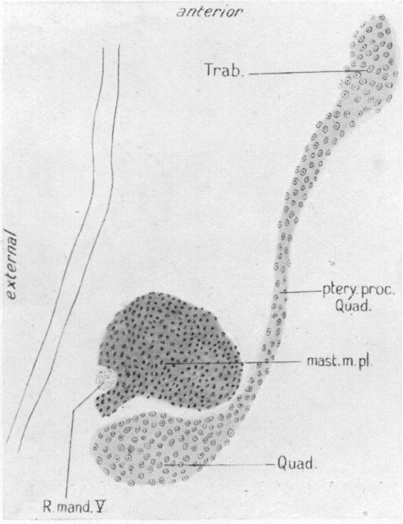

Fig. 58

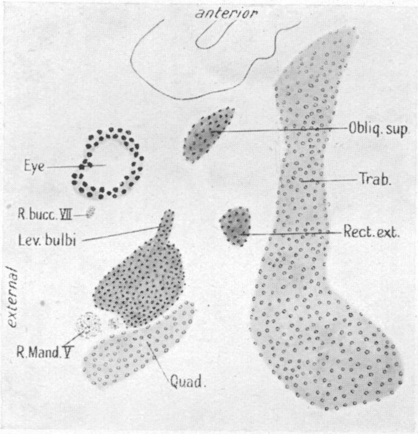

Fig. 59

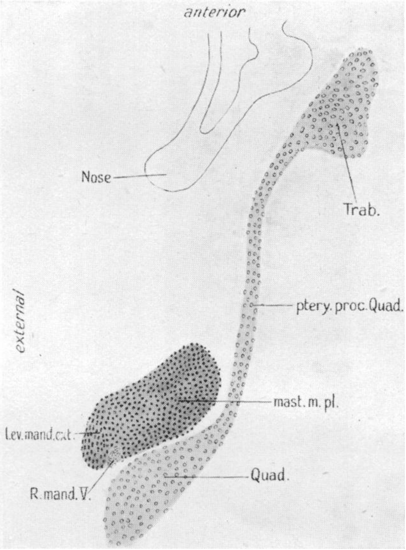

Fig. 60

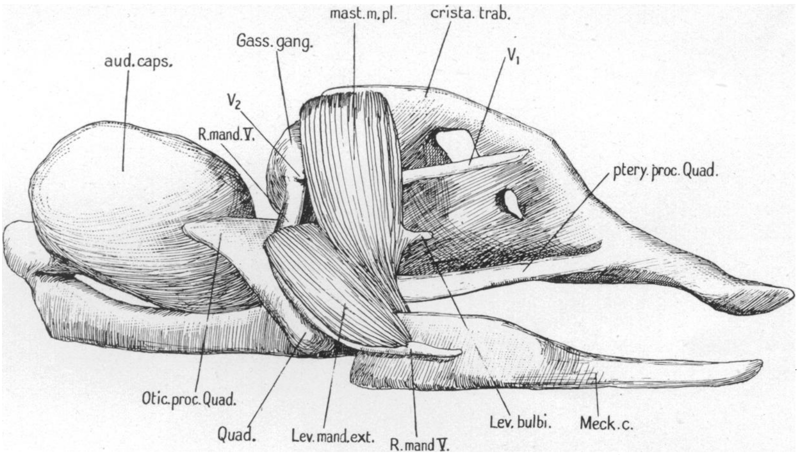

Fig 61

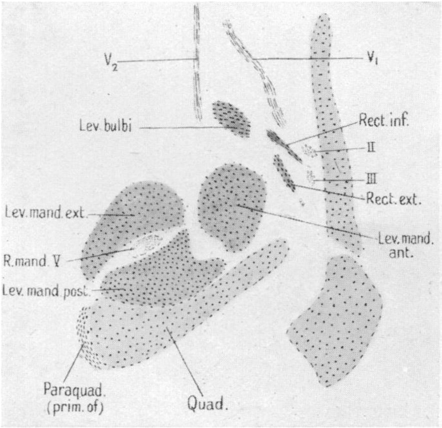

Fig. 62

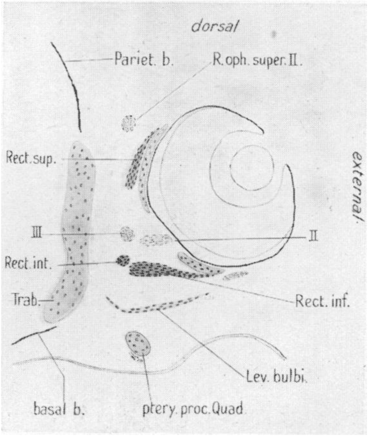

Fig. 63

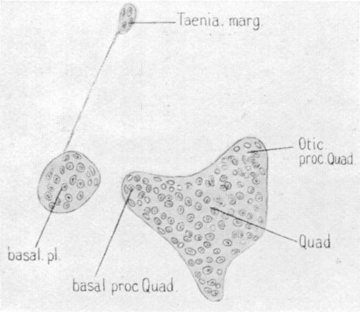

Fig. 64

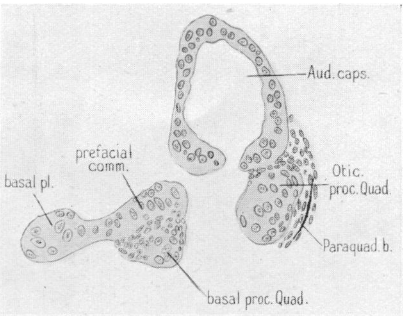

Fig. 65

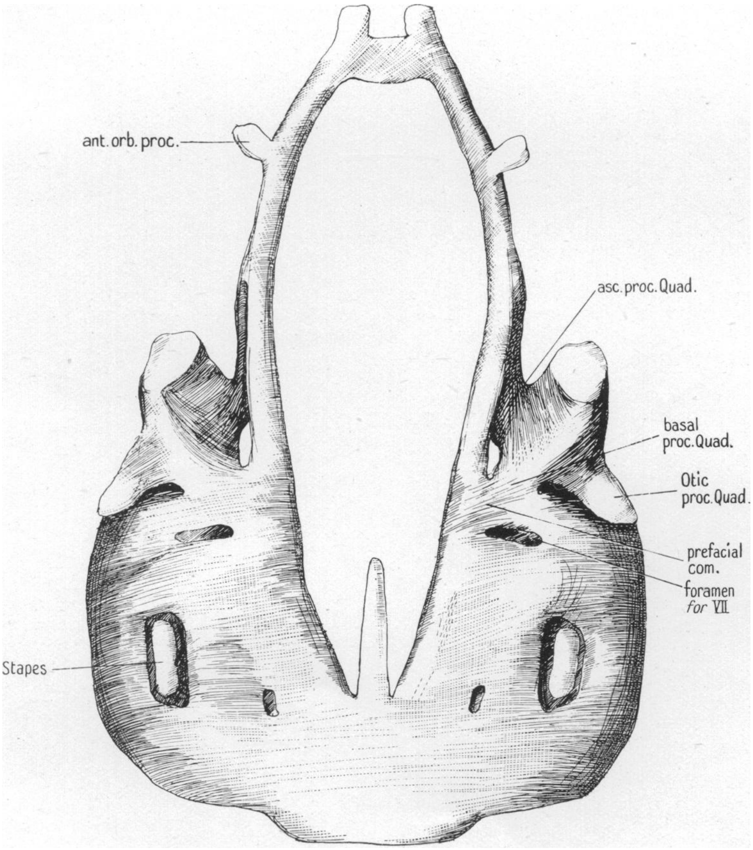

Fig. 66

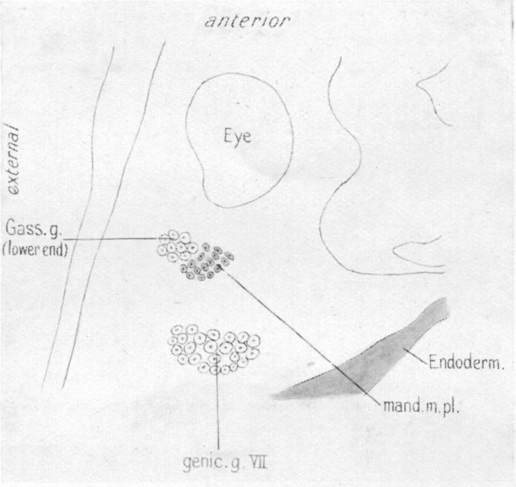

Fig. 67

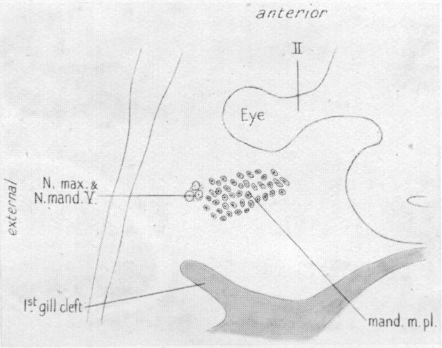

Fig. 68

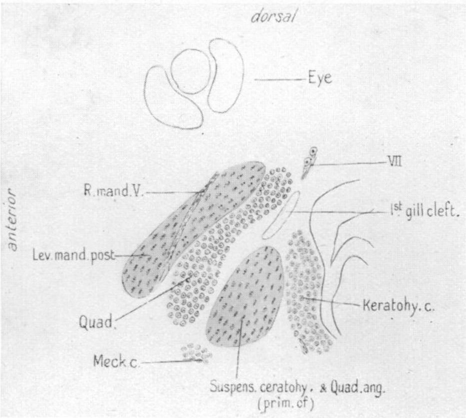

Fig. 69

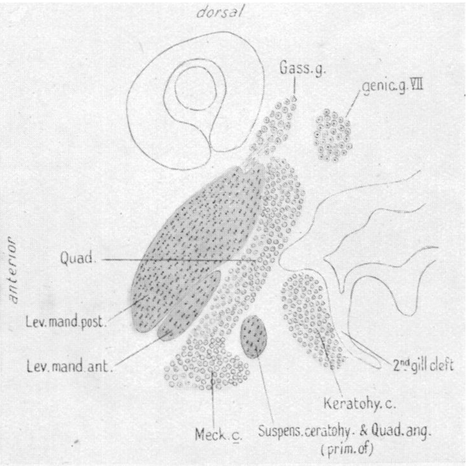

Fig. 70

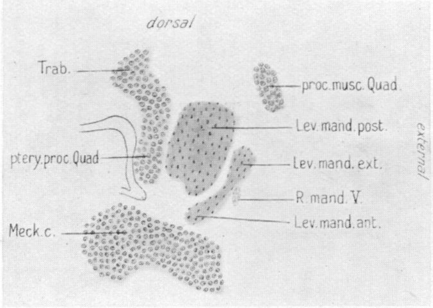

Fig. 71

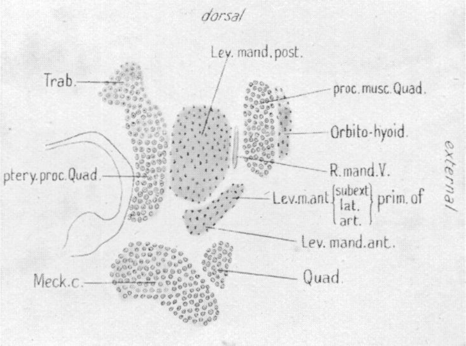

Fig. 72

EDGEWORTH—ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

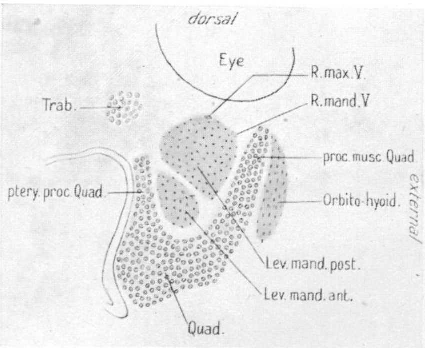

Fig. 73

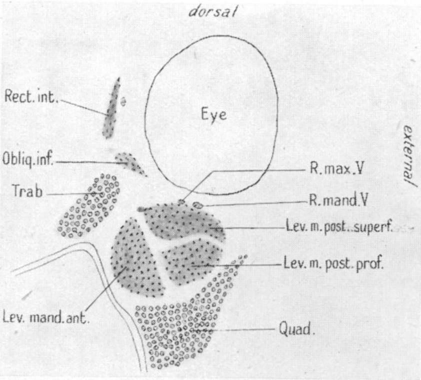

Fig. 74

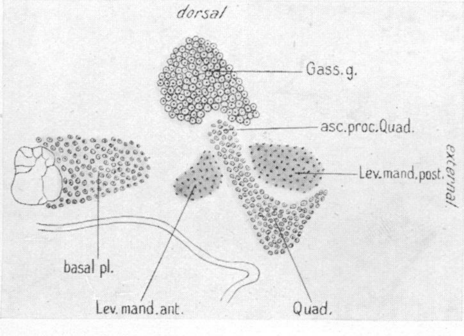

Fig. 75

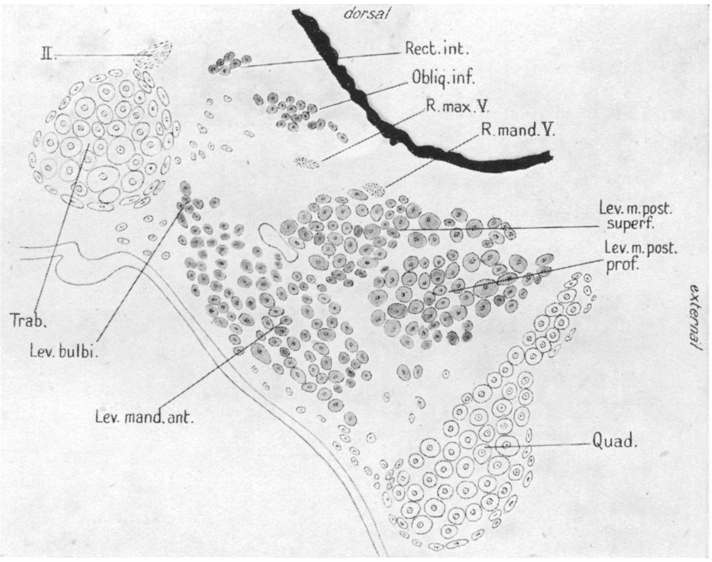

Fig. 76

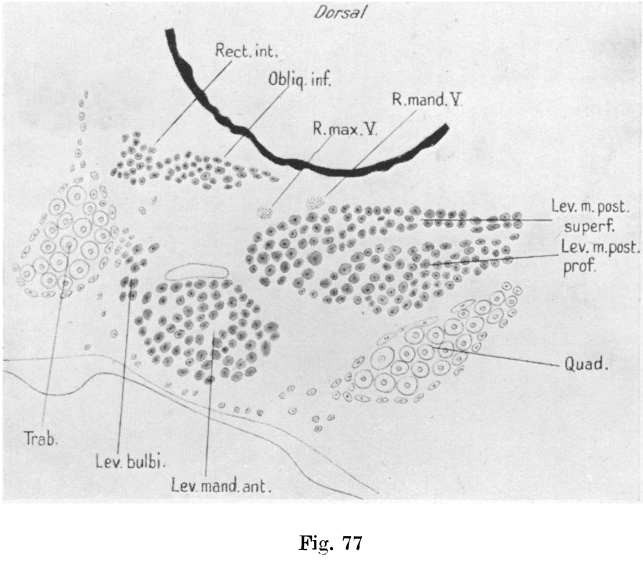

Fig. 77

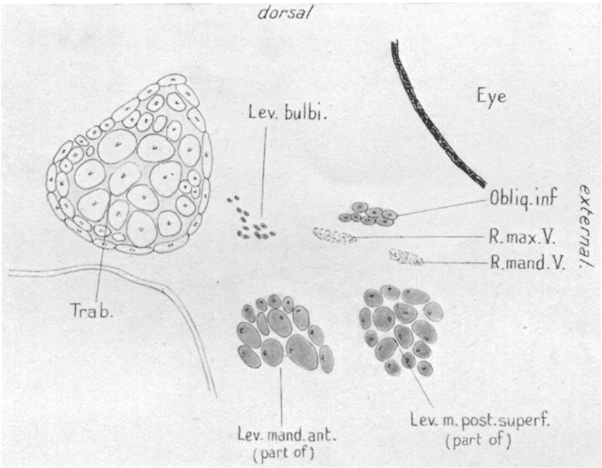

Fig. 78

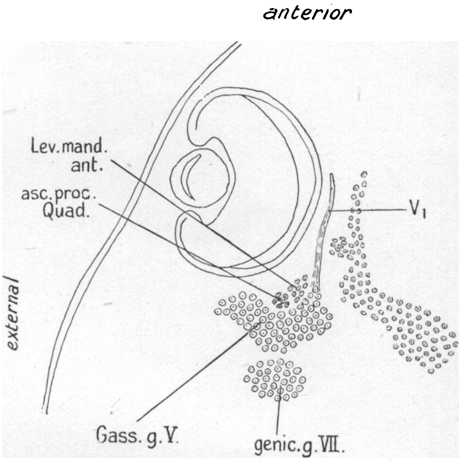

Fig. 80

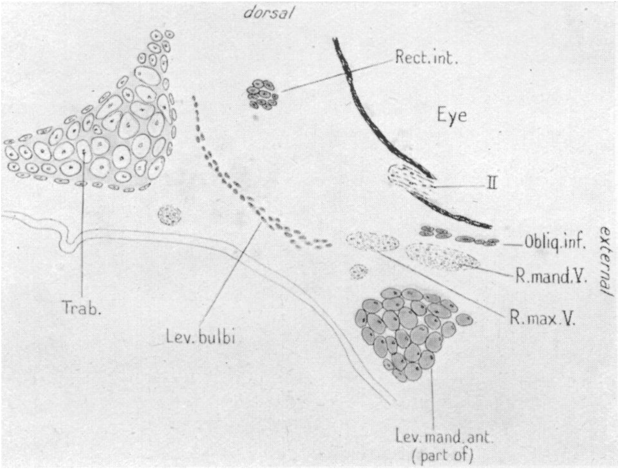

Fig. 79

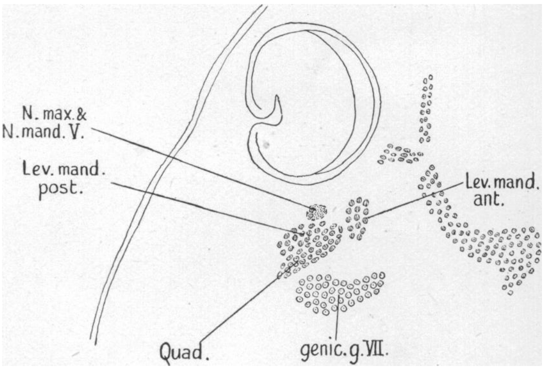

Fig. 81

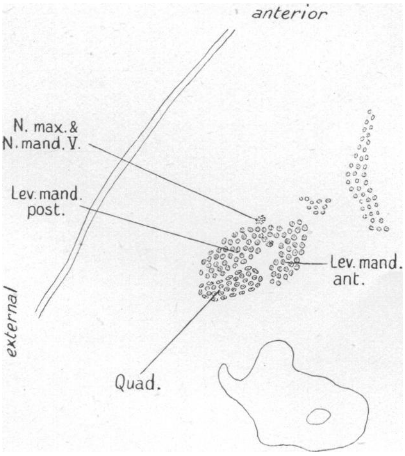

Fig. 82

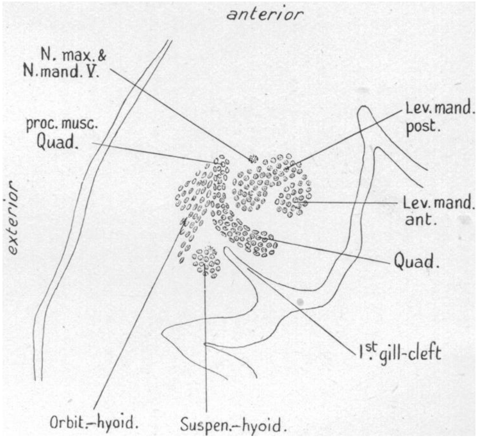

Fig. 83

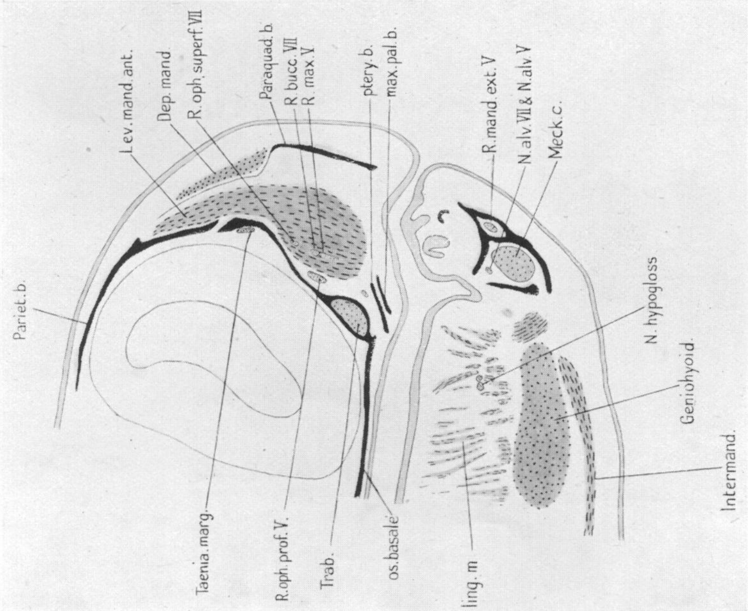

Fig. 84

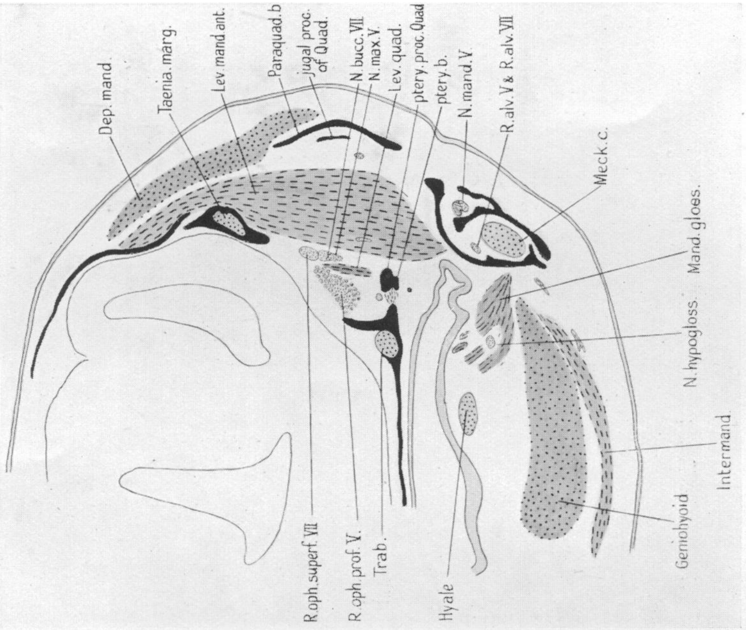

Fig. 85

EDGEWORTH—On the Autostylism of Dipnoi and Amphibia

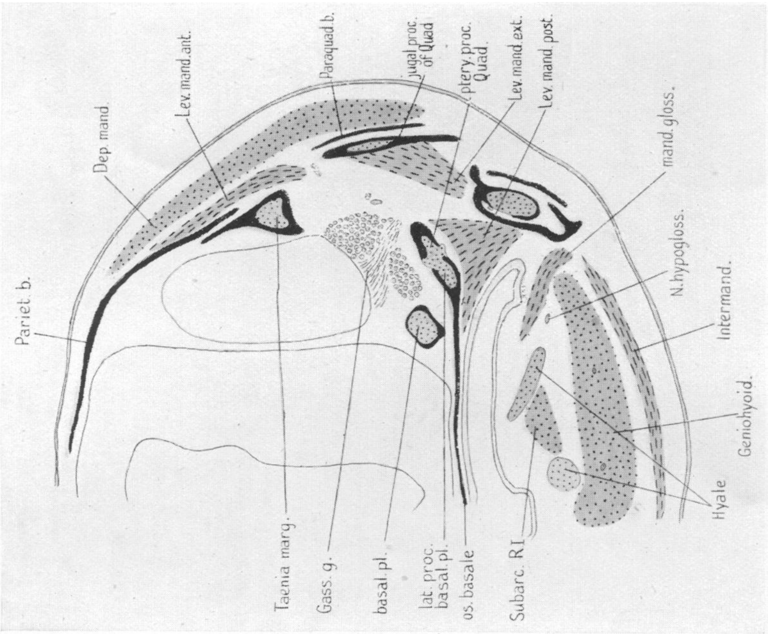
Pariet. b.
Dep. mand.
Lev. mand. ant.
Paraquad. b.
jugal proc. of Quad.
ptery. proc. Quad.
Lev. mand. ext.
Lev. mand. post.
mand. gloss.
N. hypogloss.
Intermand.
Geniohyoid.
Hyale
Taenia marg.
Gass. g.
basal. pl.
lat. proc. basal. pl.
os. basale
Subarc. R I

Fig. 87

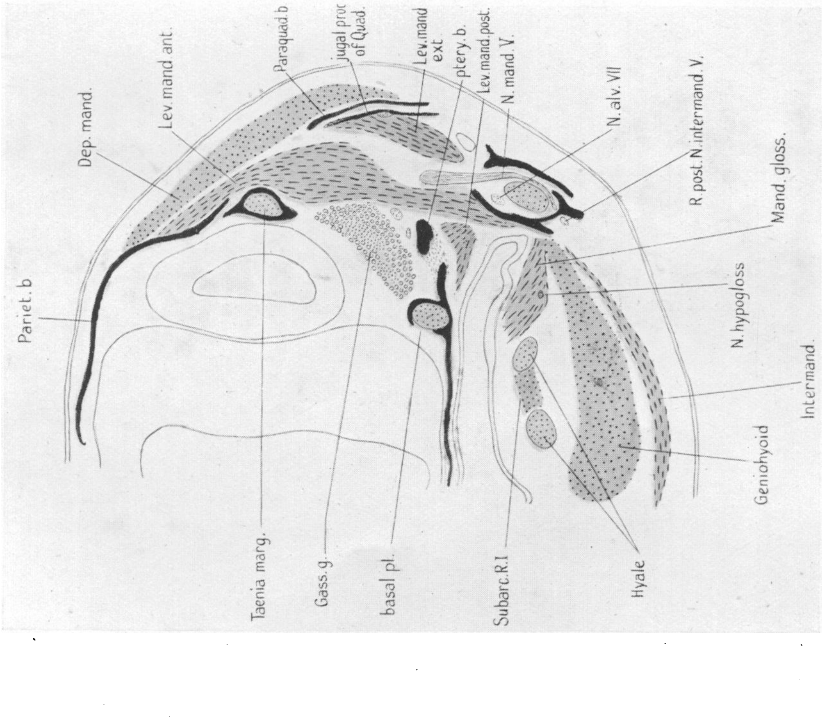
Pariet. b
Dep. mand.
Lev. mand ant.
Paraquad. b
jugal proc of Quad.
Lev. mand ext
ptery. b.
Lev. mand. post.
N. mand. V.
N. alv. VII
R. post. N. intermand. V.
Mand. gloss.
N. hypogloss
Intermand.
Geniohyoid
Taenia marg.
Gass. g.
basal pl.
Subarc. R. I
Hyale

Fig. 86

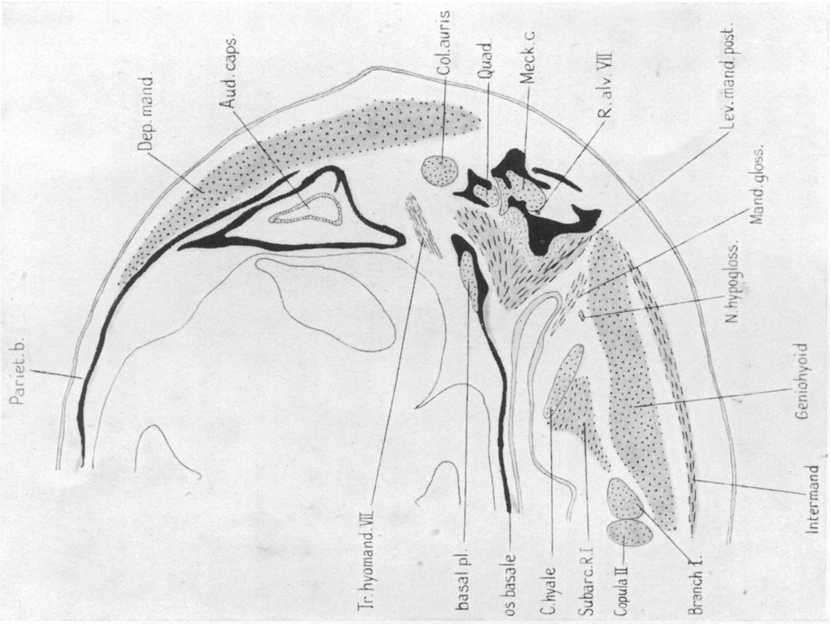

Fig. 89

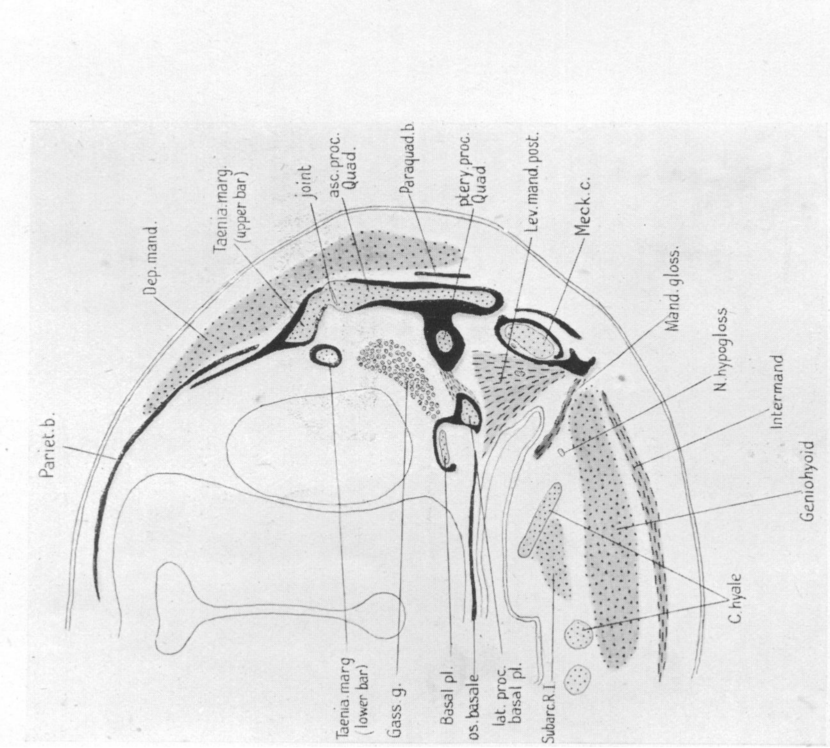

Fig. 88

EDGEWORTH—On the Autostylism of Dipnoi and Amphibia

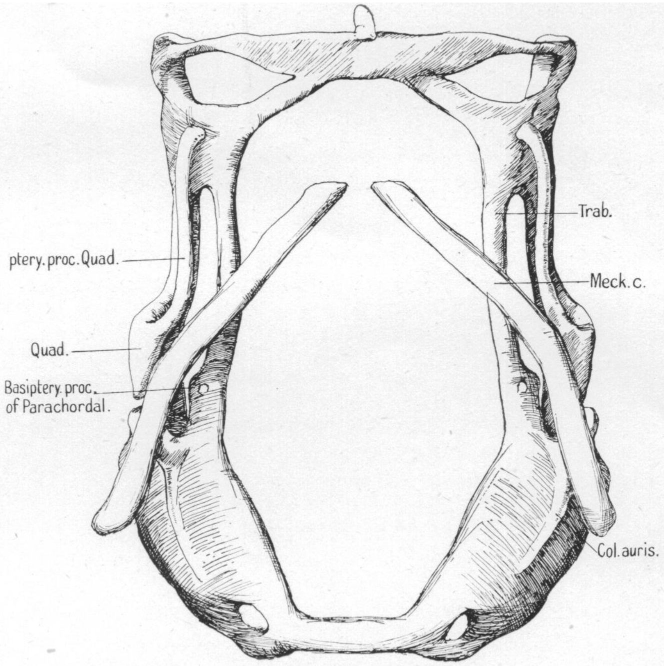
Trab.
ptery. proc. Quad.
Meck. c.
Quad.
Basiptery. proc. of Parachordal.
Col. auris.

Fig. 90

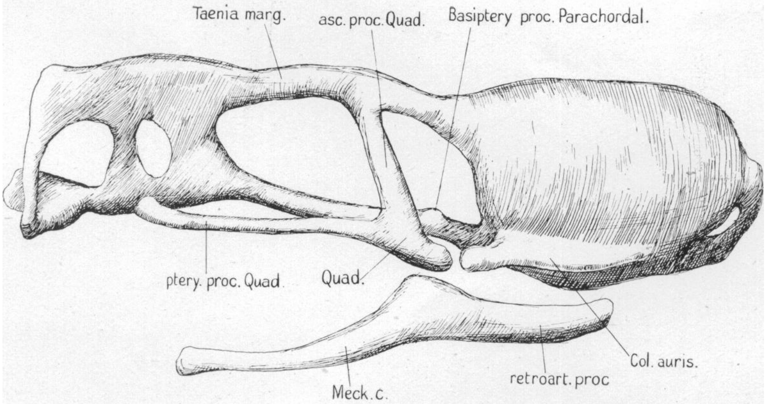
Taenia marg.
asc. proc. Quad.
Basiptery proc. Parachordal.
ptery. proc. Quad
Quad.
Col. auris.
retroart. proc
Meck. c.

Fig. 91

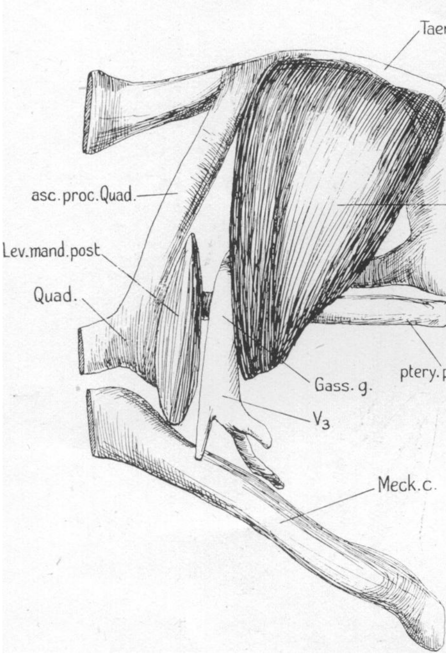

Fig. 92

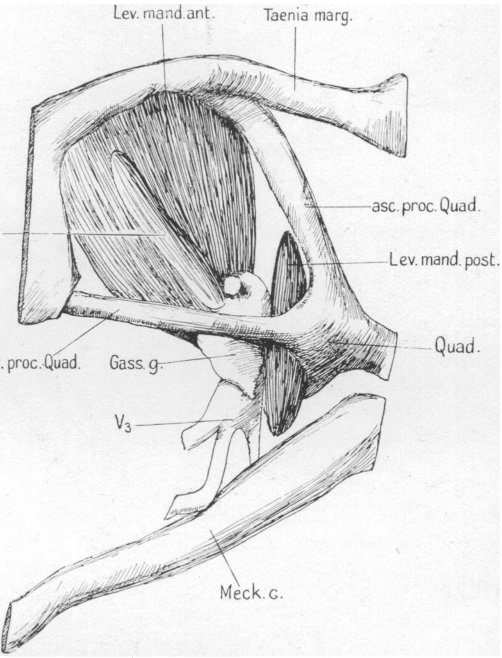

Fig. 93

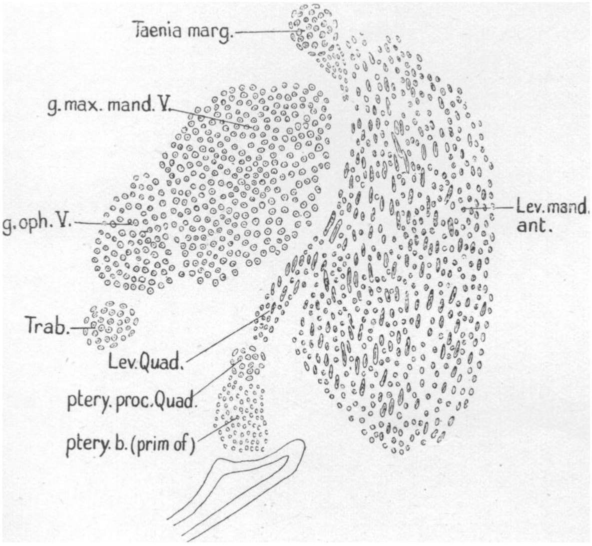

Fig. 94

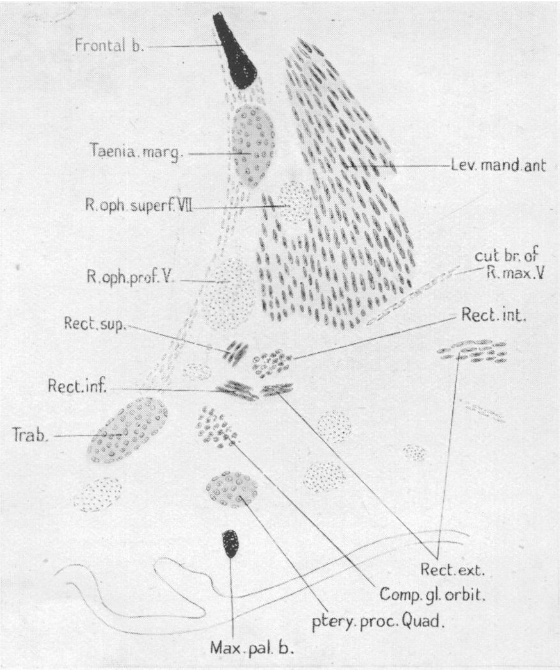

Fig. 95

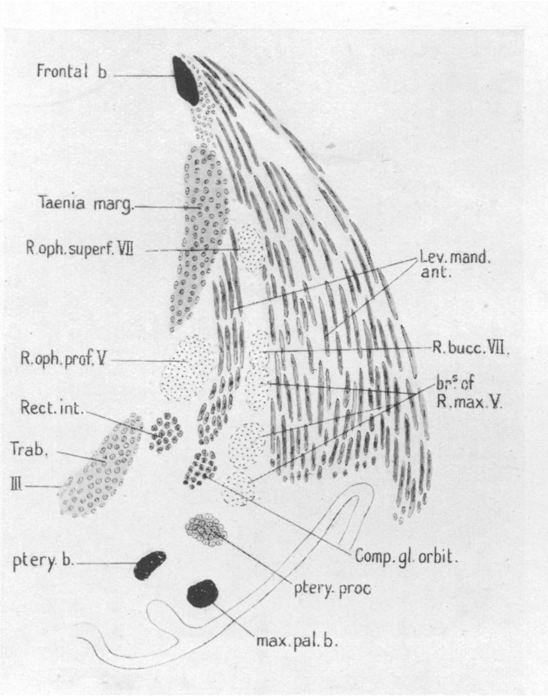

Fig. 96

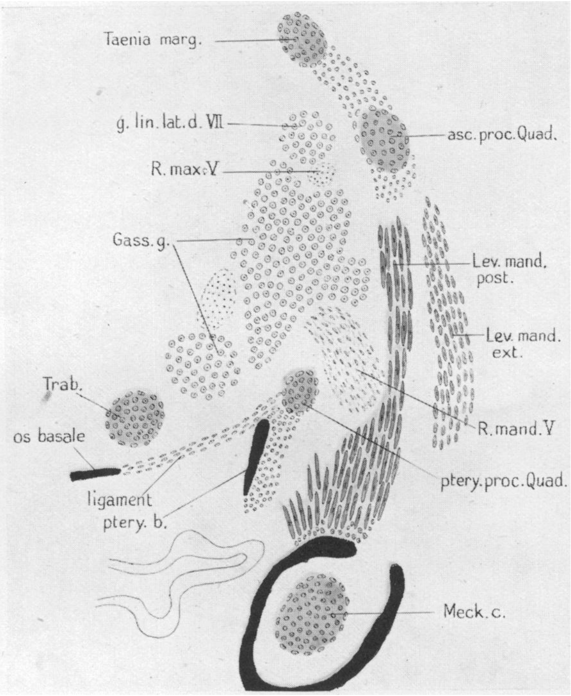

Fig. 97

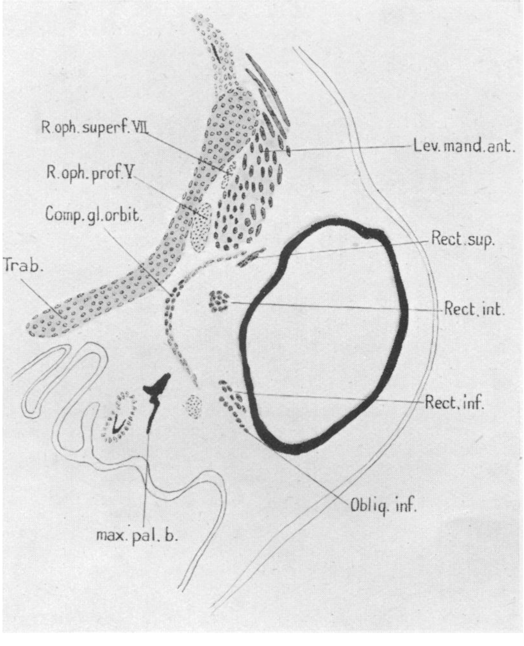

Fig. 98

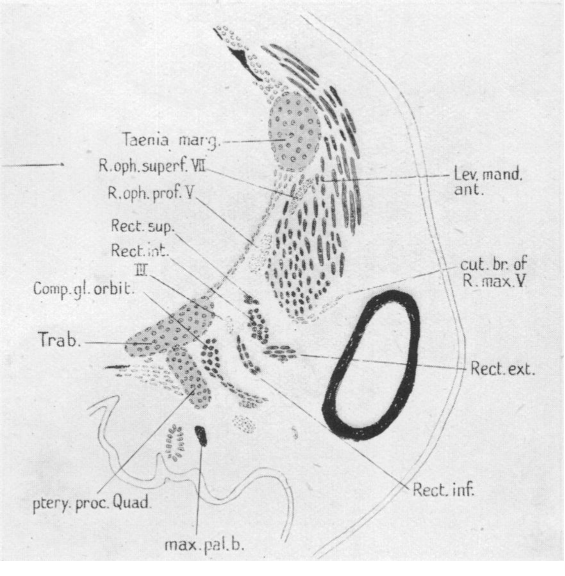

Fig. 99

EDGEWORTH—On the Autostylism of Dipnoi and Amphibia

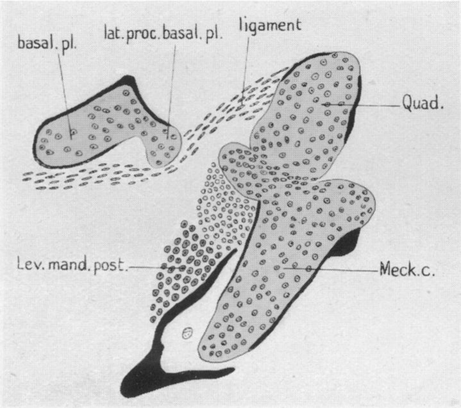

Fig. 100

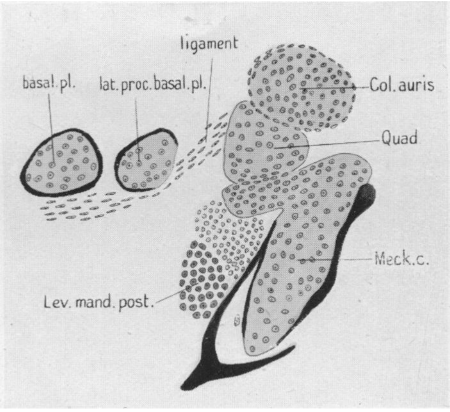

Fig. 101

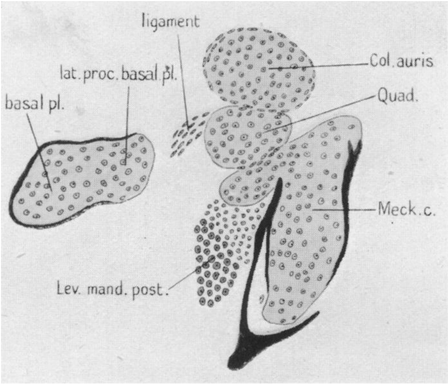

Fig. 102

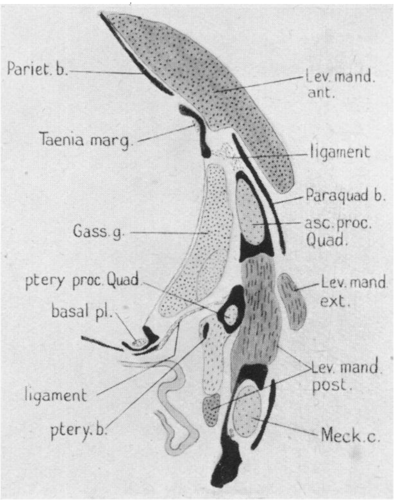

Fig. 103