THE SKELETAL MUSCULATURE OF THE KING SALMON

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CONTENTS.

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GENERAL ARRANGEMENT OF THE SKELETAL MUSCULATURE.

The general muscular structure of the king salmon has not previously been described. One must therefore be guided by the general descriptions and comparisons as between the musculature of the different parts of the body of the king salmon and that of other fishes of related groups.

The major amount of the muscle mass of the salmon is represented by the great lateral muscles. These extend from the head and pectoral arch on either half of the body straight along the sides to the base of the tail. Each great mass is grossly divided longitudinally into dorsal and ventral portions, vertically into the well-known segments or myomeres. Out of the extreme dorsal portion of the mass certain special longitudinally arranged muscles have been developed. Along the mid-ventral line similar longitudinal differentiations have occurred. In the head region the usual complex differentiations of muscles have taken place. These muscles are undoubtedly derived primarily from the great lateral muscle.

In like manner, the muscle region at the base of the tail, the caudal peduncle, has been differentiated into a number of definite and special muscles which produce the complex movements of the caudal fin.

The pectoral girdle and the pelvic girdle, together with the corresponding fins, have a number of highly specialized muscles. Also the great median fins, the dorsal fin, and the anal fin, each are supplied with a complex group of muscle filaments.

These great groups form the basis of the subdivisions which are followed in this paper in describing the muscles in anatomical detail. In gross outline the groups are as follows:

Muscles of the trunk, the great longitudinal muscles
Muscles of the head region.
Muscles of the caudal fin.
Muscles of the pectoral girdle.
Muscles of the pelvic girdle.
Muscles of the dorsal fin.
Muscles of the anal fin.

MUSCLES OF THE TRUNK, THE LONGITUDINAL MUSCLES.

The longitudinal muscles have been developed out of the great lateral muscle and form the major mass of muscle substance on each side of the body of the king salmon as in other fishes. The extreme anterior portion of the embryonic lateral muscle is differentiated into numerous highly specialized small muscles in the head region, and it is similarly, though less complexly, differentiated in the caudal region also.

The great lateral muscle is subdivided both longitudinally and transversel . Longitudinally the subdivisions are indicated superficially by more or less distinct longitudinal connective tissue areas. The most developed and largest septum however, is indicated by the connective tissue band lying immediately under the lateral line, where a thick septum extends from the under surface of the skin directly down to the lateral-ventral surfaces of the centra of the vertebral column. This septum completely divides the great lateral muscle into dorsal and ventral portions, the division extending from the base of the skull to the middle of the base of the caudal fin. Kingsley, in his Comparative Anatomy of Vertebrates, speaks of these great divisions as the epaxial and hypaxial muscles.

The extreme dorsal portion of the epaxial muscle on each side has become further differentiated by the separation of a definite cylindrical bundle extending from the occiput to the base of the tail, but interrupted at the dorsal fin, and modified at the soft dorsal fin. This muscle is the homologue of Owen's supracarinalis.

That portion of the lateral muscle lying below the lateral line, the hypaxial, has its extreme ventral portion cut off into definite masses which for the most part are cylindrical in form. This portion is the homologue of what McMurrich [a] calls in the catfish "the great ventral muscle," the infracarinalis of Owen. It extends from the gular plate to the base of the caudal fin, but is interrupted at the pelvic girdle and at the anal fin respectively.

The lateral muscles proper are further differentiated into a superficial and a deep portion. These subdivisions are rather intimately bound together at their surfaces of approximation. But in gross anatomical features, in minute histological structures, and in physiological properties, they are so characteristically different that they were considered as distinct muscles. They have been described and given distinctive names by the senior author.[b]

The entire list of longitudinal muscles, including the divisions of the lateral muscles and special differentiations at the mid-dorsal and mid-ventral regions, is as follows:

I. Divisions of the great lateral muscle proper.
   1. Musculus lateralis superficialis.
      a. The epaxial division.
      b. The hypaxial division.
   2. Musculus lateralis profundus.
      a. The epaxial division.
      b. The hypaxial division.

[a] McMurrich, J. P.: The myology of Amiurus. Proceedings of the Canadian Institute, vol. II, p. 330.

[b] Greene, Chas. W.: An undescribed longitudinal differentiation of the great lateral muscle of the king salmon. Anatomical Record, 1913, vol. 7, p. 99–101.

II. Supracarinales, the dorsal longitudinal muscles.
    3. Protractor dorsalis.
    4. Retractor dorsalis.
III. Infracarinales, the ventral longitudinal muscles.
    5. Protractor ischii.
    6. Retractor ischii (protractor analis).
    7. Retractor analis.

DIVISIONS OF THE GREAT LATERAL MUSCLE.

The great lateral muscle, as the term is applied to the adult fish, does not include the dorsal and ventral differentiations given in II and III of the above list. It does, however, include all the muscle mass extending from the base of the skull and the pectoral girdle to the base of the caudal fin except the supracarinales and the infracarinales, respectively. This mass, as just described, is divided longitudinally into four actual divisions. An epaxial and a hypaxial portion is formed by the lateral line septum. Each of these great divisions is differentiated longitudinally into a thin superficial portion and a thick deeper portion as previously indicated. Each of these may now be described in fuller detail.

MUSCULUS LATERALIS SUPERFICIALIS.

This muscle extends over the surface of the deeper division of the great lateral muscle, the profundus, for its full extent from the head to the base of the tail. It is thickest in the mid-lateral line. There are two separate and distinct portions, the epaxial and hypaxial divisions. Each of these divisions forms a thin sheet, becoming thinner as it extends out from the lateral line, dorsally in the epaxial and ventrally in the hypaxial divisions, respectively. The muscle is several millimeters thick in the king salmon in the lateral line region, while its extreme dorsal and ventral borders are represented in thickness by only a few fibers. The dorsal limit of the superficialis is along the line about two-thirds the distance from the lateral line to the mid-dorsal line of the salmon body. The ventral division varies somewhat in its extent. In the anterior portion of the body the superficialis extends only about one-half the distance from the lateral line to the mid-ventral line. In the posterior part of the body the margin of the superficialis extends two-thirds to three-fourths this distance. These epaxial and hypaxial divisions of the superficialis muscle are sharply separated from each other by the lateral line septum.

The muscle as a whole is characterized by a darker appearance than the profundus. The latter is the usual salmon pink color in the well-conditioned fish, though lighter in color in the fish of poorer quality. The superficialis is separated from the profundus by a rather weakly marked sheet of connective tissue. In macerated examples the superficialis can readily be separated from the profundus. On the whole, however, the two muscles are very intimately connected. Histologically the demarcation line is sharp and distinct, but by methods of gross anatomy this line is not so readily determined.

The superficialis has been observed by the senior author in a number of other fishes. In some of these, for example the California sardine, *Clupanodon cæruleus*, this muscle is relatively more highly developed than in the king salmon. In the

literature, however, thus far no previous reference to or description of this differentiation of the great lateral muscle in other fishes has been found other than the sentence of Miescher's quoted below.[a] Miescher speaks of "a thin muscle plate lying along the side of the body just beneath the skin which degenerates strikingly (cutaneous muscle)." I interpret this statement as referring to the lateralis superficialis, though there is nothing else in the context that suggests that Miescher recognized this portion of the lateral muscle as a differentiation out of the total mass. The differentiation is described in part by the papers of the senior author dealing with subjects in salmon anatomy and physiology.[b]

Histologically the superficialis is distinguished from the profundus by its strikingly different type of muscle fibers. The fibers of the superficialis are more compact, more uniform in diameter, and relatively smaller in size than the fibers of the profundus. The fat-storing property of this muscle has been specifically described in a previous paper.[c] Analyses made of this muscle showing the percentage of fat in the fish from the mouth of the Columbia River gave the total of the fat in the fresh wet muscle as high as 30 per cent. In no other muscle of the salmon is such an enormous quantity of fat stored, and especially nowhere else are such quantities stored within the fibers.

MUSCULUS LATERALIS PROFUNDUS.

This muscle forms the major portion of the great lateral muscle as defined above. It extends from the occiput and pectoral girdle to the base of the caudal fin. The muscle is characterized in the fish of first quality especially by its rich pink color. The body of the profundus fills the entire space between the superficialis and skin on the one hand, and the skeletal complex on the other. The two divisions, the epaxial and the hypaxial, are very sharp and distinct for the entire extent of the muscle. The attachments of the muscle are better understood after a discussion of the arrangement of its segments.

The profundus is distinguished from the superficialis always by its characteristic difference in color, as previously referred to. The king salmon in the Columbia River shows an especially rich color in this muscle, though the color fades as the period of starvation progresses during the spawning migration. The form and size of the fibers vary within wide limits while the length of the individual fibers remains more constant. In contradistinction to the superficialis the fibers of the profundus vary in diameter from 25 or 30 to as much as 200 or 250 micra. No such variation in size occurs in the fibers of the superficialis. This characteristic alone is sufficient to diagnose the two muscles.

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[a] Miescher, Friedrich: Statistische und biologische Beiträge zur Kenntniss vom Leben des Rheinlachses im Süsswasser. Schweizerischer Fischerei-Ausstellung zu Berlin, 1880, p. 186. Also reprinted in Histochemische u. Physiologische Arbeiten von Friederich Miescher, 1897, p. 145. Miescher's exact words are: "Am starksten degenerirt eine gesonderte dünne Muskelplatte, die an der Seite des Körpers direct unter der Haut liegt (Hautmuskel)."

[b] Greene, Chas. W.: The storage of fat in the muscular tissue of the king salmon and its resorption during the fast of the spawning migration. Bulletin U. S. Bureau of Fisheries, vol. XXXIII, 1913.

[c] Greene, Chas. W.: A new type of fat storing muscle in the salmon, Oncorhynchus tschawytscha. American Journal of Anatomy, vol. 13, 1912, p. 175–178.

MYOMERES OF THE GREAT LATERAL MUSCLES.

The entire lateral muscle mass, including the superficialis and profundus of both the epaxial and the hypaxial divisions, is subdivided into vertically marked segments, the myomeres (Wiedersheim). The myomeres are separated by connective tissue septa, the myocommata. The septa, and hence the myomeres, are not simple vertical sheaths but are very complexly folded "so as usually to form semiconical masses" (Owen).[a] The surface markings of the septa, forming the borders between the myomeres, present zig-zag lines across the sides of the fish. These septa are not so simple as the surface lines would indicate, as shown in the figure presented (pl. II). From this figure of three myomeres taken from about the middle portion of the body it is obvious that each myocomma as a whole forms a rather complex membrane. Owen has described the form of the myocomma in *Perca fluviatilis* and illustrated the same with a fair figure. Allis [b] figures the surface markings of the anterior portion of the body of *Amia* in his figure 33, the deep folds of the myomeres in figure 34, and the septa after dissecting away the muscles in figure 35, all of the same region. Allis' figures are splendid artistic reproductions of the anatomical facts. The region figured by him is near the pectoral girdle where the myomeres and septal folds are relatively simple.

The form of the myomere and of the septum varies somewhat in different regions of the body but is always complex and intricate. The variations are from one and the same type. In that part of the body from which the figure is taken, in fact also the myomeres of the entire side of the salmon, the surface markings have the general outline of the letter "W" with the bottom of the letter turned toward the tail. The middle limb of the curve coincides with the lateral line. (See pl. I.) For the entire anterior half of the body the myocommata at the mid-line form sweeping curves. At about the anterior border of the anal fin this curve gives way to a point of gradually increasing sharpness. On the caudal peduncle at the lateral line each myocomma makes a sharp pointed union as between the dorsal and ventral halves.

The dorsal or epaxial half of the musculature has the bend in the myocommata directed posteriorly. That portion of the myocomma on the surface between the lateral line and the mid-dorsal bend runs in a sweeping curve, almost vertical at the anterior portion of the body, set at an angle of about 60° under the dorsal fin, about 45° over the middle portion of the anal fin, and about 30° on the caudal peduncle. From the middle of the epaxial muscle to the dorsal margin the myocomma forms a sweeping curve toward the head, at first at an angle of about 50°, then curving until just at the dorsal margin the angle is about 10° to 15°, measured with reference to the lateral line. The line marking the union between the dorsal and dorso-median curves of the myocommata lies about three-fifths the distance from the lateral line to the base of the dorsal fin.

The surface of the ventral half or hypaxial muscle shows similar curves of the myocommata. The median portion very closely follows the angle formed by the ribs along the sides of the abdominal wall. Posteriorly the inclination is ever increasing, reaching its maximum of about 30° at the caudal peduncle.

[a] Owen, Richard: Comparative anatomy and physiology of vertebrates. vol. I, p. 203. 1866.

[b] Allis, Edward Phelps: The cranial muscles and cranial and first spinal nerves in Amia calva. Journal of Morphology, 1897, vol. 12, p. 487–808.

The ventral limb of the hypaxial portion of the myocomma, like the dorsal limb, is very oblique, curving anteriorly. Directly under the pectoral fin this angle is about 70°, in the neighborhood of the ventral fins the angle is about 40°, and between the ventral fin and the caudal fin it varies from 40° to 20° measured with reference to the lateral line. The myocommata are placed most nearly horizontal just above the base of the anal fin.

The form of the septum, i. e., the myocomma, is more clearly shown from plate II if one follows only the outlines of the most anterior of the four myocommata presented, considering primarily the relations of the superficial margin to the deepest margin. The deep margin is in contact with the skeleton and continuous with the median septum or skeletal membrane. Considering the whole septum the superficial zigzag markings are shallow while the zigzag outlines of the skeletal border are deep. In other words, the skeletal boundaries of the septum in the mid-lateral line are attached several centimeters in front of, i. e., cephalad to, the point at which the septum is attached to the skin on the surface. In a similar manner, the skeletal borders of the mid-dorsal and of the mid-ventral portions of the septum are attached back of, that is caudal to, the corresponding superficial borders. Posteriorly, i. e., over the anal fin (pl. 1), this arrangement of the myocommata and myomeres is much more extended in the longitudinal axis of the salmon. When a given myocomma of the posterior surface of the epaxial half of the body is exposed it is seen that the segment ends in a slender wedge directed caudally, the surface in a particular case being 27 mm. farther back, i. e., caudally, than the surface at the mid-line. The deep or skeletal attachment of the same septum was 55 mm. behind the mid-line surface point. Just at the lateral line the deep portion of the septum dips far forward. The septa of the successive myomeres form long slender conical sheaths extending from the under surface of the skin anteriorly down to the skeleton. This distance amounts in the above case to 90 mm.

The significance of this arrangement can be explained only when one keeps in mind that the individual muscle fibers [a] of the myomeres run in lines closely paralleling the axis of the fish. There are many variations from this rule; nevertheless, the general effect is a relation between the muscle fiber and its septa which gives to the latter the effect of tendons. This relation enormously strengthens the whole mechanism of myomeres and septa as a power-producing machine. Figure 1 attempts to show this advantageous arrangement in a diagrammatic way by a somewhat idealized section through the anterior conelike fold just under the lateral line and of the posterior dorsal fold above the lateral line.

The alternate contractions of the great lateral muscles accomplish the propelling of the body forward in the act of swimming. The skeleton is like a great flexible board. The masses of the myomeres of either side are mechanically so knitted into this support by the complex attachments of the myocommata to the skeleton that when a contraction occurs the force of the act is distributed over an unexpected distance along the

[a] Measurements of length of fibers in the myocommata at points on the surface: At the anterior margin of the dorsal fin at the lateral line, 7.2 mm.; at the dorsal mid curve, 6 mm.; in front of the dorsal fin near the dorso-median line, 3.6 mm.; ventrally 3 cm. below the lateral line, 7 mm.; 6 cm. below, 8.2 mm.; fibers running obliquely down and back just in front of the pelvic fin, 5.8 mm.

Measurements just over the anal fin: Dorsal, 2.5 mm.; at the bend, 6.5 mm.; at the lateral line, 8 mm.; deep fibers directly under this region and 1 cm. dorsal to the lateral line the pink fibers measure 2.8 mm. On the ventral line of the muscle apparently the same general variation in length of fibers occurs. At the point where the myocommata run most obliquely just above the base of the anal fin the fibers measure 3 mm.

length of the fish. In the caudal region, for example, this extent is so great that the contraction of a single myomere, should it occur, would bend the skeleton toward that side through an extent of several segments. The longitudinal extent of a myomere in the caudal region, opposite the anal fin, is 12 centimeters, i. e., 15 myomeres, of the muscle. The alternate cone-like folds of the septa mutually support each other. It

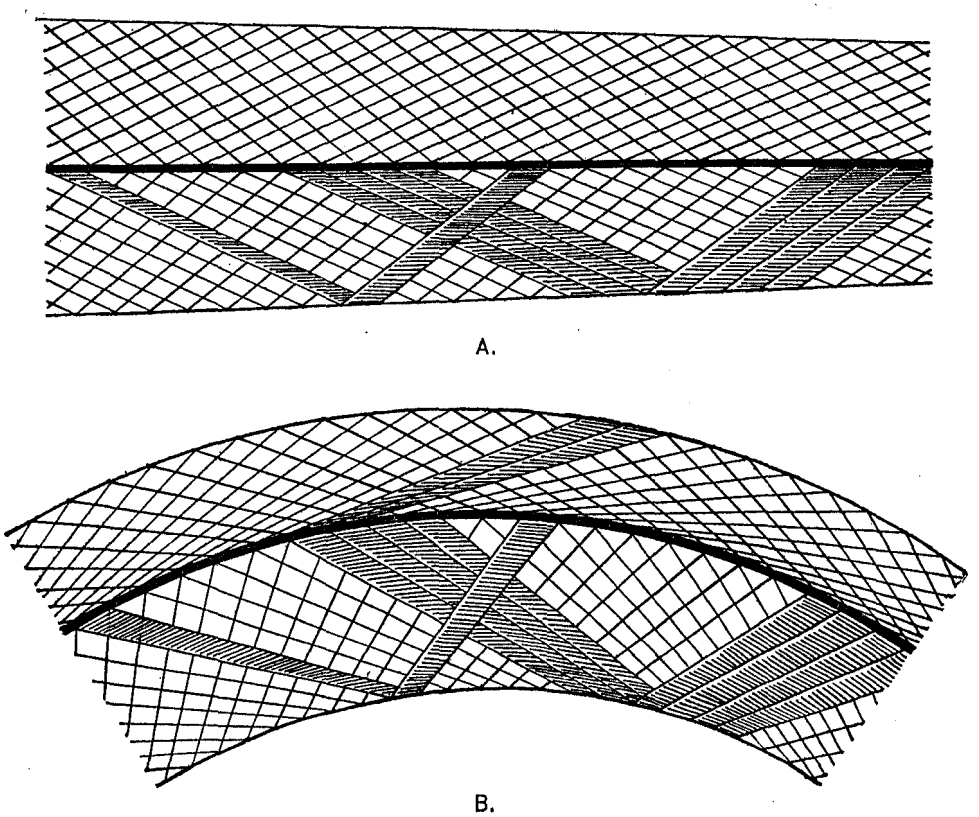

FIG. 1.—Diagrams to illustrate the mechanical relations of the muscle fibers and tendonous septa of the lateral muscles. The diagrams should be considered in comparison with the dissections presented in plates I and II. A, position in rest; B, position during contraction of the left side.

The figures are drawn to represent a composite view of an idealized transverse plane that would cut the individual myomeres and septa through the greatest longitudinal extent. This plane cuts the anterior fold in the median line and the posterior fold through a plane somewhat dorsal to the median line. The posterior folds are less oblique to the skeletal axis than are the anterior folds. More anteriorly the septa will be less oblique, posteriorly more oblique than shown (see pl. 1). This diagram is constructed for the region under the dorsal fin. Note that during contraction of one side the individual fibers on the opposite side are stretched slightly, a condition favorable to the expenditure of contractile energy. Note also that the muscle fibers retain their relatively parallel position with reference to the adjacent skeletal axis. The anterior folds of the septa of the anterior surfaces of the myomeres act as anchors against the posterior folds (dorsal and ventral) of the septa of the posterior surface. As both are inelastic they serve as admirable tendons. Considering the depth of the septa it is obvious that flexion will increase the thickness of the mass of muscle slightly. But the anchoring is such that during flexion parallel septa move or shear over each other in such a way as to produce a maximal amount of movement of the trunk of the salmon by a relatively small amount of muscle fiber shortening, a most advantageous physiological justification of a complex anatomical mechanical relation.

is obvious that the successive septa are very close together and that the fibers from one to the other run very obliquely. In other words, when a contraction occurs every individual fiber is in the best mechanical position to expend all its energy in a much more direct pull on the septal sheet and on the skeleton than would be the case if the myocommata were simple vertical septa placed at right angles to the axis of the fish.

Furthermore, as a contraction progresses and the body of the salmon is sharply curved, i. e., concave, to the side involved, the muscles pull even more directly on the skeleton than at the beginning of the movement, as the figure shows. When the lateral muscles on one side thus bend the ends of the body toward that side, the muscles will pull along the line of oblique attachment of the anterior myocommata on the one hand and the similar attachments of the posterior myocommata on the other, so that these two sheaths serve as direct tendons for the muscle fibers. The arrangement is such that this relation holds for almost every portion of the myomere.

If the septa were simple vertical connective tissue sheaths the mechanical conditions would be wholly changed. In such a case the power expended by the contraction of each myomere would result in a pull on the adjacent myomeres only and from segment to segment and not a direct pull on the skeleton. Only when the great lateral muscles contracted for their full extent would the individual myomere exercise its greatest mechanical possibility. Even then the fibers toward the surface of the myomere would at the time of their maximal contraction soon reach their physiological limit of shortening. The total effect would be to produce tension drawing the superficial part of the muscle away from the skeleton in a relatively inefficient pull. The actual and natural arrangement of the structures in the king salmon is far better and forms a wonderfully efficient and economical mechanical-physiological device.

SUPRACARINALES, THE DORSAL LONGITUDINAL MUSCLES.

Lying along the extreme dorsal margins of the lateral muscles on either side of the body are separate and well developed muscles, the supracarinales. These paired muscles are imbedded in distinct and heavy connective tissue sheaths. In describing the supracarinales the muscles should be considered as made up of two divisions: (1) That portion between the scapula and the anterior portion of the spinous dorsal, and (2) that portion between the posterior margin of the spinous dorsal and the caudal fin. This latter is sharply divided into an anterior and posterior division by the soft dorsal. These two muscle divisions acting together tend to flex the body in the dorso-ventral plane, which in the salmon would seem to be their chief function. Acting separately, each division may be assumed to move the spinous dorsal fin, the first division forward, i. e., in protraction, the second division backward, in retraction. From this latter function the homologous muscles in other fishes have received their names and these names are used here

PROTRACTOR DORSALIS.

This relatively strong muscle extends from the dorsal end of the scapula to the anterior margin of the spinous dorsal and is about 25 cm. long in an 80 cm. salmon. Anteriorly the fibers of the muscle are spread out into a relatively broad fan-shaped mass about 2.5 cm. in width. The mass of the muscle is correspondingly thin in this region. From the middle to the posterior end of the muscle the outline is almost circular, the fibers forming a distinct strong cylindrical bundle even up to the point of insertion. The diameter of this cylindrical mass is from 8 to 10 mm. in an 80 cm. standard fish. Each muscle lies in a tendinous sheath (one on either side of the mid-line of the body). The sheath is less strongly developed anteriorly. The different relations of the walls of

this sheath are as follows: Superficially there is a relatively thin connective tissue sheath separating the muscle from the skin covering it. This portion is heavily loaded with fat. On the ventral surface of the muscle is a thick septum extending from the skin to the median septum into which it is strongly knitted. The median wall is formed by the superior portion of the median septum, in which are imbedded the interneurals of the skeleton. The outlines of a cross section of the sheath are irregular though approximately circular, the outlines being slightly flattened where the septum is strongly developed.

The protractor dorsalis is segmental in the arrangement of its constituent fibers. Connective tissue septa, the homologues of the myocommata of the lateralis superficialis and profundus, extend through the muscle but in an irregular and complexly folded way. In other words, the septa are not simple transverse membranes, but form cone-like spirals. The fibers composing them are strongly interlaced producing in effect a tendinous skeletal framework in which the muscle fibers are imbedded.

The attachments of the muscles are as follows: The anterior end is attached into the posterior margin of the dorsal end of the scapula and by a strong superficial aponeurosis into the skin over the scapula and occiput. This fascia extends forward to the occipital and temporal bones. The tendinous fibers of the posterior end of the protractor are knitted into the anterior and superior margins of the two or three interneurals lying under and supporting the most anterior rays of the dorsal fin. However, all along the median border of the muscle tendinous slips are strongly inserted into the median septum and the interhemals imbedded in this portion of the median septum.

Contractions of the protractor fibers produce traction not only as between the dorsal fin and the occiput, but all along the line of the dorsal margin of the median septum. The whole mechanical effect of the attachments is more favorable for the production of a strong dorsal flexion of the body of the fish than for a protraction of the dorsal fin.

RETRACTOR DORSALIS.

That portion of the supracarinalis lying between the posterior margin of the spinous dorsal and the superior margin of the caudal fin receives the name of retractor dorsalis. This muscle is a cylinder in form. The anterior attachment is by a short tendon inserted into an irregular shaped vertical plate which forms a joint with the last interneural spine, the spine lying under the most posterior dorsal ray. The plate is a modified and enlarged free end of an interneural to receive the tendon of the retractor. The posterior tendon of the retractor is rather broadly attached to the connective tissue enclosing the dorsal ends of the interneural spines of the caudal peduncle which lie under and support the dorsal rudimentary rays of the caudal fin.

The retractor does not seem to be so intimately knitted into its division of the median septum as in the case of the protractor; it is, indeed, free for most of its course. The fact that the muscle is relatively short and smaller in its absolute size than the protractor is probably associated with a development which has separated it from the median septum. That portion of the retractor lying between the soft dorsal and the caudal fin is very slender, 2 or 3 mm. only in diameter. Under the soft dorsal the muscle is wholly tendinous and is closely attached to the base of the fin. Possibly it would be better to consider the two divisions as distinct muscles separated by the soft dorsal.

INFRACARINALES, THE VENTRAL LONGITUDINAL MUSCLES.

Longitudinal muscles lie along either side of the mid-ventral line. These muscles are the homologues of Owen's infracarinales and of McMurrich's fifth portion of the lateral longitudinal musculature. The muscle mass extends from the basibranchiostegal plate to the base of the caudal fin. It is sharply separated from the surrounding muscles for all of its extent except the anterior portion for about one-fourth of its extent.

The infracarinales in the king salmon are divided into three portions, by the interposition of the pelvic arch and of the anal fin. These portions can be described under the names of the protractor ischii, the retractor ischii (protractor analis), and the retractor analis.

PROTRACTOR ISCHII.

This term has been given by Owen to the anterior portion of the infracarinalis. In the king salmon this muscle division extends from the anterior margin of the pelvic arch to the posterior margin of the basibranchiostegal plate, the paired muscles lying on either side the mid-ventral plane. For the greater portion of its length the protractor ischii is inclosed in a cylindrical connective tissue sheath which contains a relatively large amount of adipose tissue. In the mid-line between the two muscles the adjacent portions of this connective tissue sheath form a pretty definite ventral median septum. In the anterior third of the muscle this sheath is less definite and in most specimens scarcely continuous for the full length. In this part of the muscle the form of the muscle as a whole ceases to be cylindrical. The myomeres are not definitely separated from those of the lateral muscle, and the septa are more or less continuous with those of the neighboring lateral muscle. This portion of the protractor is spread out into a slight spatula-shaped terminal mass in the region ventral and anterior to the pectoral fin. The protractor ischii is composed of myomeres, relatively simple in arrangement in the anterior third, and becoming more and more complexly folded into a sort of spiral toward the posterior end of the muscle. In an 80 cm. salmon the diameter of the most cylindrical portion of the muscle varies from 8 to 10 mm., i. e., just in front of the symphysis of the ischii.

The protractor ends in a conical tip which is inserted into the fascias of the skin and of the ventral fin muscles, the median septum, and the antero-ventral border of the ischium itself. The tendons of insertion are formed by the ends of the whorls of myocommatous connective tissue. These are best exposed by a median incision through the skin ventral to the protractor ischii itself.

Contractions of this muscle accomplish two functions. If the axis of the body is rigidly fixed by the action of other muscles then this muscle merely pulls the pelvic girdle forward. It is from this action that it receives its name. However, it seems that a more important function is found in a second action, namely, a strong ventral flexion of the body. Then, too, in the spawning act, if one is to judge by external appearances, the protractor ischii contributes sharply to the pressure that is brought upon the abdominal cavity and which produces the extrusion of the eggs.

RETRACTOR ISCHII (PROTRACTOR ANALIS).

The retractor ischii consists of a cylindrical muscular slip which extends from the posterior end of the pelvic arch directly caudalward and around the anal aperture to be inserted with its fellow into a special bony triangle at the base of the anal fin.

The relation of the pair of muscles and their insertion into this triangle is shown in figures 2 and 8. This bony triangle in its normal position in the body rests directly under and indirectly supports the most anterior rays of the anal fin, with which it is strongly connected by connective tissue fascias. It is a modified interhemal.

The contractions of this division of the infracarinalis contribute to the ventral flexion of the body. It does this by fixing both the anal fins and the pelvic fins. When other muscles are relaxed so that these fins are movable the action of the muscle is to produce retraction of the ventral fins, i. e., the pelvic girdle. If this latter arch is fixed then protraction of the anal fin results, a movement by which the muscle may well receive the alternate designation of protractor analis.

RETRACTOR ANALIS.

On either side of the mid-ventral line of the caudal peduncle lies a slender cylindrical muscle, the retractor analis. The muscle is oval in cross section, about 4 mm. broad by 2.5 mm. thick in an 80 cm. salmon. The fibers run up under the tendinous end of the most posterior erector muscle of the anal fin, to be attached by a broad tendon into the posterior margin of the modified cartilage which supports the most posterior rays as previously described and indicated in figure 14. When the skin is removed and all the muscles are in place this muscle has the appearance of running into the angle formed by the lateral muscles and the posterior margin of the fin.

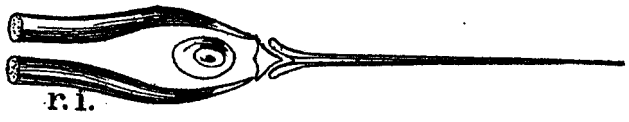

FIG. 2.—An antero-ventral view, somewhat diagrammatic, of the relation of the anterior rays of the anal fin, the supporting triangular cartilage, and the insertions of the pair of retractor ischii, i. e., protractor analis muscles. The figure shows only indistinctly that the three anal rays appear one behind the other, the most anterior of course the shorter.

Posteriorly the muscle runs under the bases of the ventral aborted rays of the caudal fin to be attached into the connective tissue and fascias and the ends of the hemal spines. The muscle is slightly conical in shape, becoming more slender posteriorly. It is only 3 or 4 mm. in diameter at its thickest part.

The function of the muscle is that of retraction of the anal fin, but the muscle is so slightly developed that it can not produce extensive motion.

MUSCLES OF THE HEAD REGION.

The muscles of the head region may be grouped and discussed under the following heads:

A. Superficial dorsal head muscles.
   1. Adductor mandibulæ, (*a*) cephalic portion; (*b*) mandibular portion.
   2. Levator arcus palatini.
   3. Dilatator operculi.
   4. Levator operculi.
B. Deep dorsal head muscles.
   5. Adductor operculi.
   6. Adductor arcus palatini.

C. Dorsal branchial arch muscles.
- 7. Levatores arcuum branchialium.
- 8. Interarcualis dorsalis obliquus, posterior.
- 9. Interarcualis dorsalis obliquus, anterior.
- 10. Adductor arcuum branchialium, anterior.
- 11. Adductor arcuum branchialium, posterior.
- 12. Transversi dorsalis, anterior.
- 13. Transversi dorsalis, posterior.

D. Ventral branchial arch muscles.
- 14. Interarcuales ventrales obliqui.
- 15. Transversi ventralis, anterior.
- 16. Transversi ventralis, posterior.
- 17. Pharyngo-clavicularis externus.
- 18. Pharyngo-clavicularis internus.

E. Mandibular and hyoid arch muscles.
- (18b. Adductor mandibulæ, mandibular portion.)
- 19. Intermandibularis.
- 20. Geniohyoideus.
- 21. Hyohyoideus.
- 22. Sternohyoideus.

SUPERFICIAL DORSAL HEAD MUSCLES.

ADDUCTOR MANDIBULÆ (THE MASSETER OF AGASSIZ, OR RETRACTOR ORIS OF OWEN).

This is the largest muscle in the head. It forms the fleshy mass just posterior to the eye which for its delicacy of flavor the fishermen prize under the name "salmon cheeks."

The adductor mandibulæ is in two divisions that are almost though not quite distinct and separate. There is a cephalic division above the angle of the jaw, and a mandibular portion lying chiefly below and along the inner border of the dentary.

The cephalic division of the adductor is in old specimens often more or less indistinctly separated into three divisions, as described by Allis[a] for *Amia*. These divisions are, however, not bounded by more than the thinnest of endomysial membranes and are intimately fused toward the tendon of insertion. In fact they are of lesser importance and scarcely justify the dignity of special designation. The cephalic division will therefore be described as a whole.

(*a*) *The cephalic division of the adductor mandibulæ* has an extensive surface of origin which includes (1) the anterior border of the preopercle for most of its extent, (2) the entire surface of the quadrate, (3) the metapterygoid, and (4) the hyomandibular. Some fibers arise (5) from the connective tissue sheath covering the levator arcus palatini and from the post-orbital septum. The muscle fibers converge in a sweeping curve or general fan-shaped whorl in the dorso-ventral direction to their attachment in the broad tendon at the angle of the jaw. The extreme posterior fibers run anteriorly and somewhat downward toward the ventral margin of attachment. This division of the muscle is attached by a short, heavy, rather broad tendon into the outer margin of the posterior part of the articulare. The tendon is intimately fused with the connective tissue that binds the articulare with the premaxillary and the quadrate bones.

[a] Allis, Edward Phelps, loc. cit.

The cephalic portion of the muscle in the medium sized fish is about 4 cm. broad in the anterior posterior extent and about 5.5 cm. in the dorso-ventral dimension. The thickness is from 1 to 1.5 cm.

(*b*) *Mandibular portion of the adductor.*—Besides the cephalic portion of the adductor there is a stout mandibular portion. It arises from the anterior border of the tendon over the quadrate bone and the angle of the mouth. It extends anteriorly to an attachment along the inner surface of the middle third of the dentary, i. e., from a point directly below the angle of the mouth forward to a point on the jaw. At the origin of this portion the fibers are continuous with the fibers of the cephalic portion. From the origin the fibers diverge slightly as they are distributed to their attachments on the dentary. The lower margin of the muscle takes a continuous attachment along the under and inner surface of the bone. The upper and outer side of the muscle remains free from attachments.

The contraction of the adductor closes the mouth with great power. In addition to its function in feeding it undoubtedly takes part in the motions of respiration.

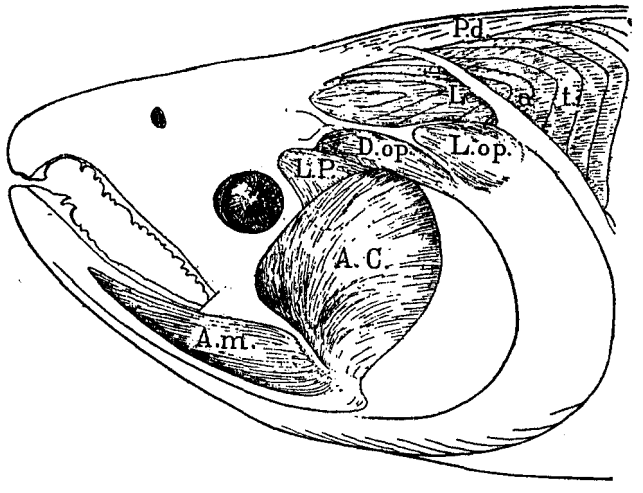

FIG. 3.—Superficial head muscles after removal of the skin and a part of the jaws. *A. C.*, adductor mandibulæ, cephalic portion: *A. m.*, adductor mandibulæ, mandibular portion; *L. P.*, levator arcus palatini; *D. op.*, dilator operculi; *L. op.*, levator operculi; *P. d.*, protractor dorsalis; *Lat.*, lateral muscle.

LEVATOR ARCUS PALATINI.

This is a short, thick, comparatively wide muscle which takes its origin from the angle formed in the external surface of the sphenotic, filling the space just posterior to the eyeball. The fibers run obliquely downward and backward to a broad insertion on the anterior surface of the superior half of the hyomandibular and also into the superior margin of the metapterygoid. The muscle at its posterior dorsal margin is intimately associated with and often inseparable from the fibers at the origin of the dilatator operculi muscle.

DILATATOR OPERCULI.

This muscle has its origin from the anterior margin of the external surface of the pterotic and the posterior border of the sphenotic. Its fibers converge sharply backward and downward to an insertion by a small but strong tendon into the upper margin of the opercle. The attachment is on the knob formed at the junction of the opercle with the hyomandibular. The muscle lies in the groove between the exposed margin of the pterotic and the hyomandibular.

LEVATOR OPERCULI.

The levator operculi is a short, triangular muscle which arises from the posterior spinous border of the pterotic. The fibers converge diagonally downward and backward to an insertion in the upper margin of the opercle. Its contraction leads to an elevation of the opercle aiding in the act of respiration.

DEEP DORSAL HEAD MUSCLES.

When the eye is removed along with the upper portion of the metapterygoid and hyomandibular bones a broad curved sheet of muscle consisting of short thick bundles is exposed. The homologous mass in *Amia* has been divided by Allis into three portions—the levator maxillæ superioris, the adductor hyomandibularis, and the adductor operculi. In *Oncorhynchus* this region can scarcely be divided except for the small group of fibers at the posterior limit of the region. The two parts are better identified under McMurrich's names, the adductor arcus palatini, and the adductor operculi.

ADDUCTOR OPERCULI.

The adductor operculi arises on the ventral surface of the pterotic directly under the origin of the levator operculi. Its origin is overlapped by the posterior fibers of the adductor arcus palatini. The fibers form a short but thick bundle, its length being from 8 to 10 mm. It is inserted into the inner surface of the opercle a little above the insertion of the dilator operculi which it opposes in action.

ADDUCTOR ARCUS PALATINI.

This muscle has an extensive origin along a line from the origin of the adductor operculi to a point in the ventral portion of the eye socket. The fibers are short, thick, and massive for the position in which they lie, but are not readily separated into distinct bundles.

The posterior half of this muscle arises just ventral to the articulation of the hyomandibular and from the ventral surface of the pterotic and sphenotic bones. The fibers are only a few millimeters in length, run directly outward, and are attached into the inner surfaces of the upper half of the hyomandibular and the posterior portion of the metapterygoid. The anterior portion of the mass, which is relatively the larger, arises from the outer surface of the orbitosphenoid. Its fibers extend outward and downward to a broad attachment on the inner surface of the metapterygoid and the dorsal surface of the mesopterygoid.

The contractions of the entire mass tend to elevate the angle of the jaw and to compress the palatine arch.

Allis [a] divides this muscle into the levator maxillæ superioris and the adductor hyomandibularis. No natural division along these lines can be observed in *Oncorhynchus tschawytscha*.

DORSAL BRANCHIAL ARCH MUSCLES

When the palatine arch is removed and the adductor arcus palatini reflected, one can, by trimming away the gill filaments, readily expose the group of muscles of the dorsal half of the branchial arches.

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[a] Allis, Edward Phelps, loc. cit.

LEVATORES ARCUUM BRANCHIALIUM.

This group consists of five diverging muscle slips which are subdivisions of one thin broad sheet. The origin of the muscle sheet is on a line immediately ventral to the origin of the middle portion of the adductor arcus palatini. At the origin the sheet is continuous and its divisions spread out to their attachments somewhat like a miniature fan.

Fifth division.—This, the most posterior slip of the group, is a very slender muscle arising from a point on the skull just in front of the foramen of the tenth nerve. The fibers run posteriorly downward and backward to an attachment on the dorsal margin of the flange of the fourth epibranchial. This muscle is about 2 to 2.5 cm. long, the longest of the group.

Fourth division.—A similar though slightly stouter muscle arises just in front of the latter and is attached on the crest of the corresponding flange of the third epibranchial.

Third division.—The next differentiated strip runs under the tendon of the fourth division and the flange of the third arch and is attached to the dorsal end of the cartilaginous rod corresponding to a fifth epibranchial.

Second division.—The second division is attached on the flange of the second epibranchial. But a tiny slip of this muscle also runs to the dorsal surface of the pharyngobranchial of the third arch.

First division.—The most anterior slip is attached superficially to the flange on the first epibranchial. But its deeper fibers run to the pharyngobranchial of the second arch. These fibers are only a few millimeters long.

The points of attachment of the first, second, and third muscle slips are also common points of union for the connective tissue and septa covering the corresponding gill clefts, i. e., the first muscle is opposite the angle of the second gill cleft, the second opposite the third, and the fourth opposite the fourth.

The pharyngobranchial attachments of the first and second divisions are apparently the homologues of McMurrich's levatores interni, while the five divisions described here would be his externi.

INTERARCUALIS DORSALIS OBLIQUUS, POSTERIOR.

There are two obliqui interarcuales on the dorsal half of the branchial arch. The most posterior dorsal oblique arises from the posterior dorsal surface of the third pharyngobranchial. The fibers run obliquely backward to an insertion on the anterior surface of the flange of the fourth epibranchial.

INTERARCUALIS DORSALIS OBLIQUUS, ANTERIOR.

The second or anterior oblique arises from the second pharyngobranchial near its union with the epibranchial. The fibers run obliquely outward to an insertion on the anterior margin of the flange of the third epibranchial.

ADDUCTOR ARCUUM BRANCHIALIUM, ANTERIOR.

There are two dorsal adductor muscles, an anterior and a posterior. The anterior adductor arises on the posterior surface of the fourth epibranchial plate and is inserted into the dorsal surface of the distal end of the corresponding ceratobranchial. Its contraction approximates the cerato and epibranchials of the fourth arch.

ADDUCTOR ARCUUM BRANCHIALIUM, POSTERIOR.

The posterior adductor muscle arises on the internal surface, i. e., median, of the bony plate of the fourth epibranchial just within the origin of the preceding. It is inserted into the external surface of the cartilaginous cap of the fifth ceratobranchial.

TRANSVERSI DORSALIS, ANTERIOR.

This thin and slightly developed muscle arises from the postero-dorsal surface of the second pharyngobranchial near its junction with the corresponding epibranchial. It runs to a similar attachment on the other side. It is one of the few unpaired muscles.

TRANSVERSI DORSALIS, POSTERIOR.

This unpaired muscle is much more strongly developed than the preceding. It arises from the dorsal surfaces of a part of the fourth pharyngobranchial and the dorsal margin of the central end of the fourth epibranchial. The fibers run to similar attachments on the other side of the body.

Some fibers arise on the dorsal surface of the fifth ceratobranchial and become continuous with the constrictors of the pharynx.

VENTRAL BRANCHIAL ARCH MUSCLES.

The ventral muscles of the branchial arch consist of three groups, the interarcuales ventrales, the transversi ventrales, and the pharyngo-claviculares.

INTERARCUALES VENTRALES OBLIQUI (VETTER).

A group of more or less distinct muscles corresponding to the interarcuales dorsales is present on the ventral side of the branchial basket. In the salmon the anterior three of these muscles are distinct and separate and not divisions of one sheet as in the dorsal group. The posterior two are intimately united. Their dissection should follow that of group E. They are exposed better beginning with the anterior one of the group.

First division.—The most anterior or first division belongs to the first arch. It is a comparatively small slip which has its origin from the ventral surface of the first basibranchial. It extends along the under surface of the hypobranchial to an attachment into the cartilage and ventral tip of the ceratobranchial near its union with the hypobranchial.

Second division.—The second division arises from the ventral surface of the second basibranchial. It runs its course over the second hypobranchial and is attached by a short strong tendon into the ventral surface of the second ceratobranchial. The first and second arch muscles are completely separated at their area of origin. A tendinous band runs over the ventral surface of the basibranchials between the two slips.

Third division.—The third division or muscle of the third arch arises from the third basibranchial and the median portion of the ventral surface of the hypobranchial. Its attachment on the third arch corresponds to that of the first and second divisions.

Fourth division.—This division is continuous with the fifth. They arise from the third basibranchial on the ventral surface somewhat median to and in close contact

with the third. The insertion of the fourth is into the extreme ventral portion of the cartilage of the fourth ceratobranchial.

Fifth division.—The fifth division is regarded as a subdivision of the preceding muscle. It has its origin in a tendinous raphé which is strongly developed at a point ventral to the insertion of the preceding. Some fibers also arise from the cartilaginous plate posterior to the insertion of the fourth division. The muscle is relatively short and thick. It is attached by a short, stout tendon to the fifth ceratobranchial, its tendon being fused with the anterior border of the tendon of the pharyngo-clavicularis externus.

TRANSVERSI VENTRALIS, ANTERIOR.

A short thick triangular bundle of fibers arises on the median surface of the ventral end of the ceratobranchial of the fourth arch. It is an unpaired muscle and runs directly across to an attachment at the corresponding point on the opposite side.

TRANSVERSI VENTRALIS, POSTERIOR.

This stout unpaired muscle is very much like the preceding, but three times larger. It runs from the inner surface of the base of the fifth ceratobranchial transversely under the esophagus to a corresponding insertion on the opposite ceratobranchial.

The transversi ventrales by their contractions approximate the ventral portions of the fourth and fifth arches of the branchial basket.

PHARYNGO-CLAVICULARIS EXTERNUS.

This is a short broad muscle band extending from the antero-dorsal surface of the clavicle directly dorsalward to the lower surface of the fifth ceratobranchial. Its length is only about three times its breadth. Its contractions depress the branchial arch.

PHARYNGO-CLAVICULARIS INTERNUS.

This is a broad thin muscle band arising from the anterior surface of the inner margin of the clavicle at about the middle of its arch. Its fibers run diagonally forward and inward to an insertion on the ventral margin of the fifth ceratobranchial just under the insertion of the pharyngo-clavicularis externus. There is a strong tendinous line along the upper margin of the muscle.

The internus muscle retracts the branchial basket, i. e., draws it backward toward the esophagus.

MANDIBULAR AND HYOID ARCH MUSCLES.

INTERMANDIBULARIS.

A short thick unpaired muscle extends transversely from the left dentary to the right. In cross section it is a rough oval 17 by 6 mm. The muscle is 2 cm. long. It is attached to the inner surfaces of the two dentaries just back of the symphysis. It serves to approximate the mandibles.

GENIOHYOIDEUS.

This is a broad flat sheet of muscle arising from the ceratohyal. The origin is along a diagonal line extending from the postero-ventral border to the antero-dorsal margin of the bone. The muscle joins with its fellow to form a practically continuous

sheet at the insertion into the inner surface of the anterior portion of the dentary around the symphysis. At its insertion the tendon is divided into an external and an internal portion, one passing above, the other below the intermandibularis to its insertion.

HYOHYOIDEUS.

This long thin sheet of muscle arises from the ventral surface of the hypohyal and passes diagonally outward and backward to insertions over the branchiostegal rays. The muscle has attachments to the internal margin of each successive ray. It also has insertions along the ventral margins of the ceratohyal and epihyal. The left hyoideus somewhat overlaps the right at its origin.

STERNOHYOIDEUS.

The name sternohyoideus is applied to a broad and thick sheet of muscle arising on the dorsal surface of the anterior end of the clavicle directly in front of the attachment of the pharyngo-clavicularis externus. Its fibers run forward and are attached to the ventro-lateral surface of the hypobranchial plate. Its differentiation from the ventral portion of the great lateral muscle is apparent and probably it would be better to group it with the longitudinal muscles.

MUSCLES OF THE CAUDAL FIN.

The modifications of the musculature which have come about for the control of the movements of the caudal fin are associated with striking modifications of the caudal skeletal structure. In order to present more accurately the form and relations of the muscles it seems desirable to give the facts concerning the caudal skeletal complex.

CAUDAL SKELETAL COMPLEX.

The caudal fin in the king salmon is regularly bilobed and symmetrical. Externally it appears of the regular homocercal type. The caudal skeleton, however, still shows the heterocercal structure as presented by figure 5. The skeleton reveals the fact that the epichordal component is limited to the rudimentary rays and at most the first two rays of the dorsal lobe. The remainder of the dorsal lobe and all of the ventral represents the hypochordal component. This modification rests on a rather complex caudal skeletal base, as was shown by Kölliker [a] for *Salmo salar*.

The axial region may be considered as composed of those vertebræ entering into the caudal peduncle, and those of the caudal fin proper. Of the three obvious vertebræ that enter into the caudal fin skeleton one only has a well developed centrum. The second and third centra are very much reduced in size, the latter being only a tiny bony nodule. The modifications of the vertebræ of the caudal peduncle begin sharply with the last three vertebræ of the group. However, the spines of the fifth and fourth, counting from the tail, have a median flange on the anterior margin of the neural spines. In the last three vertebræ these flanges are fused each with the spine in front of it. The neural spines of the first and second caudal vertebræ enter into this fusion, the five spines making a firm mass.

[a] Kölliker, Albert von: Ueber das Ende der Wirbelsäule der Ganoiden und einiger Teleostier, taf. IV, fig. 1 and 2. Leipzig, 1860.

Lying on the dorsal surface of the three centra of the caudal group, and extending out over the bases of the neural spines is an irregularly fan-shaped bony plate, the Deckknochen der Chorda of von Kölliker.[a] This plate is coalesced into the dorsal surface of the second, and usually the third, centrum. It has a caudally projecting spine extending in the direction of the axis of the third centrum.

The hemal spines of the last three vertebræ of the peduncle are also sharply modified

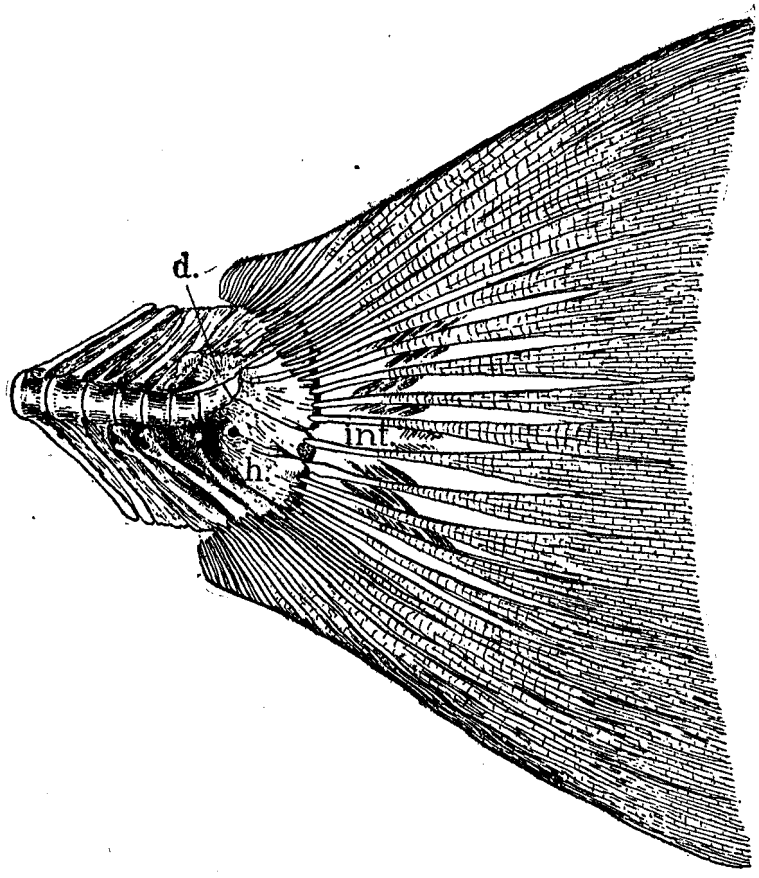

FIG. 4.—Caudal skeleton. Five centra of the caudal peduncle with their modified spines are shown. The three caudal centra are much reduced, the last quite rudimentary. The hemal spine of the basal caudal vertebra is very stout. It bears a transverse spine near its base. The lower one of the five hypurals is marked "*h.*" The large irregular plate "*d*" is von Kölliker's "Deckknochen der Chorda" of *Salmo salar*. A few of the deeper fibers of the musculi interfilamenti (*int.*) are shown.

by being greatly thickened and broader. The borders of these plate-like hemal arches are not fused, though they are intimately bound together by connective tissue.

The hemal spine of the most anterior vertebra of the three that belong to the caudal fin proper is very strong and bar-like. It is heavier than the caudal peduncle spines anterior to it, and is especially characterized by its strong and stocky base which carries a well-developed lateral process. This process stands out sharply for 3 to 5 mm.

[a] Kölliker, Albert von, op. cit., p. 12.

from the base of the spine. It is directed somewhat posteriorly and serves for the attachment of a group of the deeper caudal muscles. The last two caudal fin vertebræ are sharply modified. Ventral to the rudimentary centra there is a series of strong and broad hypurals. In the king salmon there are five hypurals, the most anterior one the strongest, and the individuals of the series diminishing in size toward the dorsal lobe of the fin base. The development of the hypurals is commensurate with that of the caudal musculature.

Saddled over the ends of the hemal spines of the last two vertebræ of the caudal peduncle, the spine of the first caudal vertebra, the hypurals, and the bony fusion of neural spines previously described, are the series of paired fin rays constituting the caudal fin. The fully developed rays are 19 in number, with about 12 rudimentary rays above and as many below. The middle ray of the fully developed series represents the axial ray. It is not only in the middle of the series but the interfilamenti caudales muscles are inserted symmetrically with reference to this axial ray (fig. 4). These rays form a joint of limited movement over the end of the skeletal complex to which they are strongly anchored in a firm mass of ensheathing connective tissue.

CAUDAL FIN MUSCLES.

The muscles of the caudal fin are derived from the posterior myotomes of the embryonic lateral muscles. The only probable exception is the interspinous muscle, which is very intimately associated with the dermal fin rays and the skin itself. The muscles are superficial and deep.

SUPERFICIAL MUSCLES.

CAUDAL END OF THE MUSCULUS LATERALIS SUPERFICIALIS.

This is a trunk muscle, but the details of its caudal insertion have been reserved for description at this point. The lateralis superficialis or dark muscle is continued over the lateral surface of the caudal peduncle to be inserted into the base of the tail. It forms a sheath on each side of the mid-line of the caudal peduncle estimated in width at two-thirds the distance from the mid-line of the peduncle to the dorsal and ventral borders respectively. The muscle substance ceases posteriorly in the middle line at a point directly under, i. e., ventral to the base of the first long dorsal caudal ray. The caudal end of the muscle, i. e., marking the termination of the myomeres in its tendon and fascias, is distinctively clavate. The dorsal myomeres are narrowed, and the myocommata run together into a strong tendon that is attached to the bases of the first, second, and usually the third long dorsal rays just exterior to and in the fascia of the profundus lateralis. In a Baird specimen (small male) the last three dorsal myomeres are modified, the last two into a muscular slip running obliquely dorsalward and caudalward to end in a delicate flat tendon or fascia. The dorsal lobe of the superficialis is rendered more prominent by the fact that the dorsal border of the muscle, just at the base of the caudal peduncle, is attached to fascias which are intimately connected with the myocommata between the ventral two-thirds and the dorsal third of the epaxial half of the lateral muscle. There is considerable irregularity in the arrangement of the muscular fibers of the last two or three myomeres of the dorsal lobes of this muscle. A rather common irregularity is that shown in figure 5. The ventral lobe of

the lateralis superficialis forms a similar attachment into the connective tissue over the bases of the first and second long ventral caudal rays.

THE TERMINAL OR CAUDAL PORTION OF THE MUSCULUS LATERALIS PROFUNDUS.

The terminal or caudal portion of the profundus is characterized by the excessive proportion of connective tissue of the myocommata. In fact the myocommata are finally reduced to tendons of insertion.

The epaxial and hypaxial portions are well separated in the region of the caudal peduncle, partly by the greater development of the superficialis which ensheathes the

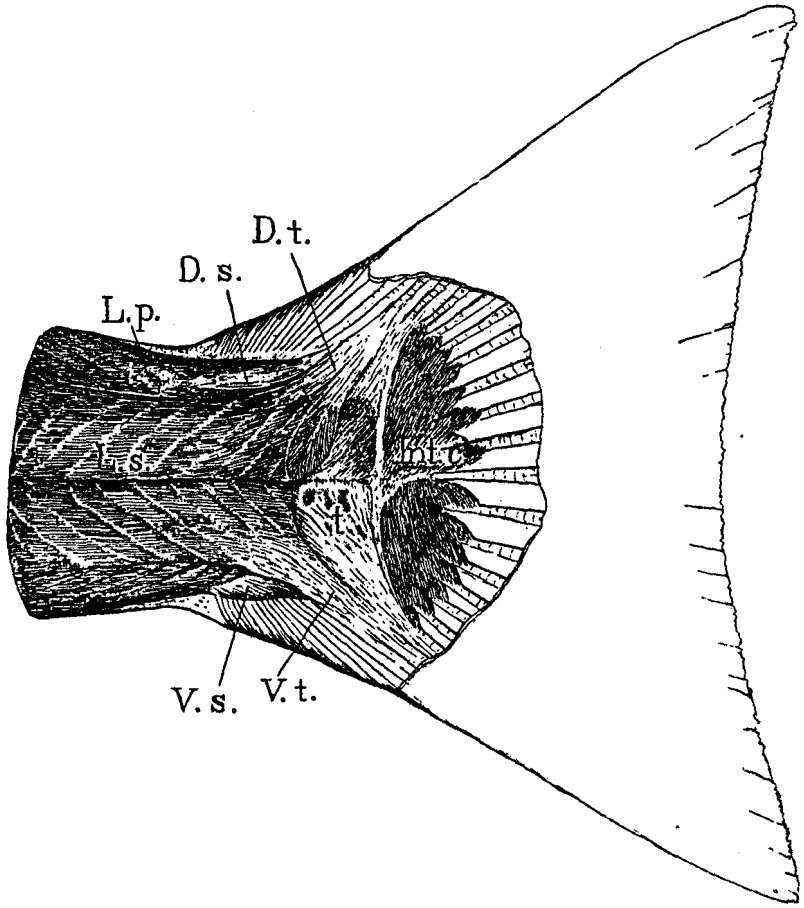

FIG. 5.—The superficial muscles of the caudal fin and the caudal peduncle. *L. s.*, lateralis superficialis; *D. s.*, dorsal slip of lateralis superficialis; *V. s.*, ventral slip of lateralis superficialis; *D. t.*, dorsal tendon of lateralis superficialis; *V. t.*, ventral tendon of lateralis superficialis, *L. p.*, lateralis profundus; *t.*, terminal tendons of the lateralis profundus; *Int. c.*, interfilamenti caudalis.

profundus next the septum. The final terminal tendons run straight back under the clavate margin of the tendon of the superficialis to a very strong insertion into the aponurosis which covers the bases of the rays of both the dorsal and the ventral lobes and includes all of the intermediate series (fig. 5).

The epaxial division covers the deeper muscles presently to be described, but is not strongly fused with their fascias. The hypaxial division is strongly attached into the tips of the hemal spines of the last vertebræ of the caudal peduncle as well as into the bases of the rays. Its superior margin covers the ventral inferior caudal flexor.

The epaxial and hypaxial aponuroses are strongly united across the median line as shown in the area between the terminal myomeres of the superficialis and the interfilamenti muscles.

MUSCULI INTERFILAMENTI CAUDALIS, THE INTRINSIC MUSCLES OF MCMURRICH.

This small superficial double fan-shaped muscle consists of dorsal and ventral portions. The fibers originate in the fascia lying over, or covering, the termination of the lateralis profundus muscle on the base of the tail. They are attached into the admesial margins and the external surfaces of the bases of the seven caudal rays lying on either side the median ray. This middle ray, so far as the muscular arrangements indicate, is axial. The muscle fibers attached to its base above run diagonally upward and caudalward, those below downward and caudalward. The superficial fibers form a continuous layer, while the deep fibers run from ray to ray, as shown in figures 4, 5, and 6. When this muscle contracts it draws the caudal rays together, narrowing the spread of the fin.

The width of the caudal interfilamenti muscles, at the best, is about 10 mm. The dorsal lobe is about 26 mm., the ventral lobe 24 mm. long.

DEEP CAUDAL MUSCLES.

The caudal fin is used by the salmon both as a steering rudder and as a propeller. The deep ventral muscles move the parts of the fin to set its form for a rudder, but the musculature which utilizes it as a propeller is limited to the great lateral muscles acting on the fin as a whole. If, during the movements of the fin as a whole, it is set in some special position or given a characteristic shape, that shape will be utilized for steering the forward motion of the salmon. This activity is accomplished by means of the deep caudal muscles, as can readily be seen by consideration of the effect of the contractions of the muscles singly or in groups. There are six pairs of these deep muscles. They vary considerably in detail of size and position but the usual type will now be described.

FLEXOR CAUDALIS VENTRALIS SUPERFICIALIS.

This is a delicate muscle slip which begins by a small flat tendon attached to the bases of the hemal spines, the third and fourth from the end of the caudal peduncle. A few fibers also arise from the fascia and tendons of the superficialis in the median line. It runs posteriorly to a slender tendon attached to the tip of the transverse spine on the first caudal vertebra. The muscle is continued from this point to an insertion on the base of the third caudal ray ventral to the axial ray. Its attachments lie over the interfilamenti. The ventral margin of the posterior division of this muscle is sometimes fused with the dorsal margin of the next.

FLEXOR CAUDALIS VENTRALIS SUPERIOR.

This caudal flexor is a rather broad group of fibers which arises from the ventral surfaces of the centra and the bases of the hemal spines of the last two vertebræ of the peduncle, also from the base of the spine and the ventral surface of the lateral process of the most anterior caudal vertebra. The fibers run slightly ventralward as they proceed to their insertion into the bases of the fifth to the eighth caudal rays below the axial ray.

The contractions of this muscle lead to a flexion of the lower half of the middle portion of the caudal fin, and of the ventral caudal lobe. The tension in this case is brought primarily on the uppermost rays of the ventral lobe. The muscle presumably acts in conjunction with the next to be described.

FLEXOR CAUDALIS VENTRALIS INFERIOR.

The origin of the inferior ventral flexor is from the surfaces of the last three hemal spines of the caudal peduncle. The attachment is in a line which begins somewhat ventral to the anterior limit of origin of the preceding muscle and runs posteriorly and toward the transverse process of the first caudal vertebra. The fibers of the border of the superior muscle arise under the ventral border of the preceding muscle.

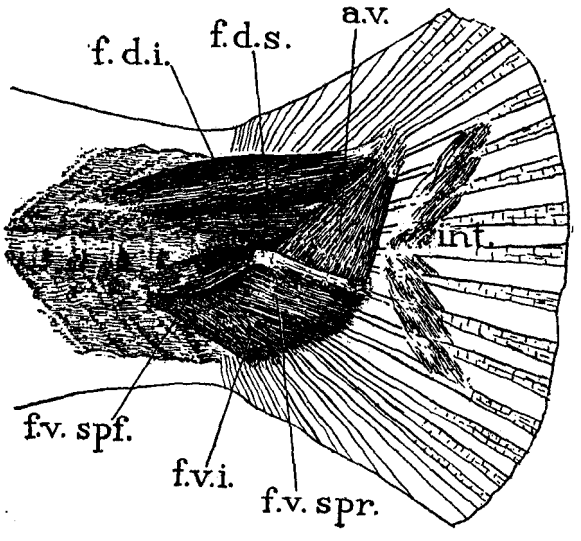

FIG. 6.—The deep caudal fin muscles. *f. v. spf.*, flexor caudalis ventralis superficialis; *f. v. spr.*, flexor caudalis ventralis superioris; *f. v. i.*, flexor caudalis ventralis inferioris; *a. v.*, adductor caudalis ventralis; *f. d. s.*, flexor caudalis dorsalis superior; *f. d. i.*, flexor caudalis dorsalis inferior; *int.*, interfilamenti caudalis.

The fibers of the inferior flexor run ventrally and caudally to insertions into the bases of the last two long ventral caudal rays and into the adjacent series ofrudimentary rays.

Contractions of this muscle sharply flex the extreme ventral border of the ventral caudal lobe. Contraction at the same time with the superior ventral flexor would sharply flex the whole ventral half of the caudal fin toward that side on which the contraction occurred.

ADDUCTOR CAUDALIS VENTRALIS, THE ADDUCTOR OF THE DORSAL CAUDAL LOBE.

This muscle is a relatively thin and broad sheet of muscle fibers lying below but in its body closely parallel with the caudal vertebral axis. The origin of the muscle is revealed by cutting away the posterior portion of the superficialis, the major portion of the interfilamenti caudalis, and the superior border of the superior ventral flexor. It has a rather broad line of origin extending from the lateral spine of the first caudal vertebra directly posterior to the second caudal ray below the axial ray. The tendon of origin is rather thickened at the spine. The line of origin is along the dorsal margin

and the surface of the lowermost hypural bone, and from the connective tissue over the bases of the corresponding caudal spines. The tendon is somewhat stronger at the ends of this broad line of origin. The fibers of the muscle run dorsally and somewhat caudally, converging as they go and ending in a broad and strong tendinous attachment into the fourth, fifth, sixth, and sometimes seventh, long caudal rays dorsal to the axial ray.

The belly of this muscle is 16 mm. wide by 3 to 3.5 mm. thick and the muscular portion is 22 mm. long, i. e., in the 80 cm. fish used as a standard.

The contractions of the adductor lead to sharp flexion and adduction of the dorsal caudal lobe. Since the tension on the lobe is almost directly from the point of attachment of the tendon toward the median axial ray, this would naturally lead to an approximation of the rays and a decrease in the spread of the fin.

FLEXOR CAUDALIS DORSALIS SUPERIOR.

The dorsal flexor is the longest and strongest muscle of the deep caudal series. It lies almost in the axial plane of the fish. It takes its origin from the median septum over the fifth and fourth neural spines and from the third and fourth vertebræ, counting from the posterior end of the caudal peduncle. Some fibers of origin are found along the tips of the second and third neural spines. Fascias of the muscle are more or less intimately attached to the median septum as far back as the first true caudal vertebra. The insertion, in conjunction with the attachment of the adductor caudalis ventralis, is by a thin flat but strong tendon ending on the lateral surface of the bases of the rays of the most superior portion of the hypaxial division of the caudal fin.

Occasionally the muscle is more strongly developed, in which case it has an origin anterior to that described.

Contractions of the superior flexor produce strong flexion of the dorsal caudal lobe toward the side on which the contractions occur. Undoubtedly this muscle and the one preceding it exert the most powerful influence in the control of the rudder-like function of the caudal fin.

FLEXOR CAUDALIS DORSALIS INFERIOR.

The inferior dorsal flexor is a much more slender muscle than the preceding one. Its origin is directly ventral to and lies parallel with the superior flexor. The fibers of origin are from the connective tissue over the basal part of the bony plate formed by the fusion of the neural spines of the last three vertebræ of the caudal peduncle. Some fibers are also attached into the myocommata at its most anterior margin. The muscle belly extends caudally in a line parallel with the general axis of the fish, running under the adductor to a flat tendinous insertion into the bases of the median two or three caudal rays next above the axial ray.

Contractions of this muscle produce simple flexion of the middle portion of the caudal fin.

From the descriptions presented and the accompanying figures it is now more clear that these muscles are the ones concerned in shaping the position and form of the caudal fin during the active movements of forward swimming. The great lateral muscles must be supposed to act on the caudal fin as a whole in the alternate propelling move-

ments. If, during this general propulsive motion, the form and shape of the caudal fin is adjusted as it would be by graduated contractions of the deep caudal muscles, it is obvious that the fin will be the guiding rudder controlling the exact direction of the forward movement. In closing the discussion of this phase of our subject we may reiterate once more the statement previously made, that these deep caudal muscles control the positions of the caudal fin which will adapt it to the purposes of a rudder. The great lateral muscles furnish the power which acts on the caudal fin as a whole, furnishing a piscine propeller seldom equaled and never excelled in the aquatic world.

MUSCLES OF THE PECTORAL GIRDLE.

The pectoral muscles of the European salmon, *Salmo salar*, have been briefly described by Harrison,[a] and more recently described and figured by Pychlau.[b] The development is given by Harrison, and by Vogel[c] for the trout, *Trutta fario*. Many instructive comparative points in the myology of fishes are to be had from the exhaustive papers by Allis[d] on *Amia calva* and *Scromber scrombcr*.

In *Oncorhynchus tschawytscha* the pectoral fin has 14 rays, the basal or external one being markedly heavier and the others successively more slender. The base of each half ray is curved sharply toward the median border of the fin. The two halves of each ray are widely separated at the base. The series of rays is seated like a saddle across the skeletal ridge of the basalia, forming a very mobile joint, as described by Pychlau for *Salmo salar*. This type of joint is also found in all the salmon fins, but with modifications.

ABDUCTOR PECTORALIS SUPERFICIALIS.

This muscle arises from the anterior ventral border and the inner or median ventral margin of the coracoid as far back as the base of the fin. Its surface of origin along the coracoid is widest about one-third the distance from the anterior end of the coracoid, where it covers a surface of about 9 mm. wide in a standard fish. The median line of origin is along the ventral ridge on the coracoid, covering this ridge for one-third its length. The fibers of the muscles run back over the deep abductor to a tendinous insertion in the tips of the processes of the ventral half rays. The ventral surface of the muscle near its origin has its tendon joined by the fibers of the protractor ischii. These occasionally spread fan-shaped over the surface of the angle between the ventral ends of the clavicles. The external fibers of the pectoralis superficialis are in close approximation to, and have tendons intimately fused with, the internal portion of the profundus.

The action of the superficialis is to bend the fin downward and forward and to close the rays.

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[a] Harrison, Ross G.; Die Entwicklung der unpaaren und paarigen Flossen der Teleostier. Archiv für Mikroskopische Anatomie, bd. 46, 1895, p. 500–578.

[b] Pychlau, Waldemar: Untersuchungen an den Brustflossen einiger Teleostier. Jenaische Zeitschrift, bd. 43, 1908, p. 692–728.

[c] Vogel, Richard: Die Entwickelung des Schultergürtels und des Brustflossenskelettes der Forelle (Trutta fario). Jenaische Zeitschrift, bd. 45, 1909, p. 499–544.

[d] Allis, Edward Phelps: The skull and the cranial and first spinal muscles and nerves in Scomber scomber. Journal of Morphology, 1903, vol. 18, 1903, p. 45–328.

Same author: The cranial muscles and cranial and first spinal nerves in Amia calva. Journal of Morphology, vol. 12, 1897, p. 487–808.

ABDUCTOR PECTORALIS PROFUNDUS.

When the superficialis muscle fibers are reflected the abductor profundus is exposed. It arises from the ventral surface of the coracoid. Beginning at a point one-third the distance from the anterior end there is a thick muscular mass intimately attached into the surface of a triangular area on the ventral face of the coracoid. The base of this triangle is marked by a line parallel with the base of the pectoral fin over the union of the coracoid with the basalia. The profundus has a short, heavy tendon divided into slips corresponding with, and inserted into, the inner margins and tips of the curved bases of the ventral half rays of the pectoral fin under the tendons of the superficialis.

The contractions of this muscle draw the fin downward, helping to balance or support the body when quietly resting on the bottom.

EXTENSOR PECTORALIS.

There is a rather thick muscular bundle which arises under the anterior origin of the abductor superficialis and along the margin of the ventral portion of the clavicle.

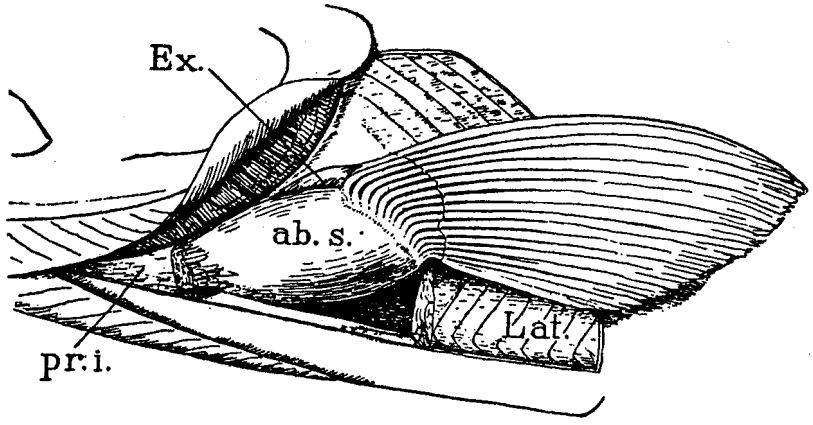

FIG. 7.—Ventral view of the pectoral fin muscles. A segment is cut out of the anterior end of the protractor ischii, *pr. i.*, together with the anterior ventral portion of the lateral muscle. This uncovers the abductor superficialis, *ab. s.*, and its attachments to the ventral half-rays of the fin. The end of the extensor, *Ex.*, with its insertion into the base of the first fin ray is shown.

This muscle lies close within the angle formed in the ventral surface of the clavicle. It is inserted by a short thick tendon into the external surface of the base of the first fin ray.

Contraction of this muscle spreads the fin out in the horizontal position. When the fin is folded back against the body the external ray forms the upper margin of the fin. From this position the extensor pectoralis throws the fin forward, bends it slightly downward and spreads the rays. The muscle tends to support the abductor.

The great lateral muscles are attached by strong slips into the clavicle just dorsal to the insertion of the pectoral fin. There is also a muscular slip from the great lateral muscle running just ventral to the base of the fin and inserted into the fascia of the dorsal wall of the pericardium. This fascia is closely attached to the internal or ventral margin of the coracoid. Undoubtedly contractions of the great lateral muscle would tend to draw the pectoral girdle posteriorly. When the fascia is dissected off a rather

thick triangular muscular mass of the adductors comes into view on the inner and the posterior surface of the coracoid.

ADDUCTOR PECTORALIS SUPERFICIALIS.

This is a short thick muscle lying in the angle between the coracoid and the clavicle and the base of the pectoral fin. It takes its origin from the posterior ventral surface of the coracoid, and the spine on the superior margin of this bone, also from the thin bony plate lying between the superior margin of the coracoid and the clavicle. The muscle fibers converge into a broad tendon which is inserted into the posterior surface of all the dorsal half-fin rays except the first five. When this muscle is reflected a deeper muscle is exposed.

ADDUCTOR PECTORALIS PROFUNDUS.

This muscle arises from the dorsal margin of the extreme ventral portion of the clavicle and the surface included in the angle between this margin and the bony ridge projecting on the side of the clavicle, also from the connective tissue septum joining the clavicle and coracoid and from the dorsal margin of the coracoid including the upper surface of the median spine. The muscle is divided into two parts. Those fibers arising in the angle between the anterior end of the coracoid and the clavicle form a stout tendon inserted into the stout base of the marginal ray. The remaining fibers converge to strong tendons inserted into the bases of the dorsal half rays of the pectoral from the second to the last.

Contractions of the profundus support the contractions of the superficial muscle in throwing the fin back against the side of the body.

INTERFILAMENTI PECTORALIS.

When the skin is removed from the basal half of the ventral surface of the pectoral fin there is exposed a series of very delicate muscle fibers running across the bases of the fin rays. These fibers run from ray to ray, being arranged diagonally so that when they contract they tend to close the rays. No fibers were observed on the dorsal surface.

MUSCLES OF THE PELVIC GIRDLE.

ABDUCTOR VENTRALIS SUPERFICIALIS.

A slender slip of muscle, the abductor ventralis superficialis, arises from the median longitudinal septum of the pelvis beginning at the ventral border of the anterior end of the ischium, also from the adjacent cutaneous fascias. It is surrounded by a strong aponurosis continuous anteriorly with that into which the tendon of the protractor ischii is partially inserted.

The superficialis runs as a slender wedge of muscle to a strong tendinous insertion into the tips of the ventral half rays of the ventral fin. A cross section of the middle of the muscle presents a wedge-shaped surface, the base of the wedge in approximation to the skin, the surface shown in figure 8, and the side in contact with the median (vertical) septum.

Contractions of the abductor ventralis superficialis produce ventral flexions of the ventral fin. It tends to bend the fin downward, i. e., away from the body. If the fin rays are at the time spread then approximation of the rays also occurs.

ABDUCTOR VENTRALIS PROFUNDUS.

This is a large and strong muscle which lies external and dorsal to the superficialis. It takes its origin from the entire ventral surface of the ischial plate, from the septum which connects the external margin of this bone with the skin, and from the similar septum that runs from the internal or median border to the mid-ventral line. This last septum joins the median longitudinal pelvic septum just at the mid-ventral line of the abdominal cavity; hence the peritoneum, the dorsal border of the median longitudinal septum and the internal border of the ischial septum are fused.

The muscle fibers from this extended origin converge in the general caudal direction toward the base of the anal fin. The insertion is by very short tendinous slips into the

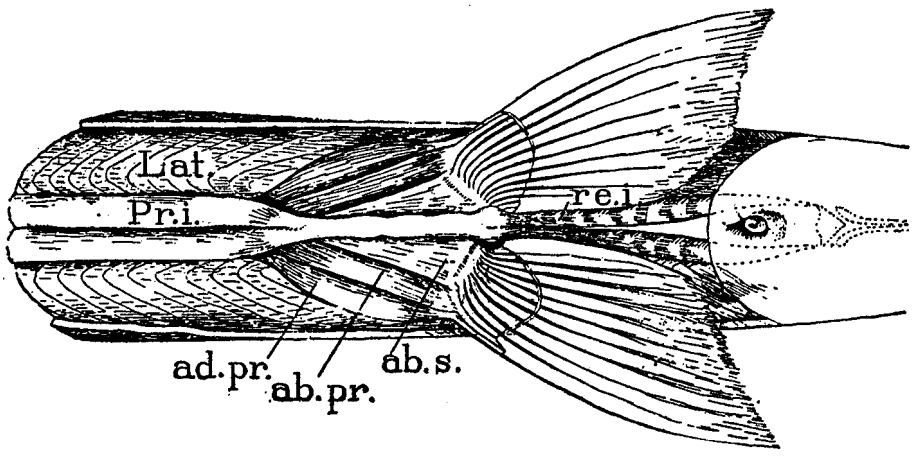

FIG. 8.—Ventral view of the superficial muscles of the ventral fins and of the pelvic arch. *ab. s.*, abductor ventralis superficialis; *ab. pr.*, abductor ventralis profundus; *ad. pr.*, adductor ventralis profundus; *Pr. i.*, protractor ischii; *re. i.*, retractor ischii; *Lat.*, lateral muscle, ventral margin.

ventral half rays of the fin. The tendons run dorsal to the tendons of the superficialis and are inserted into the inner border of the ventral half ray, i. e., the border next the median plane of the fin itself. The fibers arising most anteriorly are inserted into the rays of the external border of the fin. The fibers of the extreme posterior portion of the muscle, arising in the deep angle in front of the ischial thickening, run almost dorsally to the tips of the bases of the rays.

The two halves of the individual rays are more widely separated in the ventral fins than in the unpaired fins, and a distinct synovial joint is formed here as described for the pectoral by Pychlau.[a] The manner of insertion of the abductor profundus and the presence of this very efficient joint insures a strong abduction of the ventral fin on its contraction. There is only a minimal approximation of the fin rays, if any at all, accomplished by this muscle. This latter function seems limited to the superficialis.

[a] Pychlau, loc. cit.

ADDUCTOR VENTRALIS SUPERFICIALIS.

This muscle represents the most dorsal portion of the pelvic musculature. The muscle is separated into two divisions, as described by Harrison for *Salmo salar*.

The *pars anterior* arises from the dorsal surface of the anterior end of the ischium and along the line of aponurosis in which the median longitudinal septum, the abdominal peritoneum, and the ventral attachments of the great lateral muscles meet. The pars anterior division of the muscle runs as a flat band to end in a broad tendinous sheet which covers the dorsal surface of the caudal end of the profundus just over the posterior end of the ischium. It is inserted into the dorsal half rays of the external six or seven rays. The insertion is into the curved bases of the rays at about the middle of the curve.

The *pars posterior* consists of the short and relatively thick mass of muscle fibers which arise from the fascias along the lower border of the lateral muscle immediately dorsal to the posterior part of the ischium and the insertion of the fin. These fibers are well separated from the pars anterior. The fibers run abruptly downward and posteriorly to an insertion into the bases of the last three or four anal rays, i. e., the rays on the median border of the fin. The tendinous insertion does not seem to be sharply subdivided into slips and is extremely short.

ADDUCTOR VENTRALIS PROFUNDUS.

The profundus arises from the dorsal surface of the illium for its full extent, and from the horizontal septum extending from the inner margin of the illium to the mid-ventral line, also from a similar septum extending from the external margin to the skin. The fibers constitute the largest muscle of the pelvic series. In the middle of the belly the muscle is broad and rather thick (22 mm. broad by 6 mm. thick, in an 80 cm. fish). Posteriorly the muscle is somewhat heavier on its median border, the fibers extending transversely out and back over the posterior thickened margin of the illium, and under the tips of the dorsal half rays. When the adductor superficialis is removed the tendon of the profundus is revealed as a broad and relatively long sheath. The insertions of the tendon are on the inner, that is median, borders of all the dorsal half rays. This tendon enters also into the formation of the capsule of the movable joint by which the fin is attached to the posterior end of the illium.

Contractions of the adductor profundus lead to two motions, first, rotation of the fin over the illium at this point, i. e., throwing the fin up against the body of the fish, and second, the spreading of the rays, by throwing the outer fin margin in a lateral direction with reference to the median plane of the fish. These last motions, it will be seen, are directly the opposite of those produced by the abductor group.

The ventral margin of the lateral muscle is strongly attached into the supporting connective tissue of the posterior part of the illium by means of the myocommata. It is evident that contractions of the lower borders of the myomeres lying immediately posterior to the pelvic girdle will have a tendency to draw the pelvic arch as a whole backward. The muscular development does not seem to be of an extent which would lead one to infer that this is a chief function of the muscle. It justifies only the inference that the movement is an incidental but possible one.

MUSCLES OF THE DORSAL FIN.

Harrison [a] has briefly described the muscles of the dorsal fin of *Salmo salar* in connection with his study of the development of the fins of teleosts. The muscles in the king salmon are similar in character and arrangement. The number of dorsal fin rays is greater in *Oncorhynchus tschawytscha* than in *Salmo salar*. The muscles of the fin have a correspondingly greater number of divisions, one for each fin ray. A typical fin ray is moved by three pairs of muscles, (1) an inclinator, (2) an erector, and (3) a depressor. Beside, the fin as a whole is moved forward by the pair of protractors and backward by the pair of retractors described with the group of longitudinal muscles. The specific fin muscles may be described more fully as follows:

INCLINATOR DORSALIS (THE SUPERFICIAL LATERAL MUSCLE OF MCMURRICH).

This muscle in reality consists of a series of short muscles, i. e., independent slips, corresponding in number with the dorsal fin rays. Each tiny slip has its origin in a fascia which is strongly attached to the skin and which covers the dorsal margin of the great lateral muscle. The fibers of each muscle slip converge as a conical mass ending in a short tendon inserted into the postero-lateral margin of the base of each fin ray. These muscle slips are about 20 mm. long in the anterior members of the series and 15 mm. in the posterior. The extreme anterior three or four slips are very rudimentary and may readily be overlooked in the dissection. There are 13 free slips, 16 or 17 in all. In the sea form the spaces between muscle slips are filled with subcutaneous fat. The ends of the deep fin muscles are to be seen just between the ends or insertions of the inclinator slips.

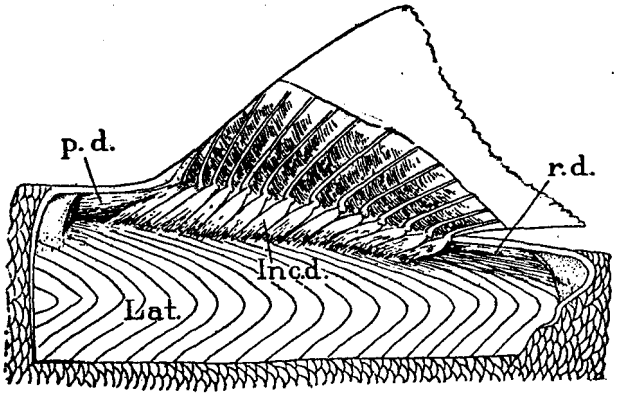

FIG. 9.—Superficial muscles of the dorsal fin after removal of the skin and subcutaneous fat, left side. *Inc. d.*, inclinator dorsalis, one slip for each fin ray; *p. d.*, protractor dorsalis; *r. d.*, retractor dorsalis; *Lat.*, great lateral muscle, epaxial portion.

Harrison was the first to describe these muscles carefully, and to him we owe the name ' 'inclinator."

The contractions of the divisions of the inclinator muscles tend to bend or incline the dorsal fin toward the side.

ERECTOR DORSALIS.

The erector muscle divisions lie between, hence alternate with, the depressor slips of the double series. Each of these arises from the fascia between its interneural spine and the one next in front of it, and from the posterior border of the latter. The mus-

[a] Harrison, Ross G., loc. cit.

cular divisions of the erector dorsalis are separated from those of the depressor by very thin connective tissue septa. But the whole group of muscle slips is encased in a much thicker and tougher sheath. When the muscles are uncovered by removing the lateral muscles the connective tissue sheath is more evident. This is seen to be intimately attached along the line where the neural spines and interneurals are interlocked and embedded in the median longitudinal septum. This sheath, the median septum, and the partitions between muscle divisions serve to form a series of slender glove-finger-like cavities enclosing the pairs of muscle slips on each side.

Each muscle division of the erector is attached by a very short tendon into the anterior margin of the base of the dorsal halfray. The largest erector divisions are 40 mm. in length. At the posterior and shorter margin of the muscle they are about 32 mm. in length. The anterior two or three muscle slips are rudimentary, very slender, and more or less fused.

The contractions of the erector muscle elevate the dorsal fin rays as the name implies. The point of attachment of the tendon of insertion above or distal to the center of movement of the joint favors the erection.

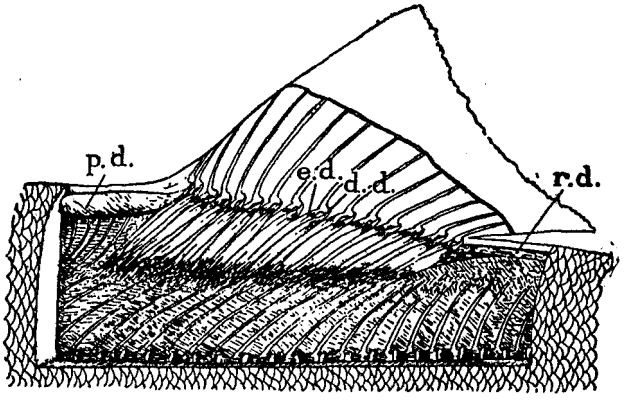

FIG. 10.—Deep muscles of the dorsal fin after removal of the great lateral muscle; *e. d.*, erector dorsalis; *d. d.*, depressor dorsalis *p. d.*, protractor dorsalis; *r. d.*, retractor dorsalis. The skeleton is shown embedded in the median longitudinal septum.

DEPRESSOR DORSALIS.

The depressor muscle of the dorsal fin is intimately associated in position and attachments with the erector dorsalis. The depressor divisions are also segmental in arrangement. They are very slender slips of muscle which arise each along the anterior border of the corresponding interneural spine, and from the fascia separating this muscle from the erector muscle in front of it. The fibers pass across the end of the interneurals to insertions on the posterior border of the base of each dorsal ray. The last muscle division of the posterior border of this series is very strongly developed. It is somewhat broader than its mates and is attached into the bony plate previously described for the retractor dorsalis muscle.

MUSCLES OF THE ANAL FIN.

The musculature of the anal fin is built on the same plan as that of the dorsal fin. The modifications are slight and more or less unimportant. The fin has a protractor, the retractor of the pelvis, and a retractor—both of which are divisions of the infracarinales previously described as the most ventral longitudinal differentiation of the lateral musculature. The proper muscles of the fin are (1) the inclinator analis, (2) the erector analis, (3) the depressor analis, and (4) the interfilamenti analis. These muscles are in divisions

corresponding to the skeletal divisions of the fin itself. Their relations are shown by a consideration of the anal fin skeletal complex.

SKELETON OF THE ANAL FIN.

The anal fin of the king salmon consists of 16 well-developed fin rays, with three rudimentary rays at the anterior margin. There are no spines. A pair of typical rays, say from the middle of the series, serves to show the general skeletal plan (fig. 11).

The ray itself consists of two half rays, the so-called dermal plates, intimately bound to each other except at the base. Near the base the plates diverge slightly and curve sharply posteriorly, not unlike the curve of a hockey stick. The ray is seated cross-saddle fashion over a median cartilage to which it is strongly bound by connective tissue ligaments but with a movable joint.

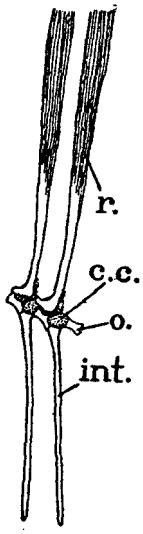

FIG. 11.—Two segments of the skeleton of the anal fin. The lettering is on the cephalic border; *r.*, ray; *int.*, interhemal spine; *c. c.*, cartilages; *o.*, ossicle forming movable joints between the interhemals and the fin rays.

The median cartilage is bound by a movable joint to the head of the supporting interhemal. The interhemal is firmly imbedded in the median longitudinal septum. The position of the interhemals alternates with the hemals but forms an acute angle with the axis of the body, the inclinations being directed caudally.

This skeleton is modified at two points. Anteriorly the whole complex just described is represented by a triangular plate, apparently the homologue of either the median cartilage or more probably of the interhemal. This plate is strongly bound to the anterior margin of the fin base. Its most dorsal angles receive the tendons of the retractor ischii (fig. 2).

Posteriorly there is also a sharp skeletal modification. The last two interhemal spines at the posterior end of the series are fused at their ventral ends forming an irregular club-shaped knob under the second from the last fin ray. This interhemal knob is larger and stronger than the ones immediately in front of it.

Just dorsal to the last rays of the anal fin, and in series with and bound by the enlarged interhemal, is a specially modified cartilaginous plate. It is rather strong and laterally compressed. This plate receives the attachment of the retractor analis. The plate is very strongly bound to the ones in front of it and to the interspinous septum by bands of fibrous connective tissue. Doubtless this modified cartilage is the homologue of one or more intermediate plates or of the interhemals.

INCLINATOR ANALIS.

The constituent serial divisions of this muscle are exposed by removing the skin from along the base of the anal fin and the ventral surface of the adjacent part of the body (fig. 13). There are muscle divisions for each ray including the rudimentary rays at the anterior margin of the fin. The largest and longest divisions are opposite the anterior full rays of the fin. The muscle slips become progressively smaller posteriorly. The muscles of the rudimentary rays are small and imperfectly separated.

The longer muscle slips of the inclinator are about 12 to 15 mm. long and from 4 to 5 mm. wide. They are broad at their origin and the fibers converge to the point of insertion into the rays.

The origin of the inclinator fasciculi is from the skin and the fascia covering the ventral border of the great lateral muscle. This broad origin gives to each slip a base which is seated on the cylindrical border of the lateral muscle. From this broad origin the fibers converge toward a short slender tendon which is inserted into the base of the corresponding ray on its lateral surface, and between the tendons of the erector and depressor respectively. The insertion is in the plane of the axis of the ray joint. The inclinator muscle slips fill the triangular space between the skin, the lateral muscle border, and the erector-depressor group of muscles (see fig. 13). The divisions are strongly embedded in connective tissue sheaths as best shown in formalin-preserved specimens.

Contractions of the inclinator muscle strongly bend the fin toward the corresponding side. This motion is most pronounced at the anterior margin of the fin where the muscle slips are longer and larger. The pull of the muscle is at an angle of about 70°, an angle that decreases with the flexion of the fin in that direction.

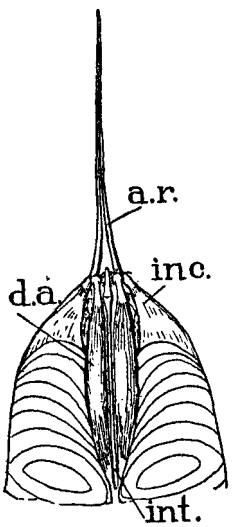

FIG. 12.—Section across the anal fin in the plane of the interhemal spines, the fin rays, and the erector-depressor group of muscles; *int.*, interhemal spine; *d. a.*, depressor analis; *inc.*, inclinator analis muscle; *a. r.*, anal ray.

ERECTOR-DEPRESSOR MUSCLE COMPLEX.

When the great lateral muscles are removed from the region of the anal fin a muscular mass is exposed lying under the superficial and deep lateral muscles and covering the interhema spines of the anal fin. This mass consists of alternate slips of muscles constituting the erector and depressor muscles of the anal fin respectively.

The whole group of muscle divisions is, like that of the dorsal fin, covered with a fibrous connective tissue sheath of considerable thickness. This sheath is continuous with that between the interhemal spines and is especially well developed in the longitudinal line marking the border between the hemal spines and the interhemals.

ERECTOR ANALIS.

The erector muscle of the anal fin is composed of the larger of the alternate divisions mentioned above as constituting the deep muscle complex. There is a muscle slip for each fin ray.

Each erector slip arises from the posterior margin of the interhemal spine in front of the one to which the ray is attached, and from the entire surface of the connective tissue septum between the two interhemals in question. Each muscle division is spindle shaped. It tapers at its ventral end into a short tendon, which runs to an attachment in the anterior basal margin of the corresponding fin ray.

The posterior slips of the erector analis are somewhat modified from the regular arrangement. The last pair of erector and depressor muscle slips is greatly enlarged, or rather the erector is greatly enlarged and the depressor moderately so. The fibers near the tendon of insertion pass over the modified interhemal cartilage to which the retractor ischii is attached, to insertions into the posterior border of the last anal fin ray. This fin ray is itself very small. The tendinous end of the muscle slides over a groove formed by the modified cartilages supporting the ray.

At the anterior margin of the series of erector divisions there is a muscular slip which seems to belong to the series, judging by its origin, but the insertion of which passes into the skin in front of the fin and near the base of the anal papilla.

The contractions of the erector muscles tend to elevate the anal fin and in continued contraction to hold it in the erect position. This is favorable in increasing the

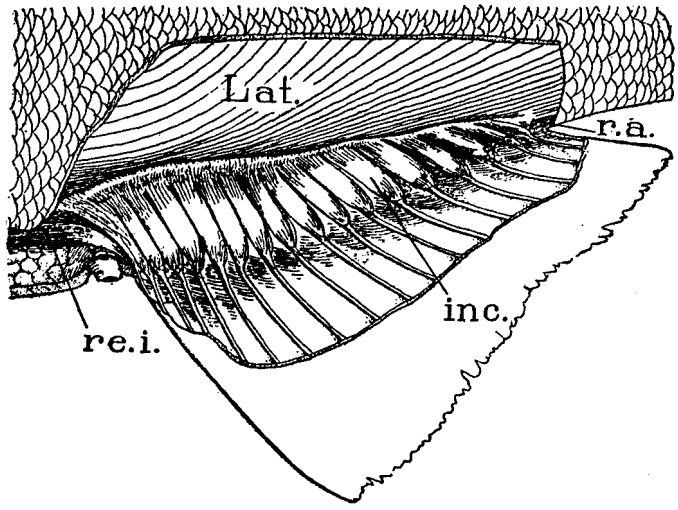

FIG. 13.—Superficial muscles of the anal fin. *inc.*, inclinator analis showing divisions for each ray; *re. i.*, retractor ischii (protractor analis); *r. a.*, retractor analis; *Lat.*, great lateral muscles. The dotted line indicates the ventral limit of the lateralis superficialis.

efficiency of the lateral movements which this fin contributes in balancing the fish in the water.

The contractions of the larger posterior muscle slip described tend to draw the posterior end of the anal fin sharply against the body and to some extent to antagonize the retractor analis. The function of the most anterior slip which has an insertion into the skin in front of the fin would seem to be in connection with the movements of the anal papilla.

DEPRESSOR ANALIS.

The depressor muscle consists of a series of slips which arise from the anterior surface and lateral margin of the interhemal of the segment to which each belongs and from the fascia separating it from the erector muscle attached to the same ray. The fibers of each slip run as a slender ribbon over the shaft of its interhemal to an insertion into the

posterior border and tip of the corresponding fin ray. Each muscle slip is somewhat thicker at its external border.

The muscle slips are from 30 to 35 mm. long anteriorly and 20 mm. at the posterior border of the series. They are about 4 mm. broad by 1 mm. thick in the middle of the muscle belly. They are closely wedged in between the bellies of the erector divisions. The anterior slips attached to the rudimentary rays are very small and slender.

The contraction of these muscles depresses the rays of the fin, tending to close it up against the body.

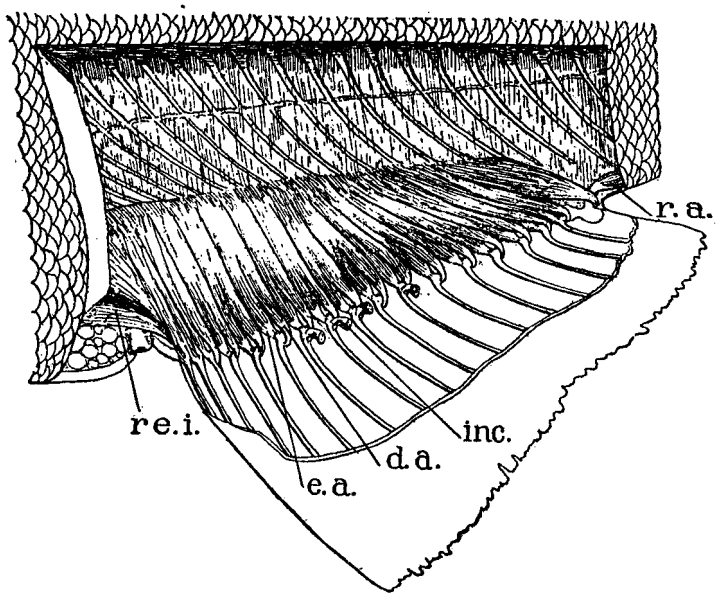

FIG. 14.—Deep muscles of the anal fin. *e. a.*, erector analis; *d. a.*, depressor analis; inc., four reflected tendons of the inclinator analis; *re. i.*, retractor ischii (protractor analis); *r. a.*, retractor analis.

INTERFILAMENTI ANALIS.

Between the fin rays of the anal fin, especially at the base and more strongly developed anteriorly, are found delicate muscle fiber bundles. These muscles are attached to adjacent fin rays, being attached nearer the base of the anterior ray, and more distally to the posterior ray, carrying them in an oblique direction from ray to ray.

Undoubtedly these slips aid in the elevation of the fin rays. They are very delicate and consist of only a very few individual fibers, a fact which easily leads to their being overlooked.

The protractor analis and the retractor analis are longitudinal muscles of the anal fin which have been described on page 34.

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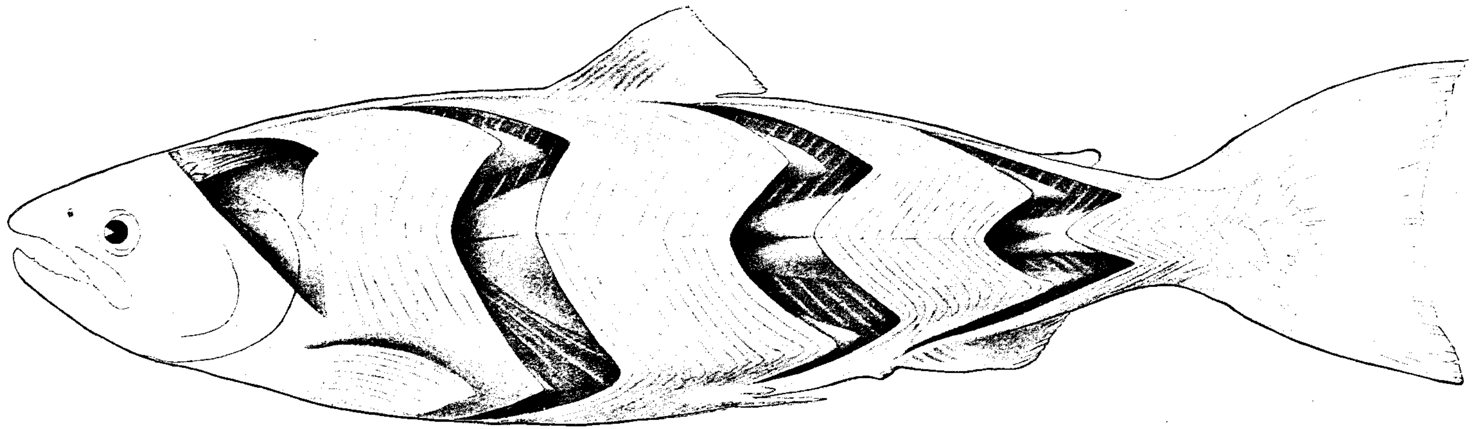
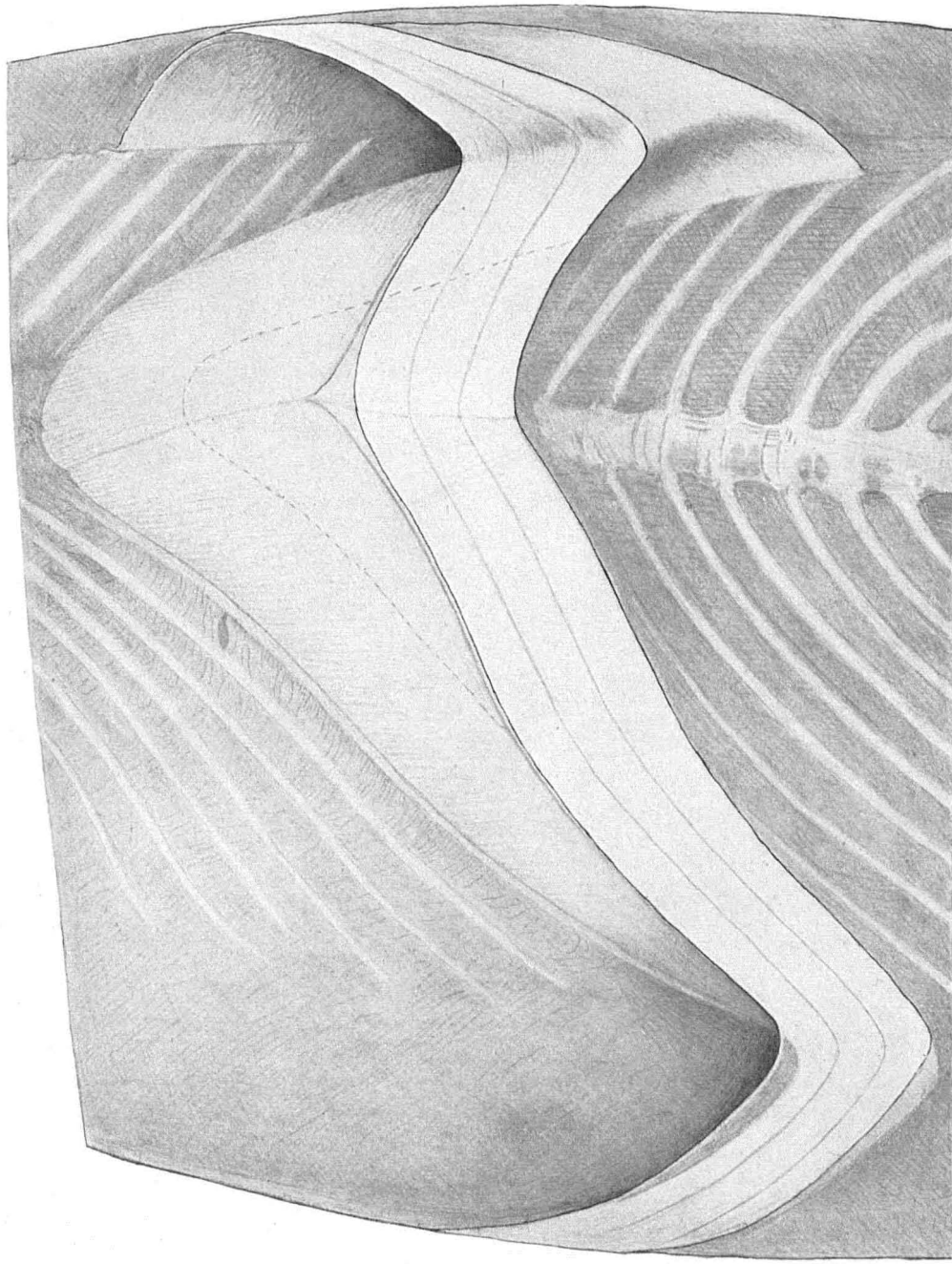


The variations in the form of the myomeres are shown in this figure of the left side of *Oncorhynchus tschawytscha*. The superficial markings of the myomeres and of the myocommata are indicated. There is some little variation, but of no great significance, at the level where the superficialis and the profundus join. It was deemed to detract from the significance of this figure to indicate this separating line, which is indicated in Plate II. The cephalic myocommata are attached to the base of the skull—to the occipital, temporal, and pterotic bones. They are not interrupted by the clavicle, which lies lightly embedded on the surface. The complexity of folding and the longitudinal extent of the myomeres increases posteriorly. The most important variation is due to the division of the anterior fold into two slender cones in the caudal half of the body. Magnification $\frac{1}{4}$.



Three myomeres isolated from the anterior part of the body, i. e., the plane just in front of the anterior border of the dorsal fin. The form of the myomeres and of the septa of the region is revealed. The longitudinal extent of the single myomere is 9 cm., though the length of the longest muscle fibers is scant 7 mm. The skeleton and its dorsal extension in the median septum are well shown. The protractor dorsalis and its supporting tissues lying between the anterior dorsal fold and the median septum have been removed. Magnification ¾.