# ON THE DEVELOPMENT OF THE HYPOBRANCHIAL AND LARYNGEAL MUSCLES IN AMPHIBIA

## By F. H. EDGEWORTH, M.D.

### Professor of Medicine, University of Bristol

THE adult anatomy of the laryngeal muscles, nerves, and cartilages, in Amphibia is now well-established, and especially by the work of Henle, Fischer, Wilder, Gegenbaur, Göppert, and Drüner. An explanation of the facts observed was sought for, and in 1892 the theory was put forward that the laryngeal muscles are branchial in origin, their nerves branchial nerves, and their cartilages modified branchial bars. A short history of the rise of this theory and of its modifications forms a preface to this paper.

In papers published in 1916 and 1919 I showed that in Mammalia and Sauropsida the laryngeal muscles, other than the Crico-thyroid of Mammalia, are developed from the Constrictor oesophagi. In this paper evidence is adduced that in Amphibia, similarly, the laryngeal muscles are developed from the Constrictor oesophagi and are not derivatives of any branchial-arch musculature.

The larynx in Amphibia comes into relation with certain hypobranchial muscles, and a description of their development and morphology precedes that of the laryngeal structures.

Many names have been employed by writers. A uniform nomenclature has been used in the following paper, both in the historical account and in the record of observations; and the following tabular statement shows its relation to the names employed by previous writers.

### Ventral muscles of the branchial arches

In this paper:

*Transversi ventrales:*

*Urodela:*

| | | |
|---|---|---|
| Transversus ventralis iii of Necturus and Proteus | Fischer | Hyo-trachealis |
| Transversus ventralis iv of other Urodela | Wilder | Hyo-laryngeus and Hyo-trachealis s. Pharyngo-branchialis iii or iv |
| | Gegenbaur | Hyo-trachealis |
| | Göppert | Hyo-pharyngeus s. Hyo-trachealis |
| | Drüner | Interbranchialis iii or iv |

*Anura:* larva

| | | |
|---|---|---|
| Transversus ventralis iv | Göppert | Hyo-pharyngeus |

*Gymnophiona:*

| | | |
|---|---|---|
| Transversus ventralis iv | Göppert | Hyo-pharyngeus. |

*Subarcuales recti and obliqui:*

*Urodela:*

| | | |
|---|---|---|
| Subarcualis rectus i | Fischer, Mivart Miss Platt, Drüner | Ceratohyoideus internus |
| Subarcualis obliquus ii of Necturus and Proteus | Fischer | Adductores arcuum |
| | Miss Platt | Constrictor arcuum |
| Subarcuales obliqui ii and iii of other Urodela | Drüner | Adductores branchialium Subarcuales obliqui Ceratohypobranchialis (in Necturus and Proteus) Constrictor arcuum branchiarum |
| Subarcualis rectus iii of Necturus and Proteus | Fischer, Gegenbaur, Mivart, Miss Platt | Constrictores arcuum |
| | Drüner | Subcerato-branchiales |
| Subarcualis rectus iv of other Urodela | Göppert | Constrictores arcuum branchialium |
| | Drüner | Subarcuales recti Constrictores arcuum branchialium |

*Anura:* larva

| | | |
|---|---|---|
| Subarcuales recti i and ii | Dugès | Ceratobranchial |
| | Schultze | Ceratohyobranchialis |
| Subarcuales recti iii and iv | Schultze | Interbranchialis |

*Gymnophiona:*

| | | |
|---|---|---|
| Subarcualis rectus i | Fischer | Ceratohyoideus externus |
| | Fürbringer | Ceratohyoideus |
| | Norris and Hughes | Ceratohyoideus internus |
| Subarcuales recti ii, iii and iv | Fischer and Göppert | Constrictor arcuum branchialium |

### *Laryngo-tracheal skeleton*

| | *Whole cartilage* | *Anterior part* | *Posterior part* |
|---|---|---|---|
| In this paper | Cartilago lateralis | Pars laryngea s. arytenoid | Pars trachealis |
| *Urodela:* | | | |
| Henle (1839) | — | Cartilago s. Pars arytaenoidea | Cartilago s. Pars laryngo - trachealis s. Cartilago lateralis |
| Fischer (1864) | — | Seitenknorpel | — |
| Wilder (1892 and 1896) | — | Arytenoidea s. C. lateralis | Tracheal elements |
| Gegenbaur (1892) | Cartilago lateralis | Arytenoidea s. Stellknorpel | — |
| Göppert (1894 and 1898) | Cartilago lateralis | Pars arytenoidea | Pars cricotrachealis |
| Drüner (1901 and 1904) | — | Cartilago lateralis s. Pro arytenoidea | Proc. trachealis |
| *Gymnophiona:* | | | |
| Henle | — | Cartilago arytenoidea | Cartilago lateralis |
| Göppert | — | Pars arytenoidea | — |
| *Anura:* larva | | | |
| Wilder | — | Arytenoidea | — |
| Göppert | — | Arytenoidea | — |
| *Anura:* adult | | | |
| Wilder | — | Arytenoid and apical cartilage | ⎰Annulus ⎱Processus bronchiales |
| Henle | — | C. arytenoidea and C. Santoriniana | C. laryngo-trachealis |
| Göppert | — | C. arytenoidea and C. Santoriniana | Pars crico-trachealis of ⎰Pars cricoidea ⎱Partes tracheales |

### Laryngeal muscles

| | Dorsal laryngeal muscle | Laryngei | Constrictor muscle |
|---|---|---|---|
| In this paper | Dilatator laryngis | Laryngeus dorsalis<br>Laryngeus ventralis | Constrictor laryngis |
| *Urodela:* | | | |
| Henle | Dilatator aditus laryngis | — | Constrictor aditus laryngis |
| Fischer | { Dorso-laryngeus and Dorso-trachealis | — | Constrictor aditus laryngis |
| Wilder | { Dorso-laryngeus and Dorso-trachealis s. Dorso-branchialis v. | Laryngei | Ring of Periarytenoideus dorsalis and ventralis |
| Gegenbaur | Dilatator aditus laryngis | — | — |
| Göppert | { Dorso-pharyngeus of Dorso-laryngeus and Dorso-trachealis | Laryngei | Sphincter laryngis |
| Drüner | Dorso-laryngeus | Laryngei | Constrictor aditus laryngis |
| *Gymnophiona:* | | | |
| Henle | Dilatator aditus laryngis | M. interlateralis | Constrictor aditus laryngis |
| Göppert | Dilatator laryngis | { Laryngeus ventralis Laryngeus dorsalis (?) | Sphincter laryngis |
| *Anura:* larva | | | |
| Wilder | { Dorso-laryngeus s. Dorso-branchialis v. | — | Sphincter laryngis |
| Göppert | Dilatator laryngis | — | Sphincter laryngis |
| *Anura:* adult | | | |
| Henle | { Oeffner des Stimmladeneingangs | { Verengerer des Stimmladeneingangs | Compressor der Stimmlade |
| Wilder | { Dilatator aditus laryngis s. Dorso-branchialis v. s. Periarytenoideus dorsalis | { Constrictor aditus laryngis s. Periarytenoideus ventralis | { Compressor aditus laryngis  { Sphincter dorsalis |
| Göppert | Dilatator laryngis | Hyo-laryngeus | { Sphincter anterior  { Sphincter posterior |
| In this paper | | Constrictor laryngis posterior | |

## HISTORICAL ACCOUNT

### Ventral muscles of the branchial arches

**Anura.** The Subarcuales recti of the larva were described by Dugès and by Schultze.

Another muscle was described by Göppert (1894) in a 11 mm. larva of Rana, arising from connective tissue surrounding the post-branchial body and passing inwards towards the middle line. In older larvae the median ends of the two muscles meet. He homologised this muscle with Transversus ventralis iv of Urodela and, further, stated that it becomes the Constrictor laryngis posterior of the adult—a muscle which arises from the processus postero-medialis and passes inwards and forwards to meet its fellow in a median raphé just in front of the Cartilagines laryngis.

Wilder, on the other hand, stated (1896) that the Constrictor laryngis posterior develops at a late larval stage (one with rudimentary hind limbs)

as a derivative of the ventral half of the Constrictor laryngis and is not identical with the larval muscle described by Göppert, which probably atrophies. Göppert in 1898 adhered to his previous statement. Neither investigator gave any figures in support of his opinion.

Differences of opinion between Göppert and Wilder in regard to Levator arcus branchialis iv are mentioned later.

*Gymnophiona.* The Subarcuales recti and the Transversus ventralis iv were described by Fischer and Göppert (*vide infra*).

*Urodela.* The larynx, owing to certain developmental changes, which will be described later, comes into relation with the Transversus ventralis (iii in Necturus and Proteus, iv in Urodela with four branchial bars). The linea alba, connecting the two halves of this muscle, underlies the pharynx and anterior part of the larynx in Siredon, Salamandra, Triton, Necturus, and Proteus; it underlies the larynx in Ellipsoglossa, and underlies the trachea in Menopoma, Megalobatrachus max. and Amphiuma. Various opinions have been expressed as to the morphology of this Transversus ventralis. Fischer (1864) considered that it was part of a single muscle system—that of a Constrictor pharyngis. Wilder (1892) described the Dilatator laryngis and Transversus ventralis as "extrinsic" laryngeal muscles. He homologised the former with the dorsal segment of the fifth branchial arch of Selachians, but could not determine whether the latter was homologous with the ventral segment of the same arch or not. Gegenbaur (1892) homologised the Transversus ventralis with the Constrictores arcuum of the branchial skeleton (called in this paper Subarcuales recti and obliqui). Göppert (1894), accepting Gegenbaur's opinion, stated that the Transversus ventralis was the hindmost member of a longitudinal series binding together the hyoid and the branchial bars, though differing from the other members in that it has generally given up its ventral attachment to skeletal parts. In Necturus and Proteus, where no fourth branchial bar is present, the hinder part of the Transversus ventralis and the Levator iii pass to an inscriptio tendinea separating them, whilst the chief part of the former muscles passes over to Ceratobranchiale iii. In Megalobatrachus max., where the third and fourth bars are absent, the Transversus ventralis and Levator iii meet in an inscriptio tendinea which forms an anterior continuation of that in the territory of Levator iv. In land-living forms such as Salamandra and Triton, no forward migration of the muscle takes place, and, on atrophy of the rudimentary fourth bar, the Transversus ventralis and Levator iv form a Cephalo-dorso-pharyngeus—a muscle-band with an inscriptio tendinea. Wilder (1896) advanced the theory that, primitively, there was a series of ventral transverse muscles attached to the visceral bars—in the mandibular segment represented by the Intermandibularis anterior, in the hyoid segment by the Intermandibularis posterior, and in the branchial region by a series of Transversi ventrales. In Necturus and Proteus the Transversus ventralis consists of Transversi ventrales iii and iv; in other Urodela only iv is present. Embryology would show whether Transversi ven-

trales i and ii are represented ontogenetically. Wilder made no reference to Vertebrates other than Amphibia. Göppert (1898) accepted Wilder's opinion that the Transversus ventralis of Urodela other than Proteus and Necturus represents a Transversus ventralis iv, but, against Wilder's opinion concerning Proteus and Necturus, stated that the muscle in those animals is an altogether simple one in which no division is possible even in the embryo. Further, no proof had been given that a Transversus ventralis iii as well as a Transversus ventralis iv existed in Urodela with a fully developed branchial skeleton.

Drüner's theory (1901 and 1904) of the segmental origin of the Transversus ventralis of Urodela was different from that of Wilder and Göppert. He found that the muscle is innervated by the N. recurrens intestinalis x, and not by branchial arch nerves. He inferred from this that the muscle had migrated forwards from more posterior segments which once existed and was not native to the segment in which it lay. His terms Transversus ventralis iii or iv are thus purely descriptive and denote merely the bar of attachment. (It may be added that this theory was adopted in all cases of the hyoid and branchial musculature of Urodela where the innervation does not harmonise with the position of the muscle—the innervation being held to be a clue to the derivation of the muscle elements. Göppert had expressed the same theory in the statement that a muscle never changes its innervation in the course of its phylogenetic development.) Drüner consequently described the muscle in most Urodela as a Transversus ventralis iv. As regards Necturus and Proteus, he stated that the muscle is homologous with Transversus ventralis iv of Salamandra and Triton in position and form, i.e. is a Transversus ventralis iv which has shifted forwards and become a Transversus ventralis iii. In Megalobatrachus max. the muscle has shifted forwards another segment and becomes a Transversus ventralis ii.

In regard to the corresponding Levatores arcuum, he stated that in Necturus and Proteus there is no demarcation possible between a Levator iii and a Levator iv, nor are there any remains of a gill-cleft. So that, unless it were proved by ontogeny that such existed, it is possible that a Levator iv, cartilage, and gill-cleft, have disappeared and that the insertion of the Levator into the inscriptio tendinea behind Ceratobranchiale iii is due solely to a caudal extension of Levator iii. In Megalobatrachus max. the Levator, which is inserted into Ceratobranchiale ii and the inscriptio tendinea behind it, may represent Levator ii, or ii and iii, or ii and iii and iv. Drüner, further, stated that there is evidence in Salamandra and Triton larvae of at least one branchial segment behind the fourth, between that and the Dorsolaryngeus. In Salamandra there is a short inscriptio tendinea extending backwards from Ceratobranchiale iv. Levator iv is separated into two portions, of which the anterior is inserted into Ceratobranchiale iv and the posterior into the inscriptio. The Transversalis ventralis is attached laterally, from before backwards, to (a) Ceratobranchiale iv, (b) the inscriptio, and (c) the ligamentum branchiopericardiacum. Between portions (b) and (c), i.e. behind the fourth branchial

arch there is, in young embryos (size not stated), an epithelial connection between the pharyngeal epithelium and the skin which represents a sixth gill-cleft. Again, on the left side of a 25 mm. Triton larva the Levator arcus iv consisted of two portions, inserted (*a*) into the cartilage, and (*b*) into the inscriptio extending back from it; whilst on the right side there was in addition a Levator v inserted at the junction of the inscriptio tendinea and the ligamentum branchio-pericardiacum. Between Levator iv and Levator v was an epithelial connection between the epithelium of the pharynx and the Plica omo-branchialis (which is formed from the fourth "Kiemenblättchen" and the skin of the shoulder region). This lies at the position where a sixth visceral-cleft would be expected and represents the remainder of it. The position agrees with that found in Salamandra larvae.

In Siredon Levator arcus iv is inserted to Ceratobranchiale iv and an inscriptio tendinea extending back from it. The Transversus ventralis arises from ceratobranchiale iv, the inscriptio and the ligamentum branchio-pectorale. Further, the fourth branchial nerve gave off an inconstant sensory branch which passed under the ligamentum branchio-pectorale, lying behind the position in which—on comparison with Salamandra and Triton larvae— the sixth gill-cleft is to be sought. This is a rudiment of a R. posttrematicus v. Once a small epithelial vesicle was found which was regarded as the remains of gill-cleft epithelium. Also a fine nerve was given off from the R. pharyngeus of the fourth branchial nerve, which was regarded as a R. pretrematicus vi.

There is thus in these larvae the remains of a sixth gill-cleft behind Cerato-branchiale iv, and the Transversus ventralis has fourth and fifth branchial elements. In Triton there is also a Levator v. The laryngeal structures— cartilage, Dilatator laryngis, and laryngeal muscles—consequently do not belong to a fifth branchial segment, as Wilder, Gegenbaur and Göppert supposed, but to some more posterior segment, at least to a sixth, possibly to one still further back.

*Laryngo-tracheal skeleton*

*Anura.* The laryngeal cartilages of Anuran larvae consist of a short rod on either side of the larynx. The adult conditions have been described by Henle and Wilder, and their development by Märtens.

*Gymnophiona.* Göppert has described the condition of the laryngeal cartilages in a late larva of Ichthyophis (*vide infra*).

*Urodela.* The laryngo-tracheal skeleton of Urodeles consists of a continuous or interrupted cartilaginous or fibro-cartilaginous rod on either side of the larynx and trachea[1].

---

[1] The pars trachealis cart. lat. is not present in Necturus where the short trachea is surrounded by fibrous tissue only; it is present in other Urodela, cartilaginous in Siredon, Salamandra, Triton, Ellipsoglossa and Proteus, fibro-cartilaginous with or without islands of cartilage in Menopoma, Megalobatrachus max., Amphiuma and Siren. It is continuous with the pars laryngea in Menopoma, Megalobatrachus max., Ellipsoglossa, Amphiuma, Siredon, Proteus and Siren. It is separated in Salamandra and Triton (Drüner).

Neither Henle (1839) nor Fischer (1864) discussed the derivation of these structures.

In 1892 similar, but not identical, theories were independently advanced by Wilder and Gegenbaur.

Wilder suggested that the pars laryngea is homologous with the fifth branchial arch of Selachians and the inferior pharyngeal bone of Teleostei, and for the following reasons: (1) Every form possesses either a fifth branchial arch or a laryngeal cartilage in the same location typographically. No animal possesses both. The sudden appearance of such well-developed hyaline structures as the laryngeal cartilages and the sudden disappearance of other well developed structures such as the fifth branchial arch are both unusual phenomena and when considered together may well point to the theory. (2) The fifth branchial arch in Selachians is supplied by $X^4$. "This same nerve follows the arytenoids and supplies this region throughout the vertebrate realm under the name of Ramus recurrens." (3) Another example of former branchial arches entering the service of the larynx is furnished by the thyroid cartilage, which develops from the second and third branchial arches (Dubois). Wilder also stated that in Triton the pars trachealis is developed from the connective tissue surrounding the trachea at a time when the pars laryngea is an already-developed hyaline structure, and regarded the laryngo-tracheal skeleton as derived from two sources—the pars laryngea from a fifth branchial arch, and the pars trachealis which is a new formation.

Gegenbaur suggested that the cartilago lateralis is homologous with the fifth branchial arch of fishes, and for the following reasons: (1) There is a similarity between the laryngeal muscles and the Mm. interarcuales ventrales of the branchial skeleton. The Transversus ventralis iv is to be compared with this musculature. (2) Amphibia show an atrophy of the branchial skeleton, increasing caudally. The cartilago lateralis has still more diminished in size and lost its union with the fourth bar—both phenomena have parallels in the branchial skeleton. (3) The fifth branchial bar of Selachii (other than Heptanchus and Hexanchus) shows signs of atrophy, and the inferior pharyngeal bone of Teleostei—which is derived from the fifth branchial arch—is a structure with many possibilities of modification. Wiedersheim (1886) had regarded the pars laryngea as the primitive portion of the laryngo-tracheal skeleton, to which the pars trachealis became secondarily united. Gegenbaur, however, found that in Salamandra larvae there is a continuous cartilage extending from larynx to bronchi, which subsequently separates into pars laryngea and tracheal skeleton. The earlier stage corresponds to that of adult Proteus and probably represents the ancestral condition.

Wilder, in 1896, abandoned his theory of an independent origin for the tracheal elements, and accepted that of Gegenbaur, as did also Göppert in 1894 and 1898.

Drüner (1901 and 1904) accepted the theory that the pars laryngea is

homologous with a branchial bar—not, however, with the fifth, but with either a sixth or a still more caudal one. This modification of Wilder's and Gegenbaur's theories was occasioned by the discovery of certain structures (*vide* pp. 129, 130) behind the fourth bar and its muscles, which, he held, represented at least one branchial segment between the fourth and that of the cartilago lateralis. He stated that the transitory continuity of the laryngo-tracheal skeleton in Salamandra is not present in Triton and Siredon where the tracheal portion develops independently in the form of many cartilaginous islands, and is no proof of a single derivation. It is paralleled by the transitory fusion of the various parts of the branchial skeleton. He consequently regarded the condition in Proteus (with a continuous laryngeal and tracheal skeleton) as rudimentary rather than primitive; and adhered to the earlier opinion of Wilder that the laryngeal and tracheal skeleton are distinct structures, and suggested that the latter might be either derived from one or more branchial bars behind the pars laryngea or be new formations.

The pars laryngea is not uniform in shape in Urodeles, and different opinions have been advanced as to which is the most primitive form. In Siredon and larvae of Triton and Salamandra it is a roundish rod-like structure. The Dilatator laryngis is inserted to it, the Laryngeus ventralis and the Laryngeus dorsalis when present[1] arise from the Dilatator laryngis by inscriptio tendinea. In Necturus and Proteus the pars laryngea, pointed in front, broadens to a flat plate, from the lateral edge of which a hook-like process projects backwards. The hind end of the process is tied to the inner limb of the plate by a ligament, which chondrifies in Proteus. The Dilatator laryngis is inserted to the lateral edge of the cartilaginous plate and the hook-like process, and the Laryngei dorsalis and ventralis arise from the upper and lower surfaces.

Göppert held that the form present in Necturus and Proteus is the more primitive and that of Siredon and larvae of Triton and Salamandra is secondary, owing to disappearance of the lateral part of the cartilage, with resulting shifting of the origins of the Laryngei dorsalis and ventralis to the tendons of the Dilatator laryngis. Drüner held the reverse opinion.

In Ellipsoglossa, Menopoma, Megalobatrachus max., and Amphiuma the pars laryngea has an oblique direction, from dorso-oral to ventro-caudal. The ventral ends meet and are tied together by connective tissue in the ventral median line (in Amphiuma by a cartilaginous bridge). The cartilage lies just beneath the mucous membrane and forms a support for the Rima glottidis which partially separates the laryngeal cavity into an anterior part— the vestibulum, and a posterior—the laryngo-tracheal cavity. In Menopoma and Megalobatrachus max., there is a processus trachealis projecting backwards from the pars laryngea close to the mid-dorsal line.

---

[1] The Laryngeus dorsalis arises from the tendon of the Dilatator laryngis in Triton, it is absent in Siredon, whilst in Salamandra larvae it was stated by Göppert to be absent, by Drüner to be present and to arise from the tendon of the Dilatator laryngis.

Drüner held that this form of the cartilage is secondary to that present in Salamandra, Triton and Siredon, and also that the processus trachealis is due to the fusion of tracheal elements with the pars laryngea.

A theory of the cartilago lateralis, absolutely different from that of the foregoing observers, was advanced by Wiedersheim (1904) from his investigations of the larynx in Ganoids and Dipnoi. He suggested, from analogy with Protopterus and Lepidosiren, that possibly the cartilago lateralis of Amphibia was primitively a tendon-chondrification without any phylogenetic relationship to the branchial bars.

*Laryngeal muscles*

*Anura.* Göppert (1894) described the laryngeal muscles of a 10 mm. larva of Rana as consisting of a s. Dilatator laryngis, Dorso-laryngeus and a Constrictor laryngis. The first named arises from the tissue lateral to the pharynx. He was of opinion, from comparison with Urodela, that the Dilatator laryngis had lost its constrictor action on the pharynx and become restricted in its action to the larynx. The Constrictor laryngis consists of a simple paired ring with median dorsal and ventral raphés, continuous ventrally with a Transversus ventralis iv. He concluded that it is homologous with the Laryngeus ventralis of Urodela. In 1898 he modified this opinion and advanced the theory that each half is homologous with the Laryngeus ventralis and the Laryngeus dorsalis of Urodela.

According to Wilder (1896) there is in the larva no Levator arcus branchialis iv, and at metamorphosis the Dilatator laryngis of the larva becomes separated into a (dorsal) Petro-hyoideus iv and a ventral Dilatator laryngis. According to Göppert (1894) a Levator arcus iv is present in the larva, and gains a new insertion into the processus postero-medialis at metamorphosis, forming the Petro-hyoidei posteriores or at least their hinder portion, and the only change in the Dilatator laryngis of the larva is that it gains an attachment to the processus postero-medialis.

*Gymnophiona.* The laryngeal muscles of a late larva of Ichthyophis were described by Göppert (1894) *vide infra*.

*Urodela.* Fischer (1864) included the Dilatator laryngis and Transversus ventralis iv in the muscle-system of a Constrictor laryngis, which appeared to be a repetition of the Levatores arcuum.

Wilder (1892) regarded the Dilatator laryngis as homologous with the dorsal segment of the fifth branchial arch of Selachii.

Göppert (1894) regarded the Dilatator laryngis as a Levator arcus v serially homologous with the Levatores of the branchial arches. This opinion was accepted by Wilder (1896).

Drüner also regarded the Dilatator laryngis as serially homologous with the Levatores arcuum, though of some segment behind the fifth branchial (*vide supra*).

Wilder (1892) put forward the theory that the laryngeal ring of muscle is a continuation of the ring musculature of the alimentary canal which the

developing respiratory tract carried with it when it arose as a diverticulum of the former. Its first action was that of a sphincter and it gained relations to the pars laryngea later.

Göppert (1894) argued, against Wilder's theory, that there is a fundamental difference between smooth and cross-striped muscle-cells; the former are single cells, whilst the latter form a syncytium, and the relationship of the two kinds of cells to nervous centres is quite different. In Siredon, ontogenetically, the Laryngeus ventralis is a derivative of the Transversus ventralis iv; and in Triton larvae, although there is no direct proof of the origin of the Laryngeus dorsalis, yet it stands in the closest relationship to the Dilatator laryngis.

Wilder (1896) abandoned his theory of 1892, and homologised the "intrinsic laryngeal muscles" (i.e. Laryngei and Constrictor) with a Transversus ventralis v, which has become separated into dorsal and ventral portions by the growth and flattening out of the arytenoids—the homologues of the fifth branchial bars.

Göppert (1898) abandoned his theory of 1894 that the Laryngeus ventralis is derived from the Transversus ventralis iv, and stated that they are serially homologous, the Laryngeus ventralis being the Transversus ventralis of a fifth branchial branch and homologous with the Transversus ventralis v of Acipenser and the Transversus ventralis posterior of Amia. The Laryngeus dorsalis is possibly derived from the same source.

Drüner (1901 and 1904) was of opinion that the Laryngei and Constrictor are homologous with a Transversus ventralis vi, or possibly with that of a still more posterior segment which has migrated forwards to that of the Dilatator laryngis and Arytenoid. The grounds for this opinion were derived from its innervation. The Dilatator laryngis is innervated in all cases from the N. intestino-accessorius X (with the addition, in Amphiuma and Siren, of branches from the N. recurrens, and in Menopoma of a fine twig from the nerve to the fourth branchial arch). On the other hand, the Laryngei and Constrictor are innervated by the N. recurrens intestinalis X. The N. recurrens intestinalis X is thus a collecting nerve in which the elements of at least two, perhaps more, branchial segments are included, and of these at least one is to be reckoned as being behind the segment of the Dilatator laryngis.

These observers have advanced various theories as to the primitive form of the intrinsic laryngeal muscles in Urodela.

Wilder (1892) considered as typical the condition present in Siren and Menopoma where the larynx is surrounded by a complete muscle-ring and the arytenoids are partly enclosed by it and partly lie in its substance. In 1896, after publication of Göppert's 1894 paper, he stated "I hardly feel like considering the Sphincter of Salamandridae as more than a modification of the original Laryngei and of thus considering the laryngeal ring of Triton as essentially different from that of Siren or of Necturus."

Göppert (1894) was of opinion that the primitive Urodelan condition is

shown by Necturus and Proteus, where there are only Laryngei, attached to a broad arytenoid, and that the Caducibranchiata (other than Amphiuma), with a Constrictor and Laryngei attached to the tendon of the Dilatator laryngis, represent a derivative condition due to a diminution in breadth of the arytenoid. This was supported by observations on Siredon (in which no Laryngeus dorsalis is found). In 13·5 mm. specimens he found a great number of young muscle-elements dorsal to the already formed Laryngeus ventralis, and in 18 mm. specimens the primordium of the Constrictor was represented by a small bundle of young muscle-elements dorsal to the Laryngeus ventralis with its median end spreading towards the dorsal median line of the larynx. Similarly, in 10 mm. larvae of Triton alpestris he found the Constrictor being proliferated from the Laryngeus ventralis. In 1898 he modified this opinion as regards Triton saying that he could now not exclude the Laryngeus dorsalis from taking part in the formation of the Constrictor, and that the method followed in Siredon was due to the absence of a Laryngeus dorsalis.

Göppert regarded the Constrictor of Amphiuma as due to the lateral union on each side of a Laryngeus dorsalis and ventralis.

Drüner regarded the condition of Siredon, Salamandra, and Triton—with Laryngei and Constrictor—as the primitive one, and that of Necturus and Proteus—with Laryngei only—as secondary. Further, Wilder had stated that, in Necturus, the first and last sections of a transverse series show continuous fibres of a circular outline entirely enclosing the Laryngei and acting as a Constrictor, and Drüner stated that in one case of Proteus he found the rudiment of a Constrictor on one side.

## OBSERVATIONS

### *Ventral branchial muscles*

*Anura.* In a 7 mm. larva of Rana temp. there are four branchial muscle-plates. That in the first branchial segment (fig. 1) has separated from the pericardium and consists, from below upwards, of the primordia of the Subarcualis rectus i, Marginalis i, and Levator i. The second, third and fourth branchial muscle plates (figs. 2, 3) are continuous, ventrally, with the pericardial wall. The fourth lies slightly posterior to the sixth gill-cleft.

In a 7½ mm. larva the second, third and fourth branchial muscle plates have separated from the pericardial wall. From the ventral ends of the second and third, Subarcuales recti ii and iii have separated off. From the ventral end of the fourth (figs. 5 and 6) Subarcualis rectus iv has separated off and the (rudimentary) Transversus ventralis iv passes ventro-medially. Each Subarcualis rectus extends forwards into the next segment.

In an 8 mm. larva Subarcuales recti i and ii have fused together forming a muscle passing from Branchiale ii to the Hyale. The Transversus ventralis iv (figs. 8, 9, 10) is better marked, passing towards the ventral aspect of the laryngeal groove.

In an 11 mm. larva (fig. 11) a muscle, passing from Branchiale i to the Hyale, has separated from the forepart of the muscle passing from Branchiale ii to the Hyale. The Subarcuales recti iii and iv have nearly fused together (fig. 12), and, in a 12 mm. larva, form a muscle passing from Branchiale iv to Branchiale ii. The Transversus ventralis iv has disappeared.

It is observable that the fourth branchial muscle-plate, before separation from the pericardium, shifts a little backward so as to lie posterior to the (rudimentary) sixth gill-cleft, and, when the fourth branchial bar becomes formed in an 8 mm. larva, it passes backwards external and posterior to the sixth gill-cleft.

Transversus ventralis iv is rudimentary and disappears early; it never forms an independent muscle passing from Branchiale iv to the middle line. It is also absent in larvae, of lengths from 10 to 12 mm. of Bufo lentig., Alytes, and Pelobates.

*Gymnophiona.* The development of the ventral branchial muscles has not yet been traced, but Fischer, Wiedersheim, Fürbringer and Göppert have partially described them.

In 3·5 and 5·9 cm. larvae of Ichthyophis (figs. 23–25) all four branchial bars are present, the third and fourth being fused at their ventral ends. Copula i, s. Basihyale and Copula ii, s. Basibranchiale i are present. Subarcuales recti iv, iii, ii and i are present, each passing from its branchial bar to the next anterior one. The foremost—Subarcualis rectus i—is broader than those behind, and, as it passes forward, divides into two portions, the inner of which is inserted into the Hyale, whilst the outer is prolonged in front of the Hyale and is inserted into the lateral edge of the Basihyale.

In a 7 cm. larva of Siphonops (figs. 26–31) the third and fourth branchial bars are fused, except at their dorsal ends, and there is no Basihyale. Subarcualis rectus iv is absent. Subarcuales recti iii, ii and i are present. i is single and inserted anteriorly into the Hyale. In the adult stage Subarcualis rectus i persists, whilst ii and iii have degenerated into tendons.

The adult stages of Caecilia palmiri and Hypogeophis are similar to the adult stage of Siphonops.

A Transversus ventralis i (not hitherto described) is present in larvae of Siphonops and Ichthyophis. In the former (figs. 26 and 27) its lateral end is attached to Branchiale i and its median end to a short transverse aponeurosis which connects it to its fellow. In Ichthyophis (fig. 24) its lateral end is attached to Subarcualis rectis i, and its median end partially to Copula ii and partially to a median raphé. The muscle is absent in the adult stages of Siphonops, Caecilia palmiri and Hypogeophis.

There are no Transversi ventrales ii and iii in the larval stages of Siphonops and Ichthyophis.

Transversus ventralis iv has been described by Göppert, in a late larva of Ichthyophis, as arising by two heads from the fused third and fourth branchial bars and passing to an aponeurosis ventral to the trachea. In the younger

larvae investigated I find that both heads arise from the fourth bar. In a 7 cm. larva of Siphonops the muscle arises from the nearly completely fused third and fourth branchial bars by a single head.

The differences in the form of Subarcualis rectus i between Ichthyophis and Siphonops are related to the presence in the former and absence in the latter of Copula i s. Basihyale. The absence of a Subarcualis rectus iv in Siphonops may be secondary and related to the greater degree of fusion of the third and fourth branchial bars.

*Urodela.* In Menopoma seven gill-clefts are developed, and correspondingly there are five branchial segments. In a larva of 15 mm. (figs. 33, 34) the sixth and seventh gill-clefts cannot be distinguished from each other; they form a lateral projection, with a slit-like lumen, of the branchial endoderm, $140\mu$ long, which reaches the ectoderm. In a larva of 17 mm. (fig. 37) the projection is $160\mu$ long, and on its ventral surface is a slight bulge, the first indication of the seventh gill-cleft. In a larva of 19 mm. the sixth gill-cleft has disappeared on the right side, leaving no trace, whilst on the left side the anterior end of the sixth gill-cleft persists as an epithelial plug or stump continuous with the branchial endoderm (fig. 43). Behind this, the seventh gill-cleft reaches the ectoderm, on both sides (fig. 44). The distance between the anterior end of the fourth and that of the fifth gill-cleft is $170\mu$. On the right side the distance between the anterior end of the fifth and that of the seventh gill-cleft is $280\mu$; on the left side the distance between the anterior end of the fifth gill-cleft and the stump of the sixth is $180\mu$, and the distance between that and the anterior edge of the seventh gill-cleft is $110\mu$. The length of the third branchial segment (between the fourth and fifth gill-clefts) is thus $170\mu$, that of the fourth branchial segment is $180\mu$, that of the fifth branchial segment is $110\mu$. The fifth branchial segment, which does not contain any branchial muscle-plate, or branchial bar, or branchial aortic arch, is thus shorter than the more anterior ones.

The seventh gill-cleft, which does not perforate, is present in larvae in this stage up to one of 22 mm.; it has disappeared in larvae of 24 mm. without leaving any trace. The stump of the sixth gill-cleft on the left side persists in larvae up to the length of 28 mm. In one of 32 mm. it has become detached from the endoderm.

Four branchial muscle plates are developed, in the first four branchial segments. In a larva of 15 mm. (figs. 32, 33) those in the first three segments have become detached from the pericardial epithelium, whilst that of the fourth branchial segment is still continuous with it. The primordium of the hypobranchial spinal muscles forms a continuous column, and extends as far forwards as the hyoid segment. In a larva of 17 mm. (fig. 36) the fourth branchial muscle-plate has also become detached from the pericardial epithelium. These muscle plates lie lateral to the branchial bars, which have begun to develop. The ventral portions of the branchial muscle-plates form the Subarcuales, and, in the fourth branchial segment, the Transversus ventralis as well. The primordium of the hypobranchial spinal muscles has

extended forwards to Meckel's cartilage and separated into Genio-hyoid and Sterno-hyoid. The hind end of the Genio-hyoid has grown backwards a little, ventral to the Sterno-hyoid. In a larva of 18 mm. (fig. 38) (in which the sixth gill-cleft is still continuous with the ectoderm) the Subarcualis rectus iv has begun to grow forward. Its hind end is continuous with the lateral end of the Transversus ventralis iv which has begun to grow transversely inwards (fig. 39). In a larva of 19 mm. Subarcualis rectus i has grown forwards to the second gill-cleft, Subarcuales obliqui ii and iii have grown forwards and down-wards and meet, laterally to the Sterno-hyoid (fig. 42). The fourth branchial bar now passes from the fourth branchial segment backwards, outside the stump of the sixth gill-cleft on the left side, into the fifth branchial segment, and then upwards; i.e. on the total or partial atrophy of the sixth gill-cleft it bulges backwards into the fifth branchial segment (figs. 43, 44). Corre-spondingly, the hind end of the Subarcualis rectus iv and the lateral end of the Transversus ventralis iv have shifted back into the fifth branchial segment (figs. 43, 44). The front end of Subarcualis rectus iv has grown for-wards into the second branchial segment. The Transversus ventralis iv has now further developed, and passes transversely inwards to the middle line, on the left side under, and behind, the stump of the sixth gill-cleft. In a larva of 22 mm. the Urobranchiale has developed (see later, p. 141), and the hind end of the Genio-hyoid has grown further back. In a larva of 24 mm., where the seventh gill-cleft has disappeared, the hind end of Subarcualis rectus iv and the lateral end of Transversus ventralis iv are relatively further back, with the result that the anterior edge of Transversus ventralis iv is oblique and lies, on the left side, posterior to the stump of the sixth gill-cleft (figs. 48, 49). The anterior end of Subarcualis rectus iv (a) reaches the first branchial bar, whilst off-shoots (b and c) are given off to the second and third branchial bars (fig. 51). The Subarcuales obliqui ii and iii unite and pass to the sheath of the Sterno-hyoid.

There is little further change in the Subarcuales; in a 32 mm. larva the ventral end of the second gill-cleft is shallower and the anterior end of Sub-arcualis rectus i is attached to the Ceratohyale. Transversus ventralis iv gradually spreads backwards, forming a broad sheet; in a 34 mm. larva its posterior edge underlies the Laryngeus ventralis. In the adult (Drüner) the muscle underlies the trachea.

Miss Platt (1897) stated that in Necturus Subarcualis rectus i is developed from the ventral end of the mesothelial tissue of the glosso-pharyngeal arch. Subarcualis obliquus ii grows forwards from the mesothelium of the first vagus arch near the point where this tissue joins the wall of the pericardium. Subarcualis iii (a and b) arises as a single muscle from the wall of the peri-cardium in the region where the mesothelium of the second vagus arch unites with the pericardial wall.

She did not mention the Transversus ventralis iii, nor state how many gill-clefts are developed, but the figures given show five.

My observations in regard to the Subarcuales of the first two branchial

arches coincide with those above stated, but they are a little different in regard to the number of gill-clefts and the development of the third branchial muscle-plate.

In a larva of 12 mm. there are five gill-clefts—the sixth not being yet developed. In a larva of 13 mm. the fifth gill-clefts are reduced to stumps attached to the endoderm, on both sides, and the sixth gill-clefts have developed and reach the ectoderm. The length of the third branchial segment (between the fourth and fifth gill-clefts) is $120\mu$, that of the fourth is $90\mu$. In a larva of 15 mm. the sixth gill-clefts have disappeared leaving no trace. In a larva of 18 mm. the stumps of the fifth gill-clefts have separated from the endoderm, and in one of 20 mm. the right one has disappeared.

In the larva of 12 mm. (fig. 57) the third branchial muscle-plate is continuous ventrally with the epithelium of the pericardium. In a larva of 13 mm. (figs. 60 and 61) the third branchial bar passes backward from the third branchial segment lateral to the stump of the fifth branchial cleft into the fourth branchial segment and then upward. The third branchial muscle-plate has separated from the endoderm, and its ventral end has developed into the Subarcualis rectus iii and the Transversus ventralis iii. The former grows forward from the fourth branchial segment laterally to the stump of the fifth gill-cleft, the latter passes inwards, partly under the stump of the fifth gill-cleft (fig. 60), and partly behind it (fig. 61). In the larva of 16 mm. (figs. 67, 68), where the sixth gill-clefts have disappeared, the hind end of the Subarcualis rectus iii and the lateral end of Transversus ventralis iii are still further back, so that the front edge of Transversus ventralis iii is behind the stump of the fifth gill-cleft.

### Morphology of the ventral branchial muscles

*Subarcuales. Anura.* In larvae of Rana the Subarcuales recti are simple. The only secondary changes are (1) Fusion of Subarcuales recti i and ii to form a long muscle, and the subsequent separation of a slip from its anterior half to form a muscle passing from the first branchial to the hyoid bar. (2) The fusion of Subarcuales recti iii and iv to form a long muscle. The resulting condition is also present in larvae of Bufo, Alytes, and Pelobates. The condition of the Subarcuales in larvae of Aglossa has not yet been described.

*Gymnophiona.* The ventral branchial muscles in Siphonops and Ichthyophis have been described above (page 136). These are the only larval forms yet investigated.

*Urodela.* Subarcualis rectus i, as shown by Drüner, passes from the first branchial bar, generally from Ceratobranchiale i to the Ceratohyale. In all the larvae examined it was found that a delay occurs in the attachment of the anterior end of the muscle to the Ceratohyale, it is for a time inserted into the epithelium of the ventral end of the second gill-cleft, which forms a groove in the floor of the branchial region, e.g. Menopoma (fig. 51). The Subarcuales obliqui have been described by Fischer and Drüner. The latter

states that in Ellipsoglossa (adult), Megalobatrachus max. (adult), Siredon, Menopoma (adult), Salamandra and Triton larvae, the muscles pass forwards and downwards, unite by their bellies or tendons, and are inserted into the fascia of either the Rectus profundus or superficialis, and so act on the Uro-branchiale.

Two exceptions to this general rule are described by Drüner. He stated that in Necturus and Proteus (with only three branchial bars) only one muscle—Subarcualis obliquus ii—is present, and that this, in Proteus, is inserted on the fascia of the Rectus profundus, but in Necturus is inserted into Hypo-branchiale i, i.e. in the latter is a Subarcualis rectus ii. In numerous embryos, however, I find the muscle inserted into the fascia of the Rectus profundus (fig. 66), i.e. it is a true Subarcualis obliquus ii. The other exception is that of Amphiuma (adult), where Drüner stated that only one Subarcualis obliquus is present, passing from Ceratobranchiale iii to Branchiale i and not to the fascia of the Rectus.

I find that in Menopoma (larva) and Ellipsoglossa (larva) the common tendon of Subarcuales obliqui ii and iii is inserted partly into the sheath of the Rectus profundus and partly into the Urobranchiale.

The above can be summarised as follows: In Urodela, with exception of Amphiuma (adult form), the Subarcuales of the second and third branchial bars (or, in the case of Necturus and Proteus, that of the second bar) do not grow forward to the next anterior bar, as in Anuran and Gymnophionan larvae, but forward and downward, becoming Subarcuales obliqui, joining together and passing into a tendon which has direct or indirect relations to the Urobranchiale.

A Urobranchiale, either continuous with the branchial skeleton or as a separate structure, has been described by Drüner in all the Urodela he examined, with exception of Menopoma (adult), Megalobatrachus max. (adult), Amphiuma (adult), and Ellipsoglossa (adult). In the larvae of Menopoma and Ellipsoglossa, however, a Urobranchiale is present, as a structure either separate or continuous with the branchial skeleton. In these two forms, there-fore, the Urobranchiale disappears at metamorphosis or earlier (it has already degenerated in a 40 mm. Menopoma), and this may also be the case in Megalo-batrachus max. and Amphiuma[1], for its development appears to be related to the overlapping of the anterior end of the Sternohyoid s. Rectus cervicis by the Geniohyoid—which is universal in Urodela. This overlapping is due to a backward growth of the hind end of the Geniohyoid ventral to the Sterno-hyoideus s. Rectus cervicis.

The development of the Urobranchiale is not uniform in Urodela. Stöhr (1880) described it in Triton as due to division into dorsal and ventral portions of an original primordium connecting together the median ends of the hyoid and first two branchial bars. Miss Platt (1897) described a second Basi-

[1] In 45 mm. larvae of Amphiuma (Hay) the second Basibranchiale and Urobranchiale are both absent.

branchiale in Necturus as developing from cells on the anterior wall of the pericardium. She inclined to regard it as a foreign element associated secondarily with the branchial arches. Gaupp (1905) pointed out the homology of this "second Basibranchiale" of Necturus with the Urobranchiale of Salamandridae larvae, but added that it was not yet shown whether it represents an independent Basibranchiale, which in Salamandridae larvae develops in concrescence with the anterior Basibranchiale.

I find that the hyobranchial skeleton of a 12 mm. larva of Ellipsoglossa (figs. 71 and 72) is in a precartilaginous condition. The median ends of the hyoid and first and second branchial bars are continuous ventrally with a median rod which represents the first and second Basibranchialia. The Urobranchiale is a ventral process of the second Basibranchiale. In a 15 mm. larva (figs. 73–76) chondrification has taken place; the Urobranchiale has extended ventro-posteriorly, and the attachment of the second branchial bars has spread along it.

The development of the Urobranchiale in Triton, Salamandra, and Amblystoma, is similar to that in Ellipsoglossa.

In a 20 mm. larva of Menopoma (fig. 46) the Urobranchiale is a ventro-posterior process of the precartilaginous second Basibranchiale. It has separated from the second Basibranchiale in a 22 mm. larva, and is chondrified as a separate structure in a 32 mm. larva (figs. 53 and 54). This condition persists in a 36 mm. larva. In a larva of 40 mm. it has degenerated into a small clump of cells. In the adult it is absent (Drüner).

In Necturus no second Basibranchiale is developed. In an embryo of 16 mm. (figs. 64–66) the Urobranchiale is a precartilaginous rod passing ventro-posteriorly from its junction with the ventral ends of the first branchial bars.

The Urobranchiale may thus be developed (1) as a ventro-posterior process of the second Basibranchiale (Ellipsoglossa, Triton, Salamandra, Amblystoma), (2) as a ventro-posterior process of the second Basibranchiale which separates off and subsequently chondrifies (Menopoma), (3) as a structure passing ventro-posteriorly from the ventral ends of the first branchial bars, no second Basibranchiale being present (Necturus).

The attachment of the ventral end of the first branchial bar extends along the Urobranchiale in Ellipsoglossa, Triton, Salamandra, and Amblystoma, but does not do so in Necturus.

These phenomena suggest that some ancestral Urodelan stock possessed a Urobranchiale as a ventral process of the second Basibranchiale, with no extension of the ventral end of the first branchial bar along it—i.e. a condition very like that of a 12 mm. Ellipsoglossa or 20 mm. Menopoma.

*Subarcualis rectus iv* has been described by Fischer and Drüner. The latter states that it is present in the larval stages of Siredon, Salamandra and Triton, and in the adult stages of Amphiuma and Menopoma: but is absent in the adult stages of Siredon, Salamandra, Triton, Megalobatrachus max. and

Ellipsoglossa. My observations show that it is also present in the larval stages of Ellipsoglossa and Menopoma.

It is a muscle that takes origin from the fourth branchial bar, passes forward and separates into three slips (*a*, *b*, *c*) which are attached respectively to the first, second and third branchial bars. In Siren only (*a*) is present. In Necturus and Proteus there is a similar Subarcualis rectus iii which takes origin from the third branchial bar, and is attached, (*a*) to the first, and (*b*) to the second, branchial bar.

The forward extension of Subarcualis rectus iv in front of the third branchial bar—to the second and first bars—is related to the secondary function and position of Subarcuales ii and iii. (It is noticeable that this secondary form of Subarcualis rectus iv also exists in Amphiuma (adult), and that in Megalobatrachus max. (adult, with only two branchial bars) though no Subarcualis rectus iv is present yet Subarcuales obliqui ii and iii and not Subarcuales recti ii and iii are present (*vide* Drüner). These facts form additional evidence in favour of the theory, suggested above, that a Urobranchiale exists in the larval forms of these Urodela also.)

There are thus five closely related phenomena in Urodela. (1) Backward growth of the hind end of the Genio-hyoid ventral to the forepart of the Rectus cervicis. (2) Formation of a Urobranchiale. (3) Formation of Subarcuales obliqui ii and iii (Subarcualis obliquus ii in Necturus and Proteus). (4) Forward extension of Subarcualis rectus iv (Subarcualis rectus iii in Necturus and Proteus) to the first branchial bar. (5) Separation of a superficial, ventral, portion of the Rectus cervicis, attached to the Urobranchiale.

No one of these secondary phenomena occur in Anuran and Gymnophionan larvae, where the conditions are more primitive. (There is a small overlap of the Genio-hyoid and Rectus cervicis in Rana temp. larvae, but it is due to a backward extension of the former along the hypobranchial plate, and so of a different character from that of Urodela. The anterior end of the Rectus becomes attached to the Crista hyoidea (of Schultze), but this, as shown by Gaupp, is a ventral process of Basibranchiale i, and so not homologous with the Urobranchiale of Urodela.)

*Transversi ventrales.* Transversus ventralis i is present in larvae of Ichthyophis and Siphonops, but not in Anuran or Urodelan larvae. Transversus ventralis ii is not found in any Amphibia. Transversus ventralis iii is present in Necturus, and probably in Proteus, but not in other Amphibia. Transversus ventralis iv is present in larvae of Anura, Gymnophiona, and Urodela with four branchial bars. In Rana the muscle is rudimentary and soon disappears. In Ichthyophis it is attached to the fourth branchial bar, and, on the fusion of this with the third, to the fused bar, by two heads in Ichthyophis, by one in Siphonops.

In Menopoma, at the stage when the sixth gill-cleft reaches the ectoderm, the ventral end of the fourth branchial muscle-plate (attached to the pericardial wall) and the primordium of the fourth branchial bar are in front of

it and do not extend outside or behind it. When the gill-cleft is reduced to a stump, the fourth branchial bar passes outwards and backwards laterally to the stump, then upwards and posterior to it, and correspondingly the primordia of the Subarcualis rectus iv and Transversus ventralis iv have migrated posterior to the stump, and from this point grow forwards and inwards respectively.

The whole series of events is due to an enlargement of the "branchial basket," whereby all the structures of the fourth branchial segment bulge backwards behind the stump of the sixth gill-cleft.

A similar series of events is observable in Rana, where—the sixth gill-cleft being never more than a stump—it occurs relatively earlier, before the ventral end of the fourth branchial muscle-plate separates from the pericardial wall.

In Necturus a similar series of events occurs in regard to the third branchial muscle-plate and the fifth gill-cleft. Only one Transversus ventralis is formed, i.e. the third. Transversus ventralis iii or iv subsequently extends backwards forming a broad sheet which underlies, to a variable extent, the respiratory tract (*vide* p. 128).

The above mentioned developments of Transversi ventrales may be tabulated as follows:

|  | 1st | 2nd | 3rd | 4th branchial segment |
|---|---|---|---|---|
| Gymnophiona, larvae ... ... | × | 0 | 0 | × |
| Anura, larvae ... ... ... | 0 | 0 | 0 | × |
| Necturus and Proteus ... ... | 0 | 0 | × | 0 |
| Urodela with 4 branchial bars ... | 0 | 0 | 0 | × |

The theory of Wilder (*vide supra*, p. 128) is supported by these facts. It has to be remarked, however, that the Intermandibularis and Interhyoideus are probably not serially homologous with the Transversi ventrales of the branchial segments; and, further, that the phenomena in Necturus and Proteus possibly admit of an explanation other than that of the persistence of an ancestral feature which is lost in other Amphibia (*vide infra*, p. 147). His theory, then, should be limited to the branchial region, and restated as follows: primitively in Amphibia there was a series of ventral transverse muscles attached to the branchial bars.

The occurrence of Transversi ventrales ii, iii and v in Ceratodus may be adduced as additional evidence in favour of the theory.

### *Summary of the characteristics of the ventral branchial muscles*

The Subarcuales are developed by forward growth of the ventral ends of the branchial muscle-plates.

In some primitive ancestral stock they probably formed a series of longitudinal muscles, the Subarcuales each passing from its branchial bar to the next in front.

In Anuran and Gymnophionan larvae few modifications occur. In Anuran larvae Subarcuales recti i and ii unite, forming one muscle, and subsequently

a lateral portion is separated from the anterior part and passes from the Branchiale i to the Hyale; and Subarcuales recti iii and iv unite forming one muscle. As regards Gymnophiona, in Siphonops larvae, where there is no Basihyale, Subarcualis rectus i is single, whereas in Ichthyophis larvae, where a Basihyale is present, Subarcualis rectus i separates into two muscles. In Urodela, whilst Subarcualis rectus i remains single, considerable modifications occur in the hinder subarcuales—probably associated with the backward growth of the Genio-hyoid and the formation of a Urobranchiale. These changes are, shortly, an insertion of Subarcuales ii and iii to the Urobranchiale directly or indirectly, so that they form Subarcuales obliqui ii and iii (in Necturus and Proteus ii only), and an extension forwards of the hindmost Subarcualis rectus (fourth in Urodela with four branchial bars, third in Necturus and Proteus) to Branchiale i.

Transversi ventrales are formed by ingrowth from the ventral ends of the branchial muscle-plates. Transversus ventralis i is present only in Gymnophionan larvae. Transversus ventralis iv (iii in Necturus and Proteus) is formed in all Amphibian groups, though it is rudimentary and soon disappears in Anuran larvae; it spreads backwards, forming a broad sheet, which in part or wholly underlies the respiratory tract.

### Innervation of the ventral branchial muscles

*Anura.* The account given by Strong is not detailed, but he states that the Recurrens does not spread into the branchial region.

*Gymnophiona.* Norris and Hughes state that in Herpele (adult) the Recurrens innervates the Transversus ventralis iv in addition to the laryngeal muscles. In a 7 cm. larva of Siphonops, and in 3·5 and 5·9 cm. larvae of Ichthyophis I find that the Recurrens innervates the same muscles as in Herpele, i.e. it does not extend into the branchial region nor does it innervate the Subarcuales recti and Transversus ventralis i.

*Urodela.* Drüner stated that Subarcualis rectus i is innervated solely by the ix in Menopoma, Megalobatrachus max., and Necturus. It has an additional nerve supply from the hinder branchial nerve or nerves and the Recurrens intestinalis in other Urodeles. Subarcualis obliquus ii in Necturus is innervated by the second branchial nerve, in Proteus by this and probably also by the Recurrens. Subarcuales obliqui ii and iii in Ellipsoglossa and Menopoma are innervated by the second and third branchial nerves, in Megalobatrachus max. and Siredon by these and the Recurrens, in Salamandra and Triton by the Recurrens, in. Siren ii by the second branchial nerve and iii by the Recurrens. In Amphiuma the single Obliquus is innervated by the second branchial nerve and the Recurrens.

Subarcualis rectus iv is absent in the adult forms of Ellipsoglossa, Megalobatrachus max., Siredon, Salamandra and Triton; in Menopoma (adult) *a* and *b* are innervated by the second and third branchial nerves, *c* by the fourth branchial nerve and the Recurrens; in Siredon (adult), Amphiuma (adult),

Salamandra and Triton larvae, *a* is innervated by the second branchial nerve and the Recurrens, *b* by the third branchial nerve and the Recurrens, *c* by the Recurrens; in Siren *a* (the only one present) is innervated by the second branchial nerve and the Recurrens. Transversus ventralis iii of Necturus and Proteus, and Transversus ventralis iv of other Urodeles, are innervated by the Recurrens. Drüner, as stated above p. 129, inferred from these facts that the Transversus ventralis iii or iv had migrated forward into the branchial region, and that a similar though less marked migration had taken place in the muscle-elements of the Subarcuales. Norris, holding with Drüner that the nerves are the most conservative structures in the branchial region, and "will thus constitute more reliable guides in the search for the primitive relations in this region than will the branchial arches themselves," states that there is "a considerable usurpation by the Ramus intestino-recurrens of territory of the ventral branchial region belonging originally to the post-trematic rami of the branchial nerves."

It is doubtful whether this statement implies a forward migration of muscle-elements, as Drüner thought; or a forward extension of nerve-fibres, the muscle-elements remaining constant.

But, however that may be, the phenomena of development show that the Transversus ventralis iv and the Subarcuales are developed from the ventral ends of the branchial muscle-plates.

It may be inferred that the ventral branchial muscles are more conservative than are their nerves.

Three processes appear to have occurred. (1) A disappearance of the ventral motor branches of the branchial nerves, in increasing degree from before backwards. (2) An additional or supplanting innervation by the Recurrens. (3) In the case of the Subarcualis rectus iv an innervation by the nerves of the branchial arches into which it grows—thus, in Menopoma, Subarcualis rectus iv (*a*)—which grows forward to the first branchial bar—is innervated by the second branchial nerve, (*b*)—which grows forward to the second branchial bar—by the third branchial nerve, (*c*)—which grows forward to the third branchial bar—-by the fourth branchial nerve and the Recurrens.

Comparison of the innervation of the ventral muscles of the branchial bars in Anuran, Gymnophionan and Urodelan larvae shows that the secondary —additional or supplanting—innervation by the Recurrens intestinalis has been developed within the Amphibian phylum, and to the greatest extent in Urodela.

*On the number of branchial bars and related muscles in Amphibia*

Maurer (1902) described five gill-clefts and a post branchial body in Amphibia, and Drüner (1901) (*vide supra*, pp. 129, 130) six gill-clefts. Kingsley[1],

---

[1] Kingsley names the clefts: (*a*) hyomandibular, (*b*) the first branchial, (*c*) the second branchial, (*d*) the third branchial, in front of the fourth cartilaginous gill-arch, and then two pits behind this arch—these, according to his statement are the fifth and sixth—according to the reckoning adopted here, the sixth and seventh gill-clefts.

however, had stated (1892) that in an embryo Amphiuma (size not stated) there were two pits behind the fourth cartilaginous gill-arch, i.e. five branchial segments. Marcus (1908) stated that in larvae of Hypogeophis seven gill-clefts are developed (*vide infra*, p. 149), i.e. five branchial segments.

In Menopoma and Ellipsoglossa seven gill-clefts are developed, the last two behind the fourth branchial bar and its muscles. No muscle-plate or cartilaginous bar is developed in this fifth branchial segment.

The sum of this evidence suggests that five branchial bars with related muscles existed in Amphibian ancestors, but that the fifth disappeared long ago.

Drüner (*vide supra*, pp. 129, 130) came to the conclusion that Urodeles originally possessed a greater number of branchial arches than four. The evidence merits discussion. As regards the nerves found by him, it is possible that they have relation solely to the sixth and seventh gill-clefts. As regards the muscles, the phenomena of development do not bear out the theory that the stump of the sixth gill-cleft separates a Transversus ventralis iv from a Transversus ventralis v. Thus in Menopoma there is only one primordium developed—that of Transversus iv. This, at first, lies solely in the fourth branchial segment, then under the stump of the sixth gill-cleft, then posterior to it. The variation is due to the fact that, on the partial atrophy of the sixth gill-cleft, the Transversus iv, the hind end of Subarcualis rectus iv, and the fourth branchial bar, migrate into the fifth branchial segment; and, on the atrophy of the seventh gill-cleft, still further back. There is a similar progressive variation of the Transversus iv in relation to the sixth gill-cleft in Ellipsoglossa, and of Transversus iii in relation to the fifth gill-cleft in Necturus. The evidence, as regards muscle elements, is thus limited to the discovery of a Levator arcus v on one side in one larva of Triton. I have not seen this, however, in the many larvae of Menopoma, Ellipsoglossa, and Triton crist. I have examined.

It is probable, therefore, that the case described by Drüner is an instance of fluctuation, possibly of atavistic fluctuation, from the usual number of four branchial bars and related muscles in Urodela.

In support of these conclusions, it may be added that in Lysorophus— a member of the ancestral Urodeles, from the Pennsylvanian deposits— Sollas found only four branchial bars, the first three consisting of cerato-branchial and epibranchial elements, and the fourth of a train of fragments.

The case of Necturus, with only three branchial bars and related muscles, probably comes under a different category. All Amphibia, with exception of Megalobatrachus max. (adult), Necturus and Proteus, have four branchial bars and related muscles. Megalobatrachus max. has two branchial bars in the adult state (Drüner), but only the early stages of larval development have been published hitherto—by de Lange. In Necturus the development, described above, permits of comparison with Menopoma.

In Menopoma seven gill-clefts are formed, all of which reach the ectoderm.

The sixth disappears on the right side, whilst on the left side it forms an epithelial stump continuous with the endoderm. This becomes detached later on. The seventh disappears on both sides, without leaving any remnant. The fourth (and last) branchial muscle-plate lies, at first, anterior to the sixth gill-cleft. No muscle-plate is developed in the fifth branchial segment.

In Necturus six gill-clefts are formed, all of which reach the ectoderm. The fifth become detached from the ectoderm on both sides and form epithelial stumps continuous with the endoderm. They become detached later on. The sixth gill-clefts disappear on both sides and leave no trace. The third (and last) branchial muscle-plate lies, at first, anterior to the fifth gill-cleft. No muscle-plate is developed in the fourth branchial segment.

The differences in the ventral branchial muscles are as follows: (1) In Menopoma there is a Transversus ventralis iv, and no Transversus ventralis iii. In Necturus there is a Transversus ventralis iii, and no Transversus ventralis iv. (2) In Menopoma two Subarcuales, i.e. the second and third, become Subarcuales obliqui ii and iii. In Necturus only one Subarcualis, i.e. that of the second branchial arch, becomes a Subarcualis obliquus ii. (3) In Menopoma Subarcualis rectus iv extends forward to Branchiale i. In Necturus it is Subarcualis rectus iii which extends forwards to Branchiale i.

There is so great a similarity between the muscles of the fourth branchial segment in Menopoma and those of the third branchial segment of Necturus, that it is improbable that the difference is due to transformation of the characteristics of the third branchial arch musculature of Menopoma into those of the third of Necturus, or conversely; nor is there any evidence of the dropping out, or intercalation, of a branchial bar between the first and last.

This suggests that a common branchial muscle-plate has been separated into four portions by the gill-clefts in Menopoma; whilst in Necturus it has been separated into three portions by the gill-clefts.

No one branchial bar of Necturus, with its related muscles, is thus exactly homologous with any one branchial bar of Menopoma, and it is only possible to speak of a collective homology.

Branchial segments may thus be reduced in number by at least two processes, by a separation of the branchial area into a fewer number of segments without loss of any one individual segment, or by a loss of the ultimate segment. The former is apparently what happens in Necturus and Proteus, as compared with Menopoma and Ellipsoglossa. The latter is apparently what happens in Amphibia generally, as compared with Dipnoi. In Dipnoi there is a fifth branchial bar and related muscles. In Menopoma and Ellipsoglossa there is an empty fifth branchial segment. In Rana there is no developmental evidence of a fifth branchial segment. The existence in Necturus of an empty fourth branchial segment suggests that the mutation to three branchial segments took place subsequent to the loss of a fifth branchial bar and related muscles.

After formation of the full number of segments, the branchial region may

become shorter by fusion. Thus Sarasin showed that, in Ichthyophis, the third and fourth branchial bars coalesce. Comparison of the 5·9 cm. larva of Ichthyophis with the, relatively later, 7 cm. larva of Siphonops suggests that this is accompanied by fusion of Levatores iii and iv, and by disappearance of Subarcualis rectus iv.

### *Development of the larynx and laryngeal muscles*

Greil stated that in Urodelan and Anuran larvae the lungs are developed from bilateral longitudinal grooves on the inner surface of the floor of the oesophagus, forming with each other an angle of about 40°, open caudally. These grooves develop at a period when only four gill-clefts are present; the fifth and sixth being formed later, between the fourth and the primordia of the lungs. The pulmonary grooves form pocket-like diverticula, which grow backwards in the thickened splanchnopleure and develop into the primitive pulmonary sacs. The pulmonary grooves are put into communication with each other by a transverse or bifurcation groove. The ventral portion of the wall of the oesophagus, in front of the bifurcation groove, forms by approximation of its walls the longitudinal laryngo-tracheal groove. It is continuous posteriorly with the bifurcation groove. In Anura it becomes temporarily closed by union of its walls, and is subsequently hollowed out into the laryngo-tracheal groove. The pulmonary and bifurcation grooves are folded off on their dorsal and caudal side from the oesophagus.

In Anura the sixth gill-clefts remain rudimentary and have no connection with the ectoderm; in Bombinator they atrophy, in other Anura the ultimo-branchial bodies are formed from their ventral portions. In Ranidae and Bufonidae the lumen of the anterior part of the oesophagus becomes temporarily obliterated and subsequently opens out—later than does the laryngo-tracheal cavity.

In Urodela (Triton, Salamandra, Siredon) the sixth gill-clefts, which are also transitory, reach the ectoderm-bands which grow towards them and fuse for a short distance. Rupture to the exterior does not take place. The ultimo-branchial body is developed from the left sixth cleft.

Greil did not investigate the development of the laryngeal-muscles.

*Anura.* In a 7 mm. larva of Rana temp. (figs. 3, 4, 5), the laryngeal groove extends from $75\mu$ behind the sixth gill-clefts, where it passes into the transverse pulmonary groove, forwards to $15\mu$ behind the sixth gill-clefts. Like the oesophagus above, it has no lumen. The coelom extends dorsally on either side of the transverse groove to the side of the oesophagus, but does not do so laterally to the laryngeal groove. Many undifferentiated cells are visible on either side of the oesophagus and laryngeal groove, proliferated from the visceral layer of the coelom (figs. 4, 5).

In a $7\frac{1}{2}$ mm. larva the laryngeal groove extends from $67\mu$ behind to the level of the sixth gill-clefts. On either side of the laryngeal groove is seen

the primordium of the laryngeal muscles, partially separated into the Constrictor and Dilatator laryngis (figs. 6, 7). It extends from $82\mu$ behind to $22\mu$ behind the sixth gill-clefts.

In an 8 mm. larva (figs. 8, 9, 10) the laryngeal groove extends from $60\mu$ behind to $7\mu$ in front of the sixth gill-clefts. There is a lumen in its ventral part, continuous with that in the transverse groove. The laryngeal muscles (figs. 9, 10) are fully formed, and extend from $127\mu$ behind to $15\mu$ behind the sixth gill-clefts. The Constrictor meets its fellow dorsally and ventrally.

In an 11 mm. larva (figs. 13–16) the laryngeal groove extends from $22\mu$ behind the sixth gill-clefts to $37\mu$ in front of them. The laryngeal muscles extend from $195\mu$ behind to $22\mu$ in front of the sixth gill-clefts. The primordium of the arytenoid s. pars laryngea cart. lat. is visible within the Constrictor laryngis. The Constrictor oesophagi is visible lateral, and ventral, to the forepart of the oesophagus.

The laryngeal groove is thus at first wholly posterior to the sixth gill-clefts, and gradually extends forwards, so that finally its anterior end is a little in front of them. The lumen in the transverse pulmonary groove extends forwards in the laryngeal groove, which opens by separation of its lips. There is no trachea. The laryngeal muscles are formed in the splanchnic mesoderm on either side of the laryngeal groove, and become fully developed behind the sixth gill-clefts. In their subsequent growth they spread backwards and forwards, so that the ventral part of the obliquely situated Constrictor laryngis comes to lie a little in front of the sixth gill-clefts, i.e. in the fourth branchial segment. There is no migration forwards of the laryngeal muscles.

The Constrictor laryngis posterior is not formed until metamorphosis begins. In a 20 mm. larva (figs. 18 and 19) there are a number of oval cells in the angle, open backwards, of the muscle-fibres of the Constrictor laryngis diverging from the ventral raphé. In a later larva (fig. 20)—one with hind legs just visible on the surface of the body—these cells have grown into muscle-cells, which pass upwards and backwards forming the primordium of the Constrictor laryngis posterior. These phenomena confirm the statement of Wilder that the Constrictor laryngis posterior is a derivative of the Constrictor laryngis.

*Gymnophiona.* In Ichthyophis five gill-clefts were mentioned by the Sarasins. In Hypogeophis Marcus described seven gill-clefts, of which the first six break through. The sixth totally atrophy. The seventh do not reach the ectoderm and form the ultimo-branchial bodies which separate from the hypoblast and develop into a small vesicle on each side. The primordium of the lungs is first seen in stage 22 in which the fifth gill-clefts are already formed, either as two lateral bulges ventral to the gut, of which the left disappears, or as a right sided one—which (from the figure given) is apparently on the level of the seventh gill-clefts. Marcus did not describe any later stages in the formation of the larynx.

Göppert stated that the laryngeal muscles of a late Ichthyophis larva

consist of a Dilatator laryngis, a Constrictor laryngis, and a Laryngeus ventralis. The first-named takes origin from the fourth branchial bar and is inserted into the lateral process of the Cartilago laryngis; the Constrictor laryngis consists of two half rings surrounding the Cartilago laryngis just behind the attachment of the Dilatator; and the Laryngeus ventralis takes origin from the lateral process of the Cartilago laryngis and passes downwards just in front of the Constrictor and meets its fellow in a ventral median raphé. The existence of a Laryngeus dorsalis was doubtful.

These structures are all present, as described by Göppert, in earlier Ichthyophis larvae, and in a late Siphonops larva. In both, however, the existence of a Laryngeus dorsalis is certain (figs. 25, 29, 30).

In adult Siphonops the Laryngei dorsalis and ventralis have disappeared, and the Constrictor is more developed. In adult forms of Hypogeophis and Caecilia the Dilatator, Laryngei, and Constrictor are all present.

Göppert also described, in a late Ichthyophis larva, a Hyo-pharyngeus internus, taking origin from the fourth branchial cartilage and from the connective tissue lateral to the pharynx and passing round it to a median aponeurosis between the pharynx and trachea and to the lateral side of the trachea.

The muscle is present in younger Ichthyophis larvae and in larval and adult Siphonops. In the 3·5 cm. larva of Ichthyophis the hinder part of the muscle is overlapped by the anterior edge of the Constrictor oesophagi, and in the Siphonops larva it is, though present, less developed—incompletely separated from the Constrictor oesophagi and with no median raphé (fig. 31).

These phenomena suggest that the muscle is a separated portion of the anterior edge of the Constrictor oesophagi which has gained attachments to the fourth branchial cartilage.

Göppert described, as one of the laryngeal muscles in a late Ichthyophis larva, fibres springing from the dorsal fascia and inserted into that covering the anterior part of the ventral trunk-muscles.

It is not yet developed in 3·5 and 5·9 cm. Ichthyophis larvae. In a 7 cm. Siphonops larvae it is a slightly marked muscle lying just lateral to and behind the fused third and fourth branchial cartilages and tendon of Levator iv, with no dorsal or ventral attachment (fig. 31). In the adult Siphonops it forms a well-marked muscle arising from the dorsal fascia just behind Levator iv, and passing downwards outside the fused third and fourth branchial cartilages to a median raphé just behind Transversus ventralis iv. These phenomena suggest that the muscle in question is possibly a derivative of Levator iv. There are, in Ichthyophis larvae and in larval and adult Siphonops, three muscles arising in common from the dorsal fascia some distance behind Levator iv—one passes downwards and inwards above the oesophagus, the second passes downwards laterally to the oesophagus and is inserted into the fascia on the medial surface of the Rectus and also to a median raphé which is connected with the skin between the two Recti, whilst the third passes

downwards and outwards lateral to the Rectus. The muscles do not appear to have any genetic relation either to the Levatores or to the laryngeal muscles.

*Urodela.* In a 15 mm. larva of Menopoma (figs. 32–35) laryngeal and transverse grooves are present, both continuous with the epithelium of the branchial region and oesophagus. The front edge of the laryngeal groove is $40\mu$ in front of the anterior border of the sixth gill-cleft; it is $180\mu$ long, extending back to the level of the hinder border of the (unseparated) sixth and seventh gill-clefts, where it passes into the transverse groove. In a larva of 17 mm. (figs. 36, 37) the conditions are the same, but, owing to growth, the laryngeal groove is $200\mu$ long. In a larva of 19 mm. (figs. 42–45) the length of the laryngeal groove is $330\mu$ of which the posterior $30\mu$ and the transverse groove have separated from the oesophagus. The anterior end of the laryngeal groove is $40\mu$ in front of the stump of the sixth gill-cleft, and it passes into the transverse groove $90\mu$ behind the border of the seventh gill-cleft. In a larva of 22 mm. the length of the laryngeal groove is $330\mu$, of which the anterior $160\mu$ is attached to the epithelium. Its front end is $70\mu$ behind the stump of the sixth gill-cleft, and $110\mu$ in front of the seventh gill-cleft. In a larva of 24 mm. (in which the seventh gill-cleft has disappeared) the anterior end of the laryngeal groove is $150\mu$ behind the stump of the sixth gill-cleft; in one of 28 mm. it is $260\mu$ behind.

Two processes thus take place; a separation, from behind forwards, of the transverse and hinder part of the laryngeal groove from the oesophagus, and possibly a subsequent slight backward migration; but in a larva of 22 mm. —the latest in which the seventh gill-cleft is present and demarcation of the branchial region from the oesophagus thus possible—the anterior end of the laryngeal groove is in the fifth branchial segment and the larynx is situated in the hindmost branchial segment and the forepart of the oesophagus.

In larvae of 15 and 18 mm. (figs. 32–35 and figs. 38–41) the epithelium of the pericardium and pericardio-peritoneal ducts, underlying the laryngeal and transverse grooves, is thickened and proliferating cells which spread up round those grooves. In a larva of 19 mm. (fig. 45) these cells have increased in number and spread dorsally round the oesophagus. Those immediately round the laryngeal groove are undifferentiated, whilst the Constrictor oesophagi and Dilatator laryngis are slightly marked out by the cells being long-oval in shape. In a larva of 22 mm. (fig. 47) the Constrictor oesophagi and Dilatator laryngis are quite distinct from the surrounding splanchnic mesenchymatous cells. The Dilatator laryngis has spread upwards, its dorsal end being lateral to the spinal musculature. In a larva of 24 mm. (fig. 50) the Laryngei are visible in front of the lower end of the Dilatator. In one of 28 mm. (fig. 52), the Constrictor laryngis is visible behind it and the primordium of the arytenoid is distinguishable.

In a 12 mm. larva of Necturus the front end of the laryngeal groove is in the third branchial segment, $50\mu$ in front of the fifth gill-cleft; its length is

$170\mu$. In a larva of 13 mm. the front end of the laryngeal groove is in the fourth branchial segment, $30\mu$ behind the stumps of the fifth gill-cleft, its length is $70\mu$, and it passes into the transverse groove at the posterior edge of the sixth gill-clefts. In a larva of 15 mm. the front end of the laryngeal groove is $100\mu$ behind the stumps of the fifth gill-clefts, and in one of 17 mm. $150\mu$ behind. In subsequent stages the stumps of the fifth gill-clefts have become detached from the endoderm.

In larvae of 12 and 13 mm. (figs. 57–59, and 60–62) the splanchnic layer of the coelomic epithelium round the laryngeal and transverse grooves is thickened and proliferating cells which spread round these grooves and the oesophagus. In a larva of 15 mm. (fig. 63) the primordia of the Constrictor oesophagi and Dilatator laryngis are visible in this splanchnic mesoderm. In a larva of 17 mm. (fig. 69) the Dilatator is more marked and its upper end has spread up laterally to the spinal musculature. The Laryngei are formed; their lateral ends are continuous with the Dilatator laryngis and do not arise from the primordium of the arytenoid. In a larva of 20 mm., the trachea has developed, $80\mu$ in length, and the Dilatator tracheae has separated from the Dilatator laryngis. In a larva of 42 mm., as shown by Göppert, the Laryngei arise from the arytenoid.

### Morphology of the larynx and laryngeal structures in Amphibia

On reviewing the above observations it is clear that, in the Amphibia examined, the transverse groove lies behind the ultimate gill-cleft, in the oesophageal region. The laryngeal groove extends forward into the ultimate (Rana) or penultimate (Menopoma, Ellipsoglossa, Necturus) branchial segment. In the latter three animals, the front end of the laryngeal groove subsequently migrates slightly backwards into the ultimate segment. The transverse groove and hinder part of the laryngeal groove are constricted off from the oesophagus. The larynx thus comes to lie in the ultimate branchial segment and the forepart of the oesophagus. The front end of the larynx subsequently lies at steadily increasing distances behind the remains of the penultimate gill-cleft or -clefts, but as this occurs after loss of the ultimate gill-clefts its meaning is doubtful. It may be simply a growth phenomena and not indicate any real backward migration. The oesophageal and laryngeal muscles and the laryngeal cartilages are differentiated from cells which are proliferated from the splanchnic layer of the coelomic epithelium—pericardium and pericardio-peritoneal ducts. The cells spread round the oesophagus and larynx. The oesophageal and laryngeal muscles become differentiated among these cells. Although, phylogenetically, the laryngeal muscles may be regarded as derivatives of the Constrictor oesophagi, in actual development they are not budded or split off from it, but the two sets of muscles develop concurrently in close proximity in the splanchnopleure sheath of the oesophagi.

Comparison of the various laryngeal muscles leads to the following conclusions. *Dilatator laryngis.* In Anuran larvae the Dilatator arises from the

connective tissue ventro-lateral to the oesophagus and passes inward and forwards to the arytenoid.. In the adult, the origin of the muscle becomes attached to the processus postero-medialis. In Gymnophiona (larva and adult), the muscle arises from the ventral part of the fourth branchial cartilage, and is inserted into the arytenoid. In Urodela the origin of the muscle extends upwards round the spinal musculature to the dorsal fascia (hence the name "Dorso-laryngeus" often applied to it).

Göppert, who (*vide* p. 133) was of opinion that the Dilatator is serially homologous with Levatores arcuum branchialium, thought that its form in Urodela is primary and that the conditions in Anuran larvae and in Gymnophiona are secondary.

But, as shown above, the Subarcuales of the branchial bars are more primitive in Anuran and Gymnophionan larvae than in Urodela, and the Dilatator is developed by upward extension from a primordium ventro-lateral to the forepart of the oesophagus. It follows that there is no *a priori* probability that the form of the Dilatator in Urodela is primitive and the phenomena of its development are against such a view. It is possible then that its form in Anuran larvae is the primitive one, and that those in Urodela and Gymnophiona represent two divergent secondary conditions.

*Constrictor laryngis and Laryngei.* In Anuran larvae a Constrictor laryngis is developed, encircling the arytenoid posterior to the insertion of the Dilatator. In Gymnophionan larvae Laryngei and a Constrictor are present, the former in front and the latter behind the insertion of the Dilatator. In Urodelan larvae, other than Necturus, Proteus, and Siren, Laryngei and a Constrictor are present, the former in front and the latter behind the insertion of the Dilatator. In Necturus, Proteus, and Siren, Laryngei only are present— a Constrictor is not developed.

Drüner stated that in Salamandra and Triton the Laryngei disappear at metamorphosis. The same is also true of Siphonops.

Göppert held that the Constrictor is proliferated from the Laryngei ventrales in Siredon, where there is a slight overlap of these muscles. But in Menopoma there is no overlap and, though the Laryngei are developed at an earlier stage, yet there is no indication that the Constrictor is developed from them.

It would appear then that the Laryngei and Constrictor are independent laryngeal constrictor muscles, of somewhat different form, developed in front of and behind the insertion of the Dilatator.

It is not known whether the absence of Laryngei in Anura is a primitive or a secondary feature. On comparison with Dipnoi (see later), it would appear that probably a Constrictor is, phylogenetically, the older structure.

The absence of a Constrictor in the Perennibranchiata, Necturus, Proteus, and Siren, is probably to be explained by the occurrence of its development at a somewhat later stage than the Laryngei, taken in association with the theory of Boas that the Perennibranchiata are persistent larval forms—

Urodela which no longer have a metamorphosis. Menopoma would be similar if development ceased at the stage of 24 mm.

Göppert (*vide* p. 132) held that the form of the arytenoids, and the attachment of the Laryngei to them, in Necturus and Proteus represents the primitive condition. But the developmental phenomena appear to negative such a view and to show that, as Drüner thought, the condition is secondary to a more primitive one, in which, as e.g. Triton, the arytenoids are narrower and the Laryngei take origin from the Dilatator.

In Siren (*vide* Drüner) there are, in front of the Dilatator, Laryngei, arising partly from the arytenoid and partly from the Dilatator, but no Constrictor. There are, however, outside the Laryngei, sphincter fibres, which have no homologues in other Amphibia. The condition needs embryological investigation—possibly the sphincter fibres are proliferated or separate from the Laryngei.

From the slightly different innervation of the Dilatator laryngis and of the Constrictor laryngis and Laryngei Drüner inferred (*vide supra*, p. 134) that these muscles have been derived from different segments. This is not borne out by developmental phenomena. Further, in Anura and Gymnophiona all the laryngeal muscles are innervated by the N. recurrens. The phenomena in Urodela are simply due to a slightly earlier giving off of the branch for the Dilatator from the N. intestino-accessorius, and have no morphological importance.

*Cartilago lateralis. Anura.* Märtens (1895) stated that in Rana temp. there is no continuous cartilago lateralis which afterwards separates into cartilago arytenoidea and C. laryngo-trachealis, but that these elements are separate from the first, the arytenoid developing during metamorphosis, and the four elements which fuse to form the annulus shortly afterwards.

I find that the arytenoid is present in a 12 mm. larva, in a precartilaginous condition, quite distinct from the surrounding mesoblast. There is no trachea at this stage, and during the rest of larval life the larynx immediately bifurcates into the two bronchi (fig. 17). In a larva during metamorphosis, at the stage when the tail has shrunk to half its original length, the trachea develops and the elements of the annulus appear. They are continuous with the dorsal end of the obliquely placed arytenoid by precartilaginous tissue (figs. 21 and 22).

*Gymnophiona.* In a 3·5 cm. larva of Ichthyophis the trachea is already formed. There is a precartilaginous arytenoid, which anteriorly is circular in shape, then broadens (with attachment of the Dilatator laryngis to its outer edge, and the Laryngei above and below) and then contracts. It is continuous posteriorly with a cellular sheath, thicker dorsally than ventrally, round the trachea. In a 5·9 cm. larva the arytenoid has chondrified and is continuous with a cellular sheath round the trachea. In this sheath are incomplete ring-shaped patches of cartilage.

In a 7 cm. larva of Siphonops the conditions are similar to those of the

5·9 cm. Ichthyophis larva (fig. 31). In the adult, with the disappearance of the Laryngei, the lateral projection of the arytenoid also disappears and its hind end is continuous with the first tracheal ring.

*Urodela.* A precartilaginous arytenoid is present in a 10 mm. larva of Triton cristatus. It is chondrified in a larva of 12 mm. No trachea is present in larvae up to a length of 28 mm. and correspondingly there is no pars laryngea. A trachea, $135\mu$ in length, has developed in a larva of 33 mm. (figs. 77 and 78). Behind the arytenoid, and continuous with it, is a cellular mass lateral to the trachea. This cellular mass is chondrified as the trachea bifurcates into the bronchi. Later on, as described by Drüner, there are many cartilaginous islands along the trachea, and subsequently, as described by Gegenbaur, a continuous arytenoid and tracheal skeleton—the cartilago lateralis.

Similarly, in Salamandra, the first cartilage developed in the tracheal sheath is found at its bifurcation into the bronchi, in a 25 mm. larva.

In a 28 mm. larva of Menopoma there is no trachea, the larynx immediately bifurcating into the bronchi. A precartilaginous arytenoid is present, with flat internal and convex external surface, and its posterior end ventral to its anterior end (fig. 52). In a larva of 32 mm. a trachea, $120\mu$ in length, has developed. This is not accompanied by any forward migration of the larynx relative to the branchial skeleton; by it the bifurcation of the respiratory tract is carried further back. The arytenoid is chondrified and has a slight lateral process at the insertion of the Dilatator laryngis. The arytenoid is continuous with a cellular sheath lateral to the trachea (fig. 55). In a larva of 34 mm. the primordium of the processus trachealis has developed in the cellular tracheal sheath, dorsal to the posterior end of the arytenoid (fig. 56). In a 40 mm. larva this process is continuous with the arytenoid. In the adult (Drüner) many cartilaginous islands have developed in the tracheal sheath.

In a 17 mm. larva of Necturus (Fig. 69) the arytenoid is present as a precartilaginous mass of cells extending laterally to the larynx, but not sufficiently far for the Laryngei to arise from it. They are continuous laterally with the Dilatator laryngis. In a 42 mm. larva, as shown by Göppert, the arytenoid is broader and the Laryngei arise from it. There is no trachea in larva up to a length of 18 mm. In one of 20 mm. (fig. 70) a trachea, $80\mu$ long, has developed. Lateral to the trachea is a sheath of connective tissue, which is continuous anteriorly with the arytenoid.

It follows from the above that the simplest and probably the most primitive form of the arytenoid is a roundish rod, surrounded by the Constrictor laryngis and with a Dilatator laryngis attached to its anterior end. This is present in Anuran larvae. In Gymnophionan and Urodelan larvae the arytenoid is relatively longer, in relation to the presence of the Laryngei. The condition, in Necturus and Gymnophionan larvae, of a broad plate with Laryngei arising from it, is probably secondary to a simpler condition such as is present in Triton. In this connection it is of interest to see that in Siphonops the arytenoid becomes roundish in outline on the atrophy of the Laryngei.

The development of the pars trachealis cartilaginis lateralis is related to the formation of a trachea which develops at the end of the larval stage in Rana, during larval life in Menopoma, Amblystoma, Triton, Siphonops and Ichthyophis, and in the 20 mm. stage of Necturus. The pars trachealis is formed as a non-chondrified backward prolongation of the pars laryngea s. arytenoid. It may persist in this condition, e.g. Necturus, or may subsequently chondrify in tracts of more or less complete rings. In Triton and Salamandra the cartilage is first developed at the bifurcation of the trachea.

The above discussion shows that further embryological investigations are needed—in particular it would be well to know the condition of the branchial skeleton and ventral branchial muscles in the larvae of Amphiuma[1] and Cryptobranchus jap., the development of the sphincter laryngeal fibres in Siren, and the development of the ventral branchial muscles, larynx and laryngeal muscles in Gymnophiona.

### On the phylogenetic history of the larynx, trachea, and laryngeal muscles

Schmidt (1913), who investigated the development of the larynx in certain Reptiles, was of opinion that the lungs of Polypterus, Amphibia, and Amniota, like the swimming bladder of Lepidosteus and Amia, develop in the same native soil ("Mutterboden"), and that, on the other hand, the trachea with the larynx of Amniota, and possibly also that of Amphibia, are phylogenetically a later formation, the development of which begins with pulmonary respiration.

The larynx of Dipnoi and Polypterus lies in the ventral wall of the gut behind the branchial region. Its musculature was described by Wiedersheim (1904) and Göppert (1904). They came to the conclusion, though without any embryological evidence, that it is developed from pharyngeal musculature and that it represents musculature of atrophied branchial arches.

Neumeyer (1904) and Kellicott (1905), independently, showed that the larynx of Ceratodus is developed in the ventral wall of the gut at some distance behind the branchial region. Greil (1913) confirmed their observations, and also showed that the free mesoderm cells round the gut and larynx become spindle-shaped and develop into smooth muscle cells, which form a mantle round the gut and larynx.

Kerr (1910) stated that in Lepidosiren and Protopterus the lung-rudiment is developed, in stage 32, as a mid-ventral bulging from the pharynx at the level of cleft vi. His figures show that its connection with the gut migrates backwards, so that in stage 35 it is distinctly posterior to the level of the 6th gill-clefts, i.e. is in the oesophageal region. In Lepidosiren, Agar (1907) stated that the ventral and lateral parts of the "Constrictor pharyngis" of Wiedersheim are formed from mesenchymatous cells, budded off from the inner walls of the pericardio-peritoneal ducts, and are thus of splanchnic origin. The dorsal part of the muscle is of somatic origin, being derived

---

[1] In larvae younger than the 45 mm. stage investigated by Hay.

from myotome Y. He did not investigate the development of the laryngeal muscles, but comparison of his figures with those of Wiedersheim suggests that they are differentiated from the ventral, splanchnic, part of the "Constrictor pharyngis."

Wiedersheim employed the term "pharynx" to denote the portion of the alimentary canal corresponding to atrophied branchial arches. In Lepidosiren, however, there is no embryological evidence that the territory surrounded by the pharyngeal constrictor represents a region of atrophied branchial arches—so that the name is hardly justified. The term "pharyngeal constrictor" in Dipnoi might perhaps be replaced by that of "oesophageal constrictor," though with the reservation that in Lepidosiren and probably Protopterus there is an added constituent from a myotome to its dorsal portion, which is absent in Ceratodus and Amphibia. In this and previous papers the name "pharyngeal" is used as synonymous with "branchial." In this latter sense it may be said that there is no pharyngeal constrictor except in Mammals.

The larynx in Dipnoi is thus developed either in the oesophageal region, or in that of the posterior branchial clefts, and migrates backwards. This variation is similar to that which obtains in Amphibia. On comparison of the figures given by Kellicott in Ceratodus with those of Kerr in Protopterus, it is seen that whereas in Ceratodus the larynx immediately bifurcates, in Protopterus there is a portion of the respiratory tract anterior to its bifurcation. In Amphibia it is the laryngeal groove which, in part, may be situated in the branchial region; the bifurcation groove is posterior to it. If this is so, then the primitive larynx, or what corresponds to it, i.e. the bifurcation groove, is situated in the oesophageal region both in Dipnoi and Amphibia, whilst the laryngeal groove—a later development—is formed in front, and in part in the branchial region.

Wiedersheim held that Protopterus and Lepidosiren, in contrast to Ceratodus, have developed in the direction of Amphibia. The Dilatator laryngis of these two Dipnoi, however, lies on the inner side of the Constrictor laryngis and is not homologous with the Dilatator laryngis s. Dorso-laryngeus of Amphibia which lies on the outside.

On comparison with Dipnoi, the new features in the larynx of Amphibia are (1) Formation of a laryngeal groove in front of the transverse groove, extending forward into the hinder portion of the branchial region. It is possible, however, as suggested above, that there is a laryngeal groove in Lepidosiren and Protopterus. (2) Formation of a Dilatator laryngis on the outside of the Constrictor oesophagi. (3) Formation of Laryngei in Urodela and Gymnophiona. (4) Formation of an arytenoidea. (5) A, late, formation of a trachea,. with extension of the arytenoid along it. It is thus possible that the features which are common to Dipnoi and Amphibia are (1) Formation of a transverse groove, or its homologue the larynx in Dipnoi, in the floor of the oesophagus. (2) Derivation of the laryngeal musculature from a pri-

mordium common to it and the Constrictor oesophagi. The only muscle which possibly may be common to Dipnoi and Amphibia is a Constrictor laryngis, which is present in Lepidosiren and Protopterus[1].

In Amniota, as in Amphibia, the transverse groove is developed behind the branchial region in the floor of the oesophagus, and the laryngeal groove is formed progressively forward into the branchial region. The differences from Amphibia are that the laryngeal groove extends into a more anterior branchial segment and that the separation of the respiratory epithelium extends relatively further forward so that the larynx lies entirely in the branchial region. Correspondingly, the primordium of the laryngeal muscles separates from that of the Constrictor oesophagi, migrates forward into the branchial region and there develops into the laryngeal muscles. This method is secondary and related to the secondary position of the larynx.

In Sauropsida the muscles consist of a Dilatator and a Constrictor laryngis which are homologous with those of Amphibia. In a few Reptiles Laryngei are developed. These, like the Constrictor, lie posterior to the insertion of the Dilatator, are modifications of the Constrictor and not homologous with the Laryngei of Urodela and Gymnophiona.

In Mammals the laryngeal muscles consist of a Dilatator, Interarytenoid and Laryngeus ventralis. The Dilatator is homologous with that of Amphibia and Sauropsida and, as in the latter, arises from the Cricoid cartilage. The Interarytenoid represents the dorsal half of a Constrictor. Both the Interarytenoid and Laryngeus ventralis lie in front of the insertion of the Dilatator. Apparently, therefore, they are homologous, not with the Constrictor of Sauropsida and Amphibia, but with the Laryngei of Urodela and Gymnophiona.

*Recurrent laryngeal nerve.* As the laryngeal muscles are not branchial in origin, their motor nerve—the recurrent laryngeal—is not a branchial nerve. It may be regarded as a specialised oesophageal branch of the vagus. In Gymnophiona and Urodela, and markedly in the latter, it extends to the ventral branchial muscles, supplementing or supplanting branchial nerves.

The phylogenetic history of the recurrent laryngeal nerve is obscure. No nerve was described by v. Wijhe or Beauregard in Ceratodus, nor by Hyrtl in Lepidosiren. Pinkus described, in Protopterus, a fine twig extending from the N. intestinalis to the mucous membrane of the pharynx and larynx, and a R. muscularis and recurrens—a strong branch from the vagus ganglion which passes down on the outside of the "Constrictor pharyngis" and divides into two branches, one of which passes forwards and sinks into the tongue muscles, whilst the other innervates the "Constrictor pharyngis." This last branch was also described by Agar. Neither observer states whether twigs from this R. muscularis to the Constrictor oesophagi can be traced into the

---

[1] It is to be noted that Greil's investigations of the larynx of Ceratodus did not extend beyond the 18 mm. stage and that Wiedersheim said that the state of his material left much to be desired. So it is possible that Ceratodus, too, has a Constrictor laryngis.

laryngeal muscles. But, whether this be so or not, it is probable that the N. laryngeus recurrens of Amphibia, Sauropsida, and Mammalia may be regarded as being derived from a homologue of this nerve.

*Laryngeal and tracheal cartilages.* The arytenoid s. pars laryngea cartilaginis lateralis of Amphibia is developed within the Constrictor laryngis or within this and the Laryngei, and like them is differentiated from cells proliferated from the splanchnic layer of the coelomic epithelium. It does not, therefore, represent a fifth, or a more posterior, branchial bar. Its development is probably, as Wiedersheim suggested, dependent on muscle action. It is possibly related to the new development of a Dilatator laryngis in Amphibia. The tracheal skeleton s. pars trachealis cartilaginis lateralis is a backward prolongation of the arytenoid and related to the development of a trachea.

In Sauropsida the ventro-median surface of the Constrictor laryngis may become attached to the hyo-branchial skeleton, but this does not enter into the formation of the larynx.

In Mammalia a thyroid cartilage is formed, derived from two (separate in Monotremes, fused in Marsupials) branchial bars, or from one branchial bar (Eutheria), and the Crico-thyroid muscle is additionally formed from the Constrictor pharyngis, with an innervation from the superior laryngeal nerve. In Monotremes, however, there is a Thyreo-cricoid muscle, innervated by the recurrent laryngeal nerve.

I have, in conclusion, the pleasure of thanking Prof. Watasé for larvae of Ellipsoglossa, J. Pearson, Esq., for larvae of Ichthyophis, Dr Harmer for specimens of Caecilia and Hypogeophis from the British Museum, Prof. J. P. Hill for the loan of sections of an adult Siphonops, and the Bristol University Colston Society for defraying the expenses incurred.

<div align="center">

**LIST OF FIGURES**

PLATES I—XV

</div>

The figures are from transverse sections, unless otherwise stated. The lowest number, from any series, denotes the most anterior section.

Figs. 18 and 19.  Larva 20 mm. long, through larynx.

Fig. 20.  Larva with the hind legs just visible, through larynx.

Figs. 21 and 22.  Larva with tail shrunk to half its original length, through trachea.

*Ichthyophis glutinosa.*  Larva 5·9 cm. long.  Figs. 23–25.  23 through basihyale, 24 through Transversus ventralis i, 25 through larynx.

*Siphonops braziliensis.*  Larva 7 cm.  Figs. 26–31.  26 and 27 through Transversus ventralis i. 28 through Subarcuales recti ii and iii.  29 and 30 through larynx.  31 through trachea.

*Menopoma s. Cryptobranchus allegheniensis.*  Figs. 32–56.

Figs. 32–35.  Larva 15 mm. long.    32 through 3rd branchial segment.

                                                33  „      4th          „

                                                34  „      6th gill-cleft.

                                                35  „      transverse groove.

Figs. 36 and 37.  Larva 17 mm. long.  36 through 4th branchial segment.

                                              37  „      7th gill-cleft.

Figs. 38–41.  Larva 18 mm. long, sagittal sections.  38 is the most external.

Figs. 42–45.  Larva 19 mm. long.  42 through Subarcuales obliqui ii and iii.

                                              43  „      Transversus ventralis iv.

                                              44  „      7th gill-cleft.

                                              45  „      larynx.

Figs. 46 and 47.  Larva 22 mm. long.  46 through Urobranchiale, 47 through Dilatator laryngis.

Figs. 48–50.  Larva 24 mm. long.  48 and 49 through Transversus ventralis iv.

                                              50 through Laryngei.

Fig. 51.  Larva 24 mm. long, sagittal section.

Fig. 52.  Larva 28 mm. long, through larynx.

Figs. 53–55.  Larva 32 mm. long.  53 through Urobranchiale.

                                              54 just behind Urobranchiale.

                                              55 through trachea.

Fig. 56.  Larva 34 mm. long, through hinder part of larynx.

*Necturus maculatus s. Menobranchus.*  Figs. 57–70.

Figs. 57–59.  Larva 12 mm. long.  57 through 3rd branchial segment.

                                              58  „      laryngeal groove.

                                              59  „      transverse groove.

Figs. 60–62.  Larva 13 mm. long.  60 through stumps of 5th gill-cleft.

                                              61  „      4th branchial segment.

                                              62  „      laryngeal groove.

Fig. 63.  Larva 15 mm. long, through laryngeal groove.

Figs. 64–68.  Larva 16 mm. long.  64–66 through 1st branchial bars and Urobranchiale, 67 and 68 through Transversus ventralis iii.

Fig. 69.  Larva 17 mm. long, through Dilatator laryngis and Laryngei.

Fig. 70.  Larva 20 mm. long, through Dilatator laryngis and Dilatator tracheae.

*Ellipsoglossa s. Hynobius nebulosus.*  Figs. 71–76.

Figs. 71 and 72.  Larva 12 mm. long, through 1st branchial bars and Urobranchiale.

Figs. 73–76.  Larva 15 mm. long, through Urobranchiale.

*Triton cristatus.*  Figs. 77 and 78.

Larva 33 mm. long, through trachea and bronchi.


## ABBREVIATIONS IN FIGURES

| | | |
|---|---|---|
| Roman numerals | ... | cranial nerves |
| Branch iii and iv | ... | fused branchialia iii and iv (in Gymnophiona) |
| br. musc. pl. ... | ... | branchial muscle plate |
| br. i-hyale | ... | muscle passing from Ceratobranchiale i to hyale, in Rana |
| br. ii-hyale | ... | „      „      Ceratobranchiale ii to hyale, in Rana |
| br. aor. arch. ... | ... | branchial aortic arch |
| cerato br. iv | ... | cerato branchiale iv |
| cer. hy. ext. ... | ... | M. cerato-hyoideus externus |
| const. oesoph. ... | ... | M. constrictor oesophagi |

Plate I.

SOC.
NEWCASTLE
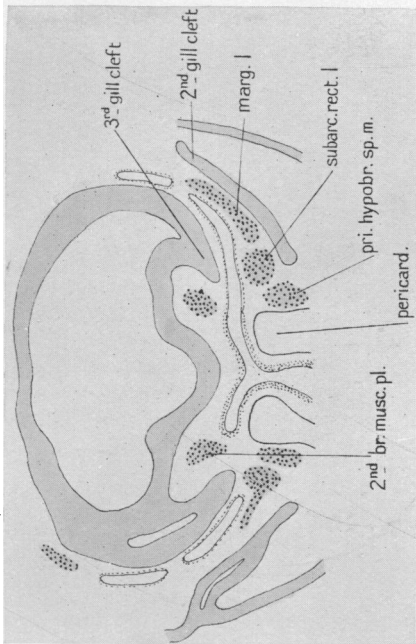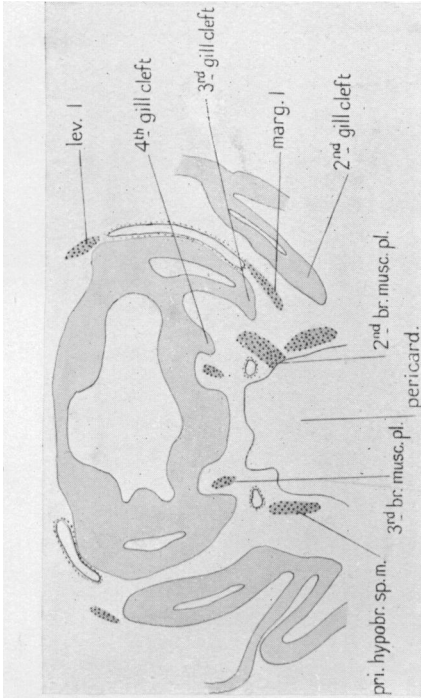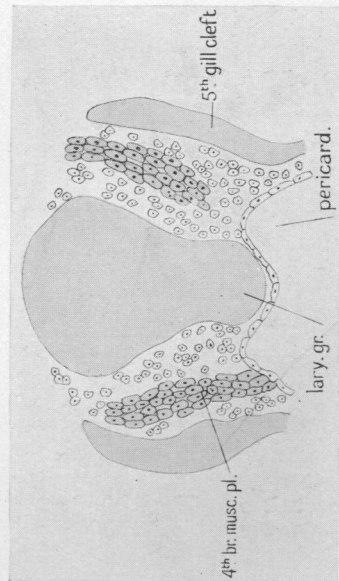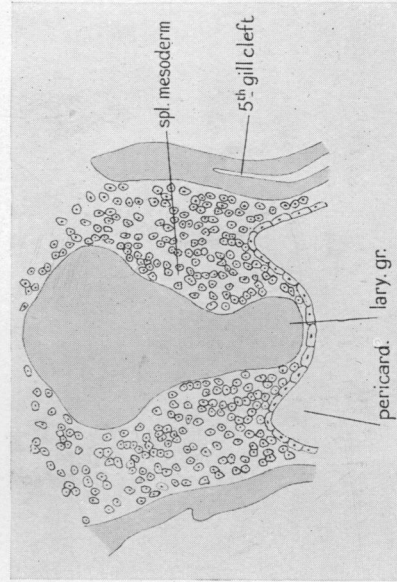


Fig. 1.

Fig. 2.

Fig. 3.
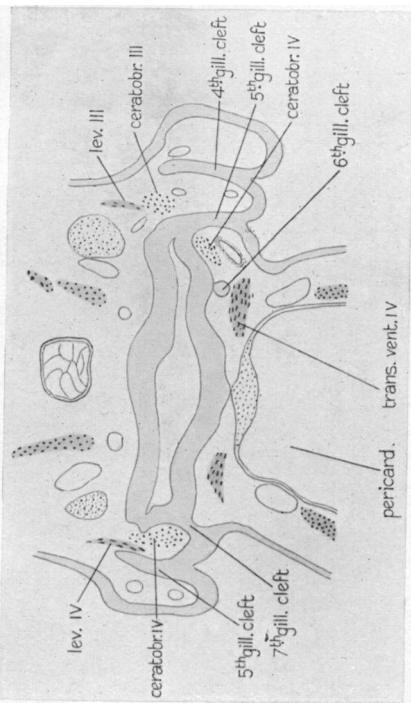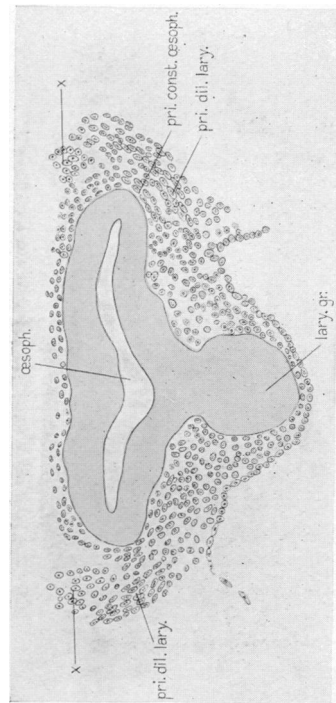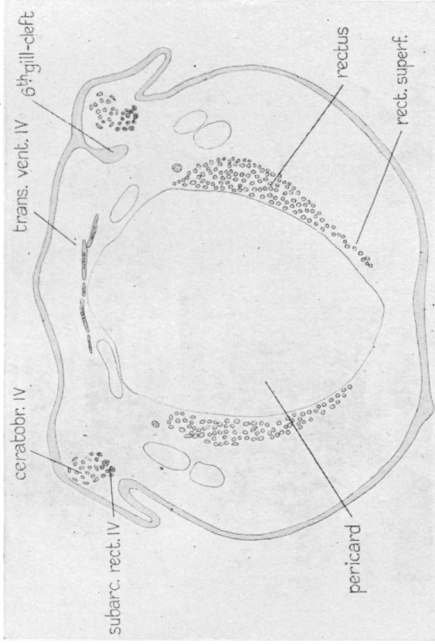
Fig. 4.
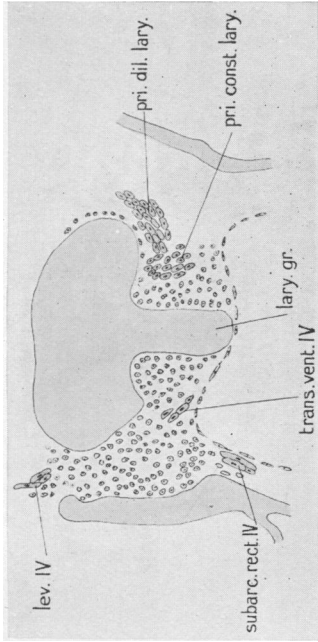
Fig. 6.
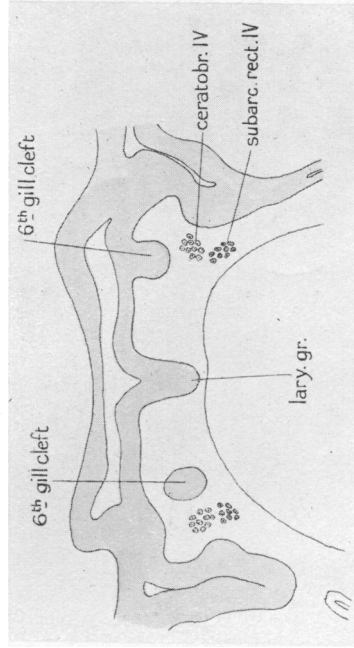


Fig. 8.
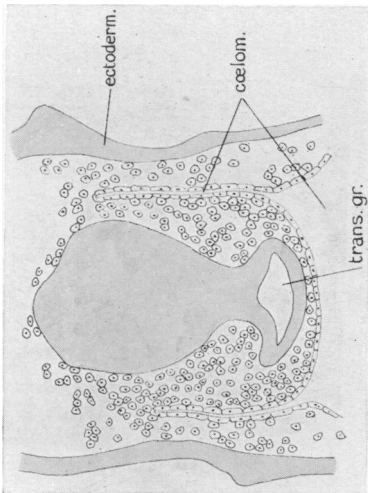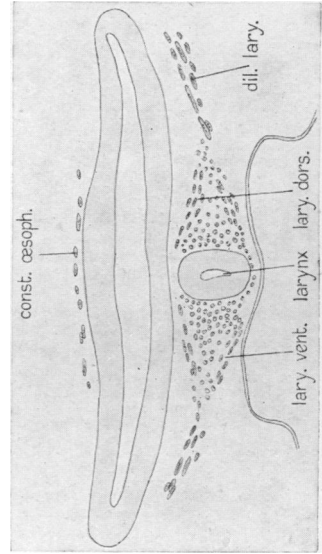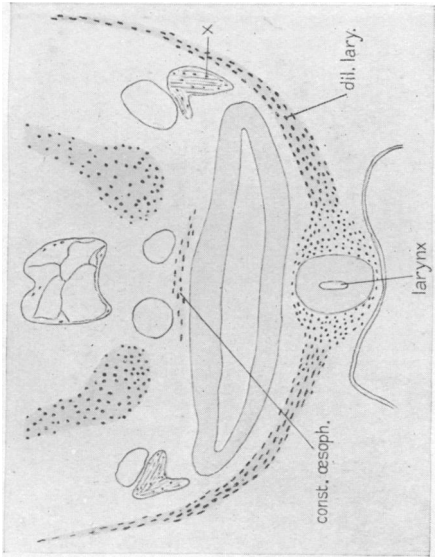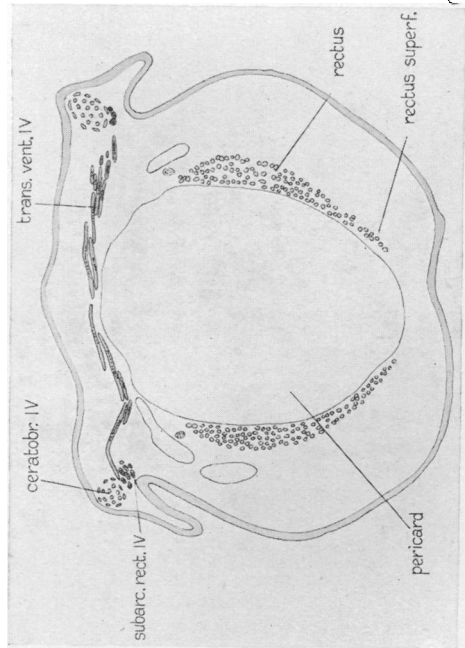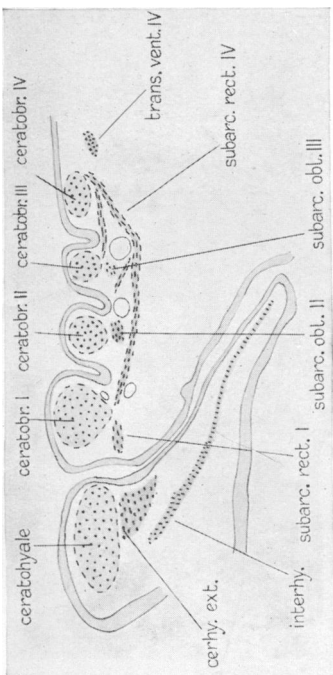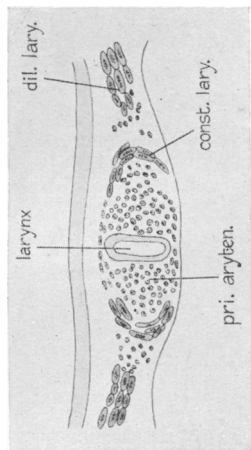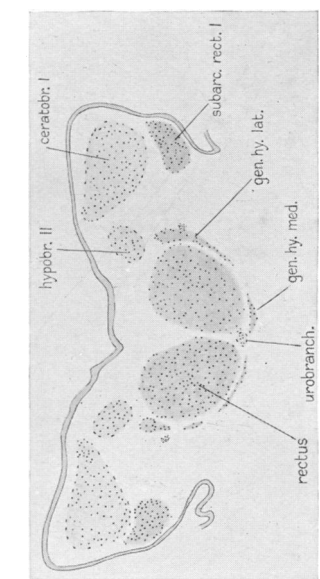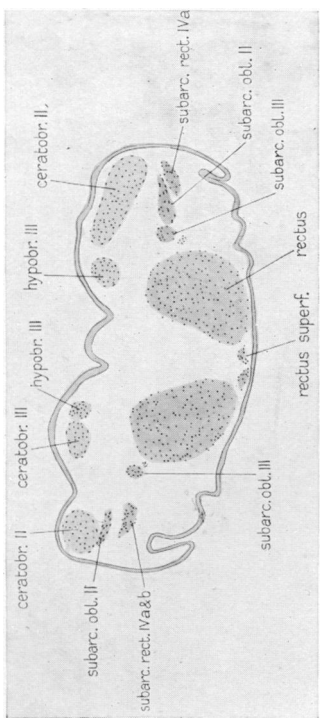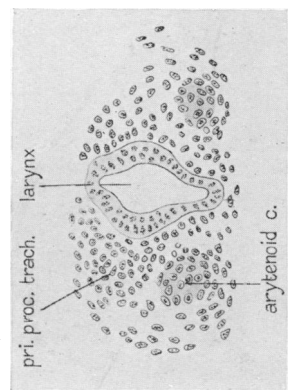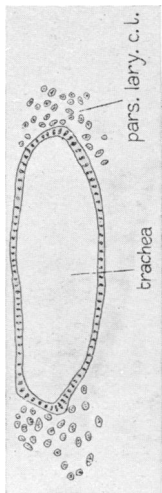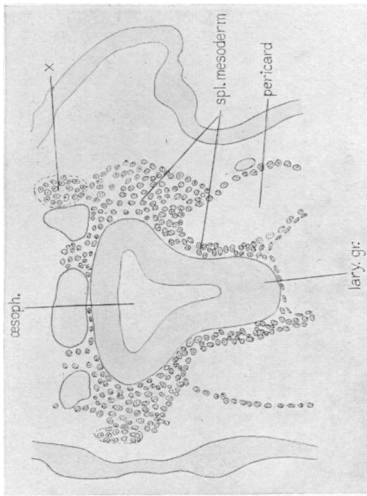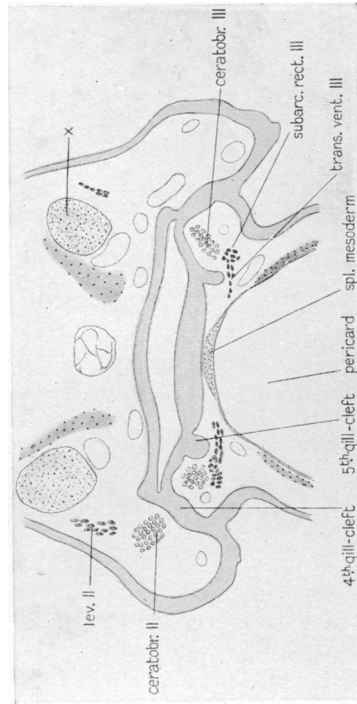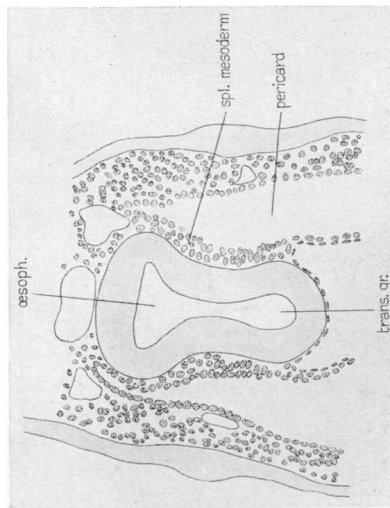


Fig. 5.
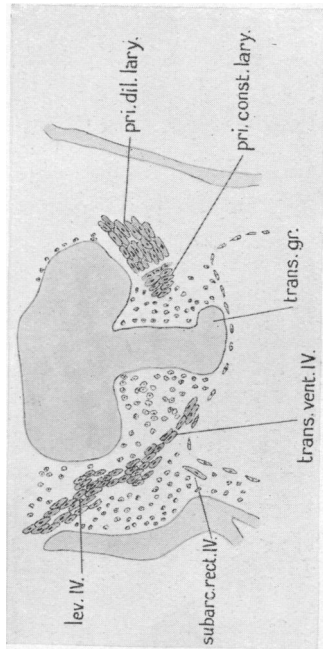


Fig. 7.
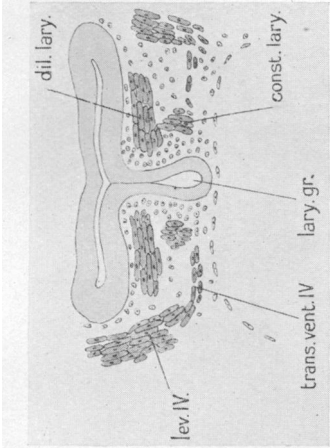
Fig. 9.
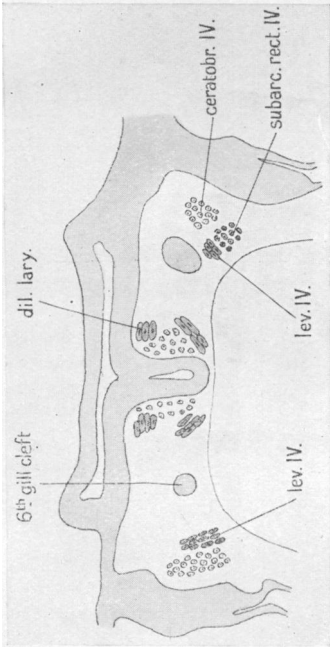
Fig. 10.
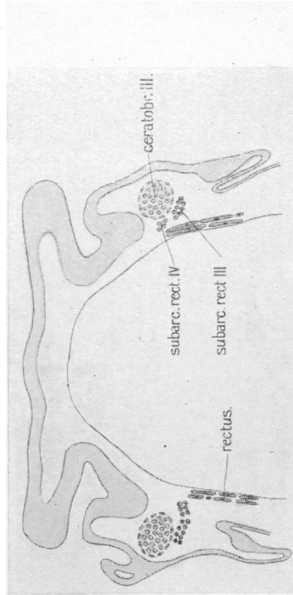
Fig. 11.
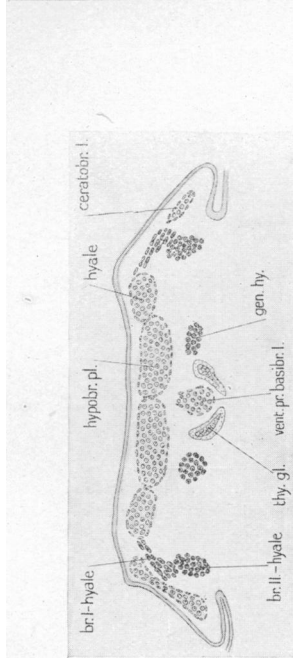
Fig. 12.
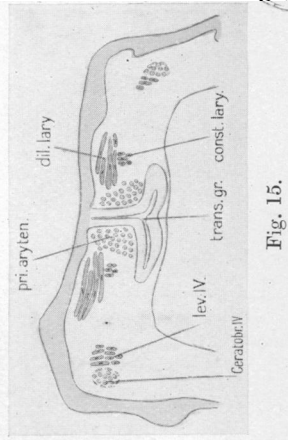
Fig. 13.
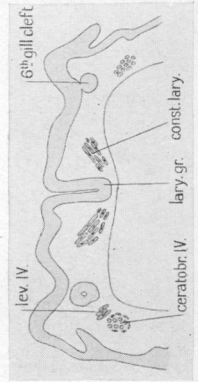
Fig. 14.
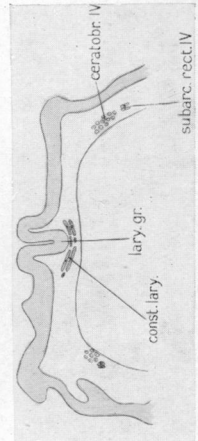
Fig. 15.
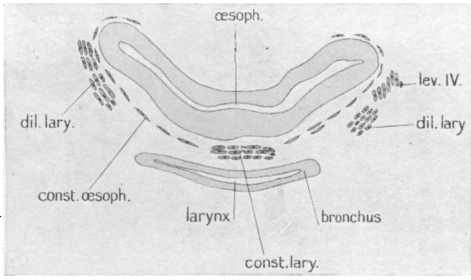
Fig. 16.
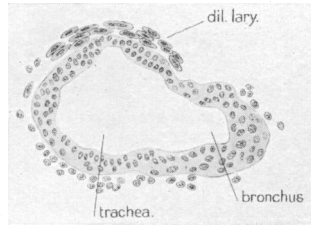


Fig. 17.
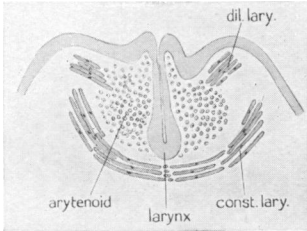


Fig. 18.
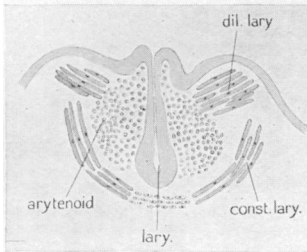


Fig. 19.
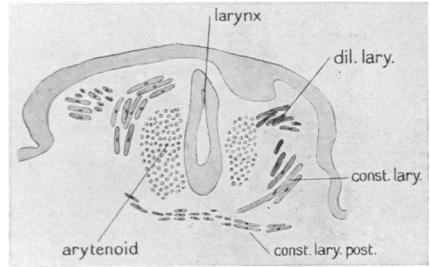


Fig. 20.
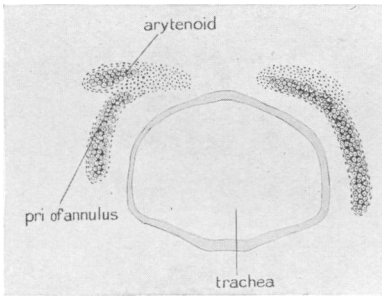


Fig. 21.
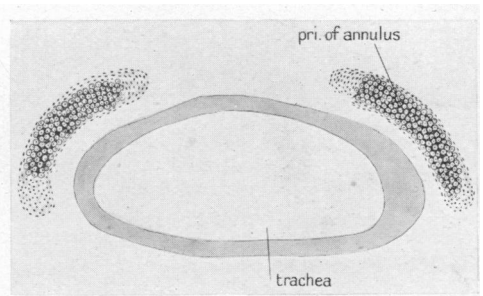


Fig. 22.
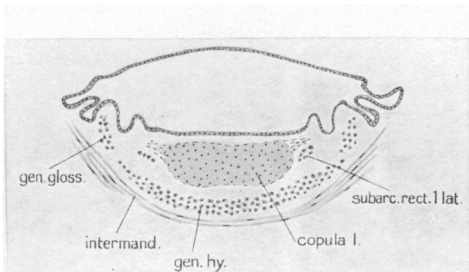


Fig. 23.
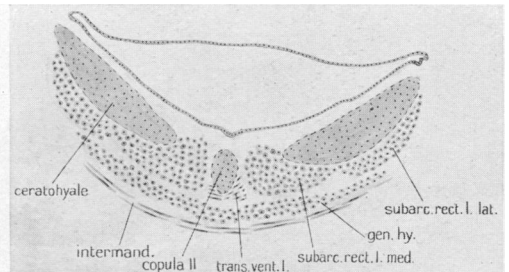


Fig. 24.
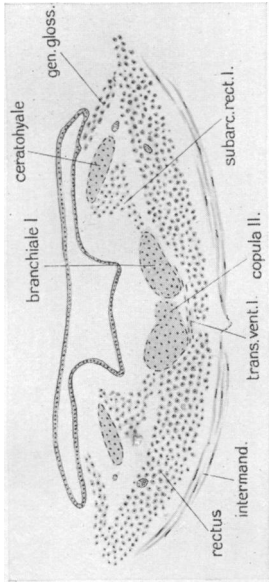
Fig. 26.
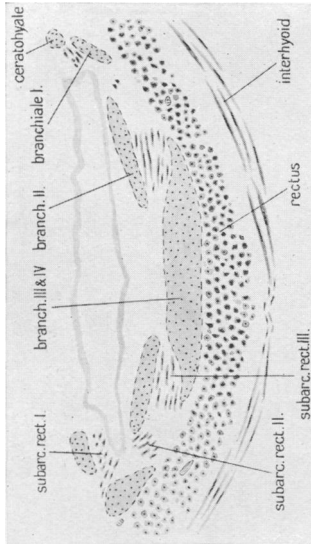


Fig. 28.



Fig. 30.



Fig. 25.



Fig. 27.



Fig. 29.

Fig. 32.

4th gill-cleft

3rd br. musc. pl.

pericard

pri. hypobr. sp. m.



Fig. 34.

spl. mesoderm

pri. hypobr. sp. m.

6th gill. cleft.

peric. p.c.



Fig. 31.

branch. III & IV

rectus

omohum. max.

hypophary. int.

trach. cart.

branchiale II

trachea

trans. vent. IV

göppert's m.



Fig. 33.

5th gill. cleft

4th br. musc. pl.

pericard

6th gill. cleft
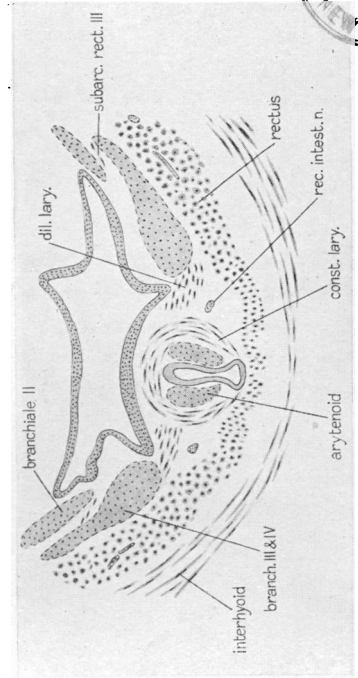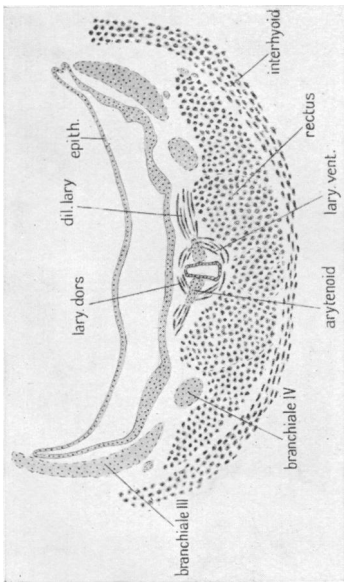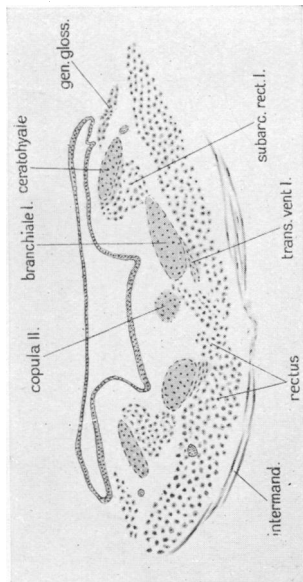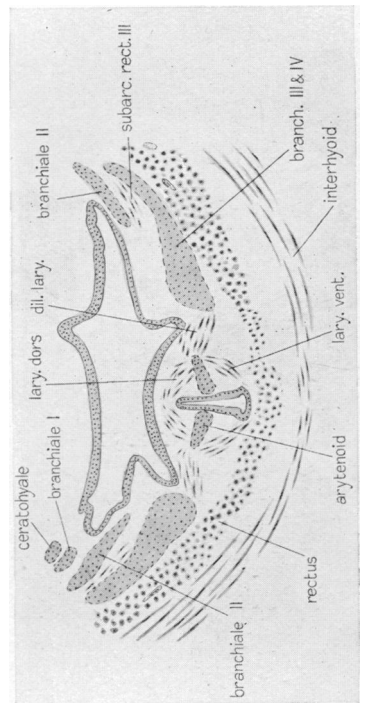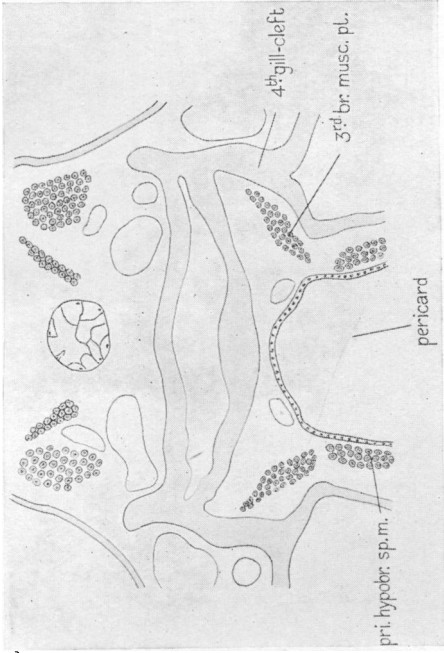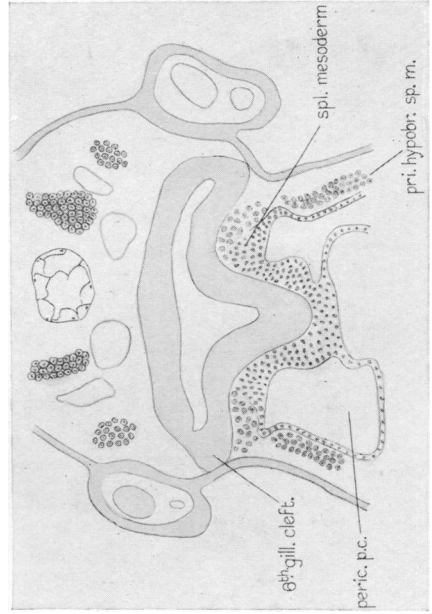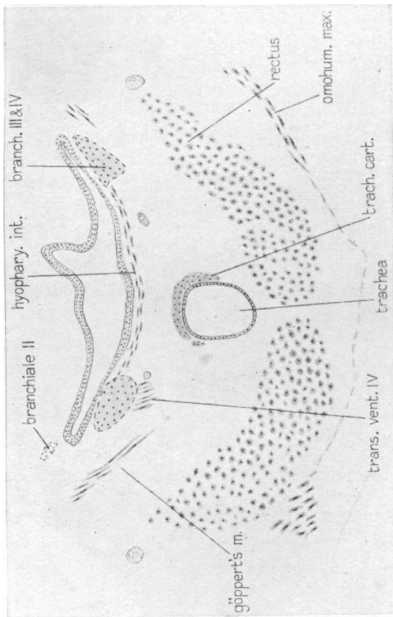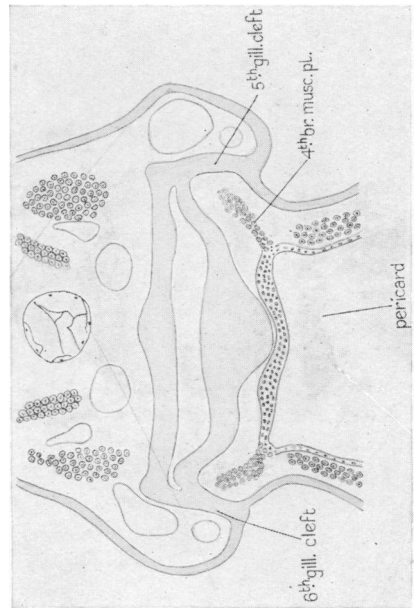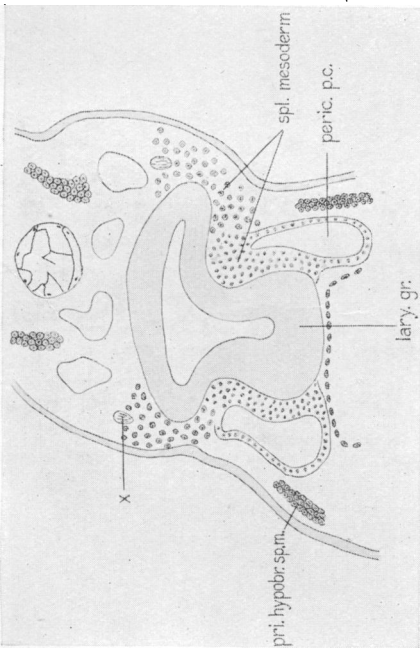
Fig. 36.

Fig. 38.

Fig. 35.
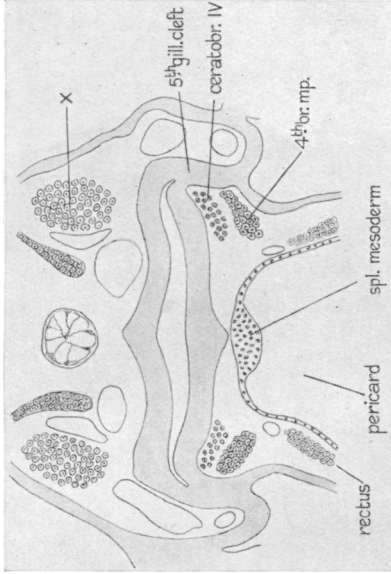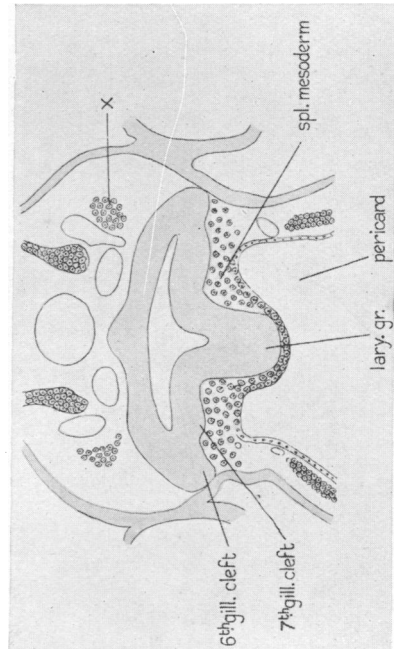
Fig. 37.
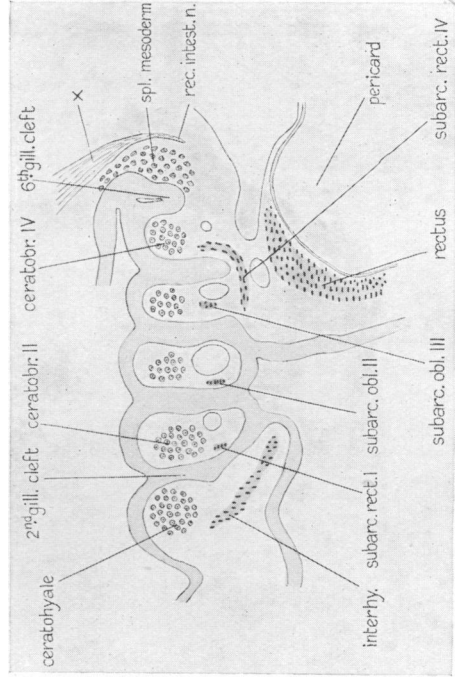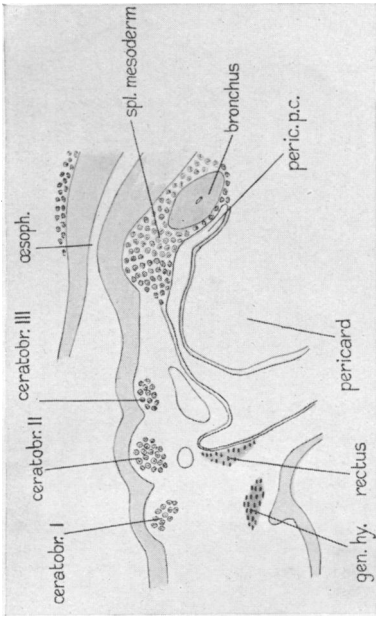
Fig. 40.
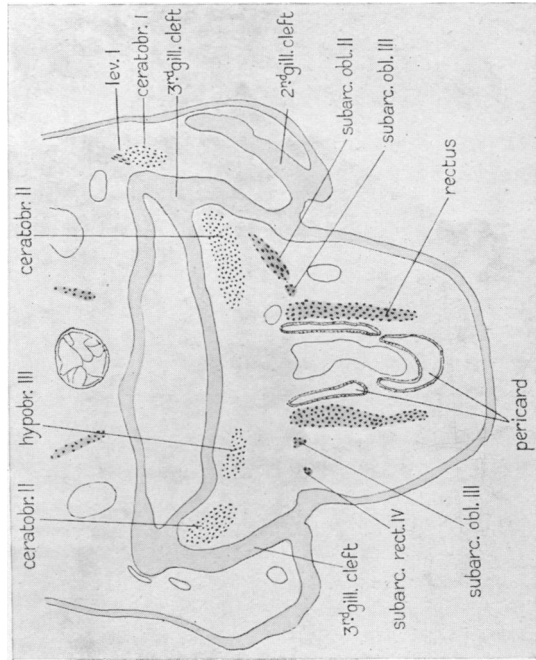


Fig. 42.
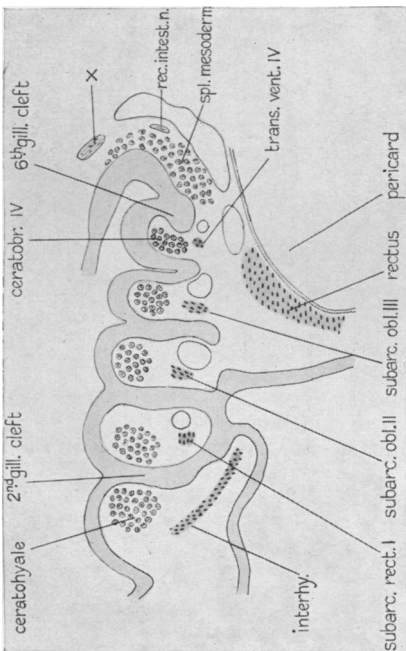


Fig. 39.
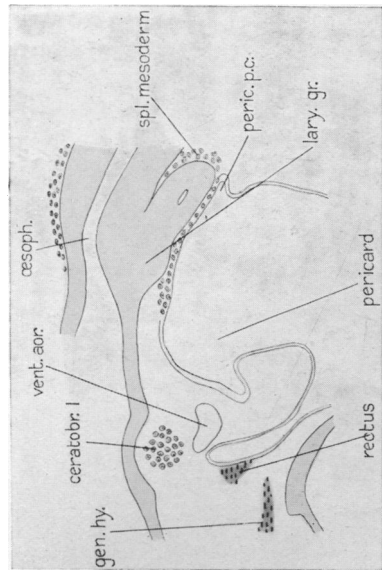


Fig. 41.
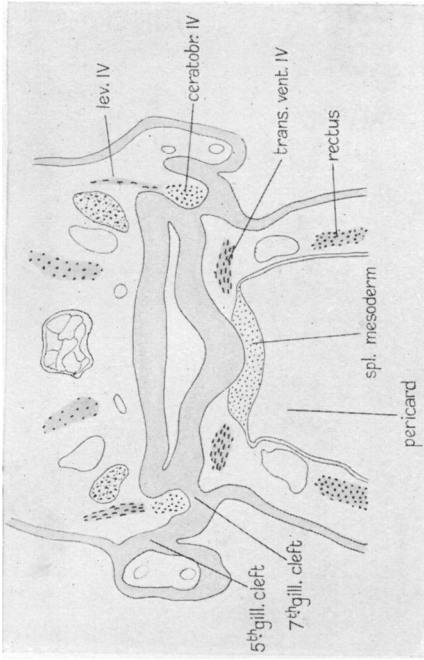
Fig. 44.
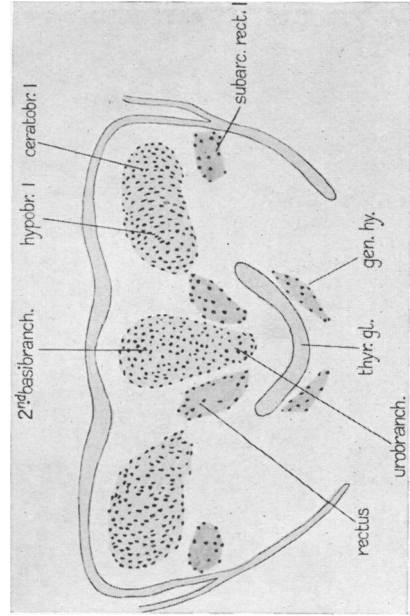
Fig. 43.

Fig. 46.

Fig. 45.

Fig. 48.

Fig. 50.

Fig. 47.

Fig. 49.

Fig. 52.

Fig. 54.

Fig. 56.

Fig. 51.

Fig. 53.

Fig. 55.

Fig. 58.

Fig. 60.
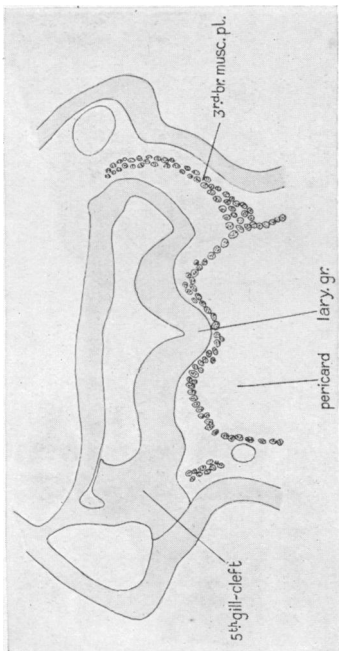
Fig. 57.

Fig. 59.
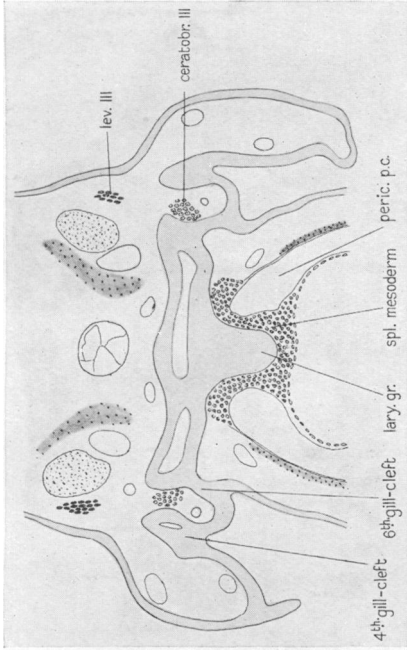
Fig. 62.
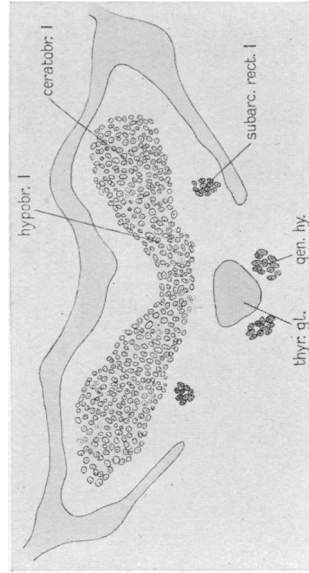
Fig. 64.
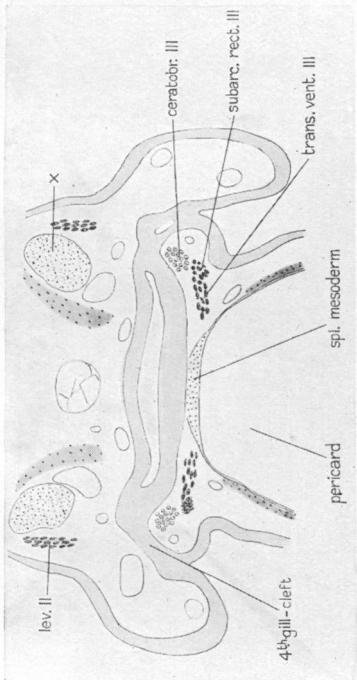
Fig 61.
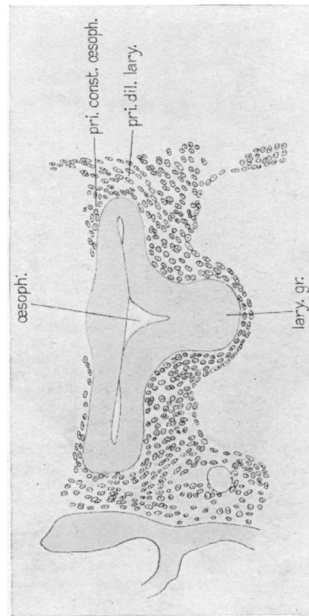
Fig. 63.
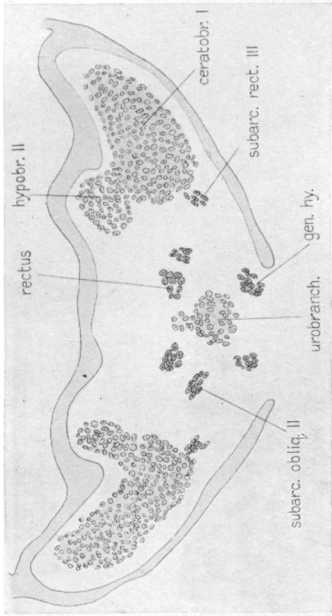
Fig. 66.
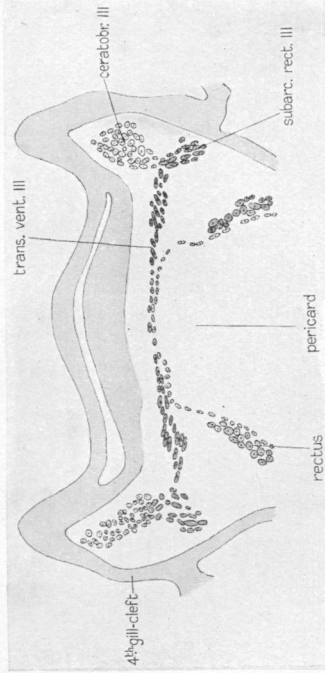
Fig. 65.

Fig. 68.
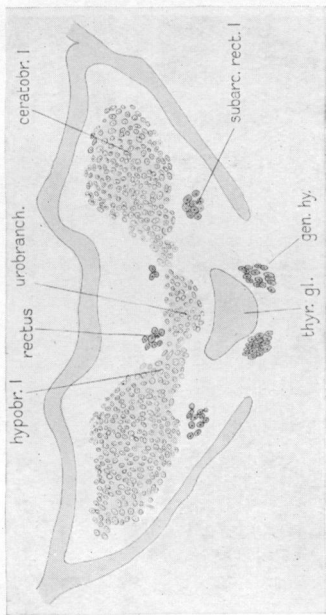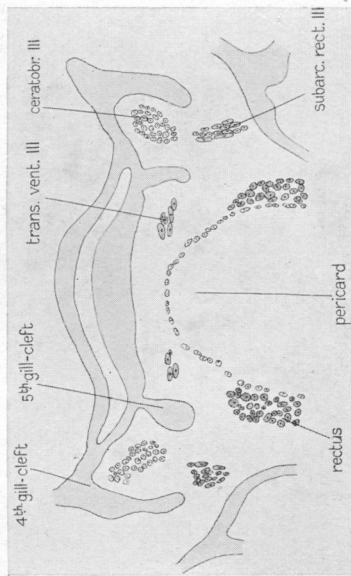
Fig. 67.

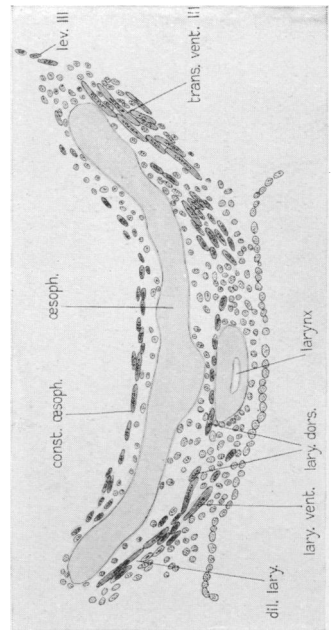Fig. 69.

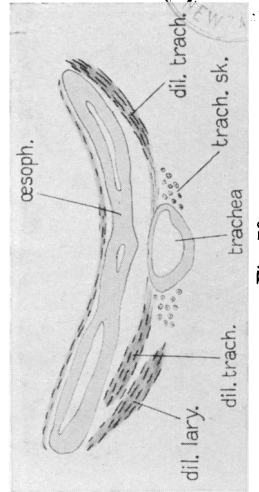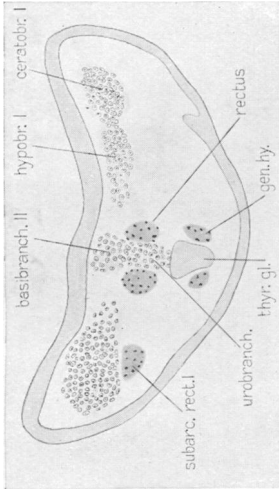Fig. 70.
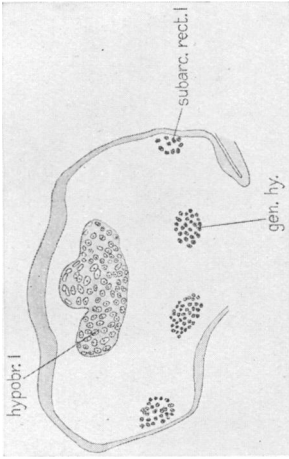
Fig. 73.

Fig. 72.
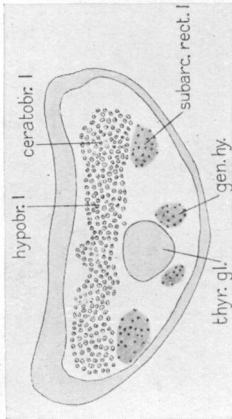
Fig. 71.
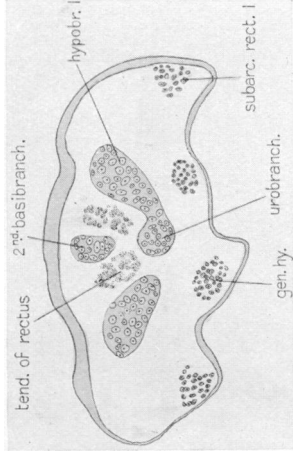
Fig. 75.
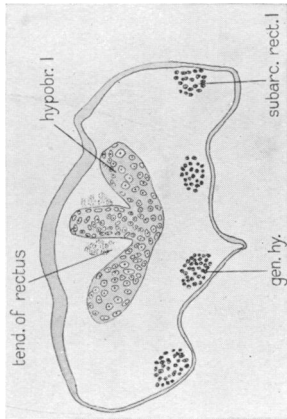
Fig. 74.
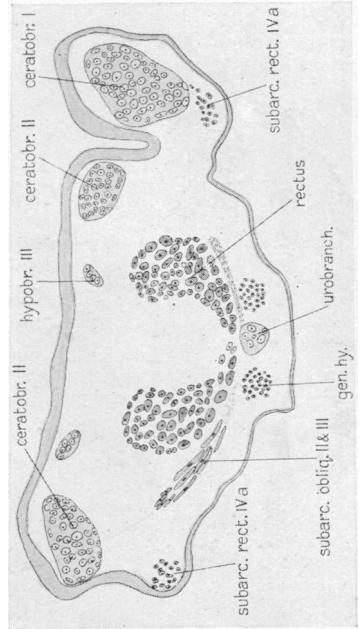
Fig. 78.

Fig. 77.

Fig. 76.
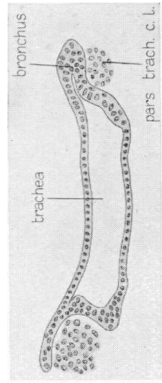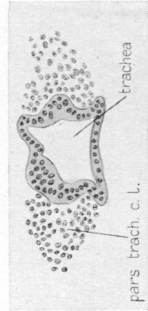
| | | |
|---|---|---|
| const. lary. ... ... | ... | M. constrictor laryngis |
| const. lary. post. | ... | M. constrictor laryngis posterior |
| dil. lary. - ... | ... | M. dilatator laryngis |
| dil. trach. ... | ... | M. dilatator trachealis |
| gen. gloss. ... | ... | M. genio-glossus |
| gen. hy. ... | ... | M. genio-hyoideus |
| gen. hy. lat. ... | ... | M. genio-hyoideus lateralis |
| gen. hy. med. ... | ... | M. genio-hyoideus medialis |
| Göppert's m. ... | ... | muscle described by Göppert |
| hyophary. int.... | ... | M. hyo-pharyngeus internus |
| hypobr. pl. ... | ... | hypobranchial plate |
| inter. hy. ... | ... | M. interhyoideus |
| intermand. ... | ... | M. intermandibularis |
| lary. dors. ... | ... | M. laryngeus dorsalis |
| lary. vent. ... | ... | M. laryngeus ventralis |
| lary. gr. ... | ... | laryngeal groove |
| Lev. ... ... | ... | M. Levator arcus branchialis |
| Marg. i ... | ... | M. marginalis of first branchial bar |
| oesoph. ... | ... | oesophagus |
| omo-hum.-maxillaris ... | | M. omo-humero-maxillaris |
| pars lary. c. l. ... | ... | pars laryngea cartilaginis lateralis |
| pericard. ... | ... | pericardium |
| peric. p. c. ... | ... | pericardio-peritoneal canal |
| pri. annulus ... | ... | primordium of annulus |
| pri. aryten. ... | ... | „ arytenoid cartilage |
| pri. const. oesoph. ... | | „ M. constrictor oesophagi |
| pri. dil. lary. ... | ... | „ M. dilatator laryngis |
| pri. hypobr. sp. m. ... | | „ hypobranchial spinal muscles |
| pri. proc. trach. ... | | „ processus trachealis |
| rec. intest. n. ... | ... | N. recurrens intestinalis |
| rect. superf. ... | ... | M. rectus superficialis |
| subarc. obl. ... | ... | M. subarcualis obliquus |
| subarc. rect. ... | ... | M. subarcualis rectus |
| thyr. gl. ... | ... | thyroid gland |
| trans. gr. ... | ... | transverse groove |
| trans. vent. ... | ... | M. transversus ventralis |
| tend. of rect. ... | ... | tendon of M. rectus |
| vent. aor. ... | ... | ventral aorta |
| vent. pr. basibra. ... | | ventral process of first Basibranchiale |
| urobranch. ... | ... | Urobranchiale |

## LITERATURE

AGAR, W. E. (1907). "The development of the anterior mesoderm, and paired fins with their nerves, in Lepidosiren and Protopterus." *Trans. R. Soc. Edin.* Vol. XLV.

BEAUREGARD, H. (1881). "Encéphale et nerfs craniens du Ceratodus Forsteri." *Jour. de l'anat. et de la physiol. de l'homme et des animaux.*

DE LANGE, D. (1916). *Studien zur Entwicklungsgeschichte des Japanischen Riesensalamanders (Megalobatrachus maximus Schlegel).* Leiden.

DRÜNER, L. (1901 and 1904). "Studien zur Anatomie der Zungenbein-, Kiemenbogen-, und Kehlkopf-musculatur der Urodelen." I. Teil, *Zool. Jahrb. Abt. f. Anat. u. Ontog.* Bd XV. II. Teil, *ibid.* Bd XIX.

DUGÈS, A. (1834). *Rech. s. l'ostéol. et la myol. des Batraciens à leurs différents âges.* Paris.

EDGEWORTH, F. H. (1916). "On the development and morphology of the pharyngeal, laryngeal, and hypobranchial muscles of Mammals." *Quart. Jour. Micr. Sc.* Vol. LXI. Part 4.

—— (1919). "On the development of the laryngeal muscles in Sauropsida." *Jour. of Anat.* Vol. LIV. Part 1.

GAUPP, E. (1905). "Die Entwicklung des Kopfskelettes." *Hertwig's Handbuch*, Bd III. Abteil 2.

GEGENBAUR, C. (1892). *Die Epiglottis.* Leipzig.

GÖPPERT, E. (1894). "Die Kehlkopfmusculatur der Amphibien." *Morph. Jahrb.* Bd XXII. Heft ii.

—— (1898). "Der Kehlkopf der Amphibien und Reptilien." I. Theil. *Amphibien. Morph. Jahrb.* Bd XXVI. Heft ii.

—— (1901). "Beiträge zur vergleichenden Anatomie des Kehlkopfes und seiner Umgebung mit besonderer Berücksichtigung der Monotremen." *Jenaische Denkschr.* VI. Semon. Zool. Forschungsreisen, III.

—— (1904). "Der Kehlkopf von Protopterus annectens." *Festschr. Ernst Haeckel.*

GREIL, A. (1904). "Ueber die sechsten Schlundtaschen der Amphibien und derer Beziehungen zu den supraperikardialen (postbranchialen) Körpern." *Verhand. d. Anat. Gesell. Anat. Anzeig.* Bd XXV.

—— (1905). "Ueber die Anlage der Lungen, sowie der ultimobranchialen (postbranchialen, supraperikardialen) Körper der Anuren Amphibien." *Anat. Hefte*, 89, Bd 29.

—— (1905). "Bemerkungen zur Frage nach dem Ursprunge der Lungen." *Anat. Anzeiger*, Bd XXVI.

—— (1913). "Entwicklungsgeschichte des Kopfes und des Blutgefässsystems von Ceratodus forsteri. Zweiter Theil." *Semon's Forschungsr.* Bd. I.

HAY, O. P. (1890). "The Skeletal Anatomy of Amphiuma during its earlier stages." *Jour. Morph.* Vol. IV.

HENLE, J. (1839). *Vergleichend anatomische Beschreibung des Kehlkopfes mit besonderer Berücksichtigung des Kehlkopfes der Reptilien.*

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

KELLICOTT, W. E. (1905). "The development of the vascular and respiratory systems of Ceratodus." *New York Acad. of Sc. Memoirs*, Vol. II. Part 4.

KERR, J. GRAHAM (1910). "On certain features in the Development of the Alimentary Canal in Lepidosiren and Protopterus." *Quart. Journ. Micr. Sc.* Vol. LIV.

KINGSLEY, J. S. (1892). "The head of an embryo Amphiuma." *Amer. Naturalist.*

MARCUS, H. (1908). *Beiträge zur Kenntnis der Gymnophionen.* I. Ueber das Schlundspaltengebiet. *Archiv f. mikrosk. Anat. u. Entwick.* Bd 71.

MÄRTENS, M. (1895). "Die Entwickelung der Kehlkopfknorpel bei einigen unserer einheimischen Anuren Amphibien." *Anat. Hefte*, Bd IX.

MAURER (1902). "Die Entwickelung des Darmsystems." *Hertwig's Handbuch*, Bd II. Teil I.

NEUMEYER, L. (1904). "Entwickelung des Darmkanales bei Ceratodus Forsteri." *Denkschr. Med. Nat. Gesell. Jena*, Bd IV.

NORRIS, H. W. (1913). "The cranial nerves of Siren lacertina." *Jour. of Morph.* Vol. XXIV. No. 2.

NORRIS, H. W. and Miss HUGHES (1918). "The cranial and anterior spinal nerves of the Caecilian Amphibians." *Jour. of Morph.* Vol. XXXI.

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

SARASIN, P. and F. (1890). *Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon*, Bd II. 4 Heft.

SCHMIDT, V. (1913). "Ueber die Entwickelung des Kehlkopfes und der Luftrohre bei Reptilien." *Anat. Hefte*, 146 Heft (48 Bd H. 3).

SCHULTZE, F. F. (1892). "Ueber die inneren Kiemen der Batrachierlarven." *Abhand. d. K. Preuss. Akad. d. Wissen. zu Berlin.*

SOLLAS, W. J. (1919). Structure of Lysorophus as exposed by serial sections. Read Roy. Soc. May 22.

STRONG, O. S. (1895). "The Cranial Nerves of Amphibia." *Jour. of Morph.* Vol. X.

VAN WIJHE, J. W. (1882). "Ueber das Visceralskelett und die Nerven des Kopfes der Ganoiden und von Ceratodus." *Niederl. Arch. f. Zool.* Bd V. H. 3.

WIEDERSHEIM, R. (1904). "Ueber das Vorkommen eines Kehlkopfes bei Ganoiden und Dipnoern sowie über die Phylogenie der Lungen." *Zool. Jahrb.* Suppl. VII.

WILDER, H. H. (1892). "Studies in the phylogenesis of the larynx." *Anat. Anzeiger*, Bd VII. 18 Heft.

—— (1896). "The Amphibian Larynx." *Zool. Jahrb. Abt. f. Anat. u. Ontog.* Bd IX.