On the skeleton of the hyoid arch in Rays and Skates.

By

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With Plates 19-21 and 1 Text-figure.

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INTRODUCTION.

In 1926 I investigated the development of the skull in *Torpedo*, and, on paying attention to the skeleton of the hyoid arch, I came to the conclusion that the interpretation placed upon it by Gegenbaur (1872), and commonly held, is incorrect. Briefly, this view is that the cartilaginous arch bearing hyal rays, which in the Batoidei is situated behind the hyomandibula, represents the hyoideum or ceratohyal which has become disconnected from the hyomandibula and has extended upwards (dorsally) behind it. To this I preferred Krivetski's (1917) conclusion to the effect that the cartilaginous arch in question represents the fused bases of the hyal rays, and that it should therefore be termed a pseudohyoid, to distinguish it from the ceratohyal of other forms with which it is not homologous. This conclusion is based on the fact that the afferent pseudo-branchial artery, on running forwards from the efferent hyoidean artery, is median to the pseudohyoid, whereas it is lateral to the ceratohyal of the non-Rajiform Selachians. It may be noted that in the latter forms¹ it is common for a number of

¹ There appears to be no convenient collective term for the non-Rajiform
hyal rays to be fused together at their base, forming little bars, and the afferent pseudobranchial artery is median to them. The morphological relations between the cartilages briefly referred to above are plainly evident in Dohrn's (1886) figures, in Krivetski's (1917), and in my own (1926).

In a recent paper, however, Edgeworth (1931) has denied the truth of these statements, referring to Torpedo ocellata with the words, 'there is no vessel passing internal to the lower part and external to the upper part of the hyoid bar', which he repeats in respect of Raja clavata. But the figures which Edgeworth gives to illustrate his paper flatly contradict his text, and the artery in question (afferent pseudobranchial), called by him afferent mandibular artery, is shown by him in Torpedo ocellata morphologically internal or median to the lower part of the bar in his figs. 2, 3, 4, 5, and 11, and morphologically external or lateral to the upper part of the bar (or hyomandibula) in figs. 9 and 10. On the other hand, in Scyllium canicula, Edgeworth shows that the afferent pseudobranchial artery passes lateral or external to the whole of the hyoid bar, i.e. to both hyomandibula and ceratohyal, in his figs. 17, 18, 19, 20, 22, 23, and 24.

As they stand, Edgeworth's figures are sufficient to confute his opinion and to substantiate the contrary one to the effect that while the upper part of the hyoid bar or hyomandibula is the same in Sharks and Rays, the lower part is not the same in its morphological relations in the two groups. He says further that, 'in an embryo of 25 mm. the hyoid bar has separated into the hyomandibula and the hyoideum'. I have not been able to reconcile this statement with my preparations, and, in view of the confused state of the problem and the conflict of evidence in regard to it, I have thought it advisable to reinvestigate the matter, and to present a few microphotographs. It may be said at once that the result of this work has been to confirm Krivetski's and my view completely.

In the preparation of the microphotographs I enjoyed the help

Selachians other than the comparatively little used Pleurotremata: the term Squailiformes is used for a particular suborder of sharks. In the present paper they will be referred to simply as 'Sharks', in contradistinction to 'Rays'. 
of Messrs. P. A. Trotman and W. Chesterman. I wish to record my appreciation of their services, and particularly to acknowledge my gratitude to Professor E. S. Goodrich, F.R.S., for the excellent facilities which I have enjoyed in his Department of Zoology and Comparative Anatomy of the University Museum, in which the work recorded in this paper was done.

The material consisted of series of sections of *Torpedo ocellata* and *marmorata* of sizes varying from 12 mm. to 30 mm., of sections of *Raja blanda* (young), and of specimens of young and adult *Rhynchobatus* and of young *Pristis* which were studied by dissection. For access to the latter I am indebted to the kindness of my friend Mr. J. R. Norman, of the British Museum (Natural History).

**Observations.**

The morphological point at issue concerns the relations of certain cartilages to an artery, the afferent pseudobranchial artery, and as a preliminary it is necessary to consider the nature of the latter.

The visceral arches of the Selachians each contain typically two efferent arteries which are interconnected about half-way up the arch by a short commissural artery which is external or lateral to the cartilaginous skeleton of the arch, and internal or median to the afferent artery and to the main trunk of the dorsal nerve corresponding to the arch. These relations hold good for all the branchial arches, as well in the Rays as in the Sharks. The first branchial arch of *Scyllium canicula* is shown in fig. 12, Pl. 20, and that of *Torpedo ocellata* in fig. 9, Pl. 20, as seen in transverse section; the first branchial arch of *Torpedo marmorata* is shown in fig. 13, Pl. 21, and that of *Raja blanda* in fig. 14, Pl. 21, as seen in horizontal section, from which the morphological relations described above can be clearly made out.

The hyoid arch differs from the more posterior visceral arches in that it contains only one (posterior) efferent artery. But at the same level as the commissural arteries of the branchial arches, the efferent hyoid artery gives off the afferent pseudobranchial artery. That the latter is serially homologous with
the commissural artery of the branchial arches there can be no
doubt, for in the Sharks it runs forwards on the outer or lateral
side of the hyomandibula and ceratohyal, and on the median
side of the afferent hyoid artery and of the main trunk of the
facial nerve. The relations of the artery to the cartilage and
the nerve are shown in Scyllium canicula in fig. 11, Pl. 20.

Now, in the Rays, the afferent pseudobranchial artery runs
forwards on the median side of the afferent hyoid artery and of
the facial nerve and is morphologically external to the hyomandi-
bula, exactly as in the Sharks; but it runs on the inner or median
side of the lower, ray-bearing part of the hyoid arch skeleton.
The position of the afferent pseudobranchial artery in the Rays,
therefore, is shown: morphologically external to the
hyomandibula in Torpedo ocellata in figs. 1, 3, 5, Pl. 19, fig. 7, Pl. 20, and in Torpedo marmorata in fig. 13, Pl. 21; morphologically internal to the facial
nerve in Torpedo ocellata in figs. 1, 3, 5, Pl. 19, and in
Torpedo marmorata in fig. 13, Pl. 21; morphologi-
cally internal to the afferent hyoid artery in
Torpedo ocellata in figs. 2, 4, Pl. 19, fig. 8, Pl. 20, in
Torpedo marmorata in fig. 13, Pl. 21, and in Raja
blanda in fig. 14, Pl. 21; and morphologically internal
to the lower ray-bearing part of the hyoid arch
skeleton in Torpedo ocellata in figs. 2, 4, 6, Pl. 19,
fig. 8, Pl. 20, in Torpedo marmorata in fig. 13, Pl. 21,
and in Raja blanda in fig. 14, Pl. 21.

Since all the morphological relations of the artery are the
same in the Sharks as in the Rays except for the relations to
the lower ray-bearing part of the hyoid arch skeleton, it follows,
if morphology is to count for anything at all, that the artery
is homologous in both groups, but that the latter cartilage is
not a ceratohyal or hyoideum, and it will be hereafter referred
to as the pseudohyoid. The questions which have now to be
answered are: what has become of the ceratohyal in the Rays;
what is the pseudohyoid, whether it is represented in the Sharks,
and, if so, by what element? These problems may best be tackled
by considering a series of developmental stages of Torpedo
ocellata.
In embryos 21 mm. long the skeleton of the hyoid arch is represented by rudiments of dense procartilage. There is (fig. 1, Pl. 19) an arch in the form of a semicircle convex outwards and forwards, with the result that the upper and lower extremities of the bar are directed slightly inwards and backwards, and respectively upwards and downwards. This arch, which may be termed the hyoid bar, is continuous from top to bottom, and is median to the afferent pseudobranchial artery. In this bar there will eventually be formed, by chondrification of the upper part, the hyomandibula; the fate of the lower part will be clearer after a consideration of later stages. But the hyoid bar is not the only skeletal element in the hyoid arch, for behind it is another bar of procartilage, more or less vertical in position, and in mesenchymatous contact with both the upper and lower extremities of the hyoid bar. This second bar, which will be termed the pseudohyoid bar, bears the rudiments of a number of hyal rays, and it is lateral to the afferent pseudobranchial artery. It is shown in fig. 2, Pl. 19, which is of a transverse section 0.2 mm. posterior to that shown in fig. 1, Pl. 19. In the pseudohyoid bar the pseudohyoid cartilage will chondrify, but it is important to note that even at this early stage, before any chondrification has set in, there are separate hyoid and pseudohyoid bars, and even if the ventral and ray-bearing cartilage of the hyoid arch of Rays be termed the hyoideum (as by Edgeworth), it is quite incorrect to say that it and the hyomandibula are formed by the separation of the lower and upper parts of one and the same hyoid bar. Indeed, the evidence from embryology confirms the conclusion arrived at from morphological considerations, to the effect that the ventral ray-bearing cartilage of the hyoid arch of Rays is not a ceratohyal or hyoideum. It may be mentioned that the rudiments of the hyal rays are quite continuous with that of the pseudohyoid.

In an embryo 22 mm. long, chondrification has just set in, and the hyomandibula is plainly visible in the upper part of the hyoid bar (fig. 3, Pl. 19). The lower part of this bar is, however, still mesenchymatous except for two small rudiments near its lower end (seen in fig. 4, Pl. 19); these are the rudiments of the ceratohyal and of the hypohyal, and it is important to notice
that while they are formed as parts of the hyoid bar which is internal to the afferent pseudobranchial artery, they are quite distinct from the pseudohyoid, which is external to that artery. The pseudohyoid is now chondrified to a certain extent, and its extremities are attached by mesenchyme, the upper to the hindmost part of the hyomandibula, and the lower to the hyoid bar in the region of the ceratohyal. Some of the hyal rays are also cartilaginous, and they appear to be continuous with the pseudohyoid, even when studied with the help of a critical cartilage-stain such as thionin.

The ceratohyal is, therefore, not entirely absent in the Rays, but it is very much reduced. It may be noted that it bears the correct relations to the afferent hyoid artery, being immediately dorsal to it. It is connected with the hyomandibula only by a string of mesenchyme, and lies at a level 0.3 mm. behind the hyomandibula. To the strand of mesenchyme between the hyomandibula and the ceratohyal there is attached a ligament which passes backwards, inwards, and downwards, dorsally to the ceratohyal, the hypohyal, and the afferent hyoid artery, to join a large paired muscle which extends backwards dorsally to the coracomandibular muscles and ventrally to the ventral aorta and to the coracobranchial muscles. This ligament is seen in figs. 3, 5, 6, Pl. 19, and fig. 7, Pl. 20, and the muscle to which it is attached in figs. 8 and 9, Pl. 20. The muscle appears to be that which Marion (1905) described in Raja as the coraco-hyomandibular. It is not an ordinary coracohyoid muscle, for it is dorsal to the afferent hyoid artery and afferent first branchial artery, instead of ventral to them as the coracohyoid muscle is in Sharks. Luther (1909) has, however, described some dorsal fibres of what he calls the coracohyoid in Stegostoma.

In addition to the coraco-hyomandibular ligament and muscle, the hyoid bar comes into relations with a part of the second superficial constrictor muscle (C$_2$hv according to Ruge’s (1897) terminology) which in Raja forms the depressor hyomandibularis muscle. This is seen in figs. 1, 3, 5, Pl. 19, and fig. 7, Pl. 20. This muscle is stated by Ruge to be wanting in Torpedo, whereas Tiesing (1896) speaks of it as present. According to Fürbringer (1897) the coracohyoid muscle of Raja is
separated from the depressor hyomandibularis by the first afferent branchial artery. Since the coracohyoid muscle must be ventral (superficial) to the artery, it follows that the depressor hyomandibularis must be dorsal to (deeper than) the artery, and so it would seem that the muscle which Fürbringer calls the depressor hyomandibularis must occupy the same position as that muscle in Raja which Marion (1905) has called the coracohymandibular. Altogether, the question of the muscles of the hyoid arch in the Rays appears to be distressingly confused, as Allis (1917) has already pointed out.

Later stages of development show little novelty, but chondrification of hyomandibula, ceratohyal, hypohyal, pseudohyoid, and hyal rays soon becomes complete (figs. 5 and 6, Pl. 19, and figs. 7 and 8, Pl. 20). It is worth noting, as well seen in fig. 8, that the ceratohyal is at a deeper level than the pseudohyoid. With regard to the hyal rays it may be mentioned that Edgeworth (1931) maintains that they are originally independent of the bar (pseudohyoid) to which they are fused. All that I can say is that I have not observed the separate nature of the rays situated at about the middle of the arch, and a study of sections and of whole preparations stained by the van Wijhe technique leads me to believe that these rays at any rate are continuous with the pseudohyoid. I have, however, seen that the more dorsal and ventral of the hyal rays do seem to possess separate centres of chondrification, and this leads to a consideration of the nature of the pseudohyoid itself.

Krivetskí (1917) regarded the pseudohyoid as formed by the fusion of the proximal ends of the hyal rays, and it is therefore necessary to turn now to the Sharks in order to see whether their hyal rays show any trace of such a fusion. Fürbringer (1903), who devoted a study to the visceral skeleton of the Sharks, showed that fusion of the hyal rays occurred to a greater or lesser extent in a number of forms, such as Chlamydoselachus, Odontaspis, Heterodontus, Spinax, Echinorhinus, Laemargus, and Scymnus. Luther (1909) demonstrated a very extensive fusion in Stegostoma, and I have observed it in Carcharodon and various species of Scyllium. Fig. 10, Pl. 20, is of a transverse section through
the posterior part of the hyoid arch of an embryo of Scyllium canicula. The section is taken behind the level of the hyomandibula and ceratohyal, but a number of hyal rays are cut, and it may be observed that five of the most ventral of the dorsal set of hyal rays are fused together forming a bar, and three of the most dorsal of the venfral set of rays are likewise fused. But most important of all it must be noticed that the bars formed by this fusion are lateral or external to the afferent pseudobranchial artery. In fact, these bars occupy precisely the same morphological position as the pseudohyoid of the Rays, and it would be very extravagant in hypotheses to suppose that they were not homologous. In the Sharks these bars, which may be termed the pseudohyoid bars, remain separate: a dorsal one and a ventral one. In the early stages of Torpedo, whole preparations stained with Victoria blue show that they have separate centres of chondrification: a little later, however (fig. 8, Pl. 20), they are joined into a single rod. Whether they remain so joined in the adult condition in Torpedo I do not know, but in adult Raja, Rhynchobatus, and Pristis they are separated into dorsal and ventral portions with a joint between.

A question now arises as to the manner in which the fusion of the hyal rays has taken place. Forbringer, Luther, and Krivetski speak of a fusion or concrescence of the proximal ends of the hyal rays. In this way it can be imagined that the pseudohyoid bar might be formed, like the cross-piece which bears the pegs of a rake. But there is another way in which it may be imagined that the process has taken place. It will be noticed that the rays which are so fused in the Sharks are the central ones, the most dorsal and most ventral rays being free. I may also repeat that it is the central rays which I have found to be continuous in their chondrification with the pseudohyoid, while the more dorsal and more ventral rays seem to possess separate centres of chondrification. This looks as if in the formation of the pseudohyoid bars the first step was the elongation and enlargement of the most ventral ray of the dorsal series and the most dorsal ray of the ventral series. On to these elongated rays the bases of the adjacent rays would be fused
in succession, in a dorsal direction for the dorsal set of rays and in a ventral direction for the ventral set. While the rays nearest the middle of the hyoid arch (the central rays) may be supposed to chondrify with the pseudohyoid bar—indeed, on this view each pseudohyoid bar itself would be an elongated ray—the more dorsal and more ventral rays may retain a certain amount of independence in chondrification.

The study of developmental stages of Torpedo has shown, therefore, that the ceratohyal is not absent but simply very much reduced; that the pseudohyoid is an element quite separate from the ceratohyal; that the pseudohyoid is formed by the fusion of hyal rays, probably on to enlarged and elongated rays; and comparison with Sharks has shown that such a fusion in them is the rule rather than the exception.

It may now be asked whether the ceratohyal is present in other Rays besides Torpedo, and the answer is that it is. A study of sections of Raja calla has revealed the existence of a small elongated splint of cartilage at each end of the hyoid copula, and median to the ventral end of the pseudohyoid of its side. A similar cartilage has been found in preparations of Pristis, but the most interesting condition of all is that shown by Rhynchobatus. This form is regarded as one of the most primitive of the Rays, and it might be expected therefore that the ceratohyal in it was not so much reduced as it is in Torpedo, Raja, or Pristis. Fig. 15, Pl. 21, is a view of the hyoid copula and pseudohyoid of Rhynchobatus, and in between these cartilages the ceratohyal can be plainly seen, and it presents evidence of its more primitive condition in that it still bears four hyal rays: all the other rays are borne by the pseudohyoid. It may also be noticed that the ceratohyal is composed of denser cartilage than the pseudohyoid, and, indeed, the latter shows a number of circular zones of incomplete chondrification, indicative of the newness of its formation.

**Discussion.**

By the recognition of the pseudohyoid of the Rays as a structure altogether distinct from the ceratohyal or hyoideum and formed by the fusion of the hyal rays, all the morphological
relations of these structures can be recognized as having been respected during the phylogenetic divergence between the Rays and the Sharks. Further, the presence of a ceratohyal in the Rays, separate from the pseudohyoid, and the presence of pseudohyoid bars in the Sharks, separate from the ceratohyal, renders it quite impossible to regard these structures as the same. In addition, this view solves the problem of why the pseudohyoid extends dorsally behind the hyomandibula and reaches a point more dorsal than that which the ceratohyal normally attains.

It is not without interest to note that the formation in the Rays of a pseudohyoid bar by fusion of hyal rays is a phenomenon which seems to have a parallel in the Dipnoi. Fürbringer (1904) has drawn attention to the conditions in Protopterus, where there is a cartilaginous rod between the hyoid and first branchial arch. He supposes that it has been formed by the fusion of the bases of rays, and he also provides a reason for this modification.

The anterior wall of the first gill-slit (second visceral cleft, referred to by Edgeworth as '2nd gill-cleft') is supported by the hyal rays, and provided that the distance between this slit and the angle of the mouth be not too great, the hyal rays can themselves be supported on the hyomandibula and ceratohyal: if not, the rays must have some other support. This argument is all the more cogent in the Rays, where, in the first place, the hyomandibula is tied to the angle of the mouth in consequence of its hyostylic function, and where the gill-slits have become separated by a considerable distance from the mouth and spiracle: the spiracle being on the dorsal side of the body while the gill-slits are on the ventral side. The normal skeleton of the hyoid arch is therefore incapable of supporting the hyal rays under such conditions, and the last vestige of this function on the part of the ceratohyal is seen in Rhynchobatus.

In the light of the present work, the relations of the skeleton of the hyoid arch in Sharks and Rays is shown diagrammatically in Text-fig. 1.

In addition to the particular conclusions to which this work has led, there may be derived from it some considerations of
more general value and application. Whether the work had been begun by a study of the anatomy of the skeleton of

TEXT-FIG. 1.
Diagrammatic representation of the relations of the skeletal structures of the hyoid arch in A, the Sharks, B, the Rays.

Rhynchobatus with its little ceratohyal still bearing rays, or of the embryology of Torpedo with its distinct hyoid and pseudohyoid bars, or of the morphology of the hyoid arch skeleton in the Selachians with the discrepancy between the relations of the afferent pseudobranchial artery to the ceratohyal
and pseudohyoid, its results would have pointed in the same direction, each line of work confirming the others. Indeed, it was because of evidence from morphology of the hyoid arch skeleton in Selachians and embryology of Torpedo that Rhynchobatus was suspected of having a ceratohyal which still retains its function of bearing hyal rays. This amounts to saying that morphological conclusions, if correct, have more than a merely descriptive value, for they enable predictions to be made, and these may be susceptible of positive verification if suitable material be available in which to test them. Investigation of such material then becomes an 'experiment', of no less philosophical value than in the so-called experimental branches of science: a fact which seems to be in danger of being lost sight of. The only handicap from which morphology suffers is the fact that, owing to the widespread extinction which has accompanied evolution, suitable material may not be available, and there may consequently be many hypotheses incapable of proof.

Summary.

1. The relations to the afferent pseudobranchial artery of the lower ray-bearing part of the hyoid arch skeleton in Rays show that the latter is not the ceratohyal, but a pseudohyoid.

2. Investigation of the development of Torpedo shows that the pseudohyoid arises distinct from the hyoid bar, and that the ceratohyal is much reduced.

3. The ceratohyal in Rhynchobatus is not so much reduced as in Torpedo, Pristis, or Raja, and it still bears a small number of hyal rays.

4. The pseudohyoid is formed as the result of fusion of hyal rays, and pseudohyoid bars are present more or less well developed in a large number of Sharks.

5. The enlargement of the pseudohyoid and reduction of the ceratohyal in Rays is associated with the increased distance between the mouth and the first gill-slit, and the necessity for providing a support for the hyal rays and the anterior wall of the first gill-slit. Similar factors have been operative in the Dipnoi and have led to analogous results.
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EXPLANATION OF PLATES 19, 20, AND 21.

PLATE 19.

Fig. 1.—Transverse section through an embryo of Torpedo ocellata 21 mm. long (section 21-4-3-6), showing the relations of the hyoid bar to the afferent pseudobranchial artery.

Fig. 2.—Ditto, 0-2 mm. posterior to fig. 1 (section 21-4-4-3), showing the relations of the pseudohyoid bar to the afferent pseudobranchial artery.

Fig. 3.—Transverse section through an embryo of Torpedo ocellata 22 mm. long (section 22-4-2-5).

Fig. 4.—Ditto, 0-3 mm. posterior to fig. 3 (section 22-4-3-8).

Fig. 5.—Transverse section through an embryo of Torpedo ocellata 27 mm. long (section 27-5-3-10).

Fig. 6.—Ditto, 0-3 mm. posterior to fig. 5 (section 27-6-1-5).

PLATE 20.

Fig. 7.—Transverse section through an embryo of Torpedo ocellata 30 mm. long (section 30-6-1-8).
Fig. 8.—Ditto, 0-32 mm. posterior to fig. 7 (section 30-6-3-5).

Fig. 9.—Transverse section through an embryo of Torpedo ocellata 22 mm. long (section 22-5-2-6), showing the relations of the skeleton of the first branchial arch to the cross-commissural artery.

Fig. 10.—Transverse section through an embryo of Scyllium canicula 35 mm. long (section 35-7-2-5), showing the fusion of hyal rays to form dorsal and ventral pseudohyoid bars.

Fig. 11.—Ditto (section 35-6-3-6), showing the relations of the hyoid arch skeleton to the afferent pseudobranchial artery.

Fig. 12.—Ditto (section 35-7-4-3), showing the relations of the skeleton of the first branchial arch to the cross-commissural artery.

PLATE 21.

Fig. 13.—Horizontal section through an embryo of Torpedo marmorata 24 mm. long (section 24-10-2-8), showing the various relations of the cartilages to the arteries and nerves.

Fig. 14.—Horizontal section through a young specimen of Raja b l a n d a (section 113), showing the various relations of the cartilages to the arteries.

Fig. 15.—Photograph of a preparation stained with Victoria blue of the skeleton of the left hyoid arch of Rhynchobatus, showing the hyoid copula, the ceratohyal bearing hyal rays, the pseudohyoid divided into dorsal and ventral portions, and a small portion of the dorsal extremity of the hyomandibula.

EXPLANATION OF LETTERING.

aba, 1 and 2, first and second afferent branchial artery; ac, auditory capsule; aeba, anterior efferent branchial artery of first branchial arch; aha, afferent hyoid artery; apa, afferent pseudobranchial artery; br, branchial ray; cb, 1 and 2, first and second ceratobranchial; cc, cross-commissural artery between anterior and posterior efferent branchial arteries; cb, ceratohyal; chm, coracohyomandibular muscle or ligament; C vh, posteroverentral portion of second constrictor muscle; cm, coracohyomandibular muscle; eba, first epibranchial; eha, efferent hyoid artery; fn, facial nerve; gn, glossopharyngeal nerve; g-s, 1 and 2, first and second gill-slit; h, hyomandibula; he, hyoid copula; hh, hypohyal; hr, hyal ray; ic, internal carotid artery; tr, ligamentous vestige of hyoid bar between hyomandibula and ceratohyal; Me, Meckel's cartilage; p, cavity of pharynx; peba, posterior efferent branchial artery of first branchial arch; ph, pseudohyoid; phd, dorsal pseudohyoid bar; phv, ventral pseudohyoid bar; t, thyroid gland.

Erratum: in fig. 2, Pl. 19, bottom right-hand corner, for apa read aha.