ON THE DEVELOPMENT OF THE CORACO-BRANCHIALES AND CUCULLARIS IN *SCYLLIUM CANICULA*

By F. H. EDGEWORTH, M.D.

A description of the development of the branchial musculature in Selachii was given by Dohrn, in 1884. He stated that each branchial muscle-plate becomes flattened antero-posteriorly, and finally separates into medial and lateral portions except at its dorsal and ventral ends. The ventral portion forms the deep portion of the Constrictor superficialis, but "diesen Namen verdienen sie freilich nur *cum grano salis*, denn der Constrictor superficialis sollte nur aus denjenigen Muskeln bestehen, welche von den distalen Portionen der ursprünglichen Muskelnschläuche abstammen. In der That sind diese Muskeln auch vorhanden, aber in der Vetter'schen Monographie falsch gedeutet worden. Er beschreibt sie als einen Theil der M. coraco-arcuales, unter dem Namen M. coraco-branchiales; sie haben aber ursprünglich nichts gemein mit M. coraco-hyoideus, setzen sich vielmehr nur an ihm an, durch eine Fascie vom ihm getrennt." (I am not sure of the meaning of the above, so quote it in the original.) No further statement was made, nor were any figures of the Coraco-branchiales published.

In a paper published in 1911 I said, after quoting van Wijhe's statements, that the Coraco-branchiales of *Scyllium* are developed from the ventral ends of all the branchial muscle-plates, which becoming cut off from the remainder of the plates grow back to the shoulder-girdle. I did not make any reference to Dohrn's paper, of which I was ignorant. Allis (1917) stated that in his opinion Dohrn and I had misinterpreted these muscles in embryos, and that they must be developed either from trunk-myotomes, or, possibly, from some part of the coelomic wall. He favoured the former theory on account of the similarity in their innervation to that of the Coraco-hyoideus and Coraco-mandibularis. Allis did not adduce any observations on the development of these muscles either in disproof of my statements or in support of either of his theories.

The following account is the result of a re-examination of the developmental phenomena in *Scyllium canicula.*

In a 12·5 mm. embryo (figs. 1–3) the first four branchial muscle-plates are developed, but the 5th not yet. They are tubular epithelial structures in the branchial segments. They are continuous below with the cephalic portion of the coelom, and their lumina are continuous with the coelomic cavity.

In a 16 mm. embryo (fig. 4) these tubular structures have broadened into plates, and their lumina have disappeared by approximation of their walls.

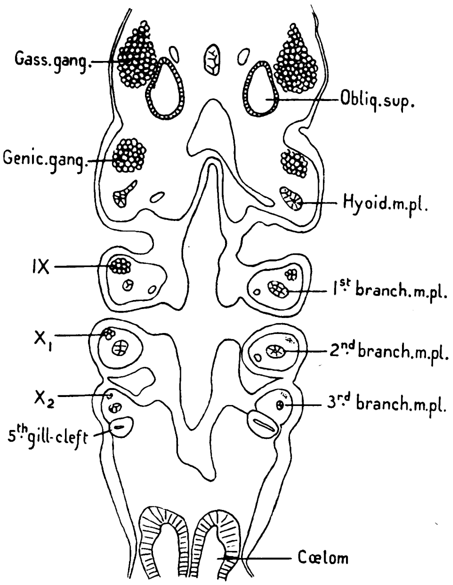

Fig. 1.

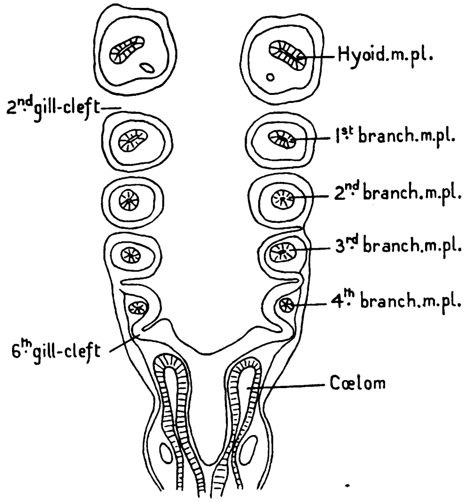

Fig. 2.

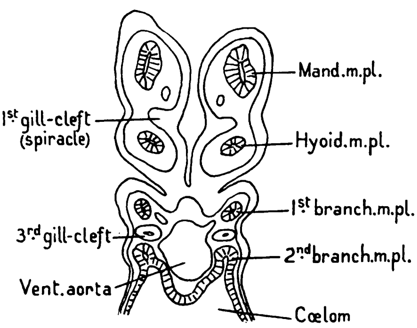

Fig. 3.

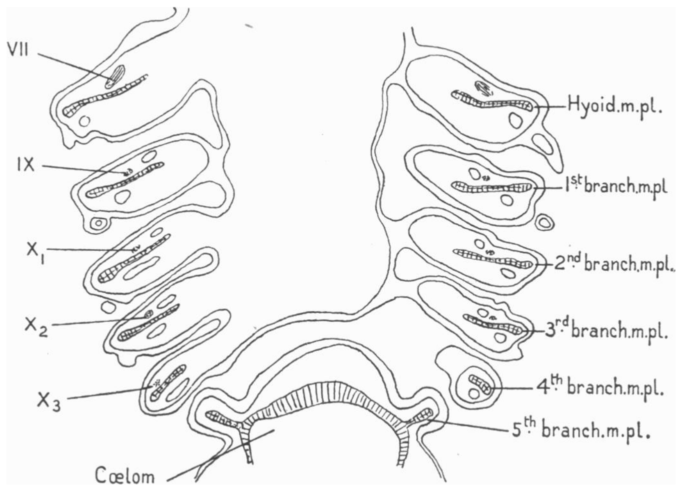

Fig. 4.

Figs. 1–3. Embryo 12·5 mm. horizontal sections. Fig. 2 is ·09 mm. below fig. 1, and fig. 3 ·24 mm. below fig. 2.
Fig. 4. Embryo 16 mm. horizontal section

Each plate consists of two strata of cells, of which the anterior is the thinner. They are directed outwards and backwards at about an angle of 30° from the transverse plane. The plates are broadest at about the middle of the pharynx. Their upper ends are narrow. Their ventral ends are still tubular and join the coelom (fig. 5). The 5th branchial muscle-plate is now developed as a short vertical column of cells which projects as an antero-lateral ridge from the coelom into the 5th branchial arch.

The Coraco-branchiales are developed from the ventral ends of the branchial muscle-plates in embryos of lengths from 23 to 28 mm. They are not formed simultaneously. There is a slight retardation in development, from before backwards, so that in any one embryo various stages of development can be seen in successive segments.

In a 23 mm. embryo (fig. 13) Coraco-branchialis i has already developed and is separated from the remainder of the 1st branchial muscle-plate. The ventral end of the 2nd branchial muscle-plate (fig. 14) is continuous with the coelomic wall. The cells have lost their epithelial character.

In a 25 mm. embryo (figs. 18–20) the 2nd branchial muscle-plate has separated from the coelomic wall. Coraco-branchialis ii is in process of development. It is a longitudinal column of cells, the anterior end of which (fig. 19) is continuous with the muscle-plate. The dorsal edge of this anterior end projects a little further forwards, towards the 2nd branchial bar (fig. 18).

Coraco-branchiales iii, iv, and v are developed similarly, but at slightly later stages—the vth not until the 28 mm. stage.

In a 27 mm. embryo, cut horizontally (fig. 21), the first four Coraco-branchiales are visible. They do not extend backwards beyond their segments of origin.

In an embryo of 29 mm. the Coraco-branchiales have begun to extend further backwards. Comparison of figs. 23 and 24 shows that Coraco-branchialis i is spindle-shaped, and extends from the 1st branchial segment backwards as far as the 3rd branchial segment.

In an embryo of 32 mm. all the Coraco-branchiales have extended backwards to the shoulder-girdle.

The above evidence shows that the Coraco-branchiales are developed from the ventral ends of all five branchial muscle-plates.

CUCULLARIS[1]

I stated (1911) that the upper ends of the branchial muscle-plates increase in antero-posterior extent and, fusing together, extend backwards as the Trapezius to the shoulder-girdle.

Allis (1917) rejected this account, though without making any investi-

[1] I employ the name "Cucullaris" in preference to "Trapezius," as the muscle though genetically connected, is not exactly homologous, with the Trapezius of man.

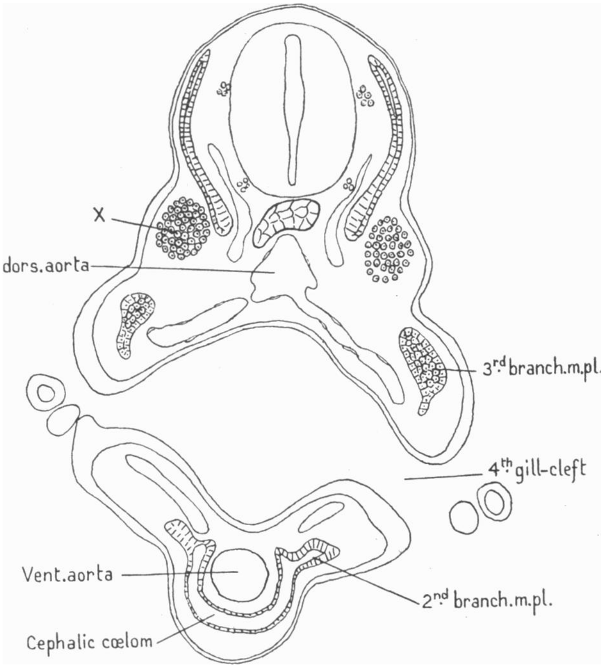

Fig 5.

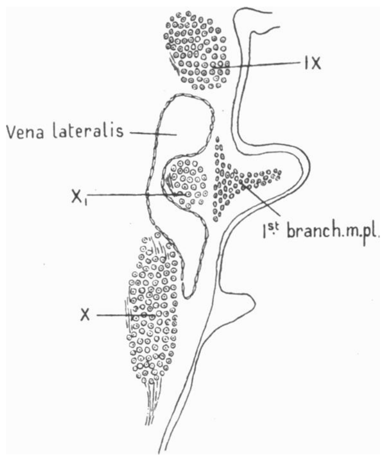

Fig. 6.

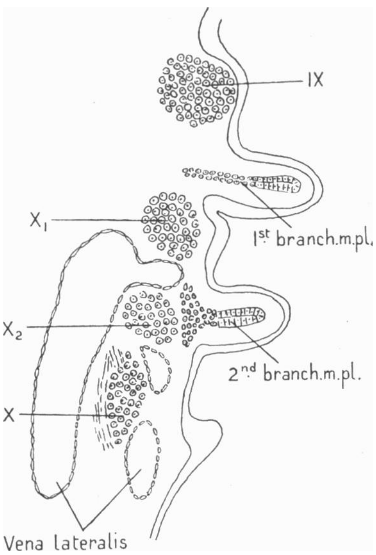

Fig. 7.

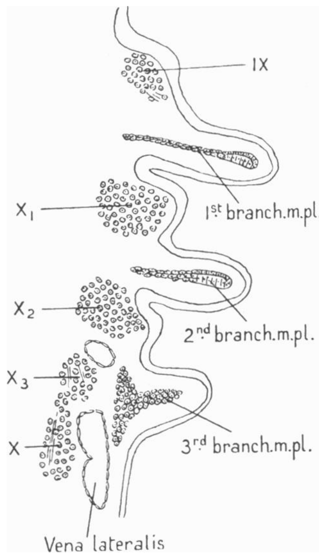

Fig. 8.

Fig. 5. Embryo 16 mm. transverse section.

Figs. 6–9. Embryo 18 mm. horizontal sections. Fig. 7 is ·07 mm. below fig. 6, fig. 8 is ·05 mm. below fig. 7, fig. 9 is ·08 mm. below fig. 8.

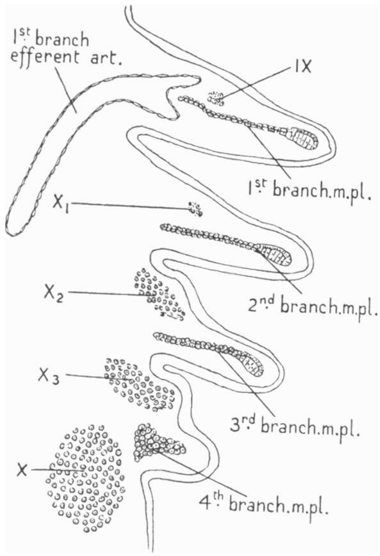

Fig. 9.

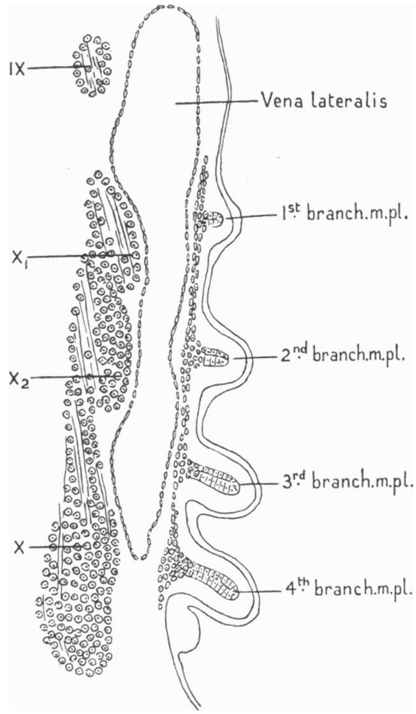

Fig. 10.

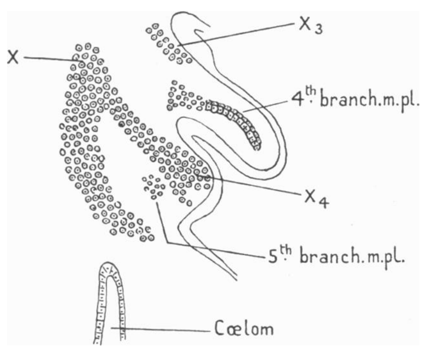

Fig. 11.

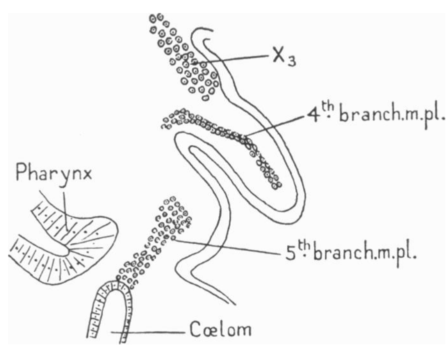

Fig. 12.

Figs. 10–12. Embryo 22·5 mm. horizontal section. Fig. 11 is ·048 mm. below fig. 10, fig. 12 is ·04 mm. below fig. 11.

gations on the development of the muscle, and stated that, in his opinion, the muscle is "a differentiation of the ultimate branchial arch," i.e. of the seventh in *Heptanchus* and of the fifth in *Acanthias*, *Scymnus* and *Mustelus*, or "possibly a differentiation of that arch and other more posterior arches if such arches primarily existed and have successively disappeared by reduction or transformation."

In a 12·5 mm. embryo (fig. 1) the upper ends of the branchial muscle-plates are rounded. In one of 18 mm. (figs. 6–9) cells have been proliferated from the inner edges of the upper ends of the first four branchial muscle-plates, forwards and backwards, so that T-shaped structures are visible. That of the 4th is not so fully developed as are those of the first three muscle-plates. The sections figured, like those of the 12·5 mm. embryo, are horizontal ones cut in a plane parallel with the notochord, and on comparison of the figures it is evident that there is a gradually declining height in the muscle-plates, from before backwards.

It may be added that the phenomena figured in the 18 mm. embryo are already present in a 16 mm. embryo, though less pronounced.

In a 22·5 mm. embryo the sections have been cut in a horizontal plane with the posterior end slightly depressed, so that fig. 10 cuts across the upper ends of the first four branchial muscle-plates. It shows that the T-shaped structures at the upper ends of these muscle-plates have coalesced and form a longitudinal column of cells—the primordium of the Cucullaris. The posterior end is just at the junction of the fourth and fifth branchial segments. The greater part of the 5th branchial muscle-plate is still continuous with the coelomic epithelium, but its upper end is free and lies just behind X_4—the branch of the vagus to the 5th branchial segment (figs. 11 and 12).

In a 24·75 mm. embryo (figs. 15–17) the upper end of the 5th branchial muscle-plate has separated from the remainder, and fused with the hinder end of the T-shaped growth of the 4th, which has extended backwards above X_4. The 5th branchial muscle-plate is connected with the coelomic epithelium only at its lower end. The sections were cut in a horizontal plane, so that the anterior part of the Cucullaris is not visible in the sections figured.

In a 28 mm. embryo (fig. 22) the Cucullaris has extended backwards nearly to the shoulder-girdle.

In a 35 mm. embryo a fasciculus diverges from the ventral edge of the muscle in the 4th branchial segment and is inserted into the 5th branchial bar.

The Cucullaris of *Scyllium* is thus developed from cells proliferated from the upper ends of all five branchial muscle-plates.

The above described investigations, which have been carried out on new material, thus confirm the statements I made in 1911 as regards the development both of the Cucullaris and the Coraco-branchiales. They invalidate both the criticisms and the theories of Allis, and show that inferences from adult anatomy are no infallible guide to the development of structures. This can only be ascertained by observation of the actual phenomena.

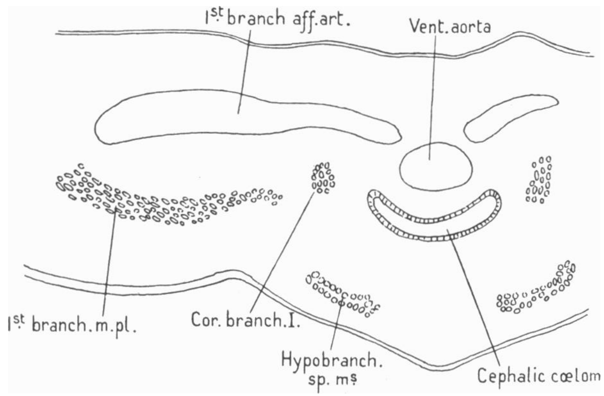

Fig. 13.

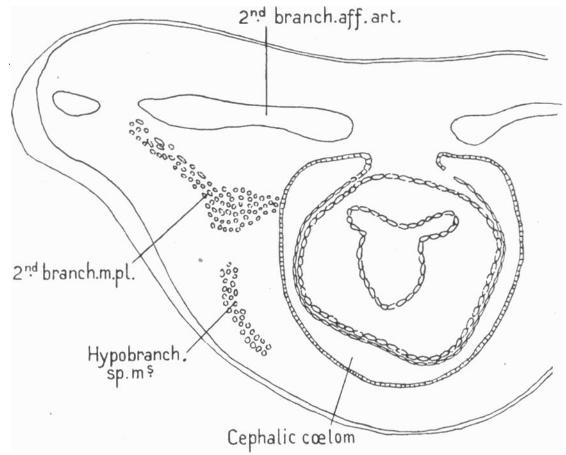

Fig. 14.

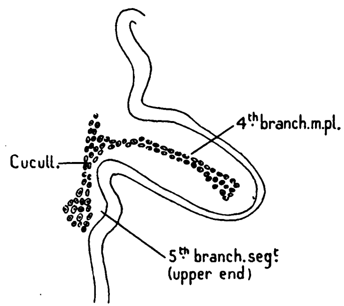

Fig. 15.

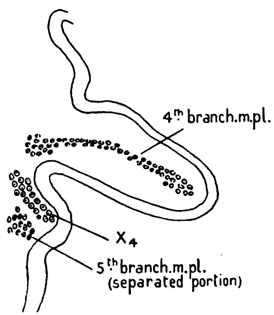

Fig. 16.

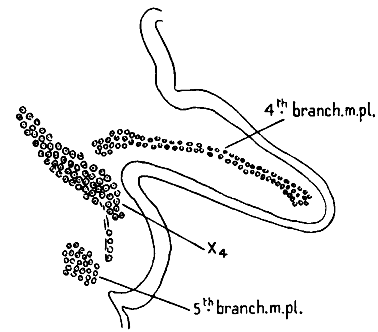

Fig. 17.

Figs. 13, 14. Embryo 23 mm. transverse sections. Fig. 14 is ·18 mm. behind fig. 13.
Figs. 15–17. Embryo 24·75 mm. horizontal sections. Fig. 16 is ·02 mm. below fig. 15, and fig. 17 ·05 mm. below fig. 16.

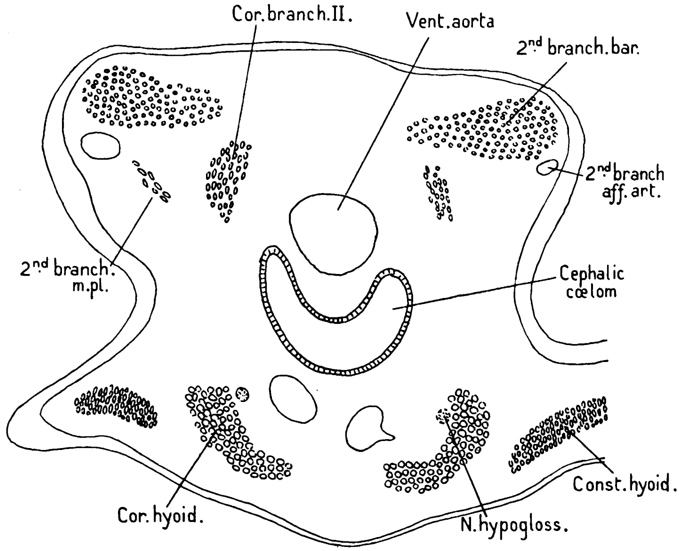

Fig. 18.

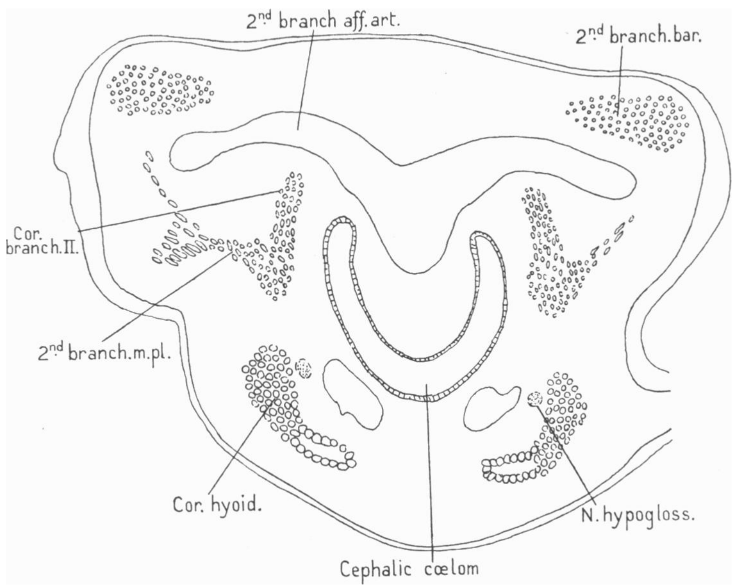

Fig. 19.

Figs. 18–20. Embryo 25 mm. transverse sections. Fig. 19 is ·032 mm. behind fig. 18, and fig. 20 ·04 mm. behind fig. 19. The right side of the sections is a little anterior to the left.

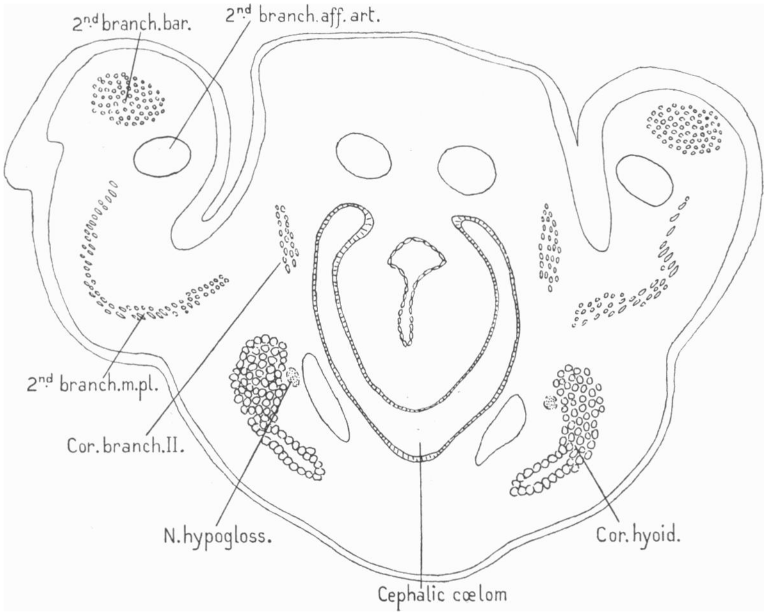

Fig. 20.

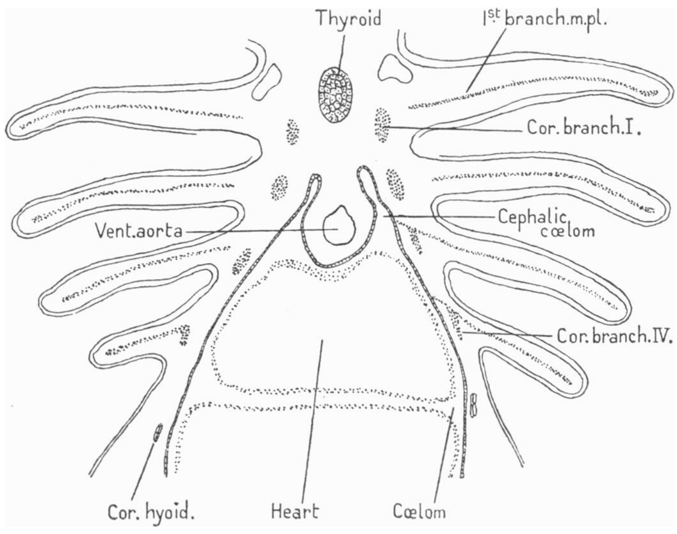

Fig. 21.

Fig. 21. Embryo 27 mm. horizontal section.

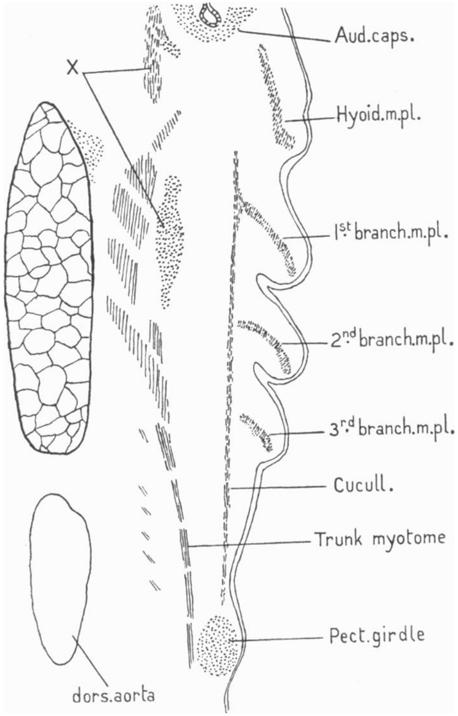

Fig. 22.

Fig. 22. Embryo 28 mm. horizontal section.

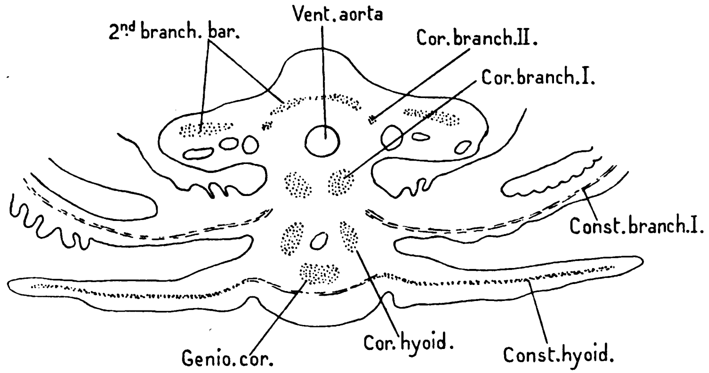

Fig. 23.

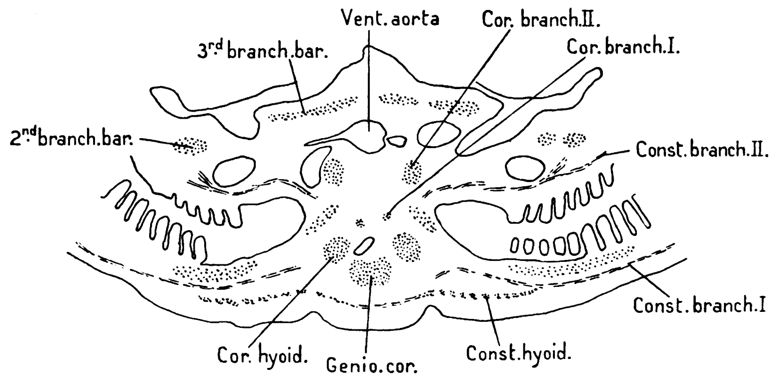

Fig. 24.

Figs. 23, 24. Embryo 29 mm. transverse sections. Fig. 24 is ·12 mm. behind fig. 23.

The development of the Cucullaris is interesting and puzzling. The question arises whether it is the primitive method, or a secondary modification.

In *Scyllium* no Levatores arcuum are developed, but only Constrictores. In *Ceratodus*, as I recently showed, Constrictores are first developed in all five branchial arches, and subsequently Levatores are separated from the inner side of the upper ends of the first four Constrictores. In Teleostomi no Constrictores are developed—but only Levatores.

These facts suggest that, phylogenetically, Constrictores are more ancient than Levatores, and that in this respect Selachii are more primitive than either Dipnoi or Teleostomi.

As regards the Cucullaris—this is developed in *Acipenser* by proliferation from the outer side of the 5th branchial Levator arcus, in *Scyllium* from the upper ends of all the branchial muscle-plates, i.e. of all the primitive Constrictores.

In view of the innervation in both cases from the vagus only—the glossopharyngeus not taking any share—it appears probable that the method of development of the Cucullaris in *Acipenser* is more primitive than in *Scyllium*.

The method of development of the Coraco-branchiales suggests that their innervation by the Plexus cervicalis s. Hypoglossus is a secondary one, and that the primary innervation was by the ixth and xth cranial nerves. In this connection it is interesting to see that there is a Coraco-branchialis v innervated by the xth in *Polyodon*, *Amia*, *Lepidosteus*, *Amiurus*, and *Menidia*, i.e. with a primitive innervation. The causes of such change, if change there has been, are doubtful—possibly by reason of the similarity in function to that of the Genio-coracoideus and Coraco-hyoideus. I hope to discuss this question in a later paper.

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April 8, 1925.

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ABBREVIATIONS

aff. art., afferent artery; aud. caps., auditory capsule; Cor. branch., Coraco-branchialis; Cor. hyoid., Coraco-hyoideus; Const. hyoid., Constrictor hyoideus; Cucull., Cucullaris; dors. aorta, dorsal aorta; eff. art., efferent artery; Gass. gang., Gasserian ganglion; Genic. gang., Geniculate ganglion; Genio-cor., Genio-coracoideus (Coraco-mandibularis of Vetter); m.pl., muscle-plate; N. hypogloss., Nervus hypoglossus; Obliq. sup., Obliquus superior; pect. girdle, pectoral-girdle; vent. aorta, ventral aorta.