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XXVI.—A Monograph on the general Morphology of the Myxinoid Fishes, based on a study of Myxine. Part II. The Anatomy of the Muscles.

Frank J. Cole

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XXVI. —A Monograph on the general Morphology of the Myxinoid Fishes, based on a study of *Myxine*. Part II. The Anatomy of the Muscles. By Frank J. Cole, B.Sc. Oxon., Lecturer in Zoology, University College, Reading. *Communicated by* Dr R. H. TRAQUAIR, F.R.S. (With Four Plates.)

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1. INTRODUCTION.

The first part of this work was published in the *Transactions* of the Society for 1905, when the present section was promised by the end of the same year. But the labour of revising the whole work on the sections and of posting all the muscles in the extensive series of key sections along with the skeleton has been much greater than was anticipated, and hence the delay. This labour, however, is amply repaid by the knowledge that one is now in a unique position for studying the blood-vessels and nerves; for not only has every fraction of the skeleton and muscles been microscopically explored, but the information obtained is immediately and completely available on reference to the key sections. When the whole work is completed and all the systems have been entered in these sections, I hope to obtain a grant to enable me to publish them as an atlas. As far as I am aware, no animal has been studied throughout in this way before.

The terminology adopted in the present part (with a few slight alterations) is that of P. FÜRBRINGER (7). I have made no attempt to revise it, for the same reason that

induced me to accept the existing nomenclature of the skeleton, *i.e.* that no revision without the evidence of the vessels and nerves could have any permanent value. It is clear, however, that a revision is necessary; and, for example, the transversus oris may possibly have to be broken up into three discrete muscles.

I am much indebted to the friendly interest of Baron A. KLINCKOWSTRÖM, who has been kind enough to present me with a number of excellent unpublished drawings of *Myxine*. Due acknowledgment will be made when these are put to any use. I also wish to express my indebtedness to the Government Grant Committee of the Royal Society for a grant which has defrayed the expenses of this research.

Perhaps I may repeat the statement made in my first Part, that although the present work is purely anatomical, the morphology of the animal will be exhaustively considered when the whole facts are available and have been co-ordinated. In conclusion, I feel it is only right to refer here to the great assistance in preparing the key sections given by EDINGER's projection apparatus, as made by Leitz. Combined with a Zeiss A lens the sections may be easily and quickly drawn with great accuracy. One may hope that this apparatus will be sufficiently improved in the future to be available with higher powers.

2. HISTOLOGY OF THE MUSCLES. (Fig. 7, *a-e*, numerals 1-5.)

I do not propose in this section to enter into the histology of the muscles proper, but simply to consider such microscopical details as have an anatomical bearing. A transverse section of the parietal muscles reveals the fact, as recognised by MAURER, that the muscle fibres are (at least) of two kinds, which are easily distinguishable even with the low power of the microscope. There are other types of muscle fibre present in *Myxine*, especially, as we should expect, in the tail, but these do not concern us here. The two types mentioned above are the small plasmic "red" fibres, which physiologists have shown to occur in rapid or strenuous muscles, and the large aplasmic "white"* fibres which are found in sluggish or tonus muscles. Of the two, the red fibres are much less numerous, but on account of their very rich vascular supply they are strikingly picked out if the section has been stained with Mann's methyl-blue-eosin. The red fibres are either absent or very sparsely scattered at the anterior end of the parietalis, and also throughout the greater part of the caudal region, and elsewhere in the thin ventral portion of the muscle. Apart from this, they may be said to characterise the parietalis generally.

The M. parietalis is formed by a number of dorso-ventrally compressed fasciuli, which in transverse section appear as flattened sausage-shaped masses, arranged (more or less) at right angles to the median vertical axis of the body. The greater part of

* I use the terms "red" and "white" on account of their convenience, but I have not examined living material to ascertain whether these fibres, as is often the case, actually are red and white in colour. Their rich vascularity at least should give the plasmic fibres a reddish tinge in *Myxine*. Well-known examples of the two kinds of fibres are the predominantly red fibres of the pectoral muscles of the pigeon and the white fibres of the similar muscles of the fowl.

the external surface, *i.e.* the surface abutting on the subcutaneous blood sinus, consists of red fibres two or three rows deep (apparently observed by SCHNEIDER), and from this crust there penetrate inwards, often right through the thickness of the muscle, numerous horizontal sheets of red fibres, each of which is shown in transverse section to be formed of a *single* row of fibres placed end to end, like a row of bricks. It is curious that, as already pointed out by MAURER, the red fibres are confined to the *ventral* surface of the fasciculi, the remainder of each fasciculus (with its dorsal surface) being formed entirely of the white fibres. Thus every fasciculus has a ventral sheath of red fibres. In the Lamprey, according to MAURER, the red fibres extend right round the fasciculi. The following descriptions are based on fibres selected from the same specimen, and take no account of the state of contraction in which they happened to be.

M. parietalis.

White Fibres (fig. 7, *a*).—These are of large size and are formed of small sarco-styles, (1),* which are very numerous and closely packed. The transverse striation is sharply marked, and there is no peripheral zone of sarcoplasm nor a peripheral blood plexus. The nuclei (2) are numerous, narrow, very elongated, and *mostly internal*, although some are situated superficially (all seen in transverse section in the figure). According to MAURER, the distorted appearance which these nuclei often present is due to the pressure of the surrounding sarcostyles. They are also said to resemble the sarcolemma nuclei.

Red Fibres (fig. 7, *b*).—These are of much smaller size and have slightly larger sarcostyles (1) which are not so concentrated (*i.e.* not so numerous). According to MAURER, the sarcostyles are here aggregations of smaller fibrillæ, but I find no evidence of this. Sarcoplasm (with an occasional stray nucleus — 2) is quite visible as a packing between the sarcostyles. According to MAURER, however, there are no internal nuclei in the red fibres; and whilst this is not literally true, it is correct to say that internal nuclei are typically absent in the red fibres. The transverse striation is not so well marked as in the white fibres, but the longitudinal striation is very apparent. Peripherally there is a zone of sarcoplasm (3) which lodges the large oval or circular true nuclei (4) of the fibre. The nuclei are here, therefore, not central, as in the white fibre, but peripheral. Round each fibre there is a rich peripheral blood plexus (5) which is very striking in longitudinal sections stained with methyl-blue-eosin. It is obvious that these are rapid fibres undergoing considerable tissue change, and hence the zone of nutritive sarcoplasm with its extensive vascular supply.

M. cordis caudalis. (Fig. 7, *c*.)

This muscle consists of red fibres only. These on an average are much smaller than the similar fibres of the parietalis, but they vary considerably in size. The figure has

* Perhaps these should be regarded rather as *fibrils* which have not collected together to form clearly defined muscle columns or sarcostyles.

been drawn from one of the medium-sized fibres, the largest being about the size of the red fibre figured from the parietalis. The sarcostyles (1) are generally quite small and closely packed, but may be of variable size. There is no appreciable internal sarcoplasm, and I have only very rarely seen internal nuclei. Most of the fibres have uniformly small sarcostyles, and the transverse striation is somewhat indistinct. The peripheral sarcoplasm (3) is relatively more abundant than in the parietalis red fibre, and contains strings of large oval or round nuclei (4). Although the muscle is very vascular (5), the capillaries are not arranged in a definite rich plexus round each fibre as in the parietalis red fibre—perhaps not necessary, owing to their smaller size.

M. velo-quadratus. (Fig. 7, d.)

Also consists of red fibres only. They are of practically uniform size, much smaller than the red fibres of the parietalis, and about equal to the medium fibres of the cordis caudalis. The sarcostyles (1) are exceedingly small, of uniform size, and fairly closely packed, and there is no appreciable internal sarcoplasm. The transverse striation generally is faint, and there is an extensive peripheral zone of sarcoplasm (3) with large unusually round nuclei (4). I have seen a large nucleus in the centre of the sarcostyles, but it may be said that the nuclei are typically peripheral. The muscle is very vascular (5), more so than the cordis caudalis, but not to such an extent as the red fibres of the parietalis. There is no plexus round each fibre as in the latter muscle, but large capillaries penetrate very freely between the fibres.

M. velo-spinalis. (Fig. 7, e.)

The histology of this muscle agrees with that of the velo-quadratus, but the following points may be noted. The fibres are smaller, and there is occasionally a patch of sarcoplasm in the centre of the fibre in which I have (rarely) found a central nucleus, but neither of these features is at all characteristic of the muscle. The striation is very faint and the muscle is highly vascular (5).

3. *M. tentacularis posterior.* (Figs. 8, 9, 10, t. p.)

J. MÜLLER, *Zurückzieher der Tentakeln* (p. 258).

Arises just behind and over the eye in the apex of the angle formed by the two limbs of the second myotome, or in some cases by the upper limb of the second myotome and the backward extension of the first (cp. fig. 9). The origin is from the strong membrane constituting the fascia superficialis externa of J. MÜLLER. The *M. nasalis* arises largely from the same membrane. The eye lies between this muscle and the palatine bar. The muscle passes forwards, most of it at the side of the lateral wall of the brain case. Opposite the posterior end of the nasal capsule it begins to

flatten out so as to become ribbon-shaped, and is opposed internally to the *M. palato-ethmoidalis superficialis*, lying at the side of the nasal capsule. In front of the capsule it courses superficially as a very broad ribbon-shaped muscle at the side of the head. Anteriorly, it separates off below a small bundle which is inserted externally into the sheath of the base of the third tentacle. The larger dorsal part then rapidly narrows down, and is inserted externally into the basal sheath of the first tentacle. It is obvious that this muscle is something more than the retractor of the first and third tentacles, and in fact most of its fibres, constituting the middle portion of *P. FÜRBRINGER*, pass straight forwards and terminate on the tough spongy tissue of the snout between, and in the region of, the first and third tentacles.

J. MÜLLER states that in *Bdellostoma* this muscle arises from the palatine bar and is inserted into the first, second, and third tentacles *only*, *i.e.* there is no middle portion. In *Myxine* it is everywhere widely separated from the palatine bar, and is, further, not inserted into the second tentacle. Any movement of the first tentacle, however, would necessarily affect the second. *P. FÜRBRINGER* also queries *MÜLLER*'s statement of the origin from the palatine bar mentioned above. The morphology of this interesting muscle I leave over until its innervation is described.

4. *M. tentaculo-ethmoidalis*. (Figs. 3, 10, 11, *t. e.*)

J. MÜLLER (in part), *Compressor des Mundes, Mundschliesser* (p. 259).

A clearly defined muscle, coursing obliquely backwards and outwards, and compressed from side to side into a vertical band, the dorsal border appearing behind on the lateral surface above the transversus oris, and the ventral border appearing on the ventral surface between the transversus oris and the copulo-ethmoidalis, but the two latter muscles approximate posteriorly, and there exclude the posterior end of the tentaculo-ethmoidalis from the ventral surface. It thus extends for a great part of its course from the dorso-lateral surface of the snout on to the ventral surface of the same, but is separated from the skin at both extremities by the elaborate blood sinuses which exist at this region, and, further, it is partly covered dorsally by the upper limb of the tentacularis posterior.

The tentaculo-ethmoidalis arises mostly from the entire lateral surface of the zone of soft cartilage forming the anterior end of the subnasal bar, but the origin was continued also on to the same surface of the hard cartilage part. It is, however, soon displaced from the latter by the copulo-ethmoidalis, when it takes up a position in the extensive concavity on the external surface of the latter muscle. In the sections, and especially on the right side, some fibres arise in front of the origin given above from the ventro-external surface of the transverse labial cartilage. There is also in the sections some confusion between the origin of the present muscle and the ethmoideo-nasalis, but I could not establish with certainty any real mingling of the fibres of the two muscles.

The tentaculo-ethmoidalis lies internal and somewhat dorsal to the transversus oris, and in fact in dissection (except in Perenyi material) there is some difficulty in satisfactorily separating them, as mentioned by P. FÜRBRINGER. J. MÜLLER evidently had this experience also, for he fails to distinguish between the two muscles, and describes them together under the name given above. The sections, however, demonstrate conclusively their complete independence.

From its origin the muscle courses backwards and outwards, wedged in between the copulo-ethmoidalis and the transversus oris, its fibres diverging ventro-dorsally like a fan, to terminate, after a short course, on the external lateral fascia between the two muscles just mentioned above in front of the base of the third tentacle and in front of the posterior vertical portion of the lateral labial cartilage. P. FÜRBRINGER asserts that it is inserted into the base of the third tentacle, but I find no evidence of this in dissections, and it is certainly not the case in the sections.

5. *M. transversus oris.* (Figs. 3, 10, 11, *t. o.*)

J. MÜLLER (in part), *Compressor des Mundes, Mundschliesser* (p. 259).

A complex and diffuse muscle, as defined by J. MÜLLER and P. FÜRBRINGER, and said by ALLIS to consist in *Bdellostoma* of "two transverse subnasal muscles." In dissections a division of the muscle into two parts seems to be indicated in *Myxine* also, although not mentioned by P. FÜRBRINGER, but a complete separation is not possible, and the sections show that the division is not a real one. Perhaps the two transverse muscles mentioned by ALLIS are the two commissures described below from the sections (cp. fig. 10), in which case he does not include the greater part of the transversus oris of other authors.

I find some difficulty in reconciling my descriptions of this muscle based on dissections and on the sections. This may be, and perhaps is, due to the fact that it is difficult in dissections, however careful, to correctly define a small and irregular muscle closely packed up with and attached to other tissues in a confined space. On the other hand, the sections fail to convey a clear impression of the *ensemble* of the muscle, and then, again, the muscle may vary considerably. I have therefore thought it advisable to give two descriptions, one of a careful dissection of a 34½ cm. Hag, and the other based on my large series of sections.

It will be convenient in the description of the dissection to divide the muscle into two regions, although, as stated above, this division is not sanctioned by the sections.

Posterior Region.—Lies, in a lateral view, apparently immediately in front of the tentaculo-ethmoidalis, to which it is somewhat closely attached, and seems to be quite distinct from the anterior region. This, however, is really due to the fact that many of the fibres, and especially the dorsal ones, are less transverse than those of the latter region. In the present specimen (see fig. 3) the most dorso-superficial fibres of the

posterior region were inserted into the first ring of the nasal tube in front of the ethmoideo-nasalis, and from thence passed obliquely backwards, outwards, and downwards under that muscle, as shown in the figure. I have not, however, seen this since. Some of the fibres arise (? insertion) from the so-called transverse labial cartilage (see Part I. p. 770) and also from the anterior extremity of the subnasal bar immediately below and in front of the origin of the tentaculo-ethmoidalis, but most of them arise from the stout ventro-lateral superficial fascia near the anterior extremity of the snout, course more or less transversely on to the adjacent dorso-lateral surface of the same side (cp. fig. 10), and are inserted (? origin) in front of the middle third of the *internal* portion of the third tentacular cartilage into the antero-internal fascia of the anterior portion of the head of the copulo-tentaculo-coronarius from the third tentacle.

Anterior Region.—More definitely transverse than the posterior region, and situated, in a lateral view, apparently anterior to it, and between it and the anterior division of the copulo-tentaculo-coronarius. Most of its fibres course direct from the tough ventro-lateral to the dorso-lateral fascia of the same side, and this region is reinforced by fibres from the first tentacle. Ventrally there is a distinct transverse commissure in front of and ventral to the anterior extremity of the subnasal bar, and seen after removal of the skin, the fibres of which arise partly from the bases of the second tentacles and partly from the antero-ventral fascia of the anterior region of the present muscle (= ventral commissure below—cp. fig. 10). All the fibres from the second tentacle, however, do not pass over into the commissure, but some of them pass on to the transverse labial cartilage and the anterior extremity of the subnasal bar (= dorsal pseudo-commissure below).

In the sections, the transversus oris arises (? insertion) by a pointed posterior extremity from the internal surface of the sheath of the third tentacular cartilage just within the contour of the body, and between the anterior division of the copulo-tentaculo-coronarius (below) and the posterior division of the same (above). The latter, however, soon dies away; and as it does so, the transversus oris is attached to its internal fascia and a number of fibres arise from this. The muscle has thus a double origin. It now courses forwards as a clearly defined muscle lying immediately above the anterior division of the copulo-tentaculo-coronarius, and external to, but somewhat below, the tentaculo-ethmoidalis. The first change noticeable is that the ventro-external fibres pursue a (very short) course of their own, and pass straight from the latero-external to the ventro-external fascia—thus giving rise in dissection to an appearance as if the muscle consisted of two divisions. The anterior division of the copulo-tentaculo-coronarius lies in a depression on the outer surface of this portion of the muscle. As the transversus oris passes forwards its fibres converge somewhat, and it now lies almost directly between the two muscles mentioned above, the latter being respectively external and internal to it (cp. fig. 10). Not much of it now appears on the lateral surface of the snout, and still less on the ventral surface. In front of this, however, it

again becomes increasingly evident on the surface, both laterally and ventrally, and continues so for the remainder of its course; and as the tentaculo-ethmoidalis narrows down in front, the transversus oris expands in the transverse plane. The dorso-internal fibres now pass upwards, and are inserted (? origin) into the entire internal surface of the sheath of the *first* tentacular cartilage after the latter has entered the contour of the snout, whilst the remaining fibres pass straight forwards and are inserted into the dorso-external surface of the sheath of the *second* tentacular cartilage, also within the contour of the snout (= transverse labial cartilage).

As far as the sections are concerned, the above represents a clearly defined and independent muscle, the object of which is to assist in the varied movements of the first and second tentacles. It therefore may be said to represent the transversus oris *sensu stricto*, although, of course, it is not a transverse muscle. There are, however, closely associated with it, two other muscle bundles, each of them strictly a separate muscle, but which I describe here, as they are evidently all included under P. FÜRBRINGER'S transversus oris. The independence of these and other muscles will be reconsidered in the concluding morphological part of this work.

Ventral Commissure (fig. 10).—Arises as follows:—(a) some fibres from the ventro-internal surface of the sheath of the root of the second tentacular cartilage (transverse labial); (b) a few fibres from the internal fascia of the anterior division of the copulo-tentaculo-coronarius; (c) the majority of the fibres from the ventro-internal fascia of the transversus oris, *sensu stricto*. I do not think the latter muscle contributes any fibres direct to this commissure, but the association between them is very close. This transverse commissure is seen on the ventral surface at the anterior end of the snout on removal of the skin, and passes without a break from the origin of one side to that of the other, *ventral* to the transverse labial cartilage and the anterior extremity of the tentaculo-ethmoidalis.

Dorsal Pseudo-Commissure.—I thought at first that this was another true transverse commissure, but a careful examination of the sections reveals that the two muscles only meet at a median linea, and that no fibres pass continuously from one side to the other. It “arises” from the dorso-internal surface of the sheath of the root of the second tentacular cartilage (transverse labial), and passes downwards, backwards, and inwards, at first lying over and closely associated with the ventral commissure, and immediately below the nasal tube. It, however, extends further back than the ventral commissure, so that it crosses the latter diagonally and appears by itself behind it. The two muscles meet at an angle at a connective tissue linea situated at the middle line just below the nasal tube. As the transverse labials pass backwards to fuse at the median line with the subnasal bar, the pseudo-commissure lies *dorsal* to them, and the more posterior fibres are “inserted” into their dorsal surface at the point of fusion not far from the middle line.

The transversus oris is not separated by J. MÜLLER, who confuses and describes it

with the tentaculo-ethmoidalis. P. FÜRBRINGER believes that its function is to assist the suctorial action of the mouth, whilst that of the transverse commissure is to approximate the second tentacles. It is, however, questionable whether the mouth of Myxinoids is ever suctorial, and further, the transverse commissure extends beyond the base of the second tentacles.

6. *M. nasalis*. (Figs. 3, 8, 9, 11, *nas.*)

J. MÜLLER, *Zurückzieher der Nasenöffnung* (p. 258).

„ *Zurückzieher der äussern Nase* (p. 322).

„ *Zurückzieher der Schnautze* (p. 323).

Arises by two small fasciculi largely from the tough membrane enclosing the roof (external superficial fascia), but also from that covering the side of the nasal chamber at about the anterior half of the latter. It passes straight forwards, partly obscuring the nasal chamber and nasal tube, and is inserted as follows:—(a) into the internal process of the *lateral* labial cartilage (cp. Part I., figs. 1 and 2, and present Part, fig. 3); (b) into the ventral longitudinal bar connecting the anterior nasal rings. This bar is also connected by ligament with the process above, in this respect differing from *Bdellostoma* according to AYERS and JACKSON, who state that the process is joined by ligament to the nasal tube, but not to any cartilages of the tube; (c) into the lateral wall of the anterior extremity of the nasal tube itself, in front of the third nasal ring; (d) into a dorsal forwardly-directed process from the second nasal ring. This process is not always found, and may be present on one side and not on the other. It is figured by POLLARD;* (e) joins with the vertical ethmoideo-nasalis (cp. fig. 3), and is inserted into the first nasal ring and the side wall of the external nasal opening. This is the only insertion mentioned by P. FÜRBRINGER.

For the greater part of its length the *M. nasalis* is seen to consist in transverse section of two large fasciculi—a dorsal triangular one and a larger ventral oval or quadrangular one. The whole forms in section a large triangular mass, with its base resting on the dorsal edge of the tentacularis posterior (behind) and on the outer dorsal surface of the palato-ethmoidalis superficialis.

According to J. MÜLLER, the muscle is very differently related in *Bdellostoma*. He states that it arises from the palatine bar, and is inserted not only into the anterior end of the nasal tube, but also into the *transverse* labial cartilage. In *Myxine* it does not even approach either of these cartilages.

The function of the nasalis, when not neutralised by the ethmoideo-nasalis, would be to draw the nasal opening and the lateral labial cartilage backwards and somewhat upwards.

* *Zool. Jahrb.*, Abt. Morph., viii., fig. 11.

7. *M. ethmoideo-nasalis*. (Figs. 3, 11, *e. n.*)

J. MÜLLER, *Compressor narium* (p. 259).

A very small cylindrical muscle, with its fibres somewhat twisted like a rope in one dissection (cp. fig. 3). Its origin, as seen by dissections, is indefinite. Many, if not most, of the fibres arose from the ventral convex protuberance at the anterior extremity of the subnasal bar (cp. Part I., fig. 1). A number of fibres, however, *appear* to be contributed by the transversus oris, of which the present muscle may conceivably be a differentiated portion. It passed vertically upwards in a curve, bent externally round the origin of the second tentacle (J. MÜLLER, by mistake, says the first), and is inserted, after a very short course, partly into the first nasal ring above the ventral anterior process, and partly into the lateral wall of the nasal tube between rings one and two, whilst the most posterior fibres intermingled with the insertion of the nasalis, as mentioned under that muscle.

In the sections the following conditions are found. The posterior fibres arise from about the dorsal third of the fascia between the opposed surfaces of the transversus oris and the tentaculo-ethmoidalis. These fibres are tightly wedged in between the two latter muscles, but a very careful examination failed to convince me that there is any mingling of the fibres of the three muscles. The posterior fibres of the ethmoideo-nasalis pass almost straight upwards, but slightly forwards, and are inserted into the dorsal-lateral wall of the nasal tube in front of the second nasal ring. These are the fibres that are confused at their insertion with the anterior extremity of the insertion of the nasalis (*q.v.*). As the tentaculo-ethmoidalis dies away in front, the ventral end of the ethmoideo-nasalis bends sharply inwards, almost at a right angle, under the dorsal pseudo-commissure of the transversus oris, to take its origin from the dorso-lateral margin of the zone of soft cartilage at the anterior extremity of the subnasal bar, just at the fusion with the transverse labial and between the origin of the tentaculo-ethmoidalis (below) and the "insertion" of the pseudo-commissure (above). On the right side the origin extended further forwards on to the external margin of the transverse labial. In front, the insertion leaves the dorso-lateral wall of the nasal tube and passes on to the dorsal margin of the first nasal ring at the point where this fuses with the forwardly-directed lateral process (cp. Part I., fig. 1). The insertion finally passes forwards as a definite narrowing bundle over the external surface of the first nasal ring on the ventral margin of the same, into which it is inserted right up to its anterior extremity, lying just below the first ring at this part of its course.

The contraction of the two ethmoideo-nasalis muscles is stated by P. FÜRBRINGER to press the first (= my second) tentacles against the nasal tube, and thus close the nasal opening; but J. MÜLLER asserts, and with more probability, that it presses the anterior end of the nasal tube against the subnasal bar, and closes the nasal opening in that way. Moreover, in my sections the muscles arise so far back that the second tentacles could not possibly be affected in the way FÜRBRINGER supposes.

8. *M. palato-ethmoidalis superficialis*. (Fig. 3, *p. e. s.*)

J. MÜLLER, *Zurückzieher der knöchernen Stütze der Schnautze* (p. 258). *Zurückzieher der Schnautzenstütze* (p. 322).

Superficially a powerful fan-shaped longitudinal muscle, with the handle directed forwards. It is roughly triangular in transverse section, the outer or superficial area representing the base of the triangle, with the apex directed inwards towards the subnasal and palatine bars. In the sections, about the middle third of the muscle was divided into two distinct portions—a dorso-horizontal plate-like portion and a ventral much larger portion. It is covered largely by the tentacularis posterior, but its dorso-external margin may appear on the surface between the latter muscle and the nasalis.

The palato-ethmoidalis superficialis has a very broad origin, as follows:—(*a*) from the lateral wall of the nasal capsule. As shown in fig. 3, this part of the origin extended back under the eye for a short distance on to the cranium. In the sections it passed back over, but not behind, the eye on the left side, but on the right side it terminated in front of the eye; (*b*) from the external fascia of the dorso-anterior border of the copulo-quadratus profundus; (*c*) from the dorso-external fascia of the palato-coronarius; (*d*) from the posterior third of the cornual cartilage (in a dissection). Except perhaps for a very few fibres from the root of the cornual cartilage, this was certainly *not* the case in the sections, the present muscle being excluded from the cartilage by the insertion of the palato-ethmoidalis profundus; (*e*) from the external margin of the anterior half of the palatine bar (dissection). In the sections this part of the origin is from the anterior three-fourths. Posteriorly, where the muscle fibres themselves do not reach the bar, the internal apex of the muscle is connected with it by a short strong ligament. The more superficial fibres are represented by *a* and *b* above, and the deeper fibres by *c*, *d*, and *e*, these latter being the deepest and constituting the apex of the triangle.

In *Bdellostoma*, according to J. MÜLLER, the palato-ethmoidalis superficialis arises from the palatine bar only, whilst in *Myxine* P. FÜRBRINGER states that it arises from the *posterior* half of the bar and from the “lateral region of the skull.”

The fibres of the palato-ethmoidalis superficialis pass forwards, rapidly converging, and were inserted, in a dissection, into about the anterior third of the subnasal bar. P. FÜRBRINGER says the middle third. In the sections the insertion covered exactly one-half of the extreme length of the bar, *i.e.* it extended through 130 sections, whilst the bar itself passed through 65 sections in front of and 65 behind it. Posteriorly, the muscle is inserted into about the dorsal half of the lateral surface of the bar, the ventral half being occupied by the origin of the palato-ethmoidalis profundus. As, however, the latter muscle dies away, the superficialis extends over the whole of the lateral surface of the bar, but at its anterior extremity it is again excluded from the lower part of the lateral surface by the commencement of the insertion of the copulo-ethmoidalis.

According to P. FÜRBRINGER, the palato-ethmoidalis superficialis produces a dorsal flexion of the subnasal bar and a retraction of the dorsal margin of the mouth, in order to bring the median tooth into a favourable position for piercing the prey.

9. *M. palato-ethmoidalis profundus*. (Figs. 3, 10, 11, *p. e. p.*)

J. MÜLLER, *Pyramidale Muskel der Schnautze* (p. 259). *Compressor der Mundhöhle* (p. 332).

Lies largely under the palato-ethmoidalis superficialis. It is a short but powerful muscle, and appears on the roof of the mouth (covered, of course, by the mucosa), as shown in fig. 10. Of this muscle ALLIS says*: "This latter muscle I find, however, in *B. dombeyi* as two wholly separate muscles, one lying dorsal to the other, and the two crossing each other at an angle. Both muscles extend from the nasal bar to the cornual cartilage, and they both must act as adductors of that cartilage, drawing it toward the nasal bar." There are certainly clear indications anteriorly of the division mentioned by ALLIS (cp. fig. 11), but behind, the two parts of the muscle are generally not separable. In front, however, the anterior, inner or ventral, division passes obliquely backwards, and the posterior, outer or dorsal, division obliquely forward. Hence, as ALLIS states, the fibres cross at an angle. In one specimen I found the two divisions entirely distinct, as in *B. dombeyi*. It is not easy to study this condition in transverse sections, but in a series of vertical longitudinal sections I found the muscle consisting of a thin postero-dorsal portion and a more extensive and greatly thicker ventral portion, the distinction being observable throughout the entire extent of the muscle. I believe, however, it is only another expression of the tendency noticeable in many of the muscles of Myxinoids for the fibres to collect into large separate divisions, which might almost be described as separate muscles. Compare, for example, the velo-quadratus muscle, where there are three of these divisions.

The palato-ethmoidalis profundus arises from the lateral (in front, ventro-lateral) and ventral surfaces of about the posterior two-thirds of the subnasal bar. P. FÜRBRINGER says the posterior half, and J. MÜLLER the *whole* in *Bdellostoma*. In the sections it works out as the posterior two-thirds exactly. The fibres of the muscle pass outwards and somewhat downwards, and converge from both extremities to be inserted into the dorso-internal surfaces (median margin—P. FÜRBRINGER) of slightly more than the posterior two-thirds of the cornual cartilage opposite the "origin" of the copulopalatinus. In the sections the insertion had precisely the same extent.

Since the area of origin is greater than that of the insertion, both as regards vertical surface and longitudinal extent (in the latter respect extending over 172 sections as against 98), it follows that all the fibres arising from the subnasal bar cannot be inserted into the cornual cartilage. Posteriorly a large number of them are inserted into the ventral fascia of the muscle extending transversely from the cornual cartilage to the median pad of soft pseudo-cartilage described on p. 765 of my first Part.

* *Op. cit.*, p. 272.

This pad of tissue commences about 50 sections in front of the posterior extremity of the palato-ethmoidalis profundus, and its tapering non-cartilaginous dorsal portion extends upwards from the mucosa like a wedge towards the subnasal bar, separating the two profundus muscles in the median plane for about 25 sections. The pad does not quite reach the subnasal bar, except where it bends upwards and backwards, and is connected by fascia with its posterior extremity, as described in my first Part. The two profundus muscles are closely opposed to the pad, but I do not think they are attached to it, as stated in my first Part.

P. FÜRBRINGER figures the present muscle as inserted into the *entire* length of the cornual cartilage, and states further that some fibres are inserted into the palatine bar itself. My dissections and sections agree with neither of these statements, but the latter is probable enough, as the fibres extend right to the boundary between the two cartilages in question. In *Bdellostoma*, according to J. MÜLLER, the muscle has a strongly pyramidal shape, the apex of the pyramid being inserted into the cornual cartilage. In *Myxine* the insertion is, on the other hand, a very broad one, although narrower than represented by P. FÜRBRINGER.

The action of the profundus muscle, by approximating the two cornual cartilages, and consequently the lateral labials, is to compress the mouth cavity laterally.

10. *M. quadrato-palatinus*. (Fig. 11, *q. p.*)

J. MÜLLER, *Anzieher des Schlundkorbes* (p. 261).

A moderately strong triangular-shaped muscle, with the apex directed forwards, and covered by the palato-coronarius in front. Internally it abuts on the lateral roof and dorso-lateral wall of the mouth.

The quadrato-palatinus arises by a broad origin (forming the base of the triangle) from the ventral margin and internal surface of the pterygo-quadrate from immediately behind the transverse zone of soft cartilage separating it from the palatine up to the similar zone of soft cartilage at about the middle of the inferior process of the pterygo-quadrate (*i.e.* mostly from the anterior process of the latter). P. FÜRBRINGER gives the origin from the lateral margin only, but both my dissections and sections support the statement of the origin given above. In the sections on the left side the origin extended back to the posterior extremity of the inferior process, and thus the muscle arose from the entire length of the anterior and inferior processes, but on the right side it did not go back so far, though further than described above.

The fibres of the pterygo-quadrate pass forwards, strongly converging, and merge into a long powerful tapering tendon which arises from the ventral surface of the muscle and courses straight forwards (but slightly inwards) under the palato-coronarius and opposed to the lateral roof of the mouth, to be inserted into the latero-ventral surface of the anterior extremity of the palatine bar, *i.e.* just posterior to where it fuses

with the cornual cartilage. In the sections it was inserted into the palatine bar just behind the palatine commissure. Shortly behind its insertion the tendon, in the sections, gave off from its external margin a small slip which passed internally under the parent tendon to some loose tissue connected with the roof of the mouth not far from the median line.

The function of this muscle will be to bend the palatine bar downwards. In *Bdellostoma* J. MÜLLER curiously describes the insertion of the muscle as the origin, and states that it draws the pharyngeal basket forwards. In *Myxine* he ascribes to it the opposite (and surely the correct) function.

11. *M. palato-coronarius*. (Fig. 11, *pl. c.*)

J. MÜLLER, *Zurückzieher des Mundrandes oder der Mundknorpel* (p. 258). *Zurückzieher des Mundes* (p. 330).

A fairly strong muscle, covered externally by the copulo-quadratus profundus, and having two heads—a large external (*pl. c.*) and a smaller internal. Between the two heads courses the R. externus of the maxillaris of P. FÜRBRINGER. According to J. MÜLLER there is only one head in *Bdellostoma*.

External Head.—Commences at the posterior portion of the zone of soft cartilage between the palatine bar and the anterior process of the pterygo-quadratus by some fibres from the external rim of this region, and from thence the origin passes obliquely forwards and inwards on to the ventral surface—first of the zone of soft cartilage above, and then on to the same surface of the palatine bar to meet the internal head, which it does near the internal rim of the cartilage. The two heads are now spread over the entire outer and ventral surfaces of the palatine bar at this region. A short distance in front of the zone of soft cartilage the muscle begins to be detached from the palatine bar, the separation commencing externally, and extending inwards and forwards until completed. The fibres of the external head pass downwards and forwards towards the pad of soft pseudo-cartilage at the anterior end of the basal plate, the fibres somewhat converging as they go.

Internal Head.—Arises at the above-mentioned region of the zone of soft cartilage, but below, internal and quite distinct from it, mostly from the ligamentous sheet connecting the palatine region with the hypophysial plate about half way between these two cartilages. The head then passes forwards, outwards, and upwards to meet the external head, and where the junction is effected a few or more fibres are contributed to this head from the inner ventral surface of the palatine bar immediately in front of the zone of soft cartilage. It is difficult to ascertain how much is contributed by the palatine bar, as the two heads here are by no means easily distinguishable either in dissections or in the sections. The fibres follow the same course as in the external head, but are completely covered by the latter in a lateral view.

The two heads pass into a common and very short but powerful tendon which arises from the ventral surface of the opposed heads, but chiefly from the external ventral surface, and which in one dissection was inserted into the pad of soft pseudo-cartilage at the anterior extremity of the external bar of the anterior segment of the basal plate, dorsal and external to the lateral labial cartilage as it was winding over the pad to fuse with the external bar. There was no union of the two heads before passing into the tendon, such as described by P. FÜRBRINGER. In another specimen, however, it was inserted largely into the dorso-posterior surface of the lateral labial itself as it was passing over the pad. In *Bdellostoma*, according to ALLIS, the insertion is into "the lateral labial cartilage, or in the tissues near that cartilage." P. FÜRBRINGER states that the tendon is inserted into the lateral labial only, which, however, he did not recognise to be cartilaginous at this region. J. MÜLLER also gives this insertion in *Bdellostoma*. In my sections I find that the tendon is large, diffuse (not easily defined), and attached to the surrounding fascia. It passed at once on to the dorsal surface of the pad of pseudo-cartilage, dorsal and *largely posterior* to the lateral labial (cp. fig. 1 of my first Part), which it certainly did not reach. Further, the two heads fused before reaching the tendon (as described by P. FÜRBRINGER), and otherwise the separation of the two heads was very difficult, although their origins were perfectly distinct. The indefiniteness of the tendon and its connection with the surrounding fascia would seem to explain the discrepancies in the statements above.

The palato-coronarius draws the anterior extremity of the basal plate, and hence the ventral margin of the mouth upwards and backwards.

12. *M. copulo-tentaculo-coronarius*. (Figs. 3, 9, 10, 11, cp. t. c., cp. t. c', cp. t. c'').

J. MÜLLER, *Zweiköpfige Herabzieher des Mundes* (p. 259).

P. FÜRBRINGER, *Copulo-tentaculo-coronarius + Tentacularis anterior* (pp. 12 and 17).

A curious and complex muscle, the anterior division of which is regarded by P. FÜRBRINGER as a separate muscle, having an independent origin from the base of the fourth tentacular cartilage, and called by him the tentacularis anterior. I have, however, invariably found, both in dissections and sections, that the latter is, with the exception of a few fibres, simply the forward continuation of the first head of the copulo-tentaculo-coronarius, and hence cannot be separated from it.

The copulo-tentaculo-coronarius arises as a first or principal head (cp. t. c.) from the median border of the external bar of the anterior segment of the basal plate at about the middle of its length, and some fibres also from the tough fibrous tissue connecting the external and internal bars (fig. 11). P. FÜRBRINGER states that some fibres arise from the outer margin of the internal bar. In the sections this head is reinforced by a small second head from the ventro-external fascia of the origin of the external head of the copulo-ethmoidalis, and which passes forwards external to the dorsal portion of

the first head, to more or less fuse with it. The posterior division (below) is formed in the sections by the fibres of this second head + the *superficial* fibres of the principal head. Also new fibres are contributed internally which arise from the internal fascia of the latter. The fibres of the first head pass straight forwards, almost parallel at the latero-ventral margin of the mouth, and opposed to the external surface of the basal plate until they reach the region of the fourth tentacle, where they are shuffled into two fairly large bundles. One of these, the *posterior division* (*cp. t. c'*.) takes an upward bend, and passes at once on to the root of the fourth tentacle just above where the latter is connected by a horizontal ligamentous sheet with the pad of soft pseudo-cartilage at the anterior end of the external bar of the anterior segment of the basal plate. As shown in figs. 3, 9, and 11, the fourth tentacle rests on the external surface of the ventral region of this muscle, and some of the external fibres passing up to it may have a separate origin from the external fascia of the principal head. A variable number of fibres arise from the cartilage of the fourth tentacle itself, and fuse with the posterior division, thus constituting another small head for the muscle. The posterior division now passes upwards, forwards, and inwards, and joins with a bundle arising from the anterior surface of the root of the third tentacle, and coursing straight upwards. This bundle in dissections only seems to *accompany* the posterior division, and not to fuse with it. In another specimen there was a second and posterior bundle arising from this tentacle. The anterior one (*i.e.* the one above) was certainly independent of the posterior division, and the posterior one also seemed distinct from, although closely opposed to it. This point is difficult to determine in transverse sections, but in a series of longitudinal vertical sections I find the head from the third tentacle comprised of anterior and posterior bundles as above, which were closely opposed to the posterior division at their insertion, but certainly did not fuse with it. These bundles, therefore, do not, strictly speaking, constitute further heads of the copulo-tentaculo-coronarius, but form small independent muscles like the coronarius, the function of which will be to move the third tentacle in the longitudinal vertical plane.

Both the posterior division and the bundle or bundles from the third tentacle are inserted into the lateral labial at the place where this receives the cartilage of the third tentacle, the latter into the ventral surface, and the former, which is related to the coronarius, as elsewhere described, into its outer ventral and inner surfaces, and also into the posterior surface of the root of the third tentacular cartilage itself.

The *anterior division*, or *Tentacularis anterior* of P. FÜRBRINGER (*cp. t. c''*.), passes forwards and upwards, largely internal to the posterior division, and internal to the fourth and third tentacular cartilages. It is not mentioned by J. MÜLLER in *Bdellostoma*. It gives off at its origin a bundle of fibres which passes upwards to the posterior surface of the third tentacular cartilage (*cp. fig. 3*), and its ventral surface is reinforced by some fibres which arise from the root of the fourth tentacular cartilage, and which therefore represent another small head of the copulo-tentaculo-coronaris.

The subsequent course of the anterior division is best dissected in specimens that have been preserved in an acid medium, such as Perenyi's fluid. It passes forwards and upwards as a compact bundle in a gentle curve at the lateral margin of the mouth, and is finally inserted into the ventro-external surface of the root of the second tentacular cartilage, or what is called by AYERS and JACKSON the transverse labial cartilage.

The copulo-tentaculo-coronarius has obviously a complex function, which can only be ascertained by direct experiment. It will, however, at least retract the lateral labial and the second, third, and fourth tentacles. In *Bdellostoma*, according to J. MÜLLER, the head from the fourth tentacular cartilage is wanting, and the origin of the first or principal head is from the *internal* bar of the anterior segment of the basal plate.

13. *M. coronarius*, F.J.C. (Figs. 3, 11, *co.*)

P. FÜRBRINGER, "*Endinsertion*" of the copulo-tentaculo-coronarius (p. 17).

According to P. FÜRBRINGER this muscle represents the final insertion of the copulo-tentaculo-coronarius, but as I find no connection between these two muscles beyond that which commonly obtains between adjacent muscles, I have separated it under the above name. Its fibres are quite independent, and if we are to regard, for example, the palato-ethmoidalis profundus as a separate muscle from the copulo-palatinus, we cannot describe the present muscle as simply the insertion of another. Its position and relations are also against this.

The coronarius is a very small muscle, with a somewhat curious anatomy. It arises from the *dorsal* surface of the lateral labial cartilage, just behind where the latter fuses with the cartilage of the third tentacle. The origin lies immediately in front of and in contact with the ligamento-cartilaginous connection between the lateral labial and cornual cartilages described on pp. 765-6 of my first Part, and shown (but not lettered) in fig. 2. Cp. also fig. 11 of present Part. This connection, by the way, I now believe to be constant.

At its posterior extremity in the sections, and in one dissection, the coronarius extended downwards from its dorsal position on the lateral labial over the *external* surface of this cartilage, and at the same time the insertion of the posterior division of the copulo-tentaculo-coronarius rose upwards from its ventral position on the same, also over its external surface, to meet it. A careful examination of both sides of two series of sections differently stained has, however, convinced me that the latter fibres are only inserted into the external *fascia* of the coronarius, and that the fibres of the two muscles are quite independent. Further, in two dissections, the muscles were obviously distinct, and almost at right angles to each other. And even if the fibres of the two were here continuous, only a small portion of the coronarius would be accounted for, and by far the major portion would have an origin of its own from the lateral

labial, and would thus, on P. FÜRBRINGER's view, constitute still another head of the copulo-tentaculo-coronarius.

In front of the origin the muscle gradually tapers down, passes upwards and forwards closely opposed to the dorso-posterior surface of the lateral labial cartilage, and is inserted into the same surface of this cartilage immediately behind the internal process. It is difficult to assign any function to this insignificant muscle, except that it may assist in manipulating the first tentacle, seeing that its posterior end is fixed.

14. *M. copulo-ethmoidalis*. (Figs. 3, 9, 10, 11, *c. e.*, *c. e'*, *c. e''*).

J. MÜLLER, *Herabzieher der knöchernen Schnautzenstütze* (p. 259).

A stout, powerful muscle arising by two heads—an antero-external (*c. e.*) and a postero-internal (*c. e'*). The former head was not distinguished by J. MÜLLER or P. FÜRBRINGER, but I find it invariably present both in dissections and sections.

The *external head* arises from the superficial fascia at the region of the antero-dorsal border, and also from that of the antero-internal margin, of the copulo-palatinus. It appears on the surface immediately in front of the latter muscle and of the anterior border of the obliquus muscle, and below the cornual cartilage. Its fibres pass upwards, forwards, and inwards in an arch underneath the cornual and lateral labial cartilages, and soon unite with the other head to form the antero-ventral portion of the insertion.

The *internal head* arises medianly to the preceding, mostly from the external surface of the bulb of soft pseudo-cartilage at the anterior end of the external bar of the anterior segment of the basal plate, but some of the ventro-external fibres arise from the dorso-external surface of the hard cartilage of the anterior extremity of the external bar itself. The fibres of the internal head pursue a similar course to those of the external head, and form the postero-dorsal portion of the insertion. The lateral labial cartilage lies in a depression on the dorsal surface of this head.

As the copulo-ethmoidalis passes forwards it becomes greatly compressed from side to side, and bent in the form of a vertical crescent with the concavity directed externally. It appears on the surface of the roof of the mouth (covered, of course, by the mucosa), as shown in fig. 10, *c. e''*, and is inserted by about the central portion of the inner or convex surface into the entire extent of the lateral surface of the subnasal bar, from about the posterior extremity of the anterior soft cartilage portion to the anterior end of the insertion into the same of the palato-ethmoidalis profundus. All the fibres are, however, not inserted into the subnasal bar, since there are some inserted into the fascia immediately above and below this cartilage, and these were in fact, in the sections, continued forwards somewhat in front of the fibres inserted into the bar.

The function of the copulo-ethmoidalis is to compress the mouth cavity vertically

by approximating the basal plate and subnasal bar. This will facilitate the rasping action of the ventral teeth.

15. *M. hyo-copulo-glossus*. (Fig. 11, *h. c. g.*)

J. MÜLLER, *Beuger des Zungenbeins* (p. 249). *Beuger des ersten und zweiten Gliedes des Zungenbeins* (p. 332).

A powerful flat longitudinal muscle which arose in a $34\frac{1}{2}$ cm. Hag from the anterior surface of the most ventral $2\frac{1}{2}$ mm. of the first branchial arch internal to the insertion here of the hyo-copulo-palatinus, but in another specimen of the same size from the most ventral $3\frac{1}{2}$ mm. This origin from the first branchial arch is wanting in *Bdellostoma* according to J. MÜLLER. In the sections the most dorsal fibres were so intimately associated with the insertion here of the hyo-copulo-palatinus that I am doubtful whether they can be separated. Some fibres also may arise from the middle segment of the basal plate anterior to where the first branchial arch fuses with it. The fibres of the muscle at first pass forwards and slightly upwards, almost parallel, but slightly converging, and alongside and external to the middle segment of the basal plate. Opposite the anterior border of the broad forward ventral process from the hyoid arch described on p. 764 of my first Part, and shown in fig. 2, and which I now believe to be of general occurrence (cp. fig. 11 of present Part), the muscle on the right side in the sections received a small reinforcing head from the *inner* surface of the membrane connecting the pharyngeal basket with the basal plate. This was also suggested on the left side. The fibres now fan out and take a more dorsal course, and are inserted partly into the fascia investing the mucous membrane of the lateral diverticulum of the mouth at the base of the dental apparatus (opposite about the dorso-middle region of the latter), but also largely into the loose ventral fascia between the dental skeleton and the basal plate and which is attached in front to the mucosa of the ventral region of the mouth. The pull on the ventro-lateral mucosa naturally retracts the fourth tentacle also, and this is doubtless the basis for the statement by J. MÜLLER and P. FÜRBRINGER that the "tendon" of this muscle is inserted into the fourth tentacle. In another specimen a few of the most posterior fibres extended on to the mucosa of the *roof* of the mouth, and this was observed in sections also.

Opposite the antero-ventral angle of the belly of the hyo-copulo-glossus, which here sends downwards a small projection, there is a wide strand of fatty connective tissue, which passes upwards and inwards to fuse with the stout membrane connecting the anterior and posterior arches of the dental plate about midway between these two cartilages. It is itself not ligamentous, but in the sections it assisted in transmitting an inconsiderable bundle of elastic fibres which arose from the tissues around the posterior arch of the dental plate and passed forwards (fused in front of the "tether" with the ventral free margin of the "tendon" of the hyo-copulo-glossus) to be inserted into the dorsal margin of the guiding rail on the anterior segment of the basal plate

(see Part I. pp. 772-3), but which had no *direct* connection with the present muscle. The strand above is the transverse tendon or "tether" of J. MÜLLER and P. FÜRBRINGER, and its object seems to be to provide a pathway under the control of the present muscle for the passage of nerves and blood-vessels to and from the "tongue." Such a movable bridge is, of course, necessary, as the position of the "tongue" is not fixed.

According to P. FÜRBRINGER, the larger part of the fibres of the hyo-copulo-glossus pass into a tendon which is inserted into the ventral [?] surface of the internal bar of the anterior segment of the basal plate throughout its entire length, a small slip being also despatched to the base of the fourth tentacular cartilage. This agrees substantially with J. MÜLLER's account of *Bdellostoma*, and I therefore feel diffident in questioning its accuracy. Nevertheless I am more than doubtful whether what these authors describe as the anterior tendon of this muscle is not too diffuse and extensive to represent a true tendon of a muscle, and I cannot regard it as other than a portion of the general fascia. It is true that a careful examination of the sections reveals its ventral margin fusing with the dorsal border of the guiding rail of the anterior segment of the basal plate, and in front of this with the large pad of soft pseudo-cartilage on the dorsal surface of the anterior extremity of the same, but it is certainly *not* connected with the fourth tentacle. Its principal relation is undoubtedly to the mucosa of the mouth as above described, whilst in front of the basal plate it loses its identity by fusing first with the external fascia of the copulo-palatinus and then with the ventro-external fascia of the first or principal head of the copulo-tentaculo-coronarius—thus indicating again that it is only a portion of the general fascia. FÜRBRINGER indeed seems to have been here influenced by MÜLLER's description of the muscle.

An important function of the hyo-copulo-glossus is stated by FÜRBRINGER to be that it acts as a tether to the dental apparatus, *i.e.* prevents by its transverse "tendon" the "tongue" from travelling too far in either direction. Here, again, FÜRBRINGER has overlooked the fact that as the play of the latter is necessarily limited by the looseness of the mucosa of the floor of the mouth, such a function is surely superfluous. A much more reasonable explanation of the "tether" is the one I have given above. FÜRBRINGER also states that the attachment of the "tether" ventrally at a position intermediate between the anterior and posterior borders of the dental apparatus would assist the pull of the protractors in toppling the latter out of the mouth by acting as a fulcrum. Further, when the "tether" is fully extended forwards, the pull of the hyo-copulo-glossus is said to reinforce the backward drag of the longitudinalis linguæ until the "tether" has swung backwards behind the anterior extremity of the belly of the former muscle, when it is stated to play a passive rôle, and simply to prevent the dental apparatus passing too far backwards. But here also it seems idle to suppose that a very powerful muscle such as the longitudinalis linguæ requires any assistance, and still more so that a strand of fatty areolar tissue is capable of arresting its action. The "tongue," of course, passes as far backwards as the anterior mucosa of the mouth and its related skin will allow it, and no further.

The real function of the hyo-copulo-glossus I believe to be that it acts as the antagonist to the copulo-glossus superficialis. We shall see that the latter muscle evaginates the mucosa anterior to the "tongue" by a ventro-lateral pull on it; and as the present muscle is also inserted into the ventro-lateral mucosa, it will naturally pull the latter back into the mouth when the "tongue" is withdrawn. It will thus have precisely the same relation to the longitudinalis linguæ as the copulo-glossus superficialis has to the copulo-glossus profundus.

16. *M. copulo-glossus superficialis*. (Figs. 3, 9, *c. g. s.*, *c. g. s'*, *c. g. s''*.)

J. MÜLLER, *Äussere Vorzieher der Zunge* (p. 250).

„ *Erste* „ „ (p. 323).

„ *Oberflächlicher* „ „ (p. 331).

A long somewhat powerful muscle, for the greater part of its course closely related to the lateral head of the copulo-glossus profundus. It arises from the dorsal margin of the posterior segment of the basal plate at about the beginning of the taper, *i.e.* at the posterior end of the anterior third, ventral and somewhat internal to the origin of the copulo-quadratus superficialis, with which it is somewhat closely associated by its dorsal border. In *Bdellostoma*, according to J. MÜLLER, it arises by *two* heads from the *posterior* end of the basal plate. Its posterior half is hidden by the lateral head of the copulo-glossus profundus. Its anterior half comes to the surface between the above two muscles (but is, of course, covered externally by the obliquus), and continues its course downwards and forwards in a slight curve, becoming laterally flattened and fan-shaped as it proceeds. In front it passes abruptly by a wide irregular border a short distance behind the ventral margin of the mouth into a wide, thin, but strong tendon, which fuses completely with that of the other side to form a concave posterior border. This tendon passes straight forwards in the mid-ventral region, and gives off one largish median (*c.g.s'*) and a few fine lateral bundles, all of which fuse with the skin immediately behind the ventral margin of the mouth, and in front of the anterior border of the obliquus. The median slip above is also described by J. MÜLLER in *Bdellostoma*, but P. FÜRBRINGER missed it in *Myxine*.

The tendon narrows slightly as it approaches the mouth, but on reaching the latter it fans out laterally, and its central portion, after giving off the median slip to the skin above mentioned, bends sharply round the anterior margin of the internal bar of the anterior segment of the basal plate into the mouth, external to the tendon of the copulo-glossus profundus, and begins to pass backwards towards the dental apparatus (this, of course, when the latter is retracted).

The subsequent fate of the tendon is not only very difficult to ascertain by means of dissections, but this method is actually misleading—at all events as far as preserved material is concerned. I have therefore worked it out in one series of transverse and another of vertical longitudinal sections. However, by splitting the basal plate

along the middle line and pinning the halves out laterally, the tendon is seen to lose its identity very quickly. The lateral portion fans out considerably, and fuses with the ventro-lateral mucous membrane at the aperture of the mouth. This portion of the tendon gives off, according to J. MÜLLER and P. FÜRBRINGER, a small lateral bundle for the cartilage of the fourth tentacle. I have found this bundle (*c. g. s''.*), and have traced it into the fascia at the base of and behind the fourth tentacle, but could not satisfy myself that any of its fibres were *continuously* connected with the cartilage of the tentacle itself. The more median portion of the tendon is apparently quickly lost on the mucous membrane of the floor of the mouth. J. MÜLLER, however, states that it is attached to the anterior margin of the "tongue" cartilage; and P. FÜRBRINGER asserts that it *splits* into two portions, which are inserted one on each side at the anterior lateral region of the dental plate, *i.e.* lateral to the insertion of the tendon of the copulo-glossus profundus. Dissections certainly favour the statements of both these writers as regards the insertion into the dental plate.

Now with regard to the sections. In transverse sections the forward course of the tendon from the muscle belly to the ventral margin of the mouth confirms what has already been stated from dissections. As, however, the tendon bends round the anterior edge of the basal plate two stout longitudinal sheets (*i.e.* one on each side) are given off at the boundary of the lateral and median portions of the tendon, and these pass almost vertically upwards, but at first somewhat medially, and are inserted into the tough fibrous submucosa of the *lateral* wall of the median ventral longitudinal diverticulum of the mouth. The median portion of the tendon, after it has rounded the basal plate, is at once inserted into the same tissue of the *ventral* wall of the diverticulum. The tendon fibres can be traced back on the ventral wall of the diverticulum for some little distance, but they are undoubtedly lost before the tongue skeleton is reached. As, however, the connective tissues of the teeth and dental plate fuse in places at the region of the anterior border of the latter, any pull on the mucous membrane is necessarily transmitted to the dental plate. Nevertheless it is quite clear that the tendon of the copulo-glossus superficialis is *not inserted into the dental plate*. The lateral slips, supposed to pass to the fourth tentacle, were traced forwards a short distance in front of the bend, but were lost in the submucosa and spongy tissue of the postero-ventro-lateral wall of the mouth without reaching the tentacle in question.

In the longitudinal sections those passing through the median plane show the median portion of the tendon curving round the basal plate anterior and external to the tendon of the copulo-glossus profundus, and at once fusing with the ventral diverticulum of the mouth as above described. Any connection with the dental plate is here out of the question. Further, the complete course of the vertical longitudinal sheets mentioned above is now visible, and we see that the fibres constituting them continue their dorsal course at the sides of the ventral diverticulum of the mouth, curving upwards and finally *backwards* to fuse with the fibrous tissue and the mucosa immediately anterior to the rows of teeth. As these fibres form a great, if not the

greater, part of the tendon, it follows that one important function of the copulo-glossus superficialis is to exercise a forward pull *on the teeth themselves*. Similarly, the other important function of the muscle is to evaginate the antero-ventral mucosa of the mouth.

The lateral slip may be traced forwards in the longitudinal sections up to a short distance behind the base of the cartilage of the fourth tentacle, where it is inserted into the skin and subcutaneous connective tissues. Some fibres of it certainly seemed to pass on to the tentacle itself. It may be, and in fact is the more probable, that the slip only fuses with other connective tissues themselves attached to the tentacle, and thus only secondarily exercises what can, after all, be but a slight control over the motion of this tentacle. The question of fact is not easy to determine, owing to the wealth of fibrous connective tissue which is at this region confused with the tendon of the muscle.

For the function of the copulo-glossus superficialis see the following muscle.

17. *M. copulo-glossus profundus*. (Figs. 3, 9, 11, *c. g. p.* (Part I.), *c. g. p'*, *c. g. p''*.)

J. MÜLLER, *Innere Vorzieher der Zunge* (p. 251).

„ *Zweite* „ „ (p. 323).

„ *Tiefe* „ „ (p. 331).

AYERS and JACKSON, *Protractor of the Dental Plate* (p. 203).

This muscle arises by two heads—a large lateral head (*c. g. p'*) and a smaller median head (*c. g. p''*), and is a very long and powerful muscle.

Lateral Head.—May arise from the posterior extremity of the ventral or keel surface of the posterior segment of the basal plate, which surface is not utilised for the attachment of the copulo-copularis muscle. In other specimens, and also in the sections, the fibres extended laterally and posteriorly below the posterior segment, and hence arose from the superficial fascia of the copulo-copularis itself. The posterior segment is, however, represented behind its true termination by the tough fibrous tissue of its sheath forming a median ventral strand. The most superficial fibres of the lateral head meet at the mid-ventral line, and are covered externally by the rectus muscle, whilst the obliquus extends over the whole. The fibres course in a weak arch outwards and forwards and then downwards at the side of the median head, and over the ventral surface of the basal plate, receiving in front in one specimen a small bundle of fibres from the copulo-glossus superficialis. In front, the median border of this head is opposed to the outer border of the rectus.

Median Head.—Has a similar origin to the lateral head, but situated immediately in front of and covered by it. The origin covers the entire surface of the posterior segment at this region, but does not extend beyond it. The median head, however, soon emerges from underneath the lateral one, and its fibres course outwards and forwards in a still weaker curve, the two heads being closely opposed as they pass forwards. At about the middle of their course the rectus muscle passes in between them to reach the middle segment of the basal plate. The two median heads are

slightly separated for a short distance at and in front of their origin, but for the greater part of their course they are closely opposed at the mid-ventral line, so that in some specimens the division is not obvious.

As the two heads approach the ventral margin of the mouth they become more concentrated, and the lateral head assumes a more ventral position, so that just behind the mouth the muscles of both sides form four small compact bundles, consisting of the four distinct heads, two on each side of the mid-ventral line. As the fibres turn abruptly round the anterior margin of the *internal* bar of the anterior segment of basal plate internal to the tendon of the copulo-glossus superficialis (*i.e.* in the relaxed condition), the four heads pass simultaneously into the single median tendon, which is narrowest at this point. The anterior margin of the basal plate is distinctly pulley-shaped—due to the external bars with their pads of soft pseudo-cartilage (cp. Part I., Pl. II. fig. 10), and this confines the tendon to the median portion of the anterior edge of the basal plate. In one specimen the two median heads fused at about the middle of their course, and were finally joined just behind the formation of the tendon by the two lateral heads, the whole mass presenting a bilobed anterior extremity where it passed into the tendon. How much is seen of the tendon ventrally depends, of course, on the position of the dental apparatus.

According to P. FÜRBRINGER, the two heads of each side first fuse up and then pass into a tendon, and the two tendons thus formed unite to form the median tendon. In one series of sections the median head of each side first of all splits into two, the two median halves first fusing up, and the resulting median mass then fusing with the lateral lobes. In this way three muscle masses are seen in transverse section—a large median one, which equals both the median heads, with the smaller lateral head on each side. Subsequently all three fused up, and the single mass so formed finally split into two at its anterior extremity, as mentioned in another case above. The conditions are doubtless subject to much variation.

The tendon of the muscle first appears on the lateral surface of the lateral heads, and then spreads inwards over the *dorsal* surface only of the muscle, to fuse in the middle line, and thus form the median tendon, as seen in dissections. This, after the bend, now passes straight backwards towards the dental apparatus, becoming rapidly wider as it proceeds, and is inserted into practically the entire anterior border of the anterior arch of the dental plate (cp. Part I., fig. 7, *c. g. p.*). As the tendon approaches the dental plate its histology changes, until it resembles a weak form of soft pseudo-cartilage. In fact, the sections irresistibly suggest the view that the anterior arch of the dental plate is merely a chondrification of the tendon of this muscle (cp. SCHAFER (16).

P. FÜRBRINGER states, in opposition to the statements of J. MÜLLER, that the tendon of this muscle does not terminate at the anterior margin of the anterior arch, but that it is continued over this on to the posterior arch, and over this again to fuse with the tendon of the *retractor* muscle of the dental apparatus (*longitudinalis linguæ*).

Examination of a series of vertical longitudinal sections shows that this is true only in a limited sense. The *superficial* fibres of the tendon pass respectively over the dorsal and ventral surfaces of the dental plate, across the fenestræ, and are ultimately continuous with the corresponding fibres of the tendon of the retractor muscle. They do not constitute the *whole* of the fibrous tissue crossing the fenestræ, nor is the soft pseudo-cartilage of the tendons prolonged beyond the particular cartilage into which each is inserted, except to a slight extent in the case of the longitudinalis linguæ. It in fact amounts to nothing more than that there is a fusion (of course inevitable) between the tendons and the fibrous sheath of the dental plate.

We may now conveniently review the *function of the two protractor muscles of the dental apparatus*, but we must first consider the very curious habit on the part of the living Hag of *entirely* protruding its dental plates when either disturbed or stimulated. When a Hag is placed in a quantity of some fixing solution, say formalin, it does not die for some time, but swims rapidly about, showing its teeth or snarling in what is certainly an alarming manner. This is effected by bringing the dental apparatus forwards and then rotating it on its anterior border round the ventral margin of the mouth through an angle of about 115° . The result is that the dental plates, which, when withdrawn, look upwards, with the teeth pointing backwards, now look forwards and somewhat downwards, with the teeth pointing anteriorly. I have succeeded in preserving several specimens with the plates extruded, but do not figure them, as satisfactory figures have already been published by P. FÜRBRINGER and AYERS. This interesting and unique phenomenon was first figured for *Myxine* by GUNNER in 1763, and described by him in the following words: * “Am schönsten liess es, wenn er anfang seine Kiefer aus beiden Seiten hervorzuschieben und zwo Reihen kleiner gelber Zähne herzuweisen, die zugleich mit dem Zahnfleisch sehr genau wie zween kleine und sehr feine gelbe Kämme anzusehen waren. Wenn er diese seinen gelben Zähne zum Vorschein brachte, so liess es fast ebenso, als wenn man einen Spiegel oder einen Schrank mit zwo halben Thieren öffnet, also dass jede Thüre auf ihre Seite fällt.”

J. MÜLLER, in 1836, severely criticises this passage without, it must be confessed, clearly understanding it, and asserts that it is “ganz unrichtig.” His reasons are negatived, partly by erroneous anatomical observation, and partly by his failure to realise that the “tongue” and mucosa are one, and therefore must both move together. In 1873 GUNNER’s observations were confirmed by W. MÜLLER (as reported by P. FÜRBRINGER) on living material of *Myxine*, and some were killed in spirit with the dental plates everted. According to W. MÜLLER, the action is very rapid and powerful, and is accompanied by a peculiar noise. In 1874–5 P. FÜRBRINGER (*op. cit.*), working with W. MÜLLER’s material, published two figures of the everted dental apparatus, and gave

* See the German translation from the Danish, *Drontheim Ges. Schrift.*, ii. p. 230, 1765.

a description of the protractor muscles, which is noticed elsewhere. In 1894 AYERS * extended the observation to *Bdellostoma*, and gives two figures of this genus, showing the teeth out, but no description of the protractor muscles. Finally GOODE and BEAN † in 1895 figure, but do not mention, this phenomenon in *Myxine australis*.

The function of the two protractor muscles has, as before stated, been already discussed in some detail both by J. MÜLLER and P. FÜRBRINGER, but their results are unsatisfactory for two reasons: (1) they failed to elucidate the anatomy of the superficial protractor muscle (copulo-glossus superficialis); (2) they did not realise that a dental apparatus derived from and attached to the mucosa cannot move without carrying the mucous membrane with it, *i.e.* the teeth cannot be everted without the mucosa of the floor of the mouth being also evaginated. This oversight of the latter point is evidently due to the fact that they worked too much with dissected specimens. If a vertical longitudinal incision be made through the roof of the head and the two halves pinned out on each side so as to expose the mouth cavity, it is seen that when the dental apparatus is at rest (*i.e.* withdrawn) there is an area of puckered mucous membrane immediately behind it, whilst the mucosa in front of it is more or less tense. Now, if a similar section be made with the dental plates everted, it is seen that the mucosa on the floor of the mouth is on the stretch, whilst externally and immediately behind the (now) ventral margin of the ventral plates there is an area of evaginated and folded mucous membrane. It therefore follows that immediately behind the "tongue" there is a special fold of loose mucosa to admit of the forward movement of the teeth, and also that there is probably some muscular apparatus for evaginating the mucosa itself in front of the teeth.

The function of the deep protractor (copulo-glossus profundus) is quite simple. It draws the "tongue" straight forwards in the mid-ventral line, but we may deduce from its attachment to what is a *ventral* skeleton that it would probably require assistance before it could topple the dental apparatus over the ventral margin of the mouth, and so on to the exterior,—*i.e.* it is adapted to produce motion in a horizontal, but not in a vertical plane. This assistance is admirably provided for by the superficial protractor, which first of all evaginates the anterior ventral mucosa (thus not only paving the way, but indirectly reinforcing the pull of the deep protractor), and finally, when the "tongue" has arrived at the anterior extremity of the mouth, exercises a sharp ventral *erecting* pull (by its *dorsal* attachment) *on the teeth themselves*, in this way supplying the jerk necessary to tumble the whole apparatus downwards out of the mouth. P. FÜRBRINGER states that the tether of the hyo-copulo-glossus assists in this final act, as described under that muscle. The two protractor muscles, therefore, though playing somewhat different parts, perform one function between them, instead of both acting in much the same way, as assumed by J. MÜLLER and P. FÜRBRINGER.

* *Biological Lectures at Wood's Holl*, ii. pp. 136-7, 141-2, 1893-4.

† "Oceanic Ichthyology," *Atlas*, pl. i. fig. 2.

THE "CLUB-SHAPED MUSCLE."

This large muscle mass, by far the most striking feature in the myology of the Myxinoids, and the development of which is by some believed to be the cause of the suppression of the anterior gills and the displacement of the functional gills, is composed of three discrete muscles, which are, however, enclosed within a tough external fascia to form the so-called "club-shaped muscle," occupying a ventro-longitudinal position, with the handle projecting straight forwards. The principal attachments of the complex are in front, where it is connected with the posterior segment of the basal plate and with the dental apparatus. It has also two slight attachments to the lateral head of the copulo-glossus profundus and the copulo-quadratus superficialis. Dorsally it is slung to the parietal muscle by the second and third divisions of the constrictor pharyngis, whilst behind it may receive the first loop of the constrictor branchiarum et cardiæ, and also a slight bundle from the ventral longitudinal tract of the same muscle, as shown in fig. 3. Posteriorly, the first pair of gill sacks overlap the club-shaped muscle dorso-laterally.

The whole mass, together with the posterior segment of the basal plate and the dental apparatus, may be easily removed from the body and studied in detail. Portions of all three muscles constituting it may then be seen without further dissection.

18. *M. copulo-copularis*. (Figs. 2, 3, *cp. c.*)

J. MÜLLER, *Hohle äussere Muskel der Zunge* (p. 254).

„ *Muskulöse Capsel [Scheide] des Längsmuskels der Zunge* (p. 315).

AYERS and JACKSON, *M. constrictor musculi mandibuli* (p. 205).

A distinctly paired (as observed by SCHNEIDER) and very powerful transverse constrictor muscle, with an extreme length of 38 mm., width 11 mm., and depth 7 mm., in a 35 cm. Hag. It is pointed in front and obliquely truncated behind, and the longitudinalis linguæ projects behind its posterior border. Its dorsal surface is flat and its ventral surface convex. The anterior extremities of the muscle are very narrow, and are situated immediately between the dorsal margins of the limbs of the U-shaped posterior segment of the basal plate so as to complete the channel dorsally. They terminate slightly in front of the greatest depth of the cartilage, *i.e.* just anterior to the commencement of the taper at the posterior end of the anterior fourth. The muscle, however, soon begins to increase both in width and depth—as regards the latter, the increase corresponding to the diminution or dorsal taper of the posterior segment of the basal plate, until the fibres appear to meet behind the point of the cartilage at the mid-ventral line. In other words, the pointed extremity of the cartilage *apparently* interrupts the course of the fibres at the mid-ventral region. In

front, the fibres of the muscle are attached to the free margin and the dorso-internal surface of each limb of the posterior segment, but behind, as the latter loses its U-shape and becomes flattened dorsally, and the muscle extends dorsally and laterally to it, the attachment spreads over the whole dorsal surface of the cartilage, and the two halves of the muscle therefore meet at the mid-dorsal line of the posterior segment of the basal plate. Hence we cannot say that the cartilage is everywhere interpolated in the course of the muscle fibres, and thus represents a modified portion of the muscle, since, anatomically, there is nothing to show that the muscle was ever more extensive than it is now. However, the connection between the cartilage and the muscle is of so intimate a nature that the former has been stated by AYERS and JACKSON to represent the tendon of the latter which has become converted into a simple form of cartilage, and which was originally inserted into the posterior extremity of the middle segment of the basal plate. To this view I assented in my first Part (p. 756), but on further consideration it seems impossible that the muscle in question can be the copulo-copularis, since this is a *transverse constrictor* muscle, and as such has no tendon at all. SCHAFFER, in two earlier papers, regarded the posterior segment as a sesamoidal formation in the tendon of the "M. retractor linguæ," but even if this is not a slip for copulo-copularis it cannot be correct. We must, however, here note that the posterior region of the copulo-copularis is U-shaped in transverse section, and in this respect is similar to the cartilage, but the conversion of the anterior region of the muscle into the cartilage postulates a series of changes of which there is at present no evidence whatever.

Dorsally, the two halves of the copulo-copularis are separated by a median ligamentous linea, which in front is a specialisation of the stout fibrous roof of the posterior segment of the basal plate. This linea is at first narrow, but gradually widens as it passes backwards. At the middle of the muscle the two halves begin to diverge dorsally, and this divergence continues up to the posterior extremity, where the two halves were 6 mm. apart in the above specimen, and the longitudinalis linguæ was plainly visible between them. They are, however, connected by a tough sheet of transparent fascia, which in front is directly continuous with the opaque linea above. The lateral margin of the linea and of the sheet of fascia throughout the greater part of the thickest portion of the muscle sends down on each side a vertical longitudinal fibrous sheet, which extends in places through the thickness of the upper half of the muscle, forming an intra-muscular fascia inclining towards the mid-dorsal line. Fibres are attached to both sides of this sheet, so that in transverse section it has a bi-pinnate appearance.

Ventrally there is also a median linea, which is wide in front before the two halves of the muscle meet at the middle line, but behind it is very narrow from side to side, although traversing the thickness of the muscle vertically so as to completely separate the two halves below. At the posterior extremity the inferior chondroidal bar plunges into the muscle and gives origin to a few of the fibres. In *Bdellostoma*, J. MÜLLER

says that *none* of the fibres of the copulo-copularis arise from the inferior chondroidal bar, but in *Myxine* I have seen it in all my dissections and sections. There is, however, no connection with the superior chondroidal bar.

It is quite clear from a merely superficial examination that all the fibres of the copulo-copularis, whilst they always pass transversely at right angles to its long axis (except at the posterior extremity), do not form complete half hoops. This is especially well seen in the longitudinal dorso-lateral spindle-shaped projection which extends from one extremity of the muscle to the other. This projection consists of short transverse fibres, the most superficial of which arose from the external fascia 3 mm. from the mid-dorsal line in a 35 cm. Hag, and after a short maximum transverse course of 4 mm. were inserted also into the external fascia (cp. fig. 3). Hence the copulo-copularis is thickest at the region of this projection. In fact by far the greater portion of the surface of the external fascia of the muscle is utilised for the origin and insertion of its fibres, so that in a surface view one sees, apart from the tract above, only the ends of muscle fibres, and not their course, as shown in the above figure. In other words, the muscle fibres become gradually longer as they pass from without inwards. Again, at the anterior region, where the muscle is flattened dorso-ventrally, the fibres are all nearly vertical, passing from the dorsal to the ventral fascia of the muscle, with, however, a slight incline towards the mid-dorsal line. Hence the most internal, and not the most external, fibres are the longest, because they traverse a greater vertical thickness of the muscle, and they, only, pass from the mid-dorsal to the mid-ventral linea. The external fascia may be described as providing the origin and insertion for the greater part of the fibres which course in a slight but internally increasing curve from the dorsal to the ventral fascial regions. At the posterior extremity the fibres do not follow a strictly transverse course, but pass obliquely downwards and *backwards*, and hence the oblique posterior margin of the muscle is formed by the *ends* of these muscle fibres.

By making a median dorsal incision through the posterior fascia and the anterior linea the two halves of the muscle may be pinned out. It is then seen that the muscle forms a hollow tube, complete in front, where it is continuous with the channel of the posterior segment of the basal plate, but only completed behind by the dorsal fascia mentioned above. In this canal is situated the *M. longitudinalis linguæ* behind, and in front its tendon. The cavity is wider behind, where it has to accommodate the belly of the *longitudinalis linguæ*, but gradually narrows in front, where it only has to lodge the tendon. Hence the copulo-copularis is thickest where the channel is narrowest, and it is important to remember this when considering the function of this muscle. Assuming, in the dead state, that the muscle is in contraction, the size of its cavity is subject to enlargement. The median ventral linea is very obvious internally, and the most internal fibres, *i.e.* those lining the cavity, are seen to be the longest and the most curved, since they arise and are inserted into the most median positions, and hence have to describe a curve in order to enclose a central cavity.

19. *M. longitudinalis linguæ*. (Figs. 2, 3, 6, *l. l.* (Part I.), *l. lg.*)J. MÜLLER, *Innere Längenmuskel der Zunge* (p. 256).AYERS and JACKSON, *M. retractor mandibuli* (p. 204).

This may also be regarded as a paired muscle. Posteriorly it projects behind the truncated extremity of the copulo-copularis, and thus far is visible without dissection, but the greater part of the belly is concealed in the cavity of the latter muscle. When its tendon leaves this cavity in front it traverses the channel of the posterior segment of the basal plate, which is roofed over and converted into a tube by tough fibrous tissue, but in front of this again the tendon works only in a groove open dorsally, the floor of which is formed by the two anterior segments of the basal plate and the sides by the paired rails described on p. 773 of my first Part. This groove gradually dies away in front, and is lost a short distance behind the anterior margin of the anterior segment of the basal plate. It serves as a guide to the dental skeleton when the latter is in the mouth, and transmits the tendon of the present muscle when the "tongue" is everted.

By making a median dorsal longitudinal incision through the copulo-copularis and the roof of the channel of the posterior segment of the basal plate, the longitudinalis linguæ, together with the attached perpendicularis, may be removed intact, along with the dental apparatus, and examined carefully under a dissecting microscope. It is then seen to arise as follows:—(a) the dorso-external fibres arise from the lateral under-surface and lateral margin of the superior chondroidal bar, *i.e.* from practically the whole ventral surface of this cartilage not occupied by the perpendicularis. It also arises, according to P. FÜRBRINGER, from the stout fascia in which this cartilage lies (= broadened out dorsal lineæ of the copulo-copularis), but I cannot confirm this either from dissections or sections; (b) the lateral and ventral fibres, comprising the greater part of the muscle, arise, like a bipinnate muscle, from a median vertical ligamentous (or pseudo-cartilaginous—cp. especially p. 780 of my first Part) partition situated in the longitudinal plane at the posterior end of the muscle; (c) a small posterior bundle, forming the most ventral fibres of the muscle, arises from the dorsal surface of the posterior tip of the inferior chondroidal bar. (Cp. figs. 2 and 3. On p. 779 of my first Part it is erroneously stated that the longitudinalis linguæ has no connection with the inferior chondroidal bar.) The above very curious reinforcement (c), which seems so small and useless, is paired, each half of the muscle receiving a bundle. In the sections the left bundle was much larger than the right. The latter first of all sharply dips down in the median plane between the fibres of the perpendicularis to reach the inferior bar, and the left one does the same immediately behind it. All the fibres of these two bundles, however, do not arise from the bar, but some of them from the vertical sheet described above.

From their origin the fibres of the longitudinalis linguæ pass outwards and forwards in a curve in order to embrace the lateral surfaces of the perpendicularis. They soon pass straight forwards (apart from their convergence), and in front of the perpendicularis the muscles of the two sides are closely opposed by their median flat surfaces, but do

not fuse. The entire mass is oval in transverse section. Dorsally, the division between the two muscles can be traced almost to the tendon, but ventrally the anterior third shows at the middle line a ligamentous cord, which is apparently continuous with the tendon of the muscle in front. The fibres converge gradually both laterally and vertically as they pass forwards, so that the whole muscle resembles a tapering pointer. Its depth behind in a 34 cm. Hag was 7 mm. and its width 9 mm., whilst the entire length of the muscle belly was 35 mm. The anterior half of the muscle, *consisting of larger and less concentrated fibres*, is spindle-shaped, and its pointed posterior end is buried in the anterior end of the posterior half (cp. the detailed description of the tendon below). The fibres of the latter half, therefore, are inserted into the outer tendinous surface of the buried end of the anterior half. Hence there is a fresh origin of (histologically different) fibres to form the anterior half of the muscle.

The belly of the longitudinalis linguæ passes into a strong laterally-compressed tendon, with a maximum depth in the above specimen of nearly 2 mm. This tendon courses straight forwards to the dental apparatus, slightly increasing in bulk as it proceeds, and having a length of 15 mm., to be inserted (in one dissection) as follows:—(a) examined dorsally, the tendon split so as to give off a pair of largish lateral bundles. These rapidly diverged, and were inserted mostly into the *lateral* portion of the posterior arch of the dental plate (Part I., fig. 9). Some of the superficial fibres, however, crossed over the posterior arch, traversed the space between the two arches, and were inserted into the anterior arch of the dental plate. These have been dissected away in the above figure. P. FÜRBRINGER states that *all* the fibres are inserted into the anterior arch (cp. the description of the tendon from sections below); (b) examined ventrally, the greater portion of the tendon formed a powerful median bundle, which passed forwards and expanded somewhat to be inserted into the *median* portion of the posterior arch of the dental plate (Part I., fig. 7). Here again the most superficial fibres crossed the posterior arch and the space in front, and were also inserted into the anterior arch, becoming there continuous with the superficial fibres of the copulo-glossus profundus, as described under that muscle (not shown in fig. 7 above).

I now describe the formation and insertion of the tendon as seen in my large series of sections, which disclose a very interesting state of affairs (cp. particularly the series of transverse sections given in fig. 6).

The tendon of the longitudinalis linguæ really commences far back in the interior of each division of the muscle at about section 1885 (the muscle itself extends back to 2287) as a vertical slip, with an inclination towards the middle line (1750, a). As we pass forwards these slips increase in length, and bend more towards the middle line, whilst a second more ventral pair are added (1570, b). The next stage is the fusion of both pairs of slips, the first pair to form a large half loop the ventral extremities of which now appear on the surface of the muscle, and the second pair to form a median vertical partition, with at first a ventral fork to indicate its paired origin (1498). The hoop encloses the larger and more spongy muscle fibres forming the

anterior half of the belly referred to above. The median division between the two muscles is somewhat early lost in the sections, but I have assumed that the partition *b* will represent the boundary between the two sides. We now find that the hoop extends vertically, and finally fuses at the mid-ventral line to form a complete circle, which encloses all the muscle fibres present (= the anterior half of the belly) and also the second division of the ligament, *b*. All the fibres outside the hoop in 1498 (= the posterior half of the belly) have now died away. At the same time the second or internal portion of the ligament loses its ventral fork, and with it all traces of its paired origin (1260). The outer or circular portion of the ligament next becomes smaller and more circular, and the fibres tend to concentrate below, leaving the dorsal half non-tendinous (cp. 720). Further, the internal tendon loses its vertical sheet-like character and becomes spherical (870). In the next stage (720) we find the dorsal half of the outer circle (*a'*) entirely non-tendinous, all the tendon fibres being concentrated below in a large *median ventral tendon* (*a*), the centre of which is invaded by a weak, soft, pseudo-cartilage. The remainder of the circle (*a'*) is membranous and lodges the nerves at the mid-dorsal line, whilst the internal tendon has now split up again to form the *dorsal paired tendon* (*1b*, *2b*) separated by a median vertical membranous partition (*a''*), and with their external membranous sheaths connected below with the dorsal non-tendinous portion (*a'''*) of the ventral tendon. Now the dorsal membranous portion of the circle (*a'*), then the median partition (*a''*), and finally the dorsal fibrous portion of the ventral tendon (*a'''*), fuse with the median ventral wall of the gut. Whilst this is happening (625), the dorsal tendons, having diverged, split vertically into two (*1b'*, *1b''*, *2b'*, *2b''*). The inner of these (*1b''*, *2b''*) are inserted into the ventro-lateral wall of the gut, and *not* into the dental skeleton. The outer ones (*1b'*, *2b'*) cross the posterior arch of the dental plate internally, and become continuous with the tissue bridging the large gap between the anterior and posterior arches of the dental plate at the posterior base of the inner row of teeth. In these two ways the tendon of the longitudinalis linguæ becomes intimately related to the gut and the dental mucosa, so that its pull will act on these structures as well as on the dental skeleton.

The median ventral tendon (*a*) fuses with the median portion of the posterior arch of the dental plate, and is in fact partly morphologically continuous with it, since a large portion of the tendon becomes converted into soft pseudo-cartilage containing nests of soft cartilage, and thus passes without any hard-and-fast break into the soft cartilage of the posterior arch. Many of the fibres, however, do not terminate in this way, but cross on either side of the posterior arch, to pass over into the stout membrane connecting the two arches of the dental plate, and also partly into the tendon of the copulo-glossus profundus, as described under that muscle. According to SCHAFER's latest paper, the whole of the above membrane is invaded by soft pseudo-cartilage, but it is only partly so in my preparations.

The extension of the dental apparatus is effected by two muscles, the superficial

protractor acting on the mucosa and teeth, and the deep protractor acting on the dental skeleton itself. Although the withdrawal of the apparatus is obviously a simple process, and is in point of fact effected by one muscle, the longitudinalis linguæ, nevertheless the division of the tendon of this muscle is of such a nature as to roughly antagonise the pull of the two protractors. The median ventral tendon corresponds to the deep protractor, and acts directly on the dental skeleton. The paired dorsal tendons correspond to the superficial protractors, and act rather on the mucosa posterior to the teeth. The protractors and retractor may, of course, represent one muscle, with the dental skeleton as a sesamoidal deposit. Cp. the function of the protractor muscles.

20. *M. perpendicularis*. (Figs. 2, 3, pp.)

J. MÜLLER, *Innere senkrechte Muskel der Zunge* (p. 257). *Senkrechter Muskel des Zungenmuskelapparates* (p. 331).

This is an unpaired median vertical muscle, and courses between and separates the posterior ends of the two longitudinalis linguæ muscles like a rod pushed through a loop. It is a short but powerful muscle, wide antero-posteriorly, and slightly compressed from side to side. In transverse section it is somewhat pear-shaped, with the narrow end anterior. In a 34 cm. Hag it had a maximum width of 5 mm. and height of 7 mm. It arises from the dorsal and lateral surfaces of the posterior two-thirds of the inferior chondroidal bar, and its parallel fibres pass upwards and somewhat forwards to be inserted into the middle ventral surface of the superior chondroidal bar, *i.e.* except for a short region anteriorly, and the lateral zones occupied by the dorsal fibres of the longitudinalis linguæ.

The function of the three muscles constituting the retractor apparatus of the "tongue" is a subject of as considerable interest as the apparatus itself is unique. The longitudinalis linguæ has been dealt with already, so that it is here only a question of the other two. According to J. MÜLLER, the perpendicularis, by compressing flat the posterior end of the muscle mass, fixes this end of the longitudinal muscle, whilst the latter, by drawing the dental apparatus sharply back, enables the ventral teeth to scratch and file away the prey already fixed by the palatal tooth. The copulo-copularis is stated to fix the longitudinal muscle in the retracted condition; but MÜLLER is undecided whether the contraction of the constrictor muscle might not also squeeze the longitudinal muscle out, and thus assist in everting the dental apparatus. On the other hand, P. FÜRBRINGER regards the constrictor muscle as a powerful supporter of the protractors of the "tongue," but agrees that the vertical muscle fixes the longitudinal muscle at its posterior end. To quote his own words, he says (p. 24)—"Durch die Contraction des Hohlmuskels wird zunächst der Hohlraum derselben erheblich verengt; dieser Volumenreduction muss natürlich auch der Längs-

muskel folgen, dessen Verkleinerung im Querschnitt zur Verlängerung des Muskels d.h. (da sein hinteres Ende fixirt ist) zu einer Vorwärtsbewegung der Sehne in dem engen vordern Abschnitt des Canals und Halbecanals führen muss." Against this view must be arranged two facts: (1) the longitudinal muscle at the region of its greatest bulk *projects beyond the posterior extremity of the constrictor muscle*; (2) as the longitudinal muscle decreases in bulk, the constrictor correspondingly increases in strength. These facts, to my mind, entirely negative FÜRBRINGER's view, and rob of any point his criticism of MÜLLER's explanation, which he appears to me to misunderstand. It is also difficult to see how the action of the vertical muscle can replace the constrictor posteriorly so as to have a similar pushing effect on the longitudinal muscle. I, however, agree with FÜRBRINGER that a movement of the ventral margin of the mouth itself at the critical moment would assist in toppling the dental apparatus out of or into the mouth, as the case might be.

I took an opportunity of demonstrating this very curious mechanism to Professor SHERRINGTON, who suggested an explanation which appears to me to meet the facts of the case, and to represent also what J. MÜLLER was driving at. We may first of all safely conclude that the tonic condition of the dental apparatus is one of rest, *i.e.* that the longitudinal muscle is at most times in a state of contraction. This muscle will correspond to a rapid or quick muscle which executes a movement that may be rapidly repeated (withdraws the dental apparatus). The constrictor will thus correspond to a sluggish or tonus muscle which preserves an attitude (maintains the tonic condition of retraction). The constrictor, therefore, neither reinforces the pull of the longitudinal muscle nor that of the protractors, but, on the dental apparatus reverting to its tonic condition after being in action, maintains that condition, whilst the longitudinal muscle becomes passive again. Consequently, when the dental apparatus is active, it is the constrictor muscle that is passive (and, of course, relaxed). Similarly, the perpendicular or vertical muscle is a tonus muscle, fixing the posterior end of the longitudinal muscles, which project beyond the sphere of the constrictor muscle. Against this view, however, I ought to state that the fibres of the longitudinal and constrictor muscles are large, of the same size, aplasmic, not richly vascular, and very distinctly cross-striated. Hence the morphological distinction we should expect to find has no existence, and both are *morphologically* tonus muscles; but as all the muscles of *Myxine* except the velo-quadratus, velo-spinalis, cordis caudalis, and the mixed parietals are of this type, this point perhaps loses in importance. I have, however, seen in at least one other muscle (the copulo-tentaculo-coronarius) a few scattered plasmic fibres.

21. *M. copulo-palatinus*. (Figs. 3, 9, *c. pl.*)

J. MÜLLER, *Heber des Zungenbeins* (p. 249). *Zungenbeinheber* (p. 324).

In the case of a muscle such as this, the terms "origin" and "insertion" can only have a purely arbitrary meaning, since neither termination of the muscle is a fixed point.

A fairly powerful flat muscle, which arises from the ventral or convex margin of the cornual cartilage at the bend immediately in front of the origin of the hyo-copulo-palatinus, and opposite the insertion of the palato-ethmoidalis profundus. It is covered externally partly by the first two myotomes behind and partly by the superficial and deep copulo-glossus muscles below. In the sections the cornual cartilage appears in about 140 sections, of which 60 are in front of the origin of the copulo-palatinus and 20 behind it.

The fibres of the copulo-palatinus course downwards and backwards, somewhat diverging, bend over the external bar of the anterior segment of the basal plate external to the first head of the copulo-tentaculo-coronarius on to the internal bar of the same, into the sheath of the ventral surface of which it is inserted near the middle line from its extreme anterior margin up to the commencement of the median fenestra. In the sections it is continued slightly behind and at the side of the fenestra, and, further, it is seen that the two muscles are joined up below the internal bar by a median ligament, and that the latter is attached, and not very securely, at about the middle line of the internal bar.

In front of the anterior margin of the internal bar of the basal plate the external fascia of the copulo-palatinus is observed in the sections to fuse with the longitudinal sheet of fascia stated by J. MÜLLER and P. FÜRBRINGER to be the tendon of the hyo-copulo-glossus (*q.v.*). It presents the appearance in the sections as if some of the fibres of the present muscle were inserted into this sheet also.

As pointed out by P. FÜRBRINGER, the function of this muscle will depend upon which end of it acts as the fixed point. As far as the copulo-palatinus is concerned the cornual cartilage can be fixed by the palato-ethmoidalis profundus, in which case the muscle would tend to approximate the external bars of the anterior segment of the basal plate, and thus compress the mouth cavity laterally, and approximate the two halves of the dental apparatus dorsally. When, however, the cornual cartilage is not fixed, the contraction of the copulo-palatinus would of course depress it. J. MÜLLER states that the muscle elevates the basal plate and draws it somewhat forwards, in that way shutting the mouth. He also recognises that it may also compress the mouth cavity laterally.

22. *M. hyo-copulo-palatinus.* (Fig. 3, *h. c. p.*)

J. MÜLLER, [*Erster*] *Vorwärtszieher des Zungenbeins* (p. 248). *Vorderer Vorzieher des Zungenbeins* (p. 322). *Erster Vorzieher des Zungenbeins* (p. 324).

A wide, powerful muscle, covered externally by about the first three myotomes, and its dorsal border situated immediately below the ventral border of the tentacularis posterior in front.

The hyo-copulo-palatinus arose, in a dissection, mostly from the external fascia of the copulo-quadratus profundus at about the middle and upper portions of its course. A few fibres, however, arose in front from about the middle of the cornual cartilage

immediately behind the posterior border of the insertion of the copulo-palatinus into the same. In the sections, the muscle arose almost exclusively from the fascia of the internal angle of the ventral border of the tentacularis posterior. Even when its dorsal border dips down so as to lose direct connection with the tentacularis posterior, it still remains attached to it for some little distance by a ligamentous sheet. Again, in the sections the dorso-anterior angle of the muscle does not reach the cornual cartilage, but it is connected with it by a short strong bundle of fibrous tissue, just where the cartilage fuses with the palatine commissure. No fibres arose, or could arise, from the palatine bar, as the hyo-copulo-palatinus is widely separated from it at its origin by the copulo-quadratus profundus and the palato-coronarius.

J. MÜLLER states that the present muscle arises from the most anterior part of the palatine bar in *Bdellostoma*, whilst in *Myxine* P. FÜRBRINGER asserts that it arises from the posterior end of the cornual cartilage, and even from the palatine bar, and he mentions finding in one specimen a bundle arising from the fascia of the copulo-quadratus profundus. His fig. 5 agrees largely with what I have found.

The fibres of the hyo-copulo-palatinus course downwards and backwards, somewhat diverging, to be inserted as follows:—(a) a few fibres are inserted into the ventro-external surface of the external bar of the anterior segment of the basal plate immediately below the insertion of the copulo-quadratus profundus. In the sections the muscle was well attached by fibrous tissue to about the ventral or inner half of the posterior sixth of the external bar; (b) two-thirds of the muscle are inserted into the ventro-external face of the middle segment of the basal plate, in front near the outer margin, then passing inwards about half way towards the middle line, and finally rising again behind so as to be situated over or external to the insertion of the rectus muscle and to reach the root of the first branchial arch; (c) a large posterior bundle, representing the remaining third, and which may be more or less distinct from the remainder of the muscle, as shown in fig. 3, courses backwards and slightly downwards, slips under the antero-ventral margin of the cranio-hyoideus, and in a 35 cm. Hag was inserted into the *anterior* surface of the most ventral 3 mm. of the first branchial arch between the insertion of the cranio-hyoideus and the origin of the hyo-copulo-glossus, *i.e.* external to the origin of the latter muscle (*q.v.*). In the sections this part of the insertion is so confused with the origin of the hyo-copulo-glossus that I could not satisfactorily separate them.

The function of the hyo-copulo-palatinus is principally to draw the basal plate (and hence the ventral margin of the mouth) upwards and forwards.

23. *M. copulo-quadratus superficialis.* (Fig. 3, c. q. s.)

- J. MÜLLER, *Hinterer Vorwärtszieher des Zungenbeins* (p. 248).
 „ *Hinterer Vorzieher des Zungenbeins* (p. 323).
 „ *Zweiter Vorzieher des Zungenbeins* (p. 324).

P. FÜRBRINGER states that this muscle may in exceptional cases be either extremely

reduced or even absent, but I have never encountered this variation either in my dissections or sections.

A fairly powerful and apparently club-shaped muscle, with the handle directed backwards, and the whole covered externally by the parietalis. The shape is due to the fact that whilst the dorsal half of the fibres passes straight back to its insertion, the ventral half bends inwards and slightly upwards at a right angle between the copulo-glossus superficialis ventrally and the constrictor pharyngis I. dorsally to reach its insertion, which is thus internal to the dorsal half.

The anterior extremity of the muscle arises—(a) from the fascia of the dorso-posterior border of the hyo-copulo-palatinus; (b) from the fascia of the dorso-posterior portion of the copulo-quadratus profundus; (c) from the fascia connecting the superior and inferior processes of the pterygo-quadratus (in the sections); and (d) largely from the inferior process of the pterygo-quadratus itself. From its origin, the muscle passes backwards and somewhat downwards, crosses transversely the cranio-hyoideus and constrictor pharyngis I., and finally bends inwards over the copulo-glossus superficialis in front, and over the lateral head of the copulo-glossus profundus for a short distance behind, to be inserted as follows: the dorsal half of the fibres is inserted partly into the ventro-lateral fascia of the anterior extremity of the copulo-copularis, but also largely into the dorsal margin of the posterior segment of the basal plate from the beginning of the taper *backwards*, and dorsal to the origin of the copulo-glossus superficialis, which for a time may even exclude it from the basal plate. For a short distance posteriorly (in the sections) it was wedged in between the lateral head of the copulo-glossus profundus and the copulo-copularis; the ventral half of the fibres is inserted into the dorsal margin of the posterior segment of the basal plate in front of the above, *i.e.* from the beginning of the taper *forwards*. The whole origin in a 35 cm. Hag extended over 7 mm. of the posterior segment. It must be remembered that the latter is here U-shaped, and that, therefore, the dorsal margin on each side is a free and somewhat thin border.

According to J. MÜLLER in *Bdellostoma*, the copulo-quadratus superficialis is “inserted” into the margin of the palatine bar where this passes over into the pharyngeal basket. As P. FÜRBRINGER points out, this “insertion” is carried much further forwards than in *Myxine*; and as the basal plate is the movable point, it is as well to call *that* extremity of the muscle the insertion.

The function of this muscle seems to be the same as that of the hyo-copulo-palatinus.

24. *M. copulo-quadratus profundus.* (Fig. 3, c. q. p.)

J. MÜLLER, *Zurückzieher des Zungenbeins* (p. 249).

A very wide, powerful muscle, situated mostly under the hyo-copulo-palatinus, and in part just external to the mucosa of the mouth. It has an irregular or ragged dorsal

origin as follows:—(a) from the skeletogenous layer of the lateral wall of the membranous cranium just external to the massed cranial ganglia (which lie in a space produced by the separation of the two layers constituting the cranial wall), commencing at its anterior end immediately behind the eye, and passing backwards in a descending curve on to the root of the superior process of the pterygo-quadrate. Some of the deeper fibres in front arose in a dissection (but not in the sections) from the anterior process of the pterygo-quadrate. This part of the origin was not found by P. FÜRBRINGER. On the right side, in my large series of sections, the origin extended further forwards so as just to cover and obscure the eye—here arising from the optic capsule; (b) the origin now extends vertically downwards in a curve over the external surface of the central portion of the pterygo-quadrate on to the root of the inferior process of the same, from the external ventral surface of the entire length of which latter it also arises; (c) the origin is finally continued backwards across the hyoid (immediately above the ventral zone of soft cartilage in front), and then rises slightly so as to pass over the posterior flat process of the hyoid, here lying internal to the cranio-hyoideus. A few fibres arose from the root of the inferior lateral cartilage, as stated by P. FÜRBRINGER. In the large series of sections the origin did not rise on to the posterior flat process of the hyoid, but passed straight on to the dorso-external surface of the root of the inferior lateral cartilage, and terminated directly the latter was separated off from the hyoid.

The fibres of the copulo-quadratus profundus course downwards and forwards in large fasciculi, only slightly converging, and are inserted into the lateral (dorsal) margin of the external bar of the anterior segment of the basal plate throughout its entire extent. A few fibres were inserted into the pad of soft pseudo-cartilage at the anterior end of the external bar, and a few also into the lateral margin of the anterior end of the middle segment. P. FÜRBRINGER states that it is inserted into the anterior third of the latter.

In the sections, the insertion into the external bar was carried anteriorly to immediately behind the fusion of the lateral labial with the external bar. In order to reach the latter, these anterior fibres had to pass over the external surface of the posterior extremity of the pad of soft pseudo-cartilage (cp. Part I., fig. 1), but I think few, if any, fibres were inserted into it. Posteriorly, in the sections, the insertion was carried over the pad of soft pseudo-cartilage between the external bar and the middle segment of the basal plate on to the lateral margin of the anterior fourth of the latter.

The function of the copulo-quadratus profundus is to draw the basal plate (and hence the ventral margin of the mouth) upwards and backwards, and in this way to widen the mouth cavity laterally.

25. *M. velo-quadratus*. (Figs. 3, 7d, 11, 12, *v. q.*, *v. q'*, *v. q''*.)J. MÜLLER, *Anzieher des Schlundsegels* (p. 260).

I describe this muscle as dissected from the ventral surface. It is an extensive and irregular muscle, with its fibres arranged into coarse fasciculi, and the fasciculi grouped into three perfectly distinct divisions (both in dissections and in the sections), which might almost be described as three separate muscles.

Ventral Division (v. q.).—Arose in one dissection—(*a*) from the lateral margin of the central expanded portion of the hypophysial plate; (*b*) from the tough tissue between the latter plate and the pterygo-quadrates; (*c*) from the internal surface of the pterygo-quadrates at, and in the immediate neighbourhood of, the zone of soft cartilage between the palatine bar and the pterygo-quadrates. In the sections a small portion of the fibres arose from the stout membrane connecting the hypophysial plate with the anterior extremity of the soft cartilage portion of the trabecula. The origin then passed on to the lateral margin of the above plate immediately before this fused with the rod from the nasal capsule. The receipt of the latter adds to the width of the plate, so that the ventral division, since it continues its origin straight backwards, no longer arises from the lateral edge of the plate, but from the ventral or external surface of it, not quite half way down. When, however, the trabecular connection is given off from the plate,* the muscle again arises from its lateral margin, until it is displaced from it by the anterior extremity of the origin of the dorsal division. There were no signs of any origin from the pterygo-quadrates.

The fibres of the ventral division pass backwards and outwards, and finally converge to be inserted into the ventro-external portion of the anterior or free surface of the expanded head of the external lateral velar bar. The ventral division almost entirely covers the middle division ventrally, but the dorsal division appears behind at its median margin.

Middle Division (v. q').—Arose in the same dissection—(*a*) apparently from the cranium slightly behind the level of the origin of the ventral division; (*b*) from the ventro-internal surface of the anterior end of the trabecula. In the sections it arose (*a*) from the ventral surface of the anterior soft cartilage portion of the trabecula; (*b*) from the same surface of the naso-trabecular cartilaginous commissure at and in the neighbourhood of its fusion with the hypophysial plate; (*c*) from the tough membrane between the latter plate and the trabecula; (*d*) from the ventro-internal surface of the zone of soft cartilage between the pterygo-quadrates and the palatine bar.

The fibres of the middle division pass backwards and outwards, and converge slightly to be inserted into a knob of *soft* cartilage at the dorso-external margin of

* The correct view to take of these cartilaginous fusions is that they represent a connection between the olfactory capsule and the trabecula which fuses with the hypophysial plate *on the way*. This is also suggested by NEUMAYER's figure and by my own sections.

the anterior surface of the expanded head of the external lateral velar bar. This is the division of the velo-quadratus one sees in a lateral external view in the anterior half of the third fenestra of the skull (figs. 3, 11, *v. q'*).

Dorsal Division (v. q'').—The most dorsal and the largest division of the three. Partly covered ventrally by the middle division. It arose in the same dissection:—(a) a few fibres from the lateral margin of the central expanded portion of the hypophysial plate; (b) the greater part apparently from the cranium at a level slightly posterior to the origin of the middle division; (c) some fibres from the ventro-internal surface of the anterior half of the trabecula behind the origin of the middle division. In the sections the origin was somewhat different. No fibres arose from the cranium, but they all arose from the ventral surface and internal margin of the trabecula opposite the posterior half of the first fenestra of the skull, and also from the lateral margin and dorso-internal surface of the hypophysial plate.

The fibres of the dorsal division pass backwards and outwards almost parallel, and finally have an oblique insertion into the internal surface of the external lateral velar bar from a short distance behind the free extremity up to and slightly beyond the origin of the internal lateral velar bar. In fact, some of the fibres were inserted into the base of the latter also, although in the sections the insertion terminated immediately in front of the origin of the internal bar.

The above account differs from P. FÜRBRINGER'S in several respects, but more particularly in that this author did not find the division of the muscle into three parts. J. MÜLLER mentions two parts in *Bdellostoma*, which are stated to be antagonistic in action (anatomically quite possible in *Myxine*); but FÜRBRINGER disputes the accuracy of this statement, and insists that in *Myxine* the insertion is quite continuous.

The velo-quadratus is stated to act as the occlusor of the naso-pharyngeal opening, but the fact that it consists of small plasmic vascular fibres, similar to those of the cordis caudalis, would indicate that it is either a rapid or a rhythmic muscle. Thus the velum may well act as an apparatus which, by a pulsating motion, draws the respiratory water into the pharynx. If this is not so, it is difficult to understand how the water reaches the gills, since the intrinsic and extrinsic musculature of the gills would only expel water from the respiratory apparatus already there. On this view the velo-spinalis is, of course, also a rapid muscle.

26. *M. velo-spinalis.* (Figs. 7e, 12, *v. s.*)

J. MÜLLER, *Anspanner des Schlundsegels* (p. 261 and p. 317, λ).

Before describing this muscle, I may mention here a ligament found in its neighbourhood. It is of course a part of the general and diffuse ligamentous system found in *Myxine*, and has a somewhat indefinite origin from the region of the dorso-internal surface of the hyoid arch. It then passes forwards, upwards, and inwards, and is

inserted into the scooped-out hollow on the ventral surface of the head, and also into the margins of the external lateral velar bar.

Like the velo-quadratus, the velo-spinalis is a small-fibred muscle. It has a long extended origin from the ventro-lateral surface of the skeletogenous layer of the notochord, commencing just behind the posterior extremity of the parachordal cartilages, and internal to the anterior portion of the origin of the first division of the constrictor pharyngis. In the sections the postero-ventral border of the origin was connected by a fibrous cord with the dorso-external margin of the anterior extremity of the anterior connecting process of the suprapharyngeal skeleton (cp. Part I., fig. 16, *sp. sk'*, about section 780). J. MÜLLER, in the description of his plates (p. 317), also mentions this connection, and in fact there describes the muscle as passing only between the two portions of the velar skeleton, and not as arising from the chorda. This, however, is figured and also described in the text. P. FÜRBRINGER describes the chordal end of the muscle as its insertion; but as this end is obviously the fixed point, this is not permissible.

From its origin the velo-spinalis, with fibres converging, passes at first downwards, and then bends sharply so as to course forwards, outwards, and downwards in a gentle curve as a small compact cylindrical muscle, lying internal to the cranio-hyoideus, and separated from the velo-quadratus by the pharyngeal diverticulum described on p. 777 of my first Part. The insertion, however, is effected immediately anterior to this diverticulum, and there the two muscles meet and are closely associated. After a course of 5 mm. in a 35 cm. Hag, the velo-spinalis was inserted into the dorso-external surface of the head of the external lateral velar bar where this appears in the third fenestra of the skull, and seems at first sight to represent the posterior continuation of the external fibres of the middle division of the velo-quadratus. In the sections it was inserted mainly into the dorso-external margin of the bar, but as it approached the extremity of the head it extended somewhat on to its external surface. Hence the velo-spinalis appears in the third fenestra of the skull immediately behind the middle division of the velo-quadratus. This portion, however, has been cleared away in figs. 3 and 11.

According to P. FÜRBRINGER, the velo-spinalis displays the velum laterally by drawing the head of the external lateral velar bar inwards, and in that way inducing a general outward rotation of the bar (but cp. the function of the velo-quadratus).

27. *M. cranio-hyoideus.* (Figs. 3, 11, *c. h.*)

J. MÜLLER, *Erster Constrictor des Schlundes* (pp. 260, 324).

P. FÜRBRINGER, on the score of innervation, objects to J. MÜLLER regarding this muscle as a division of the extensive constrictor pharyngis. There would, however, be a very strong resemblance between these two muscles if it were not for the fact that

the former passes internal to the superior lateral cartilage and the latter external to it. In the meantime, therefore, and in the absence of any information at first hand as to its innervation, I follow FÜRBRINGER in separating this muscle from the constrictor pharyngis.

The cranio-hyoideus is a small but an interesting and curious muscle. In one specimen dissected it arose as follows:—(a) a few fibres from the posterior edge of the bridge of soft cartilage connecting the auditory capsule with the upper extremity of the hyoid arch; (b) most of the fibres from the ventral and posterior surfaces of the posterior end of the auditory capsule; (c) a few fibres from the external border of the parachordal immediately behind the auditory capsule. ALLIS* states that in *Bdellostoma* this muscle arises from the notochordal sheath immediately posterior to the auditory capsule. In my sections it arose exclusively from the auditory capsule on the right side, and on the left side partly from the capsule and partly from the fascia covering the soft cartilage of the postero-lateral extremity of the parachordal.

Just below its origin the cranio-hyoideus narrows down to pass *under* the root of the superior lateral cartilage, and emerges below it between the hyoid and first branchial arches. It at once fans out so as to occupy a part of the space between the above two arches, and now proceeds in a vertical curve downwards and slightly backwards. It crosses *externally*, and obscures, the flat posterior process of the hyoid arch, the origin of the most posterior fibres of the copulo-quadratus profundus, the insertion of the hyo-copulo-palatinus into the first branchial arch, and the inferior lateral cartilage, but passes internal to the copulo-quadratus superficialis. Hence this muscle passes through the fourth fenestra of the skull.

Below the flat posterior process of the hyoid arch the fibres of the cranio-hyoideus converge again, and in a 35 cm. Hag were inserted into the *external* surface of the most ventral 2 mm. of the first branchial arch (*i.e.* just where this fuses with the basal plate), external to the insertion of the large posterior bundle of the hyo-copulo-palatinus and the origin of the hyo-copulo-glossus. In one series of sections it was inserted into the external surface of the first branchial arch somewhat dorsal to its fusion with the basal plate, but in another series the insertion was as above described.

On the right side of my large series of sections the cranio-hyoideus was vestigial, and failed to reach its usual insertion. The anterior fibres terminated mid-laterally on the hyoid arch about half way down this cartilage and opposite the dorsal border of the posterior extremity of the copulo-quadratus profundus, whilst the posterior fibres terminated opposite the dorsal margin of the posterior soft cartilage portion of the hyoid in the fascia of the dorsal border and dorso-internal surface of the copulo-quadratus superficialis.

It is difficult, as P. FÜRBRINGER says, to assign a satisfactory function to this small muscle. FÜRBRINGER regards it as a vestigial muscle representing a functional branchial muscle at a time when the first branchial arch was not fused either with the

* 1, p. 332.

cranial framework or with the basal plate. Its vestigial condition on one side described above supports this view.

28. *M. constrictor pharyngis*. (Figs. 2, 3, 11, *c. p'*, *c. p''*, *c. p'''*.)

J. MÜLLER, *Constrictor des Schlundes* [second and third portions] (p. 260). *Zweiter Constrictor des Schlundes*. *Dritter Constrictor des Schlundes* (p. 324). *Constrictor pharyngis* (p. 276).

ALLIS, *Constrictor œsophagei* (p. 334).

A very long powerful muscle, which, perhaps arbitrarily, may be divided into three sections which I have found to be separated by small breaks, as shown in fig. 3. The second and third divisions, however, may not be sharply differentiated.

First Division (c.p').—A few of the most anterior fibres may arise from the posterior extremity of the auditory capsule. In the sections none of the fibres arose from the capsule, but the origin commenced on the tough vascular fascia covering the post-auditory parachordals laterally. From here the origin extends downwards, backwards, and slightly outwards, first passing obliquely across, and at the same time arising from, the dorso-lateral surface of the notochord, until it arrives at the lateral surface of the chorda, and in a $34\frac{1}{2}$ cm. Hag, 2 mm. from the exposed ventral margin of the latter. It thus reaches the place where in transverse section the inner free surface of the parietalis meets the chorda. In front, this is about half way down the latter, but behind, the parietalis more and more involves the chorda, although it never completely encloses it ventrally, even in the tail.

The origin now passes straight backwards parallel to the chorda, and arising from the superficial internal fascia of the parietalis—at first in the angle formed by this muscle with the chorda, but behind moving out laterally away from the latter. In the above Hag the origin extended over an area of 22 mm. From the origin the fibres strongly converge, most of them passing forwards and downwards in a curve round the lateral wall of the gut. The anterior fibres describe a graceful curve, with the concavity looking forwards, and the muscle covers the pharyngeal basket *externally* from the first branchial arch backwards, except for the most ventral third of this arch. The general appearance of this part of the muscle closely resembles an open fan. The insertion (hidden by the copulo-quadratus superficialis) is as follows :—(a) the fibres forming the most anterior sixth are inserted into the *posterior* surface of the most ventral 3 mm. of the first branchial arch, *i.e.* where it fuses with the middle segment of the basal plate. *Cp.* the connection of the cranio-hyoideus, the hyo-copulo-palatinus, and the hyo-copulo-glossus with this portion of the first branchial arch; (b) a few fibres are inserted into the dorso-external surface of the root of the lower division of the second branchial arch (when present, as I now believe it generally is*) just where it fuses

* Cp. Part I. p. 763. Since my first Part was published I have dissected a *Myxine* in which the lower division of the second branchial arch fused with the upper exactly as shown for *Bdellostoma* by AYERS and JACKSON in their fig. 6. On pp. 763–4 of my first Part I state that this fusion has never been seen in *Myxine*. It is, hence, interesting to record it now.

with the first branchial arch; (c) the greater part of the fibres, however, are inserted into the dorso-lateral free border of the U-shaped posterior segment of the basal plate from its commencement to the beginning of the taper, *i.e.* to the commencement of the copulo-copularis. The whole insertion extended over 8 mm.

In the sections the insertion of the first division of the constrictor pharyngis was as follows:—the anterior fibres were wedged into the angle formed by the fusion of the first and second branchial arches ventrally, but the insertion was clearly more into the first than into the second branchial arch. The insertion then leaves both arches and passes on to the dorso-external surface of the posterior segment of the basal plate immediately below the second branchial arch. As, however, the latter rises, the muscle follows it until it reaches its characteristic insertion into the summit of the posterior segment immediately above and internal to the insertion of the copulo-quadratus superficialis.

Second Division (c. p'').—This may be distinguished from the first division by its different insertion. In the sections, however, the separation of these two divisions was not so obvious, but I was able to establish it, especially as the fibres of the first division appeared to be larger than those of the second. The second division is not so compact as the first, and consists of a number of discrete fasciculi, which, however, continue the same origin backwards, *i.e.* from the superficial internal fascia of the parietalis, not far from the middle line. The origin, in the specimen above, extended over 16 mm. The fibres, slightly converging, pass sharply forwards and somewhat downwards and outwards, to be inserted into the external fascia of the *dorso-lateral* region of the copulo-copularis from its pointed extremity backwards. The insertion extended over 15 mm.

Third Division (c. p''').—This is not present in *Bdellostoma*, unless, as seems certain, J. MULLER's first loop of the constrictor of the gills partly or entirely represents it. The third division is not so sharply defined as the other two, and the distinction may be difficult to draw in occasional specimens. It is, however, more compact than the second division, and has often a different origin behind and a slightly different insertion. In the sections, I was not able to distinguish between the second and third divisions, as there was no difference either in the origin or in the insertion. In the specimen shown in fig. 3 (but which, however, seems to be exceptional), about the first half of its fibres continued the previous origin backwards from the superficial internal fascia of the parietalis, as in the first and second divisions. The posterior half, however, arose from the ventral surface of a ligamentous sheet despatched forwards from the constrictor of the gills to the dorsal superficial internal fascia (cp. fig. 3). The whole origin extended over 11 mm. Hence, whilst the anterior fibres of this division pursued a course similar to that of the second division, the posterior fibres passed at first forwards over the afferent duct of the first gill pouch, and internal and dorsal to the pouch itself, and then downwards and outwards to reach their insertion. *All* were inserted into the external fascia of the copulo-copularis of the *dorsal* region, near the

middle line in the specimen now described, and over its last 16 mm. I have never seen the fibres of this division inserted into the protruding end of the longitudinalis linguæ. In most dissections, and also in the sections (cp. fig. 2), the posterior fibres of this division were the *direct continuation* of the dorsal fibres of the constrictor of the gills. If, therefore, in fig. 3 the ligamentous area between these two muscles remained muscular, and there was hence no origin from the dorsal fascia, this condition would be reproduced. In other words, the posterior fibres, instead of arising from the dorsal superficial internal fascia, more usually course longitudinally at the side of the gut, and are unquestionably simply the continuation forwards of the dorsal fibres of the constrictor of the gills, and, strictly speaking, are a part of that extraordinary muscle. This, as above mentioned, is borne out exactly in the sections, where the most posterior bundle of the constrictor pharyngis is clearly a portion of the constrictor of the gills, and constitutes the first loop of this muscle in connection with the first gill sack (cp. the Chart, fig. 2). The ligamentous sheet referred to above is absent.

The bearing of these facts on the question of the morphology of the constrictor pharyngis is discussed in the section on the constrictor of the gills, and we need only note here that the absence of any means of distinction between these two muscles indicates that they are essentially parts of one and the same branchial muscle, which, on the loss of the anterior gills, became modified in front as the constrictor pharyngis.

The first part of J. MÜLLER's constrictor of the pharynx = my cranio-hyoideus. His second and third parts = part I. of my C. pharyngis. The second part of the latter muscle in *Myxine* is thus absent in *Bdellostoma*, judging from J. MÜLLER's description, whilst the third section in *Myxine* (at least in part) = J. MÜLLER's first loop of the constrictor of the gills in *Bdellostoma*.

It is stated that the constrictor pharyngis, by drawing the basal plate and "tongue" muscle complex upwards and backwards, presses the gut against the parietalis and notochord, and thus occludes it.

29. *M. constrictor branchiarum et cardiae*, F.J.C. (Figs. 2, 3, 13, *c. b. c.*, *c. b. c'*., *c. b. c''*., numerals 1-14).

J. MÜLLER, *Constrictor der Athemorgane + Constrictor (Sphincter) der Cardia (Constrictor cardiae)* (pp. 270 and 273). *Constrictor der Kiemen und der Cardia* (p. 328).

As the above two muscles of J. MÜLLER are both parts of one series, I propose to consider them together under the above name. Further, my description of this muscle is based largely upon dissections, as a detailed reconstruction of this maze from the sections, after spending the whole of one long vacation in repeatedly dissecting it, was a Quixotic task I had not the courage to face. I have, however, prepared a chart which illustrates the general anatomy of the muscle in the sections, a few notes on which will be appended to the present description.

This very remarkable and unique muscle varies to such an extent, at times even in its general arrangement, that no typical description is possible. Hence the present account has not been generalised, but details the conditions as found in a perfect specimen fixed in formol-alcohol. The result of this fixative is to whiten the tissues generally, and, so far, to keep them white. Hence the present muscle, always very difficult to dissect, is too white for accurate investigation. This, however, is easily remedied by soaking the specimen in very dilute chromic acid, which colours the muscles first yellow and then brown. A number of individuals were dissected, and the more important variations are recorded in the following description.

When a lateral incision is made through the body-wall at the region of the club-shaped muscle and gills and the flaps pinned back, it is seen that the space between the notochord and these structures is occupied by a quantity of adipose tissue. When this and the vagus nerve are removed from the roof of the club-shaped muscle, the oblique fibres of the constrictor pharyngis are exposed. On turning now to the gill region, the four anterior gills are seen, more or less faintly, showing through a layer of adipose tissue, which is deposited most densely in the depressions between the gills and between their ducts, so as to render the surface of the branchial region quite level. On removing this tissue, partly with a fine needle and partly by brushing it away, we see the whole of the first gill and decreasing portions of the next four lying in their gill sacks, which are usually more or less filled with blood.* The last gill and the greater part of the fifth are covered by a thin sheet of muscle, the fibres of which (cp. especially fig. 13, *c. b. c.*) course downwards and sharply forwards, becoming more and more horizontal towards the posterior end of the muscle, until the fibres at the ventro-posterior region are quite horizontal.

In some specimens this sheet of muscle was so reduced as to be practically absent. It is not present in *Bdellostoma* according to J. MÜLLER, where only the loops are visible over the gill sacks.

At the posterior margin of the sheet there were a few fibres passing almost vertically downwards but slightly backwards on to the posterior surface of the ductus oesophago-cutaneus (fig. 13, 11, and *d. œs. ct.*). The sheet meets the corresponding one of the other side at a somewhat irregular linea situated roughly in the mid-dorsal line. In *Bdellostoma*, according to J. MÜLLER, there is an incomplete longitudinal fissure in the middle line, and the somatic arteries emerge at the lacunæ. He further states elsewhere that there is a crossing of the fibres at the mid-dorsal line in *Bdellostoma* and *Myxine*, so that the portion "was nach hinten auf der rechten Seite herabsteigt, ist die Fortsetzung der Fascikel, die vorn links heraufsteigen und umgekehrt" (p. 272). I have not seen any trace of this in *Myxine*.

The systemic aorta (*s. ao.*) passes *underneath* the two opposed sheets, *i.e.* between them and the gut. The somatic arteries, therefore, have to perforate the muscle in order to reach the back (cp. figs. 3, 13). In the specimen now described three such

* Cp. Cole, 5, p. 325.

arteries were given off—the anterior two emerging to the left of the median linea and the third to the right. In front of and behind the muscle the aorta emerges to become opposed to the notochord, *i.e.* its normal position. Ventrally the muscle extends so far as to cover the whole of the last gill and the greater part of the fifth, and also the last three ductus branchiales externi. Its ventral margin may be quite regular (cp. fig. 13) or very ragged (J. MÜLLER evidently saw this latter condition, and cp. the Chart, fig. 2), and the whole of this margin may be connected by a thin ligamentous sheet with the body-wall, either exactly opposite the dorsal border of the obliquus or the ventral border of the parietalis, or the posterior portion of the muscle may extend even further downwards so that the sheet is attached behind to the body-wall opposite the outer edge of the rectus.

Dorsally, the sheet-like portion of the constrictor extends much further forwards than ventrally—reaching as far as the second gill. Opposite the fourth gill it bifurcates, sending forward on each side a narrowing muscular limb (cp. fig. 3, *c. b. c'*), separated by a median space from that of the other side. This limb, as shown in the figure, was in this specimen separated from the main portion of the sheet by a ligamentous partition, but this was certainly not the case in other individuals. In one example the two limbs were connected by a dorsal transverse muscular bridge, itself with a median longitudinal partition, and the whole anterior portion of the muscle was modified. The anterior limb above passed forwards and slightly downwards, becoming gradually narrowed, until over the second gill it merged into a gradually narrowing ligament which curved upwards and forwards to be inserted into the superficial internal fascia of the parietalis at the side of the notochord. This ligament, which is certainly of exceptional occurrence, had a curious connection with the posterior fibres of the third portion of the constrictor pharyngis, these fibres arising from the ligament, and curving forwards over the first gill to reach their insertion on the copulo-copularis (cp. the constrictor pharyngis).

The arrangement just described seems to indicate that the third portion of the constrictor pharyngis, if not the first two, corresponds to a modified loop (or loops) of the constrictor branchiarum. If so, they would represent the loops in connection with the anterior or lost gills, the first adult gill being otherwise without a loop. We must, however, not forget that the last loop of all, *i.e.* the one immediately in front of the ductus oesophago-cutaneus (figs. 2, 3, 13, 6), is also unconnected with a gill in the adult. This view is strikingly borne out in most specimens, as there is no break whatever between the two muscles (cp. the Chart, fig. 2), the only difference being that instead of the fibres of the constrictor branchiarum passing on to the parietalis, they meet each other in the middle line over the gut, as already figured and described for *Myxine* by J. MÜLLER. Further support is to be found in the condition in *Bdellostoma*, for the third division of the constrictor pharyngis of *Myxine* unquestionably includes J. MÜLLER's first branchial loop of *Bdellostoma*.

The dorsal anterior limb of the constrictor sends downwards two muscular loops

(fig. 3, 1 and 2), but both loops were in the specimen now described, and as shown in fig. 3, separated from the limb by thin ligamentous septa, which, however, judging from my other dissections, are of exceptional occurrence, in which case the fibres of the loop are directly continuous with those of the limb, a number of fibres in the latter turning sharply downwards at right angles to form the loop. In one specimen all the loops were exceedingly reduced; nevertheless the ventral longitudinal tract (figs. 2, 3, 13, 7) was well developed. This shows that the latter tract has an existence independent of the loops—which is to be expected, seeing that the first loop, in some cases the fourth and fifth (cp. fig. 13), and generally the fifth, do not contribute any fibres to the tract. In the same specimen I found that the first loop, however, *did* unite with the ventral tract, some of the fibres passing backwards with the tract, and the others passing forwards with it to the usual insertion of the loop on the longitudinalis linguæ. Incidentally, we may here note that the second loop of *Bdellostoma*, corresponding to the first of *Myxine*, does *not*, according to J. MÜLLER, reach the longitudinalis linguæ.

First Loop (1).—Passes downwards and forwards in a curve over the external face of gill 2, then *under* the first efferent gill duct, not far from its origin from the gill, and finally bends straight forwards to fan out on the lateral fascia of the longitudinalis linguæ. In one specimen this insertion was ligamentous, and not muscular, as it generally is. In *Bdellostoma* the loops are said to course in the depressions between the gills. I have frequently seen this in *Myxine* also. A very striking difference, however, is that in *Bdellostoma*, according to J. MÜLLER, there is no ventral longitudinal tract, but all the loops are attached to the *ventral belly-wall* opposite the external branchial apertures. In many specimens of *Myxine* the loop included a number of fibres (as shown in fig. 3) which did not pass underneath the efferent gill duct, and which fanned out in the fatty tissue covering the gills; but in other individuals the first loop consisted solely of fibres for the longitudinalis linguæ. We do, however, find the non-ventral fibres of the loops, when present, more and more spread out as we pass backwards, so that the continuous posterior sheet may be regarded as having been formed by these fibres of two or more loops fusing together.

Second Loop (2).—Passes downwards and slightly forwards over the external face of gill 3, crosses over the origin of its efferent duct, then dips underneath first the second and then the first efferent ducts, to finally pass over into the ventral longitudinal tract. The latter varies considerably, and it may be very greatly reduced on one or both sides so as not to reach the second and third loops, which consequently terminate in the fatty tissue below their respective gill ducts. The formation of this ventral tract will be described subsequently. Most of the fibres of the second loop pass forwards with the tract, but a few of them turn backwards along it. This, however, here and in the other loops, is subject to variation, and the fibres of the loop may be equally divided, one half passing forwards and the other half backwards, and so on. The ventral tract, after receiving loop 2, continues its course straight forwards, and in the specimen now described terminated in two ligamentous fans, the

dorsal one of which turned upwards to become attached to the fascia at the posterior end of the longitudinalis linguæ, whilst the ventral and larger one bent downwards to effect an extensive connection with the internal surface of the rectus muscle near its outer margin. This termination just described is, however, by no means of general occurrence. The same remark as to the occasional presence of non-ventral fibres applies to the second as well as to the first loop.

Third Loop (3).—Immediately behind the origin of the anterior dorsal limb the main body of the constrictor despatches ventrally a third loop. This loop, in all the specimens I have dissected, includes a greater or lesser number of the non-ventral fibres. These fibres were very numerous in the present case, and by fanning out in front and behind largely covered the external surfaces of gills 4 and 5. The whole of the fibres of the loop were marked off at their origin from the major portion of the muscle by a ligamentous partition, but this is by no means of universal occurrence. The ventral portion of the loop passes external to the origin of efferent gill duct 4 almost straight downwards, but slightly forwards, then slips under the efferent ducts 3, 2, 1 in the order mentioned, and finally goes over into the ventral longitudinal tract in much the same way as loop 2.

The last two loops, owing to their origin from the internal surface of the now continuous posterior sheet of the constrictor some distance above its ventral border, are consequently not entirely seen until the covering sheet has been turned dorsally or its ventral portion removed. Hence in fig. 3 the latter has been done in order that all the loops may be included. The behaviour of these two loops also varies considerably.

Fourth Loop (4).—Passes external to the origin of efferent duct 5, and then downwards internal to the ducts 4, 3, 2, 1. Ventrally it may go over into the ventral longitudinal tract, the fibres diverging to accompany the latter backwards and forwards (as shown in fig. 3), or it may assist in forming the internal portion of the ventral insertion (as shown in fig. 13, 8). In the latter case the loop distinctly bifurcated, one limb passing into the ventral insertion, and the other coursing backwards as described under the *ventral insertion*, 2.

Fifth Loop (5).—Courses external to the origin of the efferent duct 6, and then ventrally internal to ducts 5, 4, 3, 2, 1. I have never seen this loop connected with the ventral longitudinal tract except by a very few fibres which it occasionally despatches to it (but cp. the description of the sections). It always passes external to the tract and on to the inner portion of the ventral insertion (figs. 3, 13, 8), but some of them turn backwards as described under the *ventral insertion*, 2.

The last two loops are very differently arranged in *Bdellostoma*, according to J. MÜLLER. Here they bend right round and fuse in the mid-ventral line over the cardiac aorta on the ventral surface of the constrictor cardiae, so as to form a distinct sphincter system of their own. Also in *Myxine* itself, according to MÜLLER, the last three loops fuse up to form on each side a ventral longitudinal tract, which, however, courses

only backwards, none of the fibres passing forwards as above described. I have seen this condition also, but only in one specimen.

Ventral Longitudinal Tract.—The fibres of the two tracts, when traced backwards, are seen to gradually converge as they approach the external branchial openings. Most of their fibres arise immediately behind these openings—the fibres of the two sides meeting at the mid-ventral line, where they are attached to the cardiac portion of the constrictor. The tract also receives dorso-ventral fibres which bend round on to it from above behind the ductus œsophago-cutaneus, as described below, and also a few fibres from the dorsal longitudinal tract, which pass round in a curve into it behind the above ductus instead of terminating at the mid-ventral line, as described below. The only traces I have seen of any decussation in the constrictor is that a variable number of fibres of, say, the right dorsal longitudinal tract may cross over into the left ventral longitudinal tract, and *vice versa*.

We must now enter into the details of the anatomy of the posterior region of the constrictor—a subject both difficult to understand and to describe. To get at the facts it is necessary to remove the constrictor *en bloc* and carefully clean it up. This is not an easy dissection, but it is the only way to understand the muscle. To do it, you remove the whole of the branchial region from the body-wall, leaving the rectus muscle attached to the latter. Then remove first the efferent gill ducts and then the gills themselves on each side, and finally snip through the large loop on the left side in front of the ductus œsophago-cutaneus, so that the latter itself may be cleared away. The constrictor is now ready to be isolated. Make a longitudinal incision through the thickness of the muscle a little on one side of the mid-dorsal line, and with a fine needle separate the constrictor from the gut, which may then be lifted out. You now have the whole of the constrictor in one piece, so that both inner and outer surfaces may be investigated, and further examination effected under the higher powers of the dissecting microscope.

The *cardiac portion of the constrictor* (figs. 2, 3, 13, *c. b. c''*.) extends a variable distance behind the gill region over the gut—in an average specimen about 5 mm. In one case the fibres were separated at the mid-dorsal and mid-ventral lines by a ligamentous septum. The fibres are loosely arranged behind, but are more compacted in front. They course transversely round the gut, but usually slightly obliquely forwards from above. Dorsally and in front the fibres surround the exit of the systemic aorta so that the latter vessel has a small constrictor of its own. In front of this region dorsally and on each side the fibres again diverge to allow the exit on the left side of œsophageal vessels opening into the left anterior cardinal (figs. 2, 3, 13, 12), and on the right side of similar vessels opening into the anterior portal vein, which is a smaller vessel, but occupies a similar position to the anterior cardinal of the other side. These openings may be provided with definite constrictor fibres. The mere divergence of the fibres could of course perform the same function, but not so effectively as a special constrictor. Ventrally in front the cardiac portion of

the constrictor is covered by the posterior extremities of the ventral longitudinal tracts, which partly arise here near or at the mid-ventral line, and between or just behind the external branchial apertures.

Anteriorly the cardiac portion of the constrictor passes imperceptibly into the branchial portion (*c. b. c.*), so that no distinction between the two portions is possible. The fibres now begin to course in various directions, but the following general tendencies may be distinguished.

Externally, Left side :—

1. A small slip may be given off to the internal fascia of the obliquus (fig. 13, 9).
2. A number of fibres bent round ventrally and anteriorly to complete the formation of the ventral longitudinal tract (for remainder, see above).
3. A large number of fibres course downwards and forwards round the postero-internal surface of the ductus œsophago-cutaneus (figs 2, 3, 10) to partly form the muscular tube through which the ductus passes, and finally to assist in forming the large external portion of the ventral insertion (figs. 2, 3, 13, 8').
4. A small slip (figs. 2, 13, 11) passes downwards and slightly backwards on the posterior surface of the ductus œsophago-cutaneus, to be mostly inserted into the ventral posterior process of the cartilage of the ductus (fig. 13, x^3 .)
5. We now come to the region where the fibres terminate below in a ventral border, which may be attached to the body-wall by a ligamentous sheet, as above described. Here the fibres nearest this ventral border, after previously coursing downwards and slightly backwards, turn forwards at a right angle and travel parallel to the ventral border (fig. 13). A few fibres, however, here pursue a rectangular course (fig. 13, part of 11), *i.e.* they pass first of all posteriorly parallel to the ventral border, and then, near the posterior surface of the ductus œsophago-cutaneus, they turn down at a right angle to be inserted as the slip (4) just described, and also into the wall of the ductus near its external opening. As we go further forwards the fibres of the posterior region of the branchial portion of the constrictor bend at a gradually increasing angle until finally attaining the downward-forward direction characteristic of the greater part of the muscle, as already described.

Externally, Right side :—

- 1 and 2. As on left side.
3. We find similar fibres coursing downwards and forwards, but this time round the postero-internal surface of the last efferent gill duct, to form the external portion of the ventral insertion. As these fibres course morphologically in front of the ductus œsophago-cutaneus, they cannot of course represent the fibres of paragraph 3 of the left side. They correspond in fact to the larger sixth loop of the left side, to be described below, and which passes between the last efferent gill duct and the ductus (figs. 2, 3, 13, 6).
4. Absent. 5. As on left side.

Internally, Both sides :—

When the internal surface of the muscle is examined it is seen that there are a number of fibres in addition to those appearing on the external surface. Ignoring the scattered fibres running in various directions, and which may occur on the external surface also, we notice, particularly in the mid-dorsal region, a large number of fibres coursing longitudinally, which may be more or less diffuse, or which may be collected together into a definite tract on each side of the mid-dorsal line. I shall call this the *dorsal longitudinal tract*. It increases in thickness as it passes backwards. In front, these fibres pass over into the anterior muscular limb already described (*c. b. c'*). It is now seen that the loops are not entirely formed by the dorso-ventral fibres of the outer muscular sheet of the constrictor, but receive from, and give fibres to, the dorsal longitudinal tract. The greater majority of the latter fibres pass from the tract on to and along the posterior margins of the loops. From the anterior margins of the loops a few fibres are given off which accompany the tract forwards. It would appear, therefore, from this, that many fibres of the loops have no beginning and no end, but course round in circles formed by the dorsal and ventral longitudinal tracts and the loops. Behind, the dorsal tract behaves as follows :—

1. A few of the fibres may pass straight backwards, ventral to the vascular gap (figs. 2, 3, 13, 12), and along the inner surface of the cardiac portion of the constrictor.

2. Most of the fibres curve downwards in front of the vascular gap (12), and behind the ductus œsophago-cutaneus on the left side and the last efferent gill duct on the right, to meet at the mid-ventral line on the gut *internal* to the origin of the ventral longitudinal tract, and thus continue forwards the cardiac portion of the constrictor.

3. On the left side a number of fibres were contributed to the sixth and largest loop (figs. 2, 3, 13, 6), which passes obliquely forwards in front of the ductus œsophago-cutaneus, and which varies less than any other portion of the constrictor.

4. A few fibres may bend forwards and go over into the external portion of the ventral insertion (fig. 13, 13).

Sixth Loop (6).—As this has already been described on the right side, the present account applies to the left side only. It arises from the inner surface of the outer branchial muscular sheet, and passes downwards and forwards into the outer portion of the ventral insertion in front of and external to the ductus œsophago-cutaneus, and internal to the last efferent gill duct. It is constituted as follows :—

1. Some dorso-ventral fibres from the internal surface of the muscular sheet above.
2. A number of fibres from the dorsal longitudinal tract, as above described.
3. The fibres forming the definite *constrictor of the ductus œsophago-cutaneus* (figs. 2, 3, 13, 14), which accompany the sixth loop in front of the ductus, but leave it above and below to complete the sphincter by curving round the back of the ductus.

For the insertion of this loop, see below.

That the sixth loop is serially homologous with the preceding five is borne out by

J. MÜLLER's description of *Bdellostoma*, where this loop has precisely the same relations as most of the others. In this region and that of the ventral insertion MÜLLER figures and describes in *Myxine* a very obvious and elaborate decussation of the fibres round the gut, both dorsally and ventrally, but the description is by no means clear (and indeed he recognises this himself), and the figures are too small and vague to be of much assistance. It is improbable that MÜLLER was mistaken in his facts; and as I have never seen any decussation of fibres except the slight one mentioned above, this can only be regarded as another of those extreme variations which this perplexing muscle exhibits. [Since this was written, however, I have found a distinct ventral decussation in one of my series of sections. The paired tracts forming the inner portions of the ventral insertion, after passing backwards under the gut, fused first with each other and then with the cardiac portion of the constrictor in such a way that each tract sent fibres both to its own and to the other side of the gut.]

Ventral Insertion.—We are now in a position to describe the ventral insertion of a large number of the fibres of the branchial portion of the constrictor. On each side a fan-like tract collects in front of the external branchial aperture (figs. 2, 3, 13, 8, 8') and passes *between* the two recti muscles, to be inserted into the internal fascia of the obliquus at the mid-ventral line. I have seen in some cases a few slips inserted into the internal fascia of the rectus itself, but generally the latter muscles may be entirely removed without in any way interfering with the insertion. J. MÜLLER describes the fibres as inserted into the rectus muscle on each side of the middle line. Apart from the few slips mentioned above, I have never seen this, either in dissections or sections [but cp. the description given below of the sixth loop in the sections], and should have concluded it to be an error on MÜLLER's part, were it not for the extensive variation characteristic of the constrictor generally. The insertion consists of an outer and an inner portion on the left side, made up from the following sources:—

1. Outer Portion (figs. 2, 3, 13, 8').—The last or sixth loop (6) forms the greater part of this section, but a tract is usually contributed by the fibres that curve round the internal surface of the ductus œsophago-cutaneus from behind (cp. fig. 3), and also a few longitudinal fibres reach it straight from their origin on the ventral surface of the cardiac portion of the constrictor at the side of the origin of the ventral longitudinal tract.

2. Inner Portion (figs. 2, 3, 13, 8).—This is not invariably separate from the outer portion, but always more or less so. It consists of a large number of fibres which curve round the ductus œsophago-cutaneus as above described, of many which pass straight on to it from the ventral surface of the cardiac portion of the constrictor, and of fibres from the loops 4 and 5. These loops may be entirely connected with the inner portion of the insertion (as in fig. 13, and, as I believe, is more frequently the case), or they may be more or less connected with the ventral longitudinal tract. In any case, however, all their fibres do not pass into the ventral insertion, or forwards into the ventral longitudinal tract, or both, but a varying number curve backwards

and upwards into the dorsal longitudinal tract, and some I have traced to an origin on the ventral surface of the cardiac portion of the constrictor.

On the right side, owing to the absence of the ductus œsophago-cutaneus, the ventral insertion is naturally the smaller by the fibres which are contributed to it on the left side by the fibres of the ductus. Hence the outer portion of the insertion is formed practically entirely by the last or sixth loop. The inner portion resembles that of the other side.

The physiology of this complex muscular apparatus can, of course, only be determined by experiment. Two points, however, are quite clear at once: (1) the œsophagus can be powerfully constricted immediately behind the branchial region so as to prevent the entrance of respiratory water into the gut; (2) the ductus œsophago-cutaneus, lying as it does for the most part in a strong muscular tube, as well as possessing an abundant intrinsic musculature, can also be occluded. For the rest, the muscle is subject to so much variation as to indicate that it is a vestigial structure of little, if any, physiological importance. It certainly cannot in the average *Myxine* "discharge the water taken in by the breathing organs" (J. MÜLLER, p. 276). For this the powerful intrinsic musculature of the gills and their ducts is amply sufficient. It is quite possible, however, that it may be concerned in controlling the blood-pressure in the elaborate system of vascular spaces surrounding the gill region. MÜLLER's statement of the physiology of the gill apparatus is evidently based merely on its anatomy, and he further does not seem to be aware that the respiratory water normally reaches the gills through the nasal tube.

I append the following notes in explanation of the reconstruction of the general anatomy of the left side of the constrictor muscle from my large series of sections (fig. 2). I do not here or elsewhere include the intrinsic musculature of the gut and gill apparatus, which will be described in my next Part when these structures are under special consideration.

The posterior external sheet (*c. b. c.*) has a very ragged ventral border, and, judging from the structure of the loops as we pass backwards, is evidently formed by the fusion of those fibres of the last three loops which are related to the gills, *i.e.* the non-ventral fibres. These become more numerous and diffuse from before backwards, and finally fuse up to cover the last gill and the greater portion of the fifth. There are numerous lacunæ here and elsewhere (not all shown in the Chart), the largest (12) transmitting the veins from the gut opening into the anterior cardinal on the left side and the anterior portal on the right. The lacuna is smaller on the right side. The two halves of the constrictor fuse dorsally at about 2970, but in front of this they are connected by three transverse bridges—a narrow anterior and posterior one, and a wide intermediate one. The constrictor envelops the systemic aorta (*s. ao.*) at the mid-dorsal line as above described. In front the muscle forks in the usual way into the pair of anterior limbs (*c. b. c'*), and each of these passes, without any obvious line of

demarcation, into the posterior section of the constrictor pharyngis (*c. p'''*). I have taken the boundary to be where the first loop merges into the anterior limb, but this is an arbitrary distinction.

First Loop (1).—On the left side this is somewhat similar to the condition represented in fig. 3, but on the right it did *not* reach the longitudinalis linguæ (*l. lg.*), but fanned out on the dorso-lateral surface of the external wall of the second pleural sack in front of its efferent gill duct. A small bundle was sent backwards on to the root of the gill duct. Hence, on the left only the ventral fibres were present, and on the right only the non-ventral, the two sides together representing the fibres which may be present on each side, as shown in fig. 3.

Second Loop (2).—Takes no part in forming the definitive ventral longitudinal tract (7), but terminates freely in front in the fatty areolar tissue slightly below and to the side of the cardiac aorta at about the level of the origin of the second afferent gill duct. This loop despatches an anterior slip to the second efferent gill duct, another anterior and smaller one at the same level to the fatty areolar tissue external to this duct, and a third postero-ventral one to the *first* efferent gill duct. On the right side the loop terminated in front mostly on the inner surface of the first efferent gill duct. There seems little doubt that the ventral forking of the loop corresponds to the anterior and posterior fibres contributed to the ventral longitudinal tract.

Third Loop (3).—Inserted by a very narrow anterior and a very wide posterior bundle into the superficial internal fascia of the parietalis, not far from its ventral border and in front of the fourth gill sack.

Fourth Loop (4).—Inserted in front into the superficial internal fascia of the parietalis in the same way and at the same level as the third loop.

Behind the fourth loop are seen the five large processes into which the ventral border of the posterior external sheet of the constrictor is prolonged. These are mostly inserted into the internal fascia at the junction of the ventral margin of the parietalis with the obliquus. The insertions of the third and fourth loops just described continue this series forwards.

Ventral Longitudinal Tract (7, 7').—The sections throw considerable light on the nature of this tract. The postero-ventrally coursing bundles, forming part of loops 3 and 4 and the whole of loop 5 (3, 4, 5), correspond unquestionably in every detail with the ventral bundles previously described from dissections, of which the third and fourth may contribute to the ventral tract, and the fifth usually does not. In the sections the ventral bundles of loops 3 and 4, after a typical course, combined to form a separate or anterior section of the ventral longitudinal tract (7), which, passing forwards immediately ventral to the first efferent gill duct, terminates in front on the obliquus muscle not far from the lateral margin of the rectus. The greater part of this section, *i.e.* between the points of entry of the loops, is formed of fibres from loop 3 passing backwards and of loop 4 passing forwards. Both loops, on entering the section, despatch fibres forwards and backwards. Posteriorly the section splits, leaving a lacuna

(cp. also fig. 13, 4), part of the fibres passing straight downwards, internal to the posterior section of the tract, to assist in forming the inner portion of the ventral insertion (8), and the remainder coursing backwards, immediately dorsal to the other fibres of the inner portion of the insertion, and forming a bundle which remains distinct from the latter up to about 3078, but which then merges into it.

The *Fifth Loop* (5) separates itself from the inner surface of the posterior external sheet of the constrictor opposite the middle of the last gill, and passes in a curve downwards and slightly backwards. It finally bifurcates into a short postero-ventral division, which penetrates between the posterior extension of the anterior section of the ventral tract and the remaining fibres of the inner portion of the ventral insertion to terminate on the internal fascia of the latter without reaching the ventral insertion, and into an anteriorly directed division. This latter constitutes the posterior section of the ventral longitudinal tract (7'), which courses forwards immediately under the anterior section, but which, except for a few connecting fibres, as shown in the Chart, is quite distinct from it. The posterior section terminates anteriorly on the internal or dorsal surface of the rectus muscle. On the right side the fifth loop splits as above stated, but the posterior division bends downwards and *forwards*, and forms the most anterior bundle of the inner portion of the ventral insertion.

The above facts show that the ventral longitudinal tract is not a definitive muscle, but is rather a complex, formed of the secondarily juxtaposed contributions from about three loops + other fibres, as above described.

The *Sixth Loop* (6), which is smaller than I found it in dissections, is detached from the internal surface of the posterior external sheet of the constrictor, and passes almost straight downwards to its insertion. This represents the outer portion of the ventral insertion (8'), but it differs very considerably from the insertion as I found it in dissections. In the first place, it is not only absolutely distinct from the inner portion, but entirely posterior to it. Then only two small bundles pass inwards and downwards between the two recti muscles at the mid-ventral line in the normal manner, most of the fibres being inserted into the lateral or outer margin of the left rectus. Posteriorly it receives the small special constrictor of the ductus cesophago-cutaneus (14), as above described.

On the right side the sixth loop is very reduced. It is continued from the ventral border of the posterior external sheet of the constrictor slightly below the ventral margin of the parietalis and at the transverse level of the posterior outline of the last gill. It then courses obliquely downwards and forwards, to be attached to the lateral margin of the right rectus. There is thus only a slight outer portion of the ventral insertion on this side. In dissections I have sometimes not found the sixth loop on the right side at all, and hence the outer portion of the ventral insertion may in some cases be entirely wanting on this side.

The inner portion of the ventral insertion (8) is formed partly by fibres from the third and fourth loops (+ the fifth on the right side), but largely by the definitive fibres

of the insertion. All these form a large paired tract which passes backwards internal to the gill and œsophageal ducts, and lateral to the cardiac aorta. As these tracts course posteriorly they spread out dorso-ventrally, and finally, together with the two recti below, by fusing at about the middle line under the gut, they form a complete muscular tube enclosing behind the vascular sinus surrounding the cardiac aorta. The mass then fuses with the posterior external sheet of the constrictor to form the cardiac portion of the muscle in such a way that fibres from *each* tract curve round *both* sides of the gut. There is thus a well-marked decussation, as mentioned above.

30. *M. parietalis*, F.J.C. (Figs. 1, 4, 5, 7, 8, 9, 14, *par.*)

J. MÜLLER, *Rücken- und Seitenmuskeln* (p. 243).

M. FÜRBRINGER, *Epibranchiale musculatur* (p. 627).

This is the muscle that constitutes the well-known alternating mytomes of the fish. Its division into dorsal and ventral portions (*Parietalis dorsalis* and *Parietalis ventralis*) by a horizontal septum stretching from the vertebral column to the lateral line, which obtains in other fishes, does not exist in *Myxine*, where this septum is wanting. WIKSTRÖM,* however, considers the septum a secondary formation of little morphological importance, and J. MÜLLER distinguishes “back” and “lateral” muscles in the parietalis of *Bdellostoma*, although this division is certainly artificial, as M. FÜRBRINGER states. WIEDERSHIEM considers the obliquus + rectus as representing the detached ventral musculature, and actually labels the dorsal border of the obliquus as the linea lateralis. Omitting the question of the morphology of the rectus, the parietalis of *Myxine* is in transverse section a single sickle-shaped muscle on each side (fig. 1), the two being separated mid-dorsally by a vertical partition arising from the cranium and neural tube, and passing over into the strong external fascia of the muscle. This septum is in front, over the cranium, wide from side to side and narrow behind, as shown in fig. 8. The parietalis terminates some distance from the mid-ventral line by a free border situated just above the slime sacks (fig. 1). The same conditions apply to *Petromyzon* for the region behind the gills, but within the branchial area dorsal and ventral parietal muscles have been differentiated.

In Fishes generally the parietalis does not extend further forward than the occipital region of the skull, but in *Myxine* it passes forwards over the membranous cranium until it almost reaches the posterior boundary of the nasal capsule (see figs. 8 and 9).

The parietalis, enclosed externally and internally by a stout fascia, the fibres of which in the outer one course obliquely downwards and *forwards*, is subdivided by the zigzag vertical partitions or *septa intermuscularia*† (ligamenta intermuscularia, J. MÜLLER; inscriptiones tendineæ) into a number of muscle segments or myotomes. These septa

* *Anat. Anz.*, xiii., 1897, p. 401.

† I have avoided the term myocomma for the septum, as this term was used by the older anatomists to indicate the myotome itself.

pass through the entire thickness of the muscle, and hence the length of the muscle fibres, which course more or less directly longitudinally from one septum to another, is confined to the intervals between the septa. Hence, as WIKSTRÖM says (p. 406): "Ein jedes Transversal-septum fungirt also zugleich als Ursprungssehne für das eine Myomer (Muskelbauch) und als Endsehne für das andere, angrenzende." Further, the fibres on the two sides of any one septum are often placed exactly opposite each other, so as to be directly continuous except for the septum.

The course of the septa through the thickness of the parietalis, *i.e.* from the fascia superficialis externa to the f. s. interna, can be studied either by a series of longitudinal radial hand sections, or, and much better, by picking and brushing away the muscle fibres from a macerated specimen. It is then seen that the septa do not everywhere pass straight through the width of the muscle, *i.e.* at right angles to the long axis of the body, but follow largely an oblique course, as shown in fig. 14. A typical septum from the middle of the body may be divided into four parts, commencing at the back, as follows (*cp.* the figure):—1. Externally commences near the middle line, and passes obliquely downwards and forwards at a sharp angle. It penetrates the muscle almost straight downwards, *i.e.* vertically, at right angles to the surface at this region, but somewhat inwards, and is attached internally at the middle of its length to the skeletogenous layer of the neural tube, near the junction of the latter with the chorda. Both behind, and in front where it bends sharply on itself opposite the junction above and turns backwards, it does not reach the neural tube or chorda, and therefore has no internal attachment at these places. 2. As seen externally, passes sharply backwards and downwards. It penetrates in a curve with the convexity external and anterior, almost straight through the muscle, *i.e.* sub-horizontally, at right angles to its external surface, but somewhat inwards, to become obliquely attached to the skeletogenous layer of the lateral wall of the chorda. 3. Externally, passes almost straight downwards, but slightly forwards, and courses obliquely through the muscle in a forwardly-directed curve, with the concavity external and anterior, to become attached to the fascia superficialis interna. 4. Continues the external course of 3, and passes practically straight through the muscle, but slightly forwards, to become attached as 3. As the muscle is thinnest at this region, the septum is here very narrow. In the Lamprey, according to J. MÜLLER, the septa are much more oblique, so that in a transverse section one sees a greater number of them than in *Myxime*.

I have counted the number of the myotomes in the different regions of the body in six Hags taken at random, with the following results (*see table, next page*).

J. MÜLLER gives 109 as the number of myotomes in *Bdellostoma*.

I have found the first few myotomes to vary somewhat. For example, the first may be quite small and quadrangular, and situated immediately below the ventral border of the tentacularis posterior, or, as is generally the case, its dorso-posterior angle may be prolonged upwards and backwards under the ventral edge of the above muscle, in some cases as far as its posterior extremity, as shown in fig. 9. In these cases the normal

Size of Hag in cm.'s.	20½		22½		24½		26½		28		37	
Left and Right Sides.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.
Anterior to Branchial Pore . . .	28	28	28	27	27	27	29	29	30	30	30	28*
Opposite Branchial Pore . . .	1	1	2	1	2	1	2	1	2	1	2	1
Between Branchial Pore and Cloacal Aperture	56	57	53	53	54	54	59	60	57	58	56	58
Opposite Cloacal Aperture . . .	2	2	2	2	2	2	2	2	2	2	3	2
Post-cloacal	20	21	22	22	20	21	19	20	24	25	20	22
Total	107	109	107	105	105	105	111	112	115	116	111	111

* Of these the first was partially subdivided into two, and obviously corresponded to the first and second of the left side. Hence there is really one more on the right side than on the left.

first myotome is doubtless the one with the posterior extension, the small quadrangular one being additional. I have, however, never seen any appreciable dorsal section to the first myotome except in one case (see fig. 9), where a few scattered fibres in front of the second myotome might have represented the dorsal portion of the first. When the first myotome is quadrangular it is entirely covered by the dorsal extension of the obliquus, but when the posterior extension is present, this is visible as far as it is developed after removal of the skin. In all cases the first myotome is considerably smaller than the succeeding ones, and never extends so far ventrally. According to J. MÜLLER, the first myotome is attached to the "cartilage process at the anterior end of the tongue bone and to the cartilage of the ventral [fourth] tentacle." This is very different from *Myxine*.

The normal second myotome is in some exceptional cases, as stated above, preceded by two distinct myotomes, in which case, of course, it becomes the numerical third. The first is then very small, whilst the second represents the normal first myotome. The normal second myotome consists of two limbs, placed at about a right angle, with the apex directed posteriorly. The dorsal limb passes upwards and forwards behind the posterior extremity of the tentacularis posterior, but does not reach the mid-dorsal line (figs. 8 and 9). The ventral limb courses downwards and forwards, at first under the ventral border of the tentacularis posterior, but afterwards behind and below the first myotome. There is a distinct furrow between the second myotome and the tentacularis posterior. Myotomes three to about eight or ten vary in external appearance, and have the form indicated in figs. 8 and 9. From myotome ten up to, generally, about twelve from the tip of the tail, all the myotomes exhibit the following external conformation (fig. 5). At the side of the mid-dorsal partition there appears to be a continuous narrow muscular band, unbroken by any septa intermuscularia. If this, however, is examined carefully in Perenyi-fixed material, it will be seen that it is traversed by very faint septa, which pass very sharply backwards. The septa then become obvious, and turn sharply forwards at an acute angle, then backwards again at a somewhat less acute angle, and finally by an obtuse angle pass downwards and slightly forwards. This agrees substantially with J. MÜLLER's description and figure of the tail region of *Bdellostoma*. On the body the arrangement is simpler, according to

him. The last twelve myotomes often exhibit a gradual simplification of this pattern, so that the last few septa appear as sinuous vertical lines. In other specimens, however, as shown in fig. 4, the pattern may be continued practically to the very extremity of the tail. The last myotome is a very small, irregular, and variable patch of longitudinal fibres at the tip of the tail. The slime sacks behind the cloaca, as described below, are partly covered dorsally by the myotomes.

The first myotome, *i.e.* of the small type, lies largely between the anterior dorsal extension of the obliquus and the copulo-palatinus, and arises from the fascia between these muscles. The succeeding myotomes, except those behind the cloaca, are all covered ventrally by the obliquus, but the dorsal and greater portions are seen at once on removal of the skin. The second, third, fourth, and fifth myotomes are thin dorsally, and roof over the membranous brain case, being closely attached to it. The anterior myotomes are also attached to the posterior extremity of the anterior process of the pterygo-quadrates, the superior and (the anterior end of) the inferior processes of the same, the auditory capsule, the dorsal portion of the hyoid arch, and the anterior end of the superior lateral cartilage. Below, the anterior myotomes cover the muscles of the head, pharynx, and the so-called "club-shaped muscle." Behind the fifth myotome the parietalis gradually thickens dorsally, where for the remainder of its length it is very fleshy, and attached to the roof and sides of the neural tube and the lateral surface of the chorda, from thence becoming thinner as it passes ventrally. From about the seventh to the twenty-third myotome a wide interval is left dorsally between the parietalis and the club-shaped muscle, in which space course the very diffuse second and third divisions of the constrictor pharyngis. This hiatus is directly continuous with the very large extra-branchial space, and the corresponding one at the dorsal region of the heart, abdomen, and tail, and is everywhere traversed by the silky adipose areolar tissue supporting nerves and blood-vessels. At the gill and cardiac regions the parietalis, together with the notochord, forms the lateral walls and roof of this space, whilst below it is bounded by the obliquus and rectus muscles. The parietalis, however, reaches its greatest development in the abdominal region. Here the muscles of the two sides are separated at the mid-dorsal line by a thin vertico-longitudinal partition arising from the roof of the neural tube. From thence the muscle extends downwards as a rapidly thickening mass at the side of the neural tube and chorda, being closely attached to these, and attaining its greatest thickness opposite the ventral surface of the latter (fig. 1). Here, with the chorda, it forms the roof of the abdominal tube. It now extends downwards, becoming gradually thinner, in order to terminate in a free border immediately over the slime sacks, and being only separated from the latter by the obliquus muscle. Here also it forms the lateral wall of the abdominal tube (fig. 1).

On the tail, where of course there is no body cavity nor any obliquus or rectus muscles, and where, apart from the transversus caudalis and the cordis caudalis, there is no other muscle present, there is a relatively greater development of the parietalis.

above the neural tube, and a thinning at the side of the neural tube and chorda. In the anterior region of the tail the slime sacks occupy the position of the body cavity, and the parietalis extends externally about half way down on each side of the slime sacks. Such extension must, of course, be purely secondary. Dorsally, the muscle extends above the neural tube at the side of the median dorsal bar, where this exists, whilst behind the slime sacks it stretches below the chorda at the side of the median ventral bar, where it is best developed, and where it coincides with the ventral boundary of the body. It soon begins to thin down, first laterally and then dorsally, and finally terminates in a very small and often irregular myotome on the fused dorsal and ventral bars, slightly behind the posterior end of the spinal cord.

The function of the parietalis is to effect the sinuous movements by which the animal swims.

31. *M. obliquus*, F.J.C. (Figs. 1, 4, 5, 9, 10, *obl.*)

J. MÜLLER, *Schiefe Bauchmuskel* (p. 246).

M. FÜRBRINGER, *M. obliquus externus* (pp. 613 and 628).

WIEDERSHEIM, *M. obliquus abdominis externus* (p. 232).

I have abbreviated the name of this muscle because it extends not only over the abdominal but also over the respiratory and cranial regions of the body. In a 31 cm. Hag it commenced 7 mm. behind the extremity of the snout as a thin sheet of fibres coursing obliquely in a curve downwards and backwards from the ventral edge of the tentacularis posterior, to which it is attached, and extending along about the middle third of the latter. This anterior more dorsal portion of the muscle entirely or largely covers the small first myotome and the ventral portion of the second (fig. 9). Behind the anterior 6 mm. the dorsal edge of the muscle descends to the more ventral level of the remainder of it, but throughout its whole course covers externally the ventral portions of the myotomes.

The obliquus is characterised in that portion of it in front of the branchial apertures by an extraordinary interdigitation of its fibres ventrally. On the abdomen the fibres arise as one continuous sheet from the superficial external fascia, but as the latter passes externally to the slime sacks and the obliquus internally to the same, the two are separated for a time. Mid-ventrally the obliquus terminates *without overlapping* at a ligamentous linea which is connected with the superficial fascia, the latter curving upwards and inwards over the median surfaces of the slime sacks to meet it. In front of the abdominal region, however, the fibres of the obliquus, as they approach the mid-ventral line, are first of all collected into definite fasciculi of very variable size, and these terminate, not at a mid-ventral linea, but are continued for some little distance over the median line on to the opposite side of the body to which they belong (fig. 10). The extent of the crossing is greatest immediately behind the mouth, *i.e.* at the anterior end. From thence it irregularly narrows down to a point at the respiratory apertures,

so that there is no sharp transition between the simple and crossing portions of the muscle. In the pre-abdominal portion of the obliquus, therefore, there is ventrally a very curious interlacing, extending from immediately behind the mouth to the branchial apertures, where it ceases, the fasciculi of one side having to pass underneath the fasciculi of the other side before emerging on to the surface of that side of the body on which they are inserted. For example, a fasciculus, let us say, of the right side arises dorso-laterally from the superficial external fascia. It courses obliquely backwards and downwards, and leaves the fascia to pass internal to the slime sacks. Median to the slime sacks it passes *internally* to the terminal portions of the fasciculi of the *left* side (being separated from the fascia by these), emerges on to the surface again at the mid-ventral line, and is now continued on the *left* side *over* the fasciculi of the latter side, separating them from the superficial fascia, into which it is inserted. Hence, in spite of the interdigitation, *all* the fasciculi arise and are inserted into the superficial external fascia. The anatomy of this portion of the obliquus is illustrated in fig. 10, which shows posteriorly two fasciculi on each side dissected clear of the overlapping fasciculi, so as to expose the whole of their course. Anteriorly the overlapping portions are wider and closer knit, and the first few fasciculi on each side are usually wider than the remainder. Omitting the very small posterior fasciculi, which are difficult to delimit, there are about 100 on each side.

Behind the heart (fig. 5) the obliquus covers superficially the ventral half or belly surface of the body. Hence its dorsal abdominal border is roughly coincident with the roof of the body cavity. Its fibres pass downwards and backwards in a slight curve, and above the line of the slime sacks it covers externally the ventral portion of the M. parietalis, whilst the slime sacks themselves in the relaxed condition lie in depressions on its outer surface. Ventrally it covers externally the M. rectus, and between the ventral border of the parietalis and the dorsal border of the rectus it forms the only muscular wall of the abdominal cavity (fig. 1). Behind the cloaca it has no appreciable existence.* The fibres of the superficial external fascia, which everywhere covers the obliquus, course in a direction *opposite* to that of the fibres of the muscle.

The function of the obliquus is to powerfully compress the walls of the body. In the region of the body in front of the gill apertures this compression, owing to the interdigitation of the fasciculi ventrally, is by far the most powerful. This is very obvious when watching a living animal, when one sees how the branchial region of the body is, as it were, wrung dry like a sponge. Another important function of the obliquus is to express the pre-cloacal slime sacks, which have no intrinsic musculature.† When the obliquus is relaxed the expanded slime sacks lie in depressions on its surface, so that when the muscle contracts they are driven against the skin, which here closely investing them and having little give, they are flattened between the obliquus and the skin.

* But cp. the description of the sphincter cloacae and the transversus caudalis.

† J. MÜLLER states, however, that in *Bdellostoma* each slime sack is surrounded by a special muscular membrane.

In *Bdellostoma*, according to J. MÜLLER, the anterior extremity of the obliquus is considerably narrowed down, and is not a blunt dorsal expansion as in *Myxine*. MÜLLER was the first to point out that there is a very striking difference between *Bdellostoma* and *Myxine*, since in the former the obliquus passes *external* to the slime sacks, the apertures of which open between the muscle fibres. Here, too, the compressing action of the obliquus affects the slime sacks, but of course in a different way.

32. *M. rectus*. (Figs. 1, 3, 5, 9, 11, *rect.*).

J. MÜLLER, *Gerade Bauchmuskel* (p. 247).

P. FÜRBRINGER and WIEDERSHEIM, *M. rectus abdominis* (p. 89 and p. 233).

M. FÜRBRINGER, *M. rectus* (pp. 614 and 628). *Hypobranchiale Musculatur* (p. 627).

I have adopted MAX FÜRBRINGER's term for this muscle, as being less misleading than his brother's. The two recti are covered throughout by the obliqui, and for the greater part of their course they lie roughly between the two rows of slime sacks (fig. 1). They arose in the specimen now described (26 cm.) 7 mm. in front of the cloaca by elongated spindle-shaped muscular strands, connected by slender fibro-muscular cords with the narrowed anterior end of the strong sphincter cloacæ. These strands soon shorten and thicken to form the paired series of (generally) alternating myomeres which constitute the rectus muscle. Throughout the entire abdomen, however, the myomeres are of a transversely wide irregular shape, are separated by extensive ligamenta intermuscularia (inscriptiones tendineæ), and, as at the remainder of their course, are in contact at the mid-ventral line. Abdominally, the rectus is in fact more or less rudimentary, and forms the mid-ventral boundary of the body cavity. It narrows down to pass between the branchial orifices, but in front of the latter at once begins to gradually increase in width and strength, until in the present specimen it was widest at about 11 mm. behind its anterior extremity. In front of its widest part it rapidly flattens from side to side into a *vertical* ribbon, which creeps between the median and lateral heads of the copulo-glossus profundus, to be inserted (usually) by a very short ligament into the sheath of the posterior extremity of the middle segment of the basal plate (near its junction with the posterior segment) at about the middle of its ventro-lateral surface.

The segmentation of the rectus may be tabularised as follows (26 cm. Hag):—

	Right Side.		Left Side.	
	Myomeres of Parietalis.	Myomeres of Rectus.	Myomeres of Rectus.	Myomeres of Parietalis.
In front of Branchial Apertures	22	19	21	22
Opposite Branchial Apertures	1	1	1	1
Between Branchial Apertures and Cloaca	50	52	56	55
Total	73	72	78	78

There is thus a close agreement in *total* number between the two segmented muscles even when the numbers of the two sides do not agree, and this agreement also extends in general to the ligamenta intermuscularia. Therefore, as the myomeres of the rectus are generally opposite those of the parietalis, the former may conceivably represent the disassociated ventral portions of the latter. Hence the myomeres of the parietalis should (and do) alternate. These statements, however, do not apply to the whole length of the rectus in every specimen, as the two sides may in parts agree or alternate with the parietalis in the same individual. The latter condition is shown in fig. 5.

These discrepancies are to be expected, since the state of contraction of the muscle will necessarily affect its position. J. MÜLLER also favours the view of the complete correspondence of the myomeres of the rectus and parietalis, and states further that these two muscles are *completely* interrupted by the row of slime sacks in *Bdellostoma*. The latter cannot be said to apply to *Myxine* (fig. 1); and if it did, its significance would be neutralised by the fact that the presence of the slime sacks has not affected the obliquus, lying *between* the rectus + parietalis and the slime sacks. Further, according to J. MÜLLER, the myomeres of the two recti are *symmetrical*; and as the myotomes of *Bdellostoma* alternate, according to AYERS and JACKSON (although this is not as easy to determine as one would imagine), this should not be the case. WIEDERSHEIM correctly states that the myomeres of the rectus alternate in *Myxine*, and assumes that this muscle represents a detached portion of the parietalis. M. FÜRBRINGER seems to favour the same view, but draws attention to a certain asymmetry between the two muscles, *i.e.* there are fewer hypobranchial (rectus) than epibranchial (parietalis) myomeres. This I also find. The whole question, however, has been reopened by the work of WIKSTRÖM,* and must therefore be left over until the nerves are considered.

The rectus clearly performs a double function. In the abdomen it assists in flexing the body ventrally, but owing to its feeble development at this region its action cannot be powerful, whilst its stronger anterior portion assists in the retraction of the basal plate, that is, when the extension of the body is preserved by the parietalis.

Ammocætes and *Petromyzon* also have an anterior representative of the rectus, as first pointed out by A. SCHNEIDER.†

Since writing the above I have dissected a 45½ cm. Hag in which the rectus was inserted, not into the basal plate, but into the external fascia of the copulo-glossus profundus. The two heads of the latter muscle diverged as usual to admit the passage of the rectus, but it terminated abruptly on both sides 14 mm. behind this place. This very interesting variation seems to emphasise the vestigial (or rudimentary?) nature of this muscle.

* *Anat. Anz.*, xiii. p. 401, 1897. He concludes from the innervation that the two muscles are *not* homologous, segment for segment.

† *Zool. Anz.*, v. p. 164, 1882.

33. GEOGRAPHY OF THE PRECEDING MUSCLES.

I include here two tables indicating the longitudinal extent of the muscles in my large series of sections on both sides of the body. These tables will be useful in subsequent sections of the work, especially those on the blood-vessels and nerves, so that when a structure is being followed forwards or backwards in the charts it can be seen by a glance at the tables what muscular region of the body is being traversed. I have excluded the tendons, when present, and hence the figures only relate to the belly of the muscles. *R* = right, *L* = left.

From Before Backwards.

R. 7-371	}	Copulo-tentaculo-coronarius (F.J.C.).
L. 27-377		
R. 12-142	}	Transversus oris.
L. 27-164		
R. 30-73	}	Ethmoideo-nasalis.
L. 35-85		
R. 44-146	}	Tentaculo-ethmoidalis.
L. 51-157		
R. 51-481	}	Tentacularis posterior.
L. 77-503		
R. 63-375	}	Nasalis.
L. 72-381		
R. 79	}	Copulo-ethmoidalis.
226 External Head		
266 Internal Head		
L. 86		
250 External Head	}	
278 Internal Head		
R. 118-184	}	Coronarius (F.J.C.).
L. 128-203		
R. 122-441	}	Palato-ethmoidalis superficialis.
L. 126-450		
R. 123-371	}	Copulo-tentaculo-coronarius (P.F., minus the coronarius, however).
L. 151-377		
R. 142-315	}	Palato-ethmoidalis profundus.
L. 144-319		
R. 201-423	}	Copulo-palatinus.
L. 222-430		
R. 222 —	}	Obliquus.
L. 249 —		
R. 273-739	}	Hyo-copulo-palatinus.
L. 289-757		
R. 287-721	}	Copulo-quadratus profundus.
L. 297-734		
R. 292-478 External and Internal Heads	}	Palato-coronarius.
L. 301		
498 External Head		
485 Internal Head	}	
R. 303 —		
L. 322 —	}	Parietalis (from first myotome).
R. 346-1021		
L. 359-1014	}	Copulo-glossus superficialis.
350		
R	}	Copulo-glossus profundus.
1214 Median Head		
1445 Lateral Head		
L		
1210 Median Head	}	
1474 Lateral Head		

R. 386-599	}	Quadrato-palatinus.
L. 410-632		
R. 465-740	}	Velo-quadratus.
L. 475-757		
R. 467 —	}	Parietalis (from dorsal cranial portion).
L. 474 —		
R. 483-723	}	Hyo-copulo-glossus.
L. 489-745		
R. 557-1081	}	Copulo-quadratus superficialis.
L. 590-1087		
R. 616-784	}	Velo-spinalis.
L. 639-787		
R. 668-727	}	Cranio-hyoideus.
L. 690-777		
R. 675 —	}	Rectus.
L. 681 —		
R. 694-2490	}	Constrictor pharyngis.
L. 703-2400		
R. 854-2089	}	Copulo-copularis.
L. 852-2090		
R. 1113-2267	}	Longitudinalis linguæ.
L. 1078-2287		
1944-2291		Perpendicularis.
R. 2371	}	3304 Constrictor branchiarum et cardiæ.
L. 2094		

From Behind Forwards.

R. — 467	}	Parietalis (to dorsal cranial portion).
L. — 474		
R. — 303	}	Parietalis (to first myotome).
L. — 322		
R. — 222	}	Obliquus.
L. — 249		
R. — 675	}	Rectus.
L. — 681		
3304	}	Constrictor branchiarum et cardiæ.
R. 2371		
L. 2094		
R. 2490-694	}	Constrictor pharyngis.
L. 2400-703		
2291-1944		Perpendicularis.
R. 2267-1113	}	Longitudinalis linguæ.
L. 2287-1078		
R. 2089-854	}	Copulo-copularis.
L. 2090-852		
R. { 1214 Median Head	}	350 Copulo-glossus profundus.
{ 1445 Lateral Head		
L. { 1210 Median Head		
{ 1474 Lateral Head		
R. 1081-557	}	Copulo-quadratus superficialis.
L. 1087-590		
R. 1021-346	}	Copulo-glossus superficialis.
L. 1014-359		
R. 784-616	}	Velo-spinalis.
L. 787-639		
R. 727-668	}	Cranio-hyoideus.
L. 777-690		

R. 740-465	}	Velo-quadratus.
L. 757-475		
R. 739-273	}	Hyo-copulo-palatinus.
L. 757-289		
R. 723-483	}	Hyo-copulo-glossus.
L. 745-489		
R. 721-287	}	Copulo-quadratus profundus.
L. 734-297		
R. 599-386	}	Quadrato-palatinus.
L. 632-410		
R. 481-51	}	Tentacularis posterior.
L. 503-77		
R. 478 External and Internal Heads-292	}	Palato-coronarius.
L. { 498 External Head		
{ 485 Internal Head		
R. 441-122	}	Palato-ethmoidalis superficialis.
L. 450-126		
R. 423-201	}	Copulo-palatinus.
L. 430-222		
R. 375-63	}	Nasalis.
L. 381-72		
R. 371-123	}	Copulo-tentaculo-coronarius (P.F., minus the coronarius, however).
L. 377-151		
R. 371-7	}	Copulo-tentaculo-coronarius (F.J.C.).
L. 377-27		
R. 315-142	}	Palato-ethmoidalis profundus.
L. 319-144		
R. { 226 External Head	}	Copulo-ethmoidalis.
{ 266 Internal Head		
L. { 250 External Head		
{ 278 Internal Head		
R. 184-118	}	Coronarius (F.J.C.).
L. 203-128		
R. 142-12	}	Transversus oris.
L. 164-27		
R. 146-44	}	Tentaculo-ethmoidalis.
L. 157-51		
R. 73-30	}	Ethmoideo-nasalis.
L. 85-35		

34. *M. sphincter cloacæ*.* F.J.C. (Fig. 4, s. cl.)J. MÜLLER, *Sphincter der Cloake* (*Ab. Ak. Berlin*, 1843, p. 167, 1845).

This muscle, in a 32 cm. Hag, surrounded the whole of the cloaca except the most postero-ventral 3 mm. When a Hag is pinned out on its back and the ventral skin removed, it is seen that the obliquus muscle extends (at least) as far backwards as the base of the cloacal elevation, and there ceases. The most posterior pre-cloacal fibres of this muscle, instead of meeting in a median ventral linea as elsewhere, bent forwards immediately in front of the cloaca, and were continued forwards external to the obliquus proper for 3 mm. in a 30 cm. Hag. When these are removed it is noticed that, behind, the ventral linea becomes indistinct, and there are indications of the

* Described from dissections only.

obliquus fibres crossing over the middle line on to their opposite side, as figured by J. MÜLLER in *Myxine*. This author, however, erroneously regards these fibres as belonging to the sphincter cloacæ. I assume that he is referring to the obliquus, and not to the sphincter, because he says that the fibres arise from the parietalis, and those of the sphincter, of course, do not. Further, the true sphincter is figured behind and distinct from them. On removal of the obliquus the sphincter cloacæ is exposed, and the rectum and cloaca may now be removed, with the sphincter intact and *in situ*. It is a powerful muscle, the origin of which occupied in the above Hag the 7 mm. in front of the cloacal aperture, and commenced just behind the posterior termination of the rectus. There is no question of crossing at the origin.

The fibres of the sphincter cloacæ arise at the mid-ventral line corresponding to the linea of the obliquus, and extend from the ventral wall of the rectum on to the descending ventral wall of the cloaca, but not over the whole of the latter, as above stated. From thence they pass as a compact mass at an obtuse angle backwards, outwards, and upwards in a curve round the lateral wall of the cloaca. Arriving at the dorso-posterior wall or roof of the cloaca, the anterior half of the fibres take a forward bend and pass over into those of the opposite side at right angles to the long axis of the gut, and there is hence (apparently) no mid-dorsal linea here. The fibres forming the posterior half, however, continue their backward course, and hence meet those of the other side at an angle. Consequently there is a mid-dorsal linea here, and there are indications that it is continued forwards throughout the entire extent of the muscle, although it is not obvious in dissection. The anterior three-quarters of the sphincter lie *external* to the terminal portions of the segmental ducts, so that the muscle will also act as a constrictor to these.

35. *M. transversus caudalis*, F.J.C.* (Fig. 4, *t. c.*)

SCHNEIDER, 17, p. 114.

I had thought that this muscle had hitherto escaped notice, but it is evidently the one briefly mentioned by SCHNEIDER.

The transversus caudalis is a long, irregular, very diffuse and ill-defined muscle, developed to take the place functionally of the obliquus behind the cloaca. It is in fact an extrinsic constrictor muscle of the post-cloacal slime sacks (which, like the others, have no intrinsic musculature), and has no existence apart from them. I include here the two slime sacks generally found *opposite* the cloacal *aperture*, since these are morphologically post-cloacal.

Anteriorly there are a few fasciculi (seven in the present case, fig. 4, *obl'*) which arise like the obliquus, but at a gradually descending level, from the superficial external fascia of the parietalis, and the largest and most anterior bundle is actually serially homologous with the obliquus. These bundles may therefore be said to represent the

* Described from dissections only.

most posterior section of the obliquus, the first of which passes *external* to the first post-cloacal slime sack (instead of internal to it, as in the pre-cloacal slime sacks), to meet at a mid-ventral linea over its anterior half. This course is the less surprising when we remember that in *Bdellostoma*, according to J. MÜLLER, the obliquus *always* passes external to the slime sacks. In addition, however, to the above, the first pair of post-cloacal slime sacks have a complete set of constrictor fibres belonging to the transversus caudalis.

We may now dissect out the two rows of post-cloacal slime sacks intact, together with the transversus caudalis, and examine the muscle *in situ*. All the slime sacks except the first pair, which are symmetrical, and the second pair, which are somewhat asymmetrical,* alternate; and not only is this the case, but space is so limited that they actually interdigitate, and hence all the external apertures except the first pair strictly alternate. The two rows are bound together into one coherent whole by the transversus caudalis, which can thus act as a powerful constrictor to them. The muscle arises at an irregular, ill-defined dorsal linea, which zigzags from side to side, following the depression between the dovetailed slime sacks. Over the first two pairs of slime sacks, however, this linea is straight, and lies in the mid-dorsal position. From the dorsal linea the fibres generally pass more or less at right angles to the long axis round the lateral surfaces of the slime sacks, which (except the last three or four) are completely covered by them dorsally. The fibres continue their course round the sacks, and the two sides become continuous on the ventral surface, *i.e.* there is no ventral linea. They do not generally diverge to pass round the openings of the sacks, but many of them end on the sack itself just above the opening. Hence there are fewer fibres below the apertures than above them, although in places fresh fibres are formed below. The muscle is usually specially strong at the depression between the sacks, but, except in the case of the first pair, the fibres encircle *both* rows of sacks, and do not extend over the opposed surfaces, *i.e.* between them; and in fact the sacks are so closely packed together that there is no room. Hence there is only one constrictor for both rows, which must therefore be discharged simultaneously without the power of independent action. At the mid-ventral line the fibres diverge to allow the exit of the ventral "fin rays." Posteriorly some of the fibres, as they traverse the lateral surfaces of the sacks, pass forwards, whilst others course backwards, so that they cross at an angle.

36. *M. cordis caudalis*. (Figs. 4, 7, *cd. c.*)

G. RETZIUS, 15, p. 96.

GREENE, 8, p. 367.

A curious small fan-shaped paired muscle, largely covered by the parietalis, the handle of the fan or insertion pointing straight forwards. It arises as follows:—(*a*) the dorsal fibres have a long origin from the skeletogenous layer of the notochord at the

* This is subject to variation.

angle formed by the junction of the latter with the median ventral bar of the caudal fin skeleton. This agrees with what I find in a series of sections I have made of the entire tail region, but in one dissection the dorsal fibres arose from the dorsal margin of the median ventral bar, and certainly did not reach the chorda. This is the condition figured; (b) posteriorly it has a diffuse origin from the entire width of the ventral bar—of course behind the region of the caudal heart; (c) the ventral fibres have a long origin from the lower margin of the ventral bar and from the roots of the anterior “fin rays” fusing with the bar—in one specimen from eleven of these, in the Hag figured from seven, but in the sections from two only, the heart and large vessels intervening between the muscle and the “fin rays” in front. This part of the origin is not mentioned by RETZIUS in *Myxine*, but it is present in *Bdellostoma*, according to GREENE.

From their origin the fibres rapidly concentrate, so that the muscle now passes straight forwards as a sharply converging belly, to terminate in a narrow insertion (immediately behind the last slime sack) into the external margin of the transversely expanded extremity of the knob projecting from the anterior margin of the median ventral bar (cp. Part I., fig. 17). The entire length of the muscle in a 30 cm. Hag was 7 mm. and its greatest width 3 mm. In *Bdellostoma*, according to GREENE, the measurements were 6.3 mm. and 2.8 mm. As *Bdellostoma* is, of course, a much larger form than *Myxine*, it would seem that the muscle is not so well developed in the former genus.

The cordis caudalis muscles are crescent-shaped in transverse section, fitting over and passing external to the paired caudal hearts, each of which lies between one of the muscles and the median ventral bar. The caudal hearts possess no intrinsic musculature, but have only fibrous walls, as pointed out by G. RETZIUS and GREENE. In this respect the caudal heart differs from the portal heart, which is controlled by intrinsic musculature.

The fibres of the cordis caudalis are in marked contrast to those of the adjacent parietalis. They are striped, but have a *very small calibre*. This is not mentioned by GREENE. I refer to the character of these fibres in another part of this paper on the histology of the muscles.

The caudal hearts and their muscles were first discovered by G. RETZIUS, who briefly described them. I shall deal with the function of the muscle when I treat of the vascular system, but in the meantime I may quote the following statement by RETZIUS, based on observations of the living animal: “Bei jeder ‘Systole’ kehrte sich der Knopf der Knorpelplatte [the knob of the median ventral bar above] von links nach rechts, und dabei entleerten die beiden paarigen Hertzsäcke ihren Inhalt in die Caudalvene. Dann kehrte der Knopf wieder nach links zurück und blieb einen Moment stille; so kam eine neue Verschiebung nach rechts mit einer Ausleerung der Säcke u. s. w. Dabei waren deutlich die beiden seitlichen platten Muskeln die Motoren, welche gleichzeitig auf die Wände der Hertzsäcke drücken und den Inhalt vorwärts verschieben.” This account differs from that given by GREENE of *Bdellostoma*, and it is quite

evident from a mere examination of RETZIUS' statement that if both hearts are to discharge simultaneously, there cannot be any lateral movement of the anterior knob. GREENE's description in fact applies also to *Myxine*.

Perhaps I may here make a preliminary announcement on another question discussed by RETZIUS in the above paper. This is as to whether the caudal hearts transmit blood from the large subcutaneous space to the veins. RETZIUS concludes, on evidence communicated to him by KLINCKOWSTRÖM, that it does, and this has since been amply confirmed both by the latter and by GREENE.* In studying the question from a new point of view, *i.e.* by serial sections, it is easy to demonstrate beyond all question that the caudal hearts *are* in communication with the subcutaneous sinus. The question now arises—How does the blood enter the latter sinus? Beyond RETZIUS, who simply mentions the matter, only KLINCKOWSTRÖM has touched on this point. I may therefore mention that there are further communications *anteriorly* between the sinus and the large internal vascular cavities of the snout which provide ample opportunity for the entrance of blood into the subcutaneous sinus. In this connection the reader may refer to my description of the communications between the afferent branchial vessels and the pleural sacks (5, p. 325).

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[In this list only those works are included which contain original observations on the muscles of Myxinoids.]

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* Cp. also FAVARO's recent note.

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EXPLANATION OF PLATES.

REFERENCE LETTERS.*

<i>a. c. m.</i> Middle cutaneous artery. <i>a. c. s.</i> Superior cutaneous artery. <i>a. sp.</i> Spinalis artery, splitting into superior and inferior spinal arteries. <i>a. v. c. i.</i> Inferior cutaneous artery and vein. <i>a. v. d.</i> Dorsalis artery and vein. <i>a. v. v.</i> Ventralis artery and vein. <i>c. ao.</i> Cardiac aorta. <i>c. b. c.</i> Branchial portion } of the M. constrictor <i>c. b. c'.</i> Paired anterior limb } branchiarum et <i>c. b. c''.</i> Cardiac portion } cardiae. The numerals (1-14) indicate the regions of the muscle referred to in the text (<i>q. v.</i>). <i>cd. c.</i> M. cordis caudalis. <i>c. e.</i> External head } of the M. copulo- <i>c. e'.</i> Internal head } ethmoidalis. <i>c. e''.</i> Fused external and } internal heads <i>c. g. p'.</i> Lateral head } of the M. copulo-glossus <i>c. g. p''.</i> Median head } profundus. <i>c. g. s.</i> M. copulo-glossus superficialis. <i>c. g. s'.</i> Median slip of tendon of above to ventral skin. <i>c. g. s''.</i> Lateral slip of tendon of above to base of fourth tentacle. Between these two slips the intermediate portion of the tendon is bending round into the mouth. <i>c. h.</i> M. cranio-hyoideus. <i>c. i.</i> R. cutaneus inferior of the spinal nerve. <i>c. m.</i> R. cutaneus medius of the spinal nerve. <i>c. o.</i> M. coronarius.	<i>c. p'.</i> First division } of the M. constrictor <i>c. p''.</i> Second division } pharyngis. <i>c. p'''.</i> Third division } <i>cp. c.</i> M. copulo-copularis. <i>c. pl.</i> M. copulo-palatinus. <i>cp. t. c.</i> First or principal head } of the M. copulo- <i>cp. t. c'.</i> Posterior division } tentaculo- <i>cp. t. c''.</i> Anterior division (= Ten- } tacularis anterior of P. Fürbringer) } coronarius. <i>c. q. p.</i> M. copulo-quadratus profundus. <i>c. q. s.</i> M. copulo-quadratus superficialis. <i>c. sp.</i> R. cutaneus superior of the spinal nerve. <i>d. m. b.</i> Dorsal motor branch of the ventral root of the spinal nerve. <i>d. r.</i> Dorsal root and ganglion of the spinal nerve. Above, it gives off the dorsal sensory branch, and below, the ventral sensory branch. <i>e.</i> Vestigial eye. <i>e. n.</i> M. ethmoideo-nasalis. <i>f. r.</i> The ventral "fin rays" of the caudal fin (those at posterior extremity removed). <i>h. c. g.</i> M. hyo-copulo-glossus. <i>h. c. p.</i> M. hyo-copulo-palatinus. <i>i. c. b.</i> Inferior chondroidal bar. <i>l. lg.</i> M. longitudinalis linguæ. <i>l. p. c.</i> Large left posterior cardinal vein, connected with the small right one by an inflated anastomosis. <i>m.</i> Mucosa enveloping dental apparatus.

* Care has been taken throughout this work not to use the same letters for different structures. Hence any letters used in the present Part but not explained in this list will be found in the list given in Part I., pp. 786-7.

- mes.* Median dorsal mesentery transmitting a genito-mesenteric artery.
nas. *M. nasalis*.
obl. *M. obliquus*.
obl'. Terminal post-cloacal section of the *M. obliquus*.
ov. Ovarian portion of the hermaphrodite gonad.
par. *M. parietalis* (forming the myotomes).
p. e. p. *M. palato-ethmoidalis profundus*.
p. e. s. *M. palato-ethmoidalis superficialis*.
pl. c. External head of the *M. palato-coronarius*.
pp. *M. perpendicularis*.
pt. Peritoneum.
p. v. Portal vein, receiving vessels from the gut and the gonad.
q. p. *M. quadrato-palatinus*.
r. d. *R. dorsalis* of the spinal nerve.
rect. *M. rectus*.
r. v. *R. ventralis* of the spinal nerve.
s. ao. Systemic aorta.
sc. b. s. Subcutaneous blood sinus.
s. cl. *M. sphincter cloacæ*.
- s. d.* Segmental duct. On the right side is shown a Malpighian body opening into it, with its arterial and venous supply.
s. s. Slime sack. On the right side of fig. 1 is shown a duct and its aperture.
s. s'. Depressions on the *M. obliquus* seen on removal of the slime sacks.
sy. Sympathetic nerve or *R. intestinalis*, formed by the fusion of the two visceral branches of the vagus.
t. c. *M. transversus caudalis*.
t. e. *M. tentaculo-ethmoidalis*.
t. o. *M. transversus oris*.
t. p. *M. tentacularis posterior*.
v. c. m. s. Middle and superior cutaneous vein.
v. q. Ventral division }
v. q'. Middle division } of the *M. velo-quadratus*.
v. q''. Dorsal division }
v. r. Ventral root of the spinal nerve formed by the fusion of four rootlets.
v. s. *M. velo-spinalis*.
v. sp. Spinalis vein formed by the union of superior and inferior spinal veins.

PLATE I.

Fig. 1. Diagram illustrating the anatomy of a typical body segment of *Myrine*, reconstructed from various series of sections. Although all the structures which may occur in one segment have been projected into the same plane, the relative positions of the same are correctly indicated as found in a 19.5 cm. Hag. On the left side the distribution of a spinal nerve is shown in black, and on the right side the course of a segmental artery and vein in red and blue. On the right side the subcutaneous space, otherwise continuous round the body, is interrupted by the opening of the slime gland. It must be understood that the diagram epitomises the possibilities of a segment, and not the actual structure of every somite.

PLATE II.

Fig. 2. Reconstruction from the large series of sections of the 25 cm. Hag of the *M. constrictor branchiarum et cardiæ* of the left side. $\times 11$. The muscle is coloured red and its lacunæ black. The shape of the third gill is somewhat distorted, owing to the fact that the specimen had to be cut into three pieces in order to get it into the microtome, and one break was through the third gill. When the tissues are cut before embedding some swell more than others and project beyond the cut surface, and this disturbs the enumeration of the sections. For the explanation of the numbers, refer to the description of the muscle based on the sections in the text.

Fig. 3. Dissection from the left side of a 34½ cm. Hag, to illustrate the superficial anatomy of the muscles of the head and branchial region. $\times 3$. The following structures have been removed: *M. tentacularis posterior*; the myotomes (except dorsally in front of the gill region); *M. rectus* (except insertion and a detached portion at the level of the first gill); *M. obliquus*; greater portion of the continuous external posterior sheet of the *M. constrictor branchiarum et cardiæ*; efferent gill ducts and the ductus œsophago-cutaneus (position of latter indicated by its constrictor—14); heart and left anterior cardinal and inferior jugular veins. Tentacles 3 and 4 cut off. Tentacles, gill sacks, and the regions of the *M. constrictor branchiarum et cardiæ* indicated by numerals (cp. text). Soft cartilage, blue; hard cartilage, red. Arteries, red and cross-striated; nerves, black.

Fig. 4. Lateral dissection of the left side of the tail of a 32 cm. Hag. $\times 3$. Last two pre-cloacal slime sacks removed. Dorsal and postero-ventral "fin rays" cut away. Obliquus and parietalis cut away ventrally—the latter behind the last slime sack only to expose the *M. cordis caudalis*. Myotomes and post-cloacal slime sacks numbered from before backwards.

Fig. 5. Dissection from the left side of a 36 cm. Hag, to illustrate the musculature of the body taken at about the middle of the abdominal region. Perenyi fixation. $\times 2$. A = anterior, D = dorsal. In front, the *M. obliquus* and the slime sacks have been removed; in the middle, the slime sacks only (leaving depressions behind); whilst posteriorly the figure represents the surface of the body as seen after removal of the skin.

PLATE III.

Fig. 6. Broken series of transverse sections of the *M. longitudinalis linguæ* and its tendon, selected from the large series of a 25 cm. Hag, to illustrate the formation and fate of the tendon. Muscular tissue, red; tendinous portions, black; soft pseudo-cartilage, dotted; fibrous connective tissue, shaded. The figures refer to the numbers of the sections; and for the lettering cp. the description of the tendon of the *M. longitudinalis linguæ* in the text. In 720, two small nerves are shown dorsally cut in transverse section; and in 625, a portion of the median ventral channel formed by the mucosa of the mouth appears dorsally. All the sections were drawn with Edinger's projection apparatus to the same scale, and are $\times 26$.

Fig. 7. Transverse sections of muscle fibres, all taken from one 31 cm. Hag, fixed in formol + alcohol, and all drawn to the same scale, in order to illustrate the differences in size. Stained with Mann's methyl-blue-eosin. Zeiss apochr. 1.5 mm., apert. 1.30, compens. oc. 4.

- (a) Aplanic fibre from the *M. parietalis* at about the middle of the back.
- (b) Plasmic fibre of ditto from the same region.
- (c) Medium-sized plasmic fibre from *M. cordis caudalis*.
- (d) Plasmic fibre from the dorsal division of the *M. velo-quadratus*.
- (e) Plasmic fibre from the *M. velo-spinalis*.
- (f) Contractile elements (sarcostyles or fibrils?); (2) narrow elongated nuclei seen in transverse section (generally central, and characteristic of the aplanic fibres); (3) peripheral zone of sarcoplasm of the plasmic fibres; (4) peripheral round or oval nuclei of the plasmic fibres; (5) peripheral blood capillaries of the plasmic fibres.

PLATE IV.

Fig. 8. Superficial muscles of the dorsal surface of the head of a 25 cm. Hag, as seen after removal of the skin. Perenyi fixation. $\times 3$. The anterior lobes of the brain are seen showing through the membranous brain case in front of the second myotome. The small first myotome is not shown in the figure, being covered, as well as the ventral portion of the second, by the dorsal extension of the *M. obliquus*. Note the alternation of the myotomes of the two sides. The numbers indicate the identity of the tentacles and the myotomes.

Fig. 9. Superficial muscles of the left lateral surface of the head of a 30 cm. Hag, after removal of the skin. Perenyi fixation. $\times 3$. The dots indicate the line of insertion of the *M. obliquus* of the left side, whilst the dashes mark the line of origin of the corresponding muscle of the right side, both of which have been completely removed. The position of the first slime sack over the seventh myotome is shown by the dotted outline. Tentacles and myotomes numbered from before backwards.

Fig. 10. Superficial muscles of the ventral surface of the head of a 31 cm. Hag, after removal of the skin. Perenyi fixation. $\times 3$. The lateral portion of the *M. obliquus* is foreshortened by the perspective. The fourth tentacle is displayed to illustrate its shape. Tentacles and myotomes numbered from before backwards.

Fig. 11. Same dissection and magnification as fig. 3 (*q.v.*), but with the following additional muscles removed:—copulo-quadratus superficialis, copulo-quadratus profundus, copulo-glossus superficialis, lateral head of the copulo-glossus profundus, copulo-palatinus, hyo-copulo-palatinus, and the palato-ethmoidalis superficialis. Hard cartilage, red; soft cartilage, blue; hard pseudo-cartilage, blue dotted; soft pseudo-cartilage, obliquely striated. Tentacles numbered from before backwards.

Fig. 12. Dissection of the roof of the mouth of a $31\frac{1}{2}$ cm. Hag, to expose the skeleton and muscles of the pharyngeal velum. $\times 4$. Mucosa, *M. quadrato-palatinus*, and both heads of the *M. palato-coronarius* removed. The figure gives a ventral view of the structures shown. Hard cartilage, red; soft cartilage, blue.

Fig. 13. Dissection from the left side of a $32\frac{1}{2}$ cm. Hag, to illustrate the superficial anatomy of the posterior portion of the *M. constrictor branchiarum et cardiæ*. $\times 4$. The body-wall, the efferent gill ducts (so far as seen), cardiac cord, left anterior cardinal vein, inferior jugular vein, and vagus nerve have been removed, whilst the definite ventral muscle bundles have been cut off short. The ligamentous sheet attaching the ventral border to the body-wall is not shown. This figure should be compared with figs. 2 and 3. For explanation of the numerals, cp. text.

Fig. 14. Lateral dissection from the right side of a 34 cm. Hag, to illustrate the relations of an inter-muscular septum, as found at about the middle of the body. $\times 3$. The specimen was macerated, and the muscle fibres picked off and brushed away. *A* = anterior, and *D* = dorsal. The numbers indicate the parts of the septum from above downwards (see text).

M^r F. J. COLE ON THE MORPHOLOGY OF MYXINE. — PART II, PLATE I.

Fig. 1.

MR F. J. COLE ON THE MORPHOLOGY OF MYXINE. — PART II, PLATE II.

Fig. 2. x 11.

Fig. 3. x 3.

Fig. 4. x 3.

Fig. 5. x 2.

Fig. 6. x 26.

Fig. 7.

MR F. J. COLE ON THE MORPHOLOGY OF MYXINE. — PART II, PLATE IV.

Fig. 8. x 3.

Fig. 10. x 3.

Fig. 12. x 4.

Fig. 14. x 3.

Fig. 11. x 3.

Fig. 9. x 3.

Fig. 13. x 4.