

MANDIBULAR AND PHARYNGEAL MUSCLES OF ACANTHIAS AND RAIA.¹

GUY ELLWOOD MARION.

INTRODUCTION.

THE following paper deals only with the muscles of the jaw and branchial region in the common dogfish (*Acanthias vulgaris*), and in one of the common skates (*Raia erinacea*). The existing literature upon this subject is very scanty, and aside from a few scattered references to the muscles, I have found only the detailed papers by Vetter ('74) upon the mandibular and branchial regions of the sharks, and a similar paper by Tiesing ('95) who discusses in the same way the muscles of the skates. Drüner (:03) uses the Selachians in describing the visceral muscles of the Urodeles.

The present article follows very closely the work of Vetter and Tiesing, especially that of the former. Tiesing classifies and arranges the muscles upon the basis of innervation; Vetter upon that of position and function. That the former method has its advantages is admitted, but convenience leads me to adopt the scheme of Vetter; and although not agreeing with him in all points, I have adopted as far as possible his nomenclature and lettering of the figures. As was said above, Vetter deals only with the sharks, and Tiesing with the skates, while I have tried to draw homologies between the two groups, and this has led me at times to differ from my predecessors.

The mandibular and branchial muscles may be divided into four main groups:—

1. Superficial circular muscles.
2. Interarcuales (muscles between the upper ends of the branchial arches).
3. Adductores (flexors at the middle of the arches).

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4. Ventral longitudinal muscles.

Each of these in turn contains several muscles which are capable of arrangement under subordinate headings. In the following account, the muscles of one of the major divisions will be described for *Acanthias*, and then the corresponding muscles for *Raia*.

SUPERFICIAL CIRCULAR MUSCLES.

Of these there are seven groups:—

1. Superficial constrictors; *a*, dorsal; *b*, ventral.
2. Interbranchiales (lying between the walls of the gill clefts).
3. Levator maxillæ superioris (raising the upper jaw).
4. Trapezius (raising the shoulder girdle and drawing it forward).
5. Levator labialis superioris (raises the upper lip).
6. Levator rostri (raises the rostrum). In *Raia* only.
7. Depressor rostri (depresses the rostrum). In *Raia* only.

Superficial Constrictors.

Acanthias.

The superficial constrictors are the most external of the muscles which cover the gill pouches and form the surface of the region of the 'neck.' They may be divided, from position, into dorsal and ventral constrictors and are six in number on either side. Between them the five gill slits are placed, the first lying between the second and third, the fifth gill slit occurring behind the sixth constrictor (Figs. 1, 2). The gill slits are slit-like in character, about 18 mm. in extent, and are vertical in position, located near the ventral portion of the side of the body.

Dorsal Constrictors.—The first and most anterior dorsal constrictor (Fig. 2, *Csd 1*) takes its origin from the lateral surface of the cranium just below the posterior end of the dorso-lateral ridge. Its point of origin is not separated from that of the levator maxillæ superioris, to be described below. Its fibers run ventrally and forward, curving around the anterior wall of the

spiracle in front of the spiracular cartilages, and are inserted upon the inner surface of the lower jaw just below the 'coro-

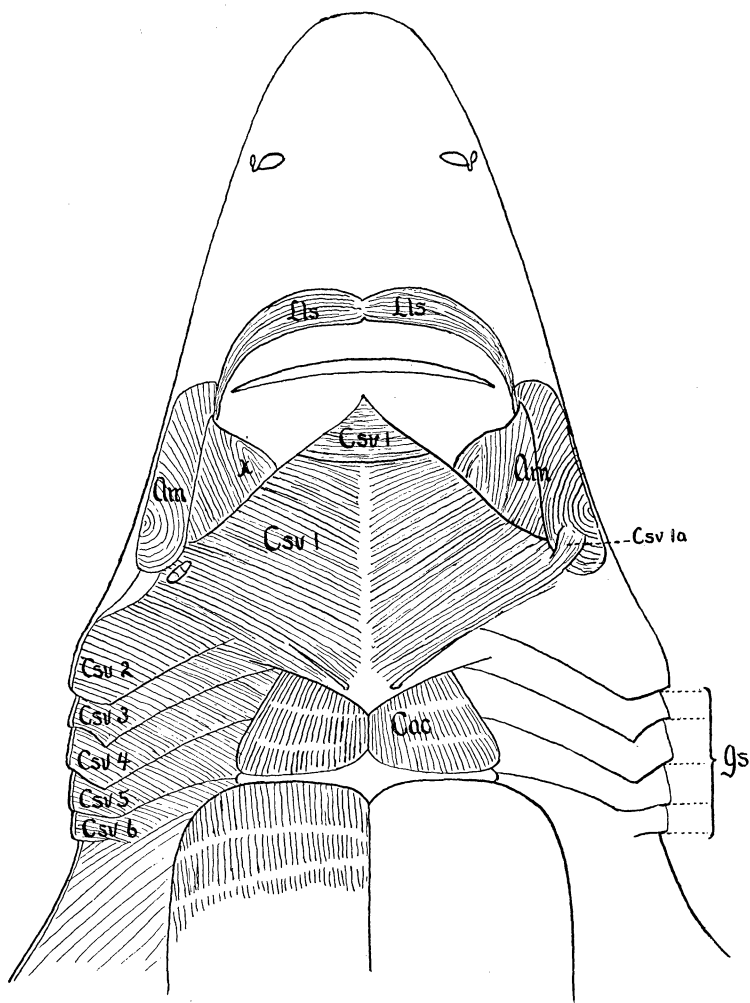


FIG. 1.—Ventral muscles of *Acanthias* after removal of skin. *Am*, adductor mandibularis; *Cac*, coraco-arcualis communis; *Csu 1-6*, constrictores superiores ventrales; *Csu 1a*, constrictor superioris ventralis, anterior fibers; *Gs*, gill slits; *Lls*, levator labialis superioris; *x*, tendon in adductor mandibularis.

noid' process. The general course of the fibers is curved, while that of the levator maxillæ superioris is straight, the only

feature distinguishing these two muscles, which Vetter does not regard as separate. I believe that of this common mass of muscles the anterior straight fibers alone represent the true levator maxillæ superioris, while the posterior curved fibers represent a

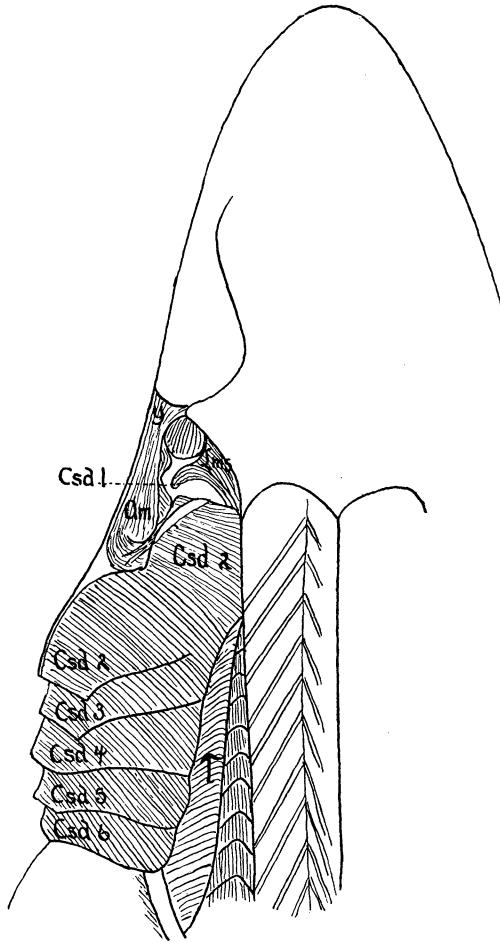


FIG. 2.—Dorsal muscles of *Acanthias* after removal of the skin. *Am*, adductor mandibularis; *Csd 1-6*, constrictores superiores dorsales; *Lms*, levator maxillæ superioris; *j*, tendinous mass back of eye; *T*, trapezius.

dorsal constrictor. In this connection Vetter ('74, pp. 420-421) says: "Die beiden Spritzlochknorpeln, welche fast senkrecht

zum Faserverlauf dieser Partie nach aussen gerichtet sind, lagern sich dabei ihrer hintern Fläche dicht an, so dass diese zu den Spritzlochknorpeln genau in dieselber Beziehung tritt, wie sie zwischen den *Mm. interbranch.* und den knorpeligen Rädien des Kiemenbogen, oder zwischen *Csd 2* und *Csv 2* und den Rädien des Zungenbeinbogen besteht."

Vetter has not carried his comparisons far enough. If these fibers nearest the spiracular cartilages bear the same relation to these cartilages as do those of the second dorsal and ventral constrictors to the rays of the hyoid arch, then why do they not represent another constrictor muscle *Csd 1* exactly like *Csd 2* in general relations? By a further comparison with *Raia* (Fig. 6) we see that the general course of the fibers of the posterior part as well as the insertion make this part distinctly comparable to the *Csd 1* of that form.

The second dorsal constrictor (Fig. 2, *Csd 2*) is by far the largest of the dorsal constrictors. It is a wide flat muscle extending from just behind the spiracle to the first gill slit. In front it arises from the postero-lateral surface of the cranium, farther back from the strongly fibrous fascia which completely covers the dorsal muscles. This origin extends as far back as the anterior end of the trapezius (Fig. 11) and even beyond that the fibers send tendinous attachments through the trapezius to their origin in the main tendinous fascia covering the longitudinal muscles. The first dorsal aponeurosis between the constrictors runs from the point where the fibers enter the trapezius in an obliquely ventral direction to the dorsal end of the first gill cleft. From this aponeurosis the more posterior fibers of *Csd 2* take their origin. The fibers of the muscles run obliquely from their origin on the dorsal margin of the muscle.

The insertion is also diverse. The most anterior fibers, which bound the spiracle behind, are inserted at the quadrate end of the upper jaw. The next fibers run around and cover the hyomandibula and are inserted upon the ceratohyal cartilage. This portion of the muscle corresponds to the levator hyomandibularis of *Raia*, where, attached to the same visceral arch, it has become much further developed. Beyond this portion the fibers are inserted upon a tendinous bridge connecting the dorsal and ven-

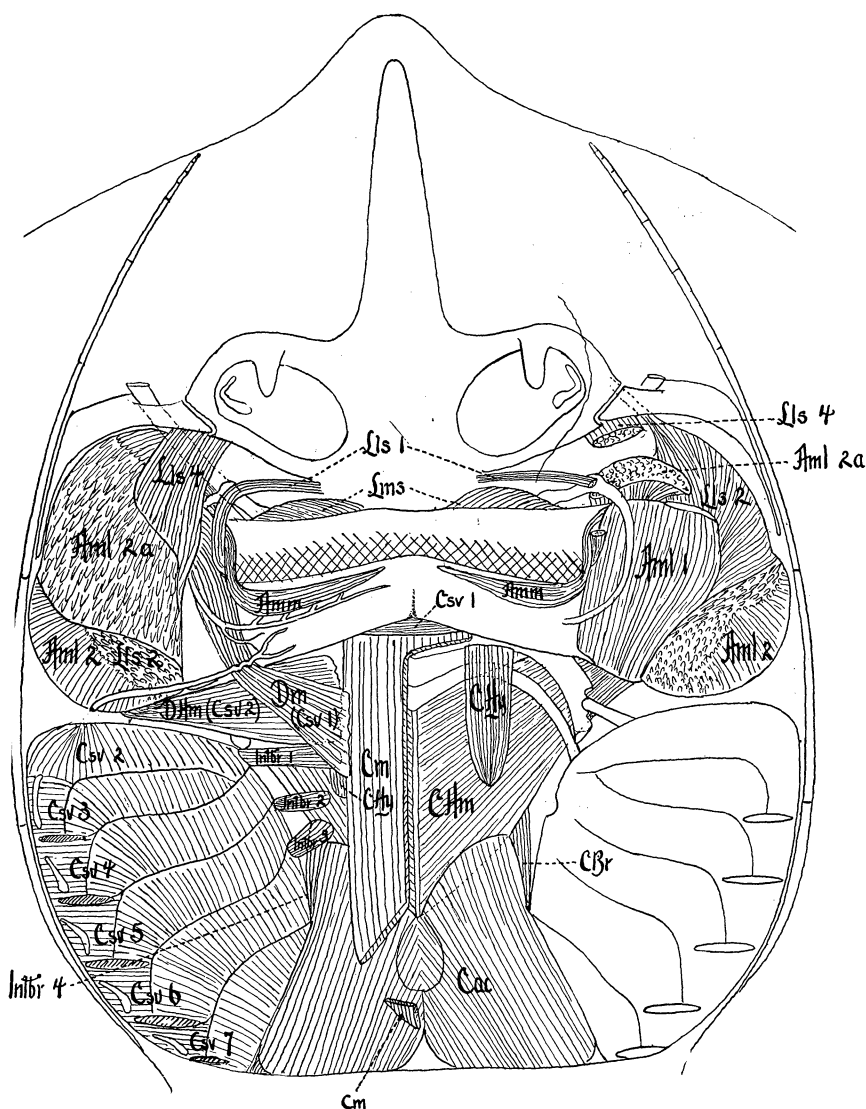


FIG. 3.—Ventral view of *Raia*, the right half a deeper dissection than the left. *Aml 1, 2*, adductores mandibularis lateralis (superficial layer, posterior); *Aml 2a*, adductor mandibularis lateralis (superficial layer anterior); *Amm*, adductor mandibularis medialis; *Cac*, coraco-arcualis communis; *CBr*, coraco-branchialis; *CHm*, coraco-hyomandibularis; *CHy*, coraco-hyoideus; *Cm*, coraco-mandibularis; *Csw 1-7*, constrictores superiores ventrales; *DHm*, depressor hyomandibularis; *Dm*, depressor mandibularis; *Intbr 1-4*, interbranchiales; *Lls 1-4*, levatores labialis superioris; *Lms*, levator maxillae superioris.

tral constrictors. This bridge extends about halfway from the end of the hyoid arch to the first gill slit. The remaining fibers pass over into those of the ventral constrictors, forming a continuous muscle. The fibers follow the direction of the gill slit in their course.

The remaining dorsal constrictors (three to six) are so closely similar that one description will serve for all (Fig. 2). The tendinous aponeuroses between them are somewhat curved, each ending at the top of a gill cleft and covering an underlying extrabran- chial cartilage. The muscle fibers run nearly vertically and those attached to the aponeuroses are often also attached to the extrabran- chials. Towards the dorsal margin some of the fibers converge to a tendon at the posterior edge of the muscle, and these tendons, after piercing the trapezius (Fig. 11, *Csd* 2-6), have their points of origin among the fibers of the dorsal longi- tudinal muscles, the last being also attached to the shoulder girdle. The more ventral fibers arise from the aponeurosis behind each muscle and are in part inserted on the aponeurosis in front, and in part continuous with the fibers of the ventral constrictors.

Ventral Constrictors.—The ventral constrictors (*Csv*) do not differ markedly from the dorsals, and like them are six in num- ber. Here I am at variance with Vetter ('74, p. 416) who does not describe a first ventral constrictor for *Acanthias*, but begins with *Csv* 2. This is, however, clearly the first ventral constrictor, while his *Csv* β 2 is really the *Csv* 2, for if we compare ven- tral with dorsal sides, we find that the muscle in front of the spiracle which is inserted on the upper jaw is, as *Raia* shows, the first, while that upon the hyoid is the second dorsal con- strictor. Just so, upon the ventral side the muscle attached to the lower jaw should be designated *Csv* 1, that upon the hyoid, *Csv* 2. With this exception my account of the ventral constrictors agrees well with that of Vetter.

On removing the skin and dissecting away the large amount of connective tissue upon the ventral side of the body (Fig. 1), we find immediately in front of the pectoral girdle, a pair of muscles, the coraco-arcuales communes (*Cac*) which, running forward, soon disappear under large sheets of muscle (*Csv* 1, 2)

which have their origin from a median line of aponeurosis and run obliquely forward and laterally to the cartilage of the lower jaw. This median aponeurosis starts at the level of the first gill slit, about half an inch in front of the pectoral girdle, and

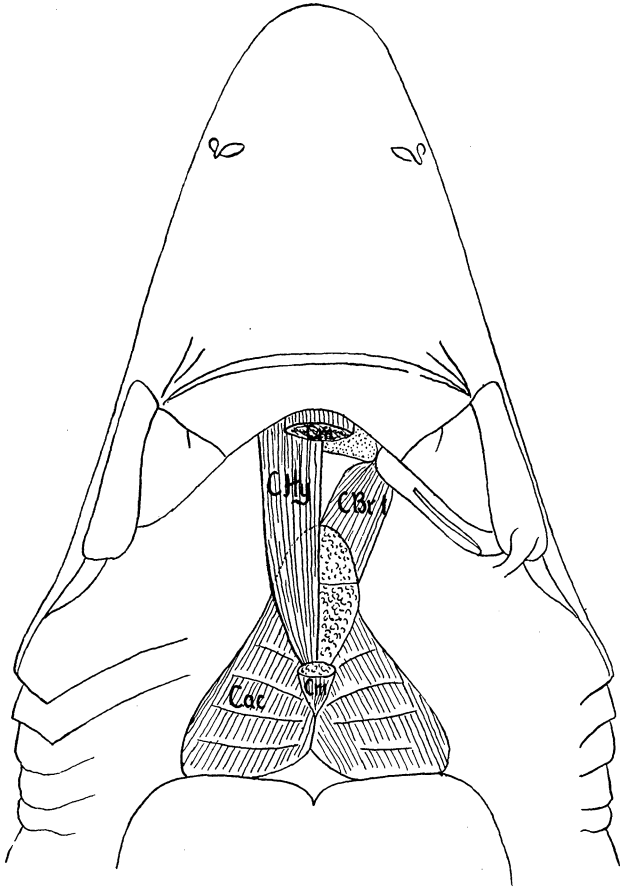


FIG. 4.—Ventral view of *Acanthias* showing the ventral longitudinal muscles. The right half a deeper dissection than the left. *Cac*, coraco-arcualis communis; *CBr 1*, coraco-branchialis; *CHy*, coraco-hyoideus; *Cm*, coraco-mandibularis.

extends to within half an inch of the symphysis of the lower jaw. The other ventral constrictors (*Csv 2–6*) are visible at either side of the coraco-arcuales communes.

The first ventral constrictor (Fig. 5, *Csv 1*) arises from the

median aponeurosis in common with, but ventral to, the second (*Csv 2*). Its fibers run obliquely forward and are inserted by means of small tendinous portions upon the ventral edge of the lower jaw. A few of the more posterior fibers (*Csv 1a*) are

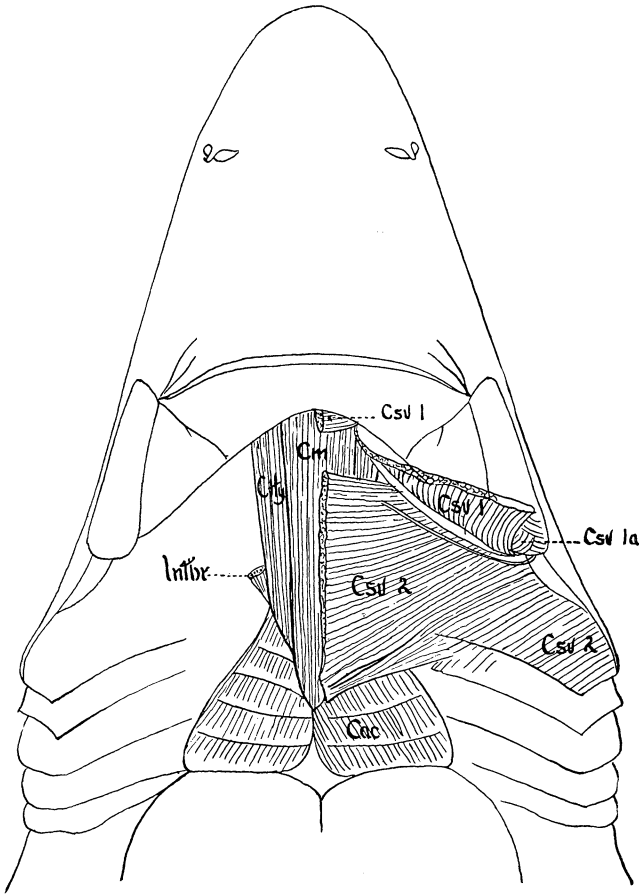


FIG. 5.—A deeper dissection of *Acanthias*. On the right, *Csv 1* has been turned back to show the whole of *Csv 2*. *Cac*, coraco-arcualis communis; *Chy*, coraco-hyoideus; *Cm*, coraco-mandibularis; *Csv 1-2*, constrictores superiores ventrales; *Csv 1a*, constrictor superioris ventralis, anterior fibers; *Intbr*, interbranchiales.

inserted upon the adductor of the lower jaw instead of upon the Meckelian cartilage, and here the fibers of *Csv 1* and *Csv 2* become fused so that at this point there is no sharply defined

margin to the first constrictor. In front the fibers of this muscle are not separated by a median aponeurosis, but run from one half of the jaw to the other.

Like the second dorsal, the second ventral constrictor (Fig. 5, *Csv 2*) is much the largest of the series. It does not extend as far forward as *Csv 1*, but, on the other hand, it extends back to the first gill cleft. About half of its fibers arise from the median aponeurosis, run parallel with those of the first ventral constrictor, and are inserted on the ventral edge of the ceratohyal cartilage. The posterior fibers, on the other hand, have their origin in the aponeurosis separating the second and third ventral constrictors, and, as they become too posterior to find attachment to the lower jaw or to the ceratohyal, they are inserted upon the fibrous bridge mentioned in connection with the second dorsal constrictor (p. 895), while still farther back the fibers run over into those of the first dorsal constrictor, passing in front of the first gill slit and running parallel to its margin.

The remaining ventral constrictors (*Csv 3*–*Csv 6*) are closely similar to each other, the only difference being in the points of origin. Excepting 3 and 6, the origin is either in the aponeurosis between each and the next succeeding muscle, or, in the case of the median fibers, from the fascia between the gill cavities and the common coracoid muscles. The most medial fibers of the second muscle take their origin, like those of *Csv 2*, in the median line ventral to the common coracoids, while the sixth has its origin in the pectoral girdle and in the fascia covering the ventral fin-muscles. The fibers of all of these muscles are either inserted in the aponeurosis in front, or are continued dorsally and laterally over into the dorsal constrictors.

The function of the constrictors is to compress the pharyngeal chamber, eject the water, and close the gill slits. The first dorsal constrictor may assist in raising the upper jaw, and the second may raise the hyoid arch, while the first and second ventral constrictors lower the under jaw and the hyoid respectively, thus assisting in the opening of the mouth.

Rai.

In removing the skin from the skate, there is less connective tissue than in *Acanthias*, the constrictors are not so conspicuous, and more muscles occur, as for instance those which control the rostrum. The muscles, too, have been altered in relative size and position in accordance with the modification of form in this extreme type, but the same general relations are easily followed.

The constrictors have increased in number to seven, and, associated with the extreme flattening of the branchial region, the dorsal and ventral constrictors are not continuous as in *Acanthias*, but are distinct, being separated at the lateral part of the branchial region by what Tiesing has called the horizontal tendon. This tendon starts from the lateral end of the hyomandibular cartilage, and running along the anterior surface of the gill region, connects with the propterygium and continues back in the lateral branchial region, affording insertion to both dorsal and ventral constrictors. Since the gill slits lie wholly upon the ventral surface, the ventral constrictors in turn have divided into median and lateral portions, the line of division occurring at the median ends of the gill clefts (Fig. 6).

Dorsal Constrictors.—The first dorsal constrictor (Fig. 6, *Csd 1*) takes its origin from the lateral labyrinth region of the skull, ventral and posterior to the postorbital process, and is continuous posteriorly with the levator maxillæ superioris, these two muscles, as in *Acanthias*, having a common origin. The fibers run forward, curving laterally along the anterior margin of the spiracle, and are inserted on the dorsal surface of the hyomandibula, a short distance from its anterior end. A sheet of fascia (*F*) to be described later, has a part of its origin from this muscle near its insertion; in part it also arises from the posterior margin of the spiracle.

The second dorsal constrictor (*Csd 2*) is larger and more differentiated than in *Acanthias*, having developed into distinct muscles with different functions—an anterior levator hyomandibularis and a posterior portion which agrees with the other constrictors in position and shape.

The levator hyomandibularis (*LHm*) arises from the postero-

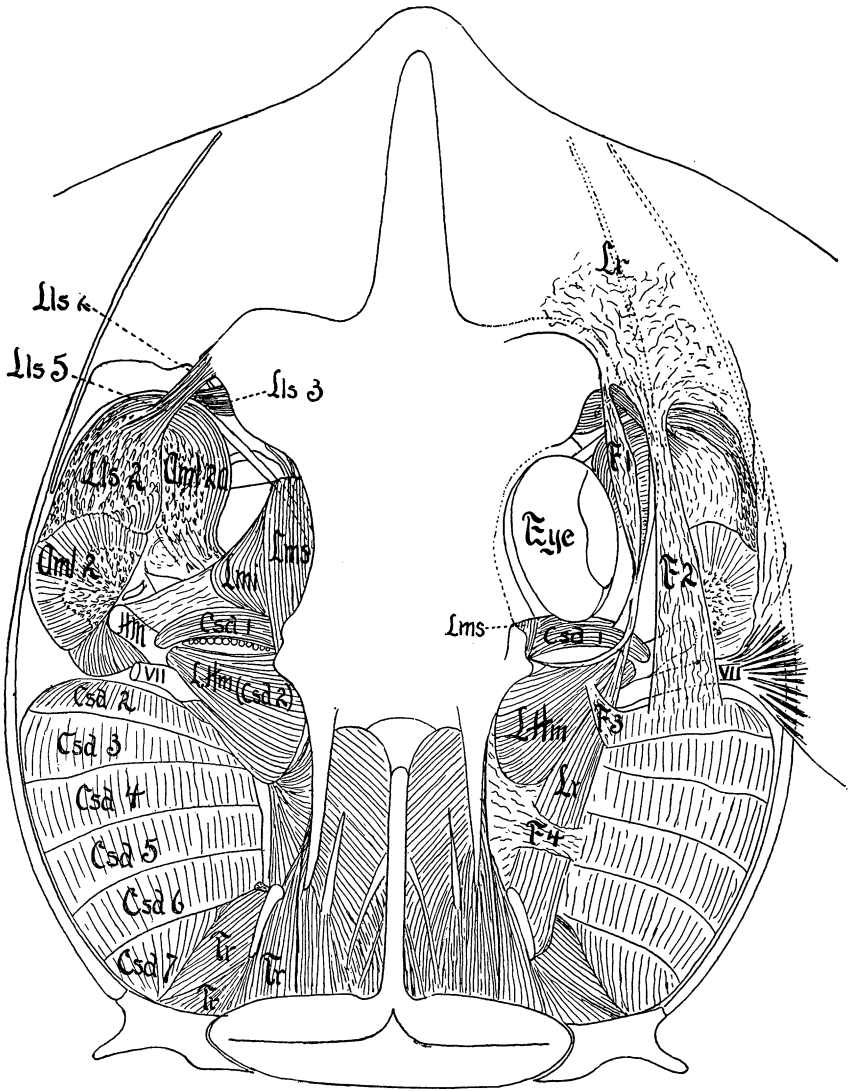


FIG. 6.—Dorsal view of *Raia*, more deeply dissected on the left. *Aml 2*, adductor mandibularis lateralis (superficial layer, posterior); *Aml 2a*, same, superficial layer, anterior; *Csd 1-7*, constrictores superiores dorsales; *F 1-4*, fasciæ; *HM*, hyomandibula; *LHM*, levator hyomandibularis; *Lls 2, 3, 5*, levatores labialis superioris; *Lmi*, levator maxillæ inferioris; *Lms*, levator maxillæ superioris; *Lr*, levator rostri; *Tr*, trapezius.

lateral part of the labyrinth region of the cranium. Its fibers run obliquely forward and outward, forming the posterior wall of the spiracle, while the large lateralis nerve penetrates the middle of the muscle in order to reach the region of the fin. The muscle is inserted upon the hyomandibula, the line of insertion beginning behind that of the first dorsal constrictor and extending the length of the rest of the cartilage. This muscle has become differentiated from the rest of the constrictor system and is only used to raise the hyomandibula.

The other more lateral and posterior portion of the second dorsal constrictor (*Csd 2*) is associated with the others of the series. Its fibers are entirely distinct from those of the levator hyomandibularis and arise from the tendon separating the second and third constrictors. This tendon is not so extensive as the succeeding and does not extend laterally to the horizontal tendon which is correspondingly interrupted opposite this point.

The remaining dorsal constrictors (*Csd 3-7*) are practically alike. Each arises from the tendon between itself and the next following muscle and is inserted on the tendon in front. The seventh forms an exception in that it is smaller than the others, and its fibers are not parallel to the main axis of the body, but converge to the point of origin upon the shoulder girdle. The intermuscular tendons incline more and more from the transverse direction as we go farther back, and, as the muscles extend to the horizontal tendon, they bend downward at the lateral margin in order to reach it. A few of the fibers of (*Csd 3*) are inserted in a strong tendon (*F 3*) which extends forward from the intermuscular tendon between constrictors 2 and 3, ventral to all the adductors of the jaws, to be inserted on the skull and surrounding tissue lateral to the nostrils.

The ventral constrictors (Fig. 3, *Csv*) are likewise seven in number. The first, instead of forming a broad sheet as in *Acanthias*, is divided into two portions, an anterior part, which extends from one mandibular half to the other just behind the symphysis, and a posterior portion. The anterior portion is not constantly present; I failed to find it in one specimen.

The posterior part of the first ventral constrictor is a flat fan-shaped muscle which arises in connection with the depressor

rostri (to be described later) in the fascia covering the coracoarcualis communis, and is inserted upon the mandible at about the center of its posterior edge. This part of this ventral constrictor thus forms a distinct depressor mandibuli (*Dm*). Only the anterior edge of the origin of this muscle can be seen until the depressor rostri (Fig. 15, *Dr*) is removed, but the method of description necessitates its mention here.

The second ventral constrictor is likewise much modified from the condition in *Acanthias*, being divided into an anterior depressor hyomandibularis (*DHm*) and a posterior second ventral constrictor proper (*Csv 2*).

The depressor hyomandibularis has its origin in the fascia overlying (ventral to) the coraco-hyoideus, the fascia connecting the depressors of the two sides dorsal to the coraco-mandibularis. The general course of the muscle is transverse to the longitudinal axis of the body. The fibers converge from a broad flat origin to a cylindrical muscle which then runs dorsally and becomes inserted upon the posterior end of the ventral edge of the hyomandibula and upon the horizontal tendon. The posterior portion of the second ventral constrictor has its origin in part in the tendon (less developed than the others) separating it from the third ventral constrictor, while the more lateral fibers are continuous with those of the third constrictor, there being no aponeurosis between them. The fibers run forward, converging from either side toward their insertion on the horizontal tendon.

Each of the remaining ventral constrictors (*Csv 3*–*Csv 7*) is composed of two parts, a large median and a smaller lateral portion, the muscle becoming smaller toward the lower limits of the gill region. The tendons separating the constrictors (the first two are united medially) run obliquely outward and backward to the median ends of the gill slits and then turn abruptly and pass to the middle of the gill slit behind, so that this portion of the tendon serves to separate the median from the lateral parts of the muscle.

The origin of the median portion of the seventh ventral constrictor is from the fascia covering the ventral edge of the coraco-branchialis. The other muscles arise from the tendon

behind. In all, the fibers are inserted upon the tendon in front, and their courses are somewhat oblique near the median side, and nearly at right angles to the body axis at their outer margins.

The lateral portions of the constrictors arise from the tendons between them and the median muscle, and the fibers run laterally to some small cartilages (not always present) and then turn dorsally to be inserted on the horizontal tendon.

Interbranchiales.

Acanthias.

It is a question whether these should be included among the superficial circular muscles or not, since they are in no sense

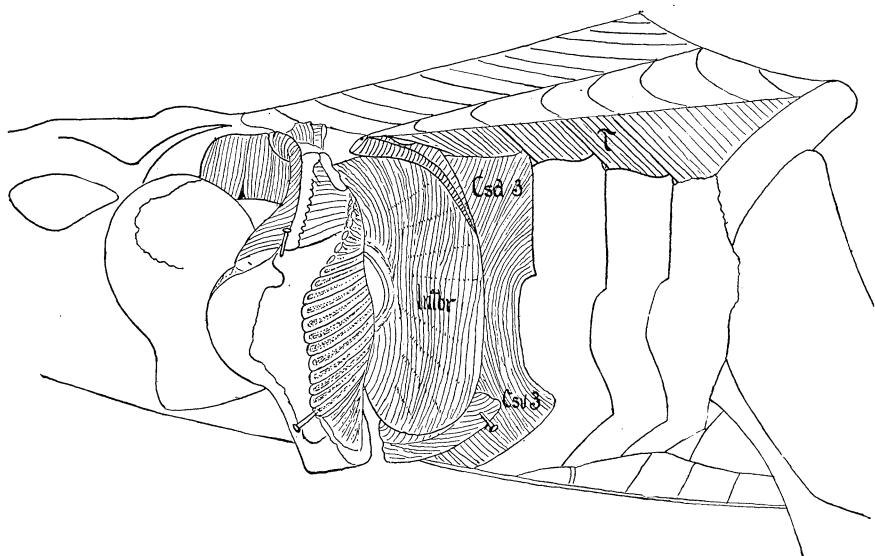


FIG. 7 — Lateral view of *Acanthias* to show the interbranchiales. *Csd 3*, constrictor superioris dorsalis 3; *Csv 3*, constrictor superioris ventralis 3; *Intbr*, interbranchialis; *T*, trapezius.

superficial, nor circular in the same sense that the other muscles are, and they lie in a different plane. However, they are closely allied with the constrictors in function, assisting in the general contraction and expansion of the gill basket, and since comparisons with Vetter are made easier, they are retained here.

These muscles (Figs. 5, 7, 8, 11, *Intbr*) are fewer in number and lie between the demibranchs of the four complete gills. Each is extremely thin and consists of a sheet of fibers, anterior to the cartilaginous gill rays, and extending between the gills

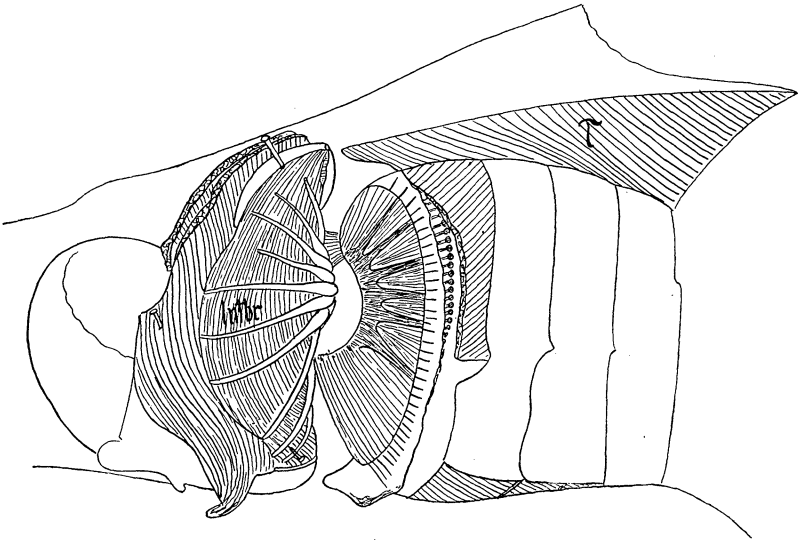


FIG. 8.—Lateral view of *Acanthias*, showing the interbranchiales (*Intbr*). *T*, *trapezius*.

from top to bottom of the septum. A tough white fascia extends from the dorsal longitudinal muscles to the extra-branchial cartilages, holding the latter in place below the aponeurosis between the dorsal constrictors, and connecting them with the interarcual muscles to be described later. The most dorsal of the interbranchial muscle fibers arise from the fascia just described, while the rest have their origin in the aponeurosis between the dorsal constrictors. The more median of the fibers curve outward and downward toward the median line, to become inserted on the anterior margin of the epibranchial cartilage (Fig. 7). The more lateral fibers are larger and follow a broad curve from the dorsal to the ventral side of the gill septum, and thus pass into the ventral fibers about to be described, just as the dorsal and ventral constrictors merge in part into each other.

The ventral fibers arise from the extrabranchials as well as

from the tendinous fasciæ connecting these cartilages, while the fibers on the median side arise from the fascia between the longitudinal muscles (Fig. 5 shows an instance of origin at the end of the common coraco-arcualis). This point is of some importance in the interpretation of the condition in Raia. The fibers near the middle line are inserted upon the anterior surface of the cerato-branchial cartilage, while the lateral fibers are continuous with those of the dorsal side as noted above. Often the muscle fibers stop at a gill ray, the tissue becoming aponeurotic, and then the muscle fibers continue on the other side.

These interbranchial muscles draw the gill radii together and thus aid in the contraction of the gill basket. In the case of the hyoid arch, the second dorsal and ventral constrictors replace the interbranchialis, since here the gill radii lie immediately beneath the surface (constrictor) muscles.

Raia.

The interbranchiales of Raia are much like those of Acanthias in position and number, the muscle of the first arch being replaced by the posterior part of *Csv2* and *Csd2*. Owing to the shape of the branchial region they do not form a continuous arc but are divided into a dorsal and a ventral portion, so that the line of division coincides with the angle separating the halves of each branchial arch. The muscle fibers of the dorsal portion arise from the aponeuroses between the dorsal constrictors, and run ventrally (Fig. 12) until they become inserted upon the dorsal surface of the epibranchial cartilages or upon the ray which runs out from the angle to the horizontal tendon. The ventral fibers take their origin from the tendons between the ventral constrictors and run dorsally to their insertion upon the ventral surfaces of the cerato-branchials or upon the horizontal ray just referred to. The fibers never become continuous, as in Acanthias, from dorsal to ventral surfaces. A few bundles of the most median fibers of the ventral portion are overdeveloped, and have extended so as to take their origin from fasciæ covering the coraco-mandibularis muscle (Fig. 3, *Intbr*). A similar condition was noted above for Acanthias but these fibers were not as

prominent there as here. Tiesing, basing his opinion on the work of Vetter upon *Heptanchus*, has regarded these fibers as a deeper layer of the constrictor but *Acanthias* shows this not to be tenable. There is no resemblance to a constrictor. In the case of the fourth arch the corresponding fibers extend into

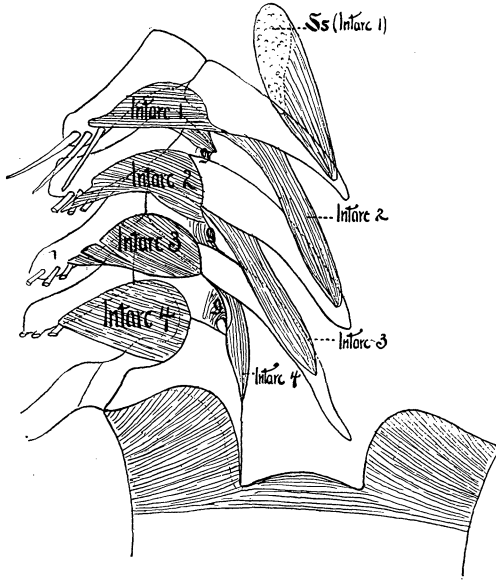


FIG. 9.—Dorsal view of gill arches of *Acanthias* to show the interarcuals. *g*, groove; *Intarc 1-4*, interarcuals; *Ss*, subspinalis.

tough tendons connected with the coraco-arcualis communis muscle (Fig. 3). On the dorsal side there is but one instance of this extension of the interbranchials (Fig. 6, at the inner posterior angle of *Csd 6*). A few fibers take their origin from the sides of the first vertebra. This could not be considered a constrictor.

This muscle (Figs. 2, 11, 14, *Lms*), already mentioned in connection with the first dorsal constrictor, arises in common with it from the lateral surface of the cranium just posterior to the

postorbital process. It is larger than the first dorsal constrictor and fills the entire bay back of the postorbital process. The fibers extend anteriorly and ventrally to their insertion on the dorsal margin of the palatal process of the upper jaw, just anterior to the attachment of the first dorsal constrictor. In fact the only distinction that can be drawn is that in the levator the fibers go directly to the jaw while those of the first dorsal constrictor curve around the anterior margin of the spiracle.

Raia.

In the skate the levator of the upper jaw (Figs. 3, 6) is composed of a thick dorsal and a thinner ventral layer, the two united at their point of insertion. The thicker layer (*Lms*) arises from the side of the skull, just ventral to the postorbital process, and its fibers run almost straight forward, then dorsal and backward in front of the oral cavity to their insertion on the upper jaw. The thinner and more ventral layer (*Lmi*) arises just below and behind the facial foramen whence its fibers run forward, laterally, and backward to unite with the dorsal layer. This course involves a strong lateral bend from which a strip of fascia extends to the hyomandibular cartilage (Fig. 6). Some of the more ventral fibers are inserted in the membranous wall of the roof of the mouth.

Tiesing maintains that the levator maxillæ superioris is only a deeper part of the first dorsal constrictor,—a view rendered very probable from the relations in *Acanthias* in which the conditions are the more primitive. It is very similar to a constrictor in origin and function, although differing widely in form.

Trapezius.

Acanthias.

The trapezius (Figs. 2, 7, 8, 11, *Tr*) has its origin in fascia covering the sides of the dorsal longitudinal muscles. Its fibers arise from a straight line extending from the posterior end of the cranium to the dorsal part of the shoulder girdle, although the

muscle extends through only the posterior three fourths of this. The fibers, which become thinner posteriorly, run obliquely downward and backward, the majority being inserted on the anterior edge of the pectoral girdle, while the more anterior fibers turn directly downward and are inserted on the dorsal edge of the last branchial arch. At intervals tendinous strands of the dorsal

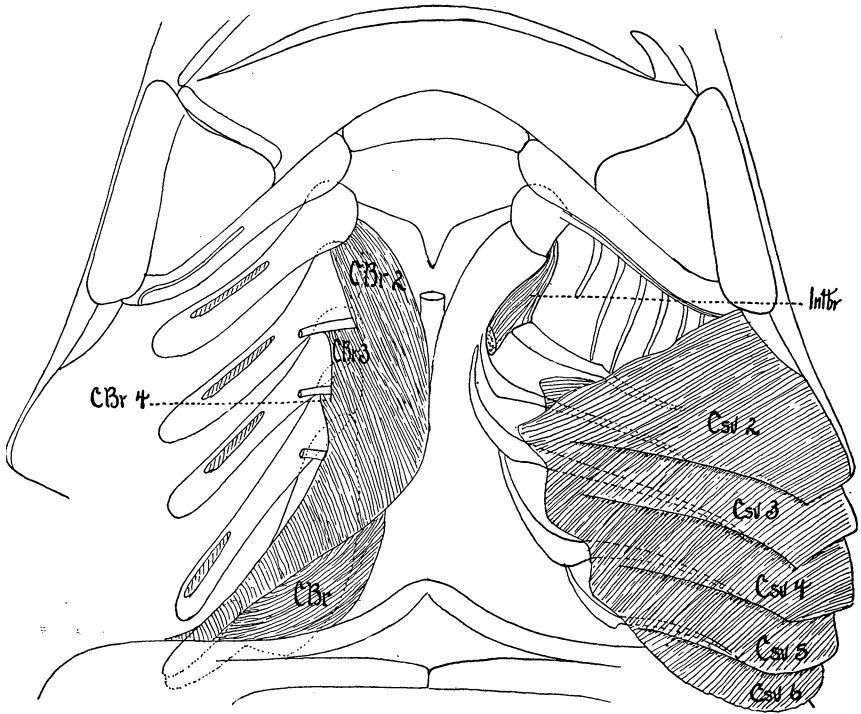


FIG. 10.—Ventral view of *Acanthias* showing the coraco-brachiales. *CBr*, coraco-brachiales; *Csd 2-6*, constrictores superiores dorsales; *Intbr*, interbranchialis.

constrictors (Fig. 11, *Csd*) as already described, pass through this muscle. The function of the trapezius is to raise the girdle and draw it forward.

Raia.

A trapezius has not been described in the skates but there occurs here a muscle (Fig. 6, *Tr*) which in its attachments and

the direction of its fibers somewhat resembles it although it does not in all respects fulfill the conditions found in *Acanthias*. There are here three parts to the muscle: a small median portion and two more lateral in position.

The median, the smallest, arises from the side of the first vertebra and its fibers run obliquely backwards to be inserted on the anterior edge and ventral surface of the suprascapula. The most lateral portion arises near the first and its fibers run obliquely backward and outward to the insertion upon the upper surface of the last visceral arch and on the anterior edge of the girdle far down towards the ventral edge. The remaining portion arises just ventral to the part just described and its fibers are attached to the scapular portion of the pectoral girdle. (In *Raia radiata* the median portion is greatly reduced and its origin is from the lateral process of the vertebra, just back of that of the next division.)

The two lateral portions of the muscle in *Raia* are apparently partly antagonistic, that first described elevating, the other depressing the girdle to a certain extent.

Levator Labialis Superioris.

Acanthias.

Although Vetter classifies this muscle among the adductors he says ('74, p. 448): "Er erscheint als seriales Homologon des M. levator max. sup. und aller der andern Theile des grossen Constrictors, welche vom Schadel oder von der epaxionischen Muskulatur zu der Visceralbogen gehen, und ist sonach passenden als M. levator labii sup. zu bezeichnen." For this reason I have included it among the other similar constrictors. This muscle (Fig. 1, *Lls*) has its origin from the ventral surface of the cranium, in front of the basal process and to one side of the middle line. The fibers run outwards and backwards, describing an arc to the angles of the mouth where they converge to a straight fibrous tendon which passes dorsal to the labial cartilages, crosses the angle of the mouth at right angles, and is inserted among the fibers of the adductor mandibularis.

Raia.

The levator labialis superior in the skate has been differentiated into five parts (Figs. 3, 6, *Lls* 1-5). Of these the first (*Lls* 1) most nearly resembles the single muscle of *Acanthias*. It is small, cylindrical, and arises from the ventral surface of the cranium near the orbit and just behind the base of the ethmoid process. It runs laterally and then backward to the angle of the mouth, which it passes, to become inserted in the fascia

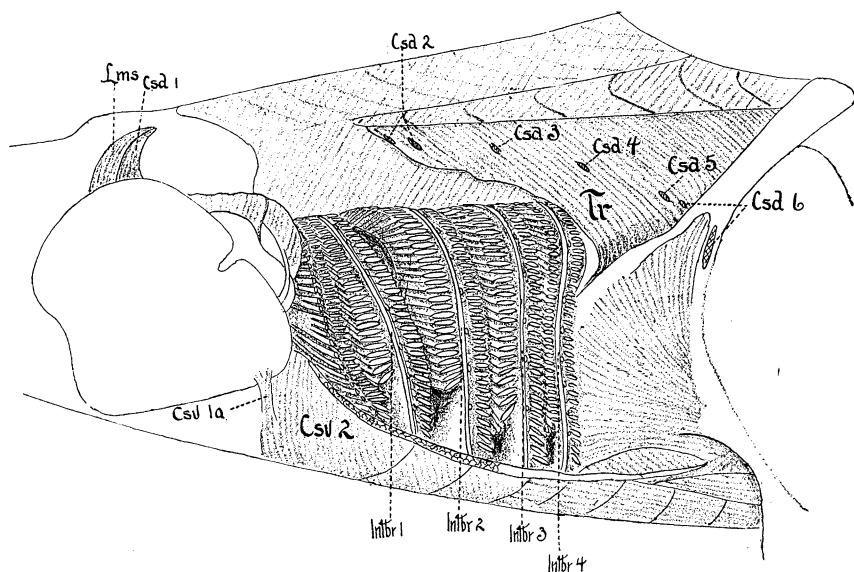


FIG. 11.—Lateral view of *Acanthias* showing interbranchiales and trapezius. *Csd* 1-6, constrictores superiores dorsales; *Csl* 1a, constrictor superioris ventralis, anterior fibers; *Csl* 2, constrictor superioris ventralis 2; *Intbr* 1-4, interbranchiales; *Lms*, levator maxillae superioris; *Tr*, trapezius.

between the adductores mandibularis medialis and lateralis which it separates.

The second division (Fig. 6, *Lls* 2) is much the largest of the labial muscles. It arises from the dorsal surface of the most lateral part of the ethmoid region in front of the antorbital process. The origin is small and of rather soft fibrous material. After passing dorsally of the large mass of the adductor man-

dibularis lateralis 2*a*, it widens into a large muscle which disappears under the adductor mandibularis lateralis 2 to become inserted on the mandibular cartilage while a portion of its fibers become confused with the posterior portion of *Aml* 2 (Fig. 3).

The third division (Fig. 6, *Lls* 3) is the smallest of the system: a short thick muscle running from the postero-lateral edge of the dorsal surface of the nasal capsule, laterally, to the posterior dorsal angle of the antorbital process, the fibers converging towards the insertion.

The fourth division (Fig. 3, *Lls* 4) is broad, thin, and flat, and its origin is continuous with and ventral to that of the third division. It lies upon the adductor mandibularis lateralis and covers a portion of it ventrally. The mandibularis branch of the fifth nerve runs between the two. Its general course is posterior and the fibers which are not inserted in the fascia covering the adductor mandibularis lateralis converge to a strong tendon, which makes its way through that muscle, to their insertion on the ventral surface of the mandible.

The fifth division (Fig. 6, *Lls* 5), though included by Tiesing among the muscles, is but a group of strong tendinous fibers having its origin just posterior to that of the second division and its insertion on the strong fascia enveloping that muscle. Muscular tissue is lacking in it, and it is scarcely more than a second origin of that muscle.

Levator Rostri.

This muscle (Fig. 6, *Lr*), together with the next, would be treated first among the superficial muscles were we describing Raia alone, but since it is lacking in Acanthias it has been left until now. Upon removing the skin from the dorsal surface, the levator rostri is the first seen and most superficial of the muscles. It takes its origin from the lateral edge of the lateral process of the first vertebra which projects above the surrounding muscles, and from the tendinous fascia covering the muscles in this region. The fibers run obliquely forward, converging to the region where they cross the levator maxillæ superioris and the first dorsal constrictor where they pass into a strong cylin-

drical tendon. This tendon continues forward, passing outside the spiracle and the eye and over the various jaw muscles and the antorbital cartilage, into the fascia of the rostral region where it is inserted in the strong membranous tissue stretching between the rostrum and the propterygium.

Depressor Rostri.

The depressor rostri (Fig. 15, *Dr*), the antagonist of the last, is a broad, flat, thin muscle arising from the fascia covering the coraco-mandibularis and from the fibers of the coraco-arcualis communis. The muscle extends forward and outward in the direction of the adductor muscles where some of the lateral fibers are inserted in the white fascia covering these muscles,¹ while the majority are collected into a strong tendon which extends forward, lateral to the nasal capsule and ventral to the antorbital process, then coming towards the median line is inserted in the membranous tissue between the tip of the rostral cartilage and the propterygium.

INTERARCUALES.

Acanthias.

The interarcuales (Fig. 9) are divided into two systems of muscles: one more medial, the other more lateral in position, each consisting of four muscles, similar in function, the first of the medial system being the subspinalis of Vetter ('74, p. 444).

Medial System.—The most anterior of the medial interarcuales has been treated as a distinct muscle, the subspinalis, by Vetter but as it agrees closely with the others in function and differs only in its origin from the rest, it is here regarded as but one of the set. Its origin is from the fascia on the under side of the dorsal longitudinal muscles, from the vertebræ near the cranium, and from the under side of the cranium itself just in front of the foramen magnum. From this broad origin it

¹ In *Raia radiata* most of the fibers have this insertion, while a small proportion are continued into the rostral depressor tendon.

tapers to a tendon which is inserted upon the dorsal posterior end of the first pharyngo-branchial. It draws the first pharyngo-branchial forward in the same way that the succeeding muscles draw the pharyngo-branchials upon which they are inserted.

The second, third, and fourth medial interarcuales arise from the posterior surface of the first, second, and third pharyngo-branchials respectively, a little in front of the middle of each and are inserted upon the dorsal surface of the second, third, and fourth pharyngo-branchials. The point of attachment is at about the middle of the cartilage except in the case of the second where the attachment is behind the middle. These muscles have a larger surface of insertion than of origin and decrease in size from in front backwards.

Lateral System.—A description of the first of the four will answer for the first three muscles of this system. The first lateral interarcuale has a double origin. The majority of the fibers arise from the posterior edge of the anterior end of the first pharyngo-branchial and a few from the anterior end of the second pharyngo-branchial just in front of the groove (*g*) for the passage of the blood vessel. The fibers are inserted on the dorsal surface of the epibranchial along a line which is a continuation of the line of insertion of the interbranchial muscle. Some of the fibers are inserted so far laterad as to be in front of the most dorsal gill rays, so that the muscle appears to be almost a portion of the interbranchial which has been forced deeper for its origin. The last lateral interarcuale differs from the rest only in its origin. Since the fourth and fifth pharyngo-branchials are fused the origin is not divided.

Raia.

The interarcuales are much reduced in the skate; indeed only the lateral system persists while the medial system is represented by non-muscular membranes connecting the pharyngo-branchial cartilages in the same way. Each of the muscles of the lateral system arises from the posterior edge of the anterior end of the pharyngo-branchial and is inserted upon the medial end of the epibranchial of the same arch.

It may be a question whether the interbranchiales, the interarcuales, and the adductores (next to be described) do not form a system of deep as opposed to the superficial constrictors. Each contributes toward the constriction of the whole branchial region, and, with the exception of the largest mandibular adductor, each lies beneath the more superficial system.

ADDUCTORES.

The adductor muscles draw together the ventral portions of each visceral arch. In the case of the mandibular arch they close the mouth, while in the gill arches they occur at the lateral hinge and approximate the ceratobranchial and epibranchial por-

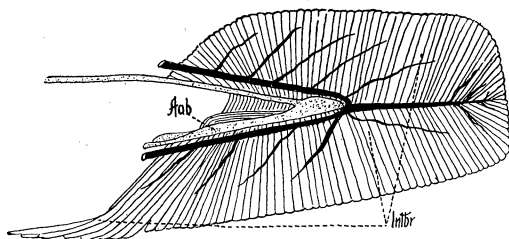


FIG. 12.—Anterior side of interbranchial muscle of *Raia*. *Aab*, adductor arcus branchialis; *Intbr*, interbranchiales.

tions of each. The adductors of the first (mandibular) arch are enormously developed in correlation with the use of these parts, while those of the gill arches are very small. In *Acanthias* the adductors are much simpler than in *Raia*.

Adductores Mandibulares.

Acanthias.

The mandibular adductor (Figs. 1, 2, 13, 14, *Am*) has a very strong tendinous envelope. Its fibers arise from the quadrate region of the upper jaw, and are attached to the entire lateral surface as well as to the medial surface of the muscle process on its dorsal margin. The course of the fibers is down-

ward and backward to the lower jaw where they are attached to the entire width of Meckel's cartilage. The details of the course of the fibers are rather difficult to express. On the lower jaw (Fig. 1) they extend nearer to the middle line than on the upper, and this portion (*x*) instead of coming from the fascia which separates it from the rest, comes from the posterior part of the upper jaw. A strong tendon is attached to this part which runs forward into the levator labialis superioris muscle. Other fibers are specialized in function. A broad thin sheet of fibers is extended on the upper half of the adductor and has its true origin from the under surface of the postorbital process, while a strong mass of tendinous material at the angle of the eye (Fig. 13, *y*) gives origin to some of the fibers. A few fibers of the first ventral constrictor, which have already been referred to as *Cstr Ia*, are attached to the outer surface of the adductor.

Raia.

In the skate the adductor muscles are more complicated. They cover and surround the lateral ends of the jaws and are divided into distinct and easily separated layers. Following Tiesing, they may be grouped into a small medial, and a larger lateral portion, the latter in turn divisible into deeper and superficial layers.

Adductor Mandibularis Medialis.—This, the smallest of the adductors (Figs. 3, 6, *Amm*) arises from the anterior edge of the upper jaw. Its fibers run back across the angle of the mouth and then medially to become inserted near the anterior (occludent) margin of the lower jaw not far from the symphysis. Its origin is in common with the deeper layer of the lateral adductor and the two separate where the levator labialis superioris passes to become attached to the fascia between them.

The *adductor mandibularis lateralis* is subdivided into a deep layer (Figs. 3, 6, *Aml 1*), and a more superficial portion (*Aml 2* and *Aml 2a*). The deep layer is largely covered by the superficial. The majority of its fibers arise from the anterior edge of the upper jaw as well as from the entire outer surface of the muscle process, and they find their insertion upon the outer surface of the lower jaw about opposite the point of origin.

The second division of the levator labialis superior, in its course to its insertion on the ventral surface of the lower jaw, crowds into the superficial layer of the lateral mandibular adductor, separating it in part into anterior and posterior portions. The anterior of these divisions (*Aml 2a*) arises in part from the dorsal surface of the lower jaw, directly opposite to its point of attachment to the deeper layer, and in part from the ventral

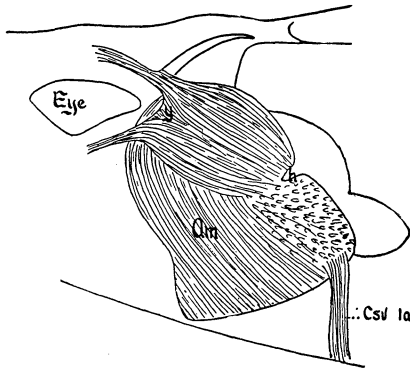


FIG. 13.—Lateral view of adductor mandibularis of *Acanthias*. *Am*, adductor mandibularis; *Csu Ia*, constrictor superioris ventralis, anterior fibers; *y*, tendinous mass back of eye.

surface by means of a very strong fibrous tendon. It runs forward, passing dorsally to the upper jaw and immediately broadens out into a large mass of fibers which curve ventrally and run backward, covering the deeper layer of the adductor and finally becomes inserted upon an aponeurosis surrounding the deeper layer. From this aponeurosis the fibers start again and continue backward, completely encasing the ends of both jaws, to the insertion directly and by means of tendons upon the lower jaw.

Adductores Arcus Branchialis.

The hyomandibular and hyoid cartilages are bound together at their articulation by strong ligaments, but no adductors are present connecting the two. In the branchial arches proper such muscles occur.

Acanthias.

A few short adductor muscle fibers extend between the cerato- and epibranchial cartilages of each branchial arch. They have their origin in small grooves on the inner surface of the epibranchials and are inserted in similar grooves on the inner (dorsal) surfaces of the ceratobranchials. Their function is to flatten the branchial region.

Raia.

In the skates (Fig. 12, *Aab*) the adductors of the branchial arches closely resemble those of *Acanthias*. They arise from

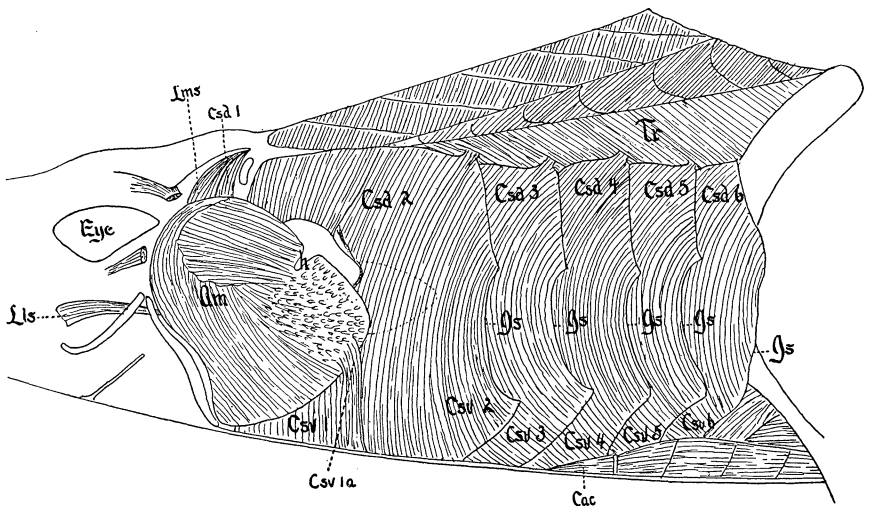


FIG. 14.—Side view of *Acanthias* after removal of the skin. *Am*, adductor mandibularis; *Cac*, coraco-arcualis communis; *Csd 1-6*, constrictores superiores dorsales; *Csv 1-6*, constrictores superiores ventrales; *Csv 1a*, constrictor superioris ventralis, anterior fibers; *Gs*, gill slits; *h*, hinge of jaws; *Lls*, levator labialis superioris; *Lms*, levator maxillae superioris; *Tr*, trapezius.

and are inserted in similar grooves in epi- and ceratobranchial cartilages, while a few of the fibers extend some distance along the ceratobranchial before finding their insertion.

VENTRAL LONGITUDINAL MUSCLES.

The location and character of these muscles is apparent from this name. In *Acanthias* they are usually thick and solid, while, correlated with the depressed body, they are flat and thin in *Raia*.

Coraco-mandibularis.

Acanthias.

In the dogfish the coraco-mandibularis is an azygos muscle lying in the median line of the body, and is exposed (Fig. 5, *Cm*) by removing the ventral constrictors. It is the most superficial of the ventral longitudinal muscles. It arises from the fascia between the coraco-arcuales communes and its fibers rapidly diverge near the origin, where the muscle is nearly circular in section, to form a flattened band which is inserted on the posterior edge of the lower jaw on either side of the symphysis.

Raia.

In the skate the coraco-mandibularis (Figs. 3, 15, *Cm*) also lies in the median line but is not covered by the ventral constrictors, since these are here more lateral in position, with the exception of a few fibers (Fig. 3, *Csv 1*) already described. In origin and insertion there is a close agreement with *Acanthias*, but the muscle is thinner and flatter than in that form. With the exception of the depressor rostri and the depressor mandibuli, whose origins overlap its margin, it is the most superficial of all the ventral muscles.

Coraco-hyoideus.

Acanthias.

The coraco-hyoideus muscles (Fig. 4, *Chy*) are exposed by removing the coraco-mandibularis, which lies close to the median line. They are the largest of the ventral longitudinals.

The origin of each is very long, extending along the fibrous aponeurosis between it and the coraco-branchialis and the coraco-arcualis communis, from beneath the origin of the coraco-mandibularis halfway to its insertion on the ventral side of the hyoid copula just behind the lower jaw. The muscle is as thick as broad and only diminishes slightly in size in front.

Raia.

In the skate the coraco-hyoideus muscles (Fig. 3, *Chy*) are reduced, flat, and thin. Each arises from the fascia covering the large coraco-hyomandibularis, near the origin of the second interbranchial muscle and is inserted upon the ventral surface of the hypohyal cartilage. It lies deeper than the depressor rostri, the depressor mandibularis, and the depressor hyomandibularis, and directly upon the coraco-hyomandibularis.

Coraco-branchialis.

Acanthias.

The coraco-branchialis (Figs. 4, 10, *Cbr*) is the deepest and most dorsal of the ventral longitudinal muscles and forms the lateral wall of the pericardial cavity. It is composed of five parts, of which the last four have a common origin. The first division (*Cbr 1*) arises from an aponeurosis directly beneath the coraco-hyoideus, and running dorsally becomes inserted on the dorsal surface of the medial end of the hyal cartilage. It is much shorter than the ceratohyoid and is contracted near its insertion.

The four remaining coraco-branchials (Fig. 10, *Cbr 2-4*) arise from a strong membrane running from the girdle to the origin of the ceratohyoid. As the fibers pass forward and laterally they divide into separate portions, the anterior of which becomes inserted on the branchial arches, while the last, which is much the largest, is inserted upon the fifth arch and upon the lateral half of the copula. Blood vessels pass through the arches between the divisions of the muscle.

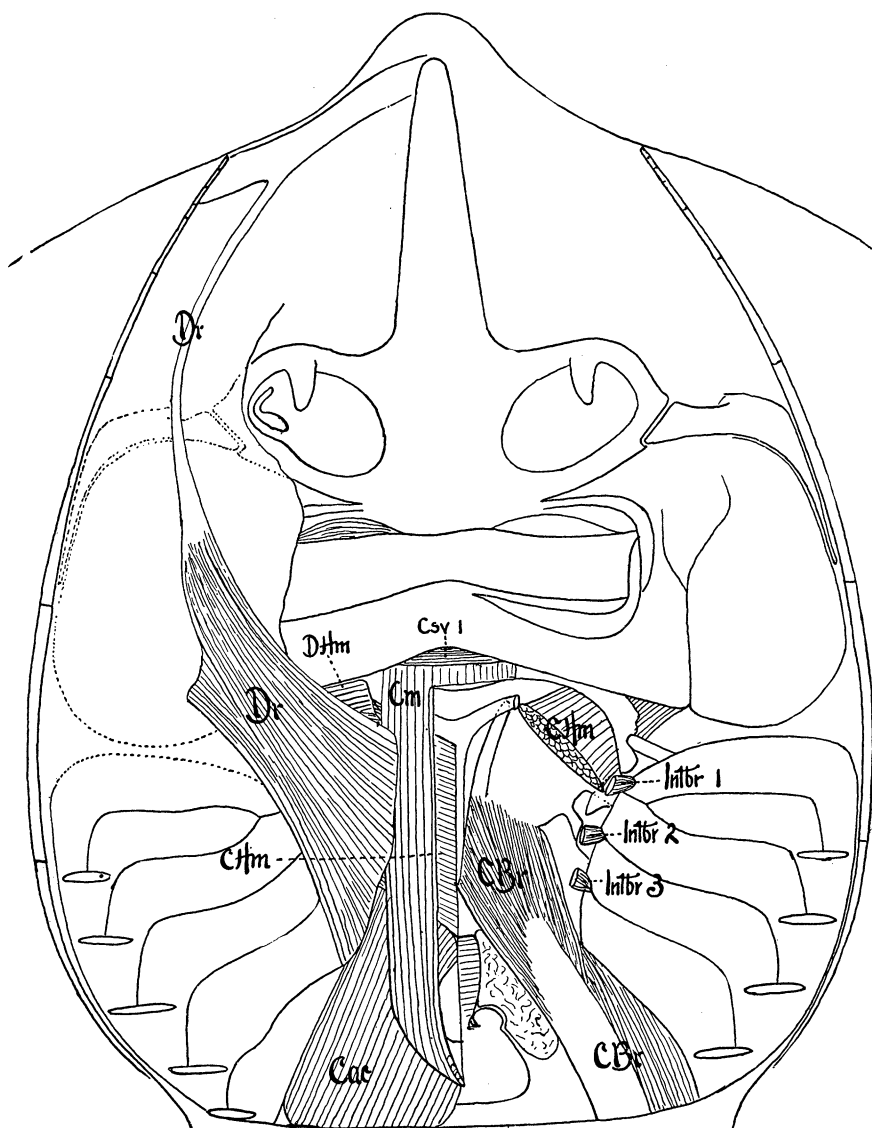


FIG. 15.—*Raia*, ventral view, after removal of the skin; right half more deeply dissected. *Cac*, coraco-arcualis communis; *CBr*, coraco-branchialis; *CHm*, coraco-hyomandibularis; *Cm*, coraco-mandibularis; *Csv 1*, constrictor superioris ventralis 1; *DHm*, depressor hyomandibularis; *Dr*, depressor rostri; *Intbr 1-3*, interbranchiales.

Raia.

In *Raia* this muscle (Fig. 15, *Cbr*) which forms the lateral wall of the pericardial cavity, arises from the pectoral girdle. Farther forward the muscle expands and the tendon gives place to muscle fibers which are inserted on the anterior process of the basibranchial and the membranous floor of the mouth. The other fibers run dorsally and become attached to the ends of the cerato- and hypobranchials. The divisions between these parts, as in *Acanthias*, permit the passage of blood vessels, and extend nearly back to the origin dividing the muscles into superimposed layers.

Coraco-arcuales communes.

Acanthias.

The paired coraco-arcuales communes muscles (Figs. 4, 5, *Cac*) lie immediately beneath the skin and arise from the coracoid region of the girdle. The fibers run inward and forward, and the medial fibers become inserted in the strong membrane which forms the floor of the pericardium, while the lateral parts are inserted upon the fascia dorsal to the origin of the ceratohyal. Each muscle is crossed by four myosepta, which makes it resemble somewhat the ventral body muscles behind the girdle.

Raia.

In the skate (Figs. 3, 15, *Cac*) this muscle closely resembles that in *Acanthias* in origin, direction, and insertion.

Coraco-hyomandibularis.

This wide, comparatively thick, and long muscle occurs only in *Raia* (Figs. 3, 15, *Chm*) of the forms studied, where it is the largest and most important of the ventral longitudinal muscles. It arises from a fascia in the middle line, and runs forward nearly to the division of the ventral aorta. The muscle runs obliquely

forward and outward, passes the first hypobranchial on the dorsal side, and converges to a small flat tendon on the anterior ventral surface of the hyomandibula.

SUMMARY.

In the foregoing, all of the muscles of the head and the branchial region, with the exception of the eye muscles, have been considered. The two forms studied agree very closely when their difference in shape is considered.

In the skate, as might be expected from its extreme modification, a few muscles are developed which are not found in the dogfish. These are the levator and depressor of the rostrum, and the cerato-hyomandibularis which, from its position, seems adapted to the protrusion of the jaws.

The muscles of the skate referred to by Tiessing as "*Csvp* 3-5," are here interpreted as fibers of the interbranchials which have acquired an extreme development.

The muscles in *Acanthias*, marked *Csv* 2 and *Csβ* 2 by Vetter, are here regarded as the first and second ventral constrictors respectively.

The deeper ventral longitudinal muscles of *Raia* are described for the first time.

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