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ON THE HOMOLOGICAL RELATIONS TO ONE ANOTHER OF THE MESIAL AND LATERAL FINS OF OSSEOUS FISHES. By PROFESSOR HUMPHRY.
PL. II.

THE use of the terms 'median' and 'lateral' with reference to the fins of fishes, though founded on obvious facts, appears to me nevertheless to have in some measure the effect of contributing to maintain a misconception with regard to the real nature of those parts and their relation to one another and to surrounding structures. More especially is this so forasmuch as the term 'median' is by anatomists pointedly contrasted with 'lateral' when they are indicating as one among the special features of fishes that certain of their locomotory organs are placed in the middle line.

The most rudimentary knowledge of development tells us that, with the exception of the parts lying in the axis of the body, none are really mesial, that is, formed in the middle line. All are formed in the lateral layers which ascend or descend from the axial line. The most, therefore, that we can say of any part is that it has acquired a mesial position and character by the coalescence of two lateral elements in the middle line. This must be the case with the dorsal, caudal and anal fins of fishes; and it is in this way that, though not essentially median organs, they have acquired their claim to that title. Nor is this an unimportant distinction, especially when we seek to compare them morphologically with other structures. Each of these fins, like the tongue and every other organ mesially situated, and at a distance from the axis, is a double organ and may be the representative of any other organ which is actually double, in which, that is, the two lateral constituents have not coalesced¹.

¹ A similar view was, I find, entertained by that eminently philosophical anatomist, John Goodsir. After giving his reasons for considering that the interspinous bones and mesial fin-rays are elements of the neuro- or endoskeleton, he goes on to say: "With reference to the mesial position and characters of these bones, I would remark, that it appears to me quite permissible, on morphological grounds, to look upon each interspinous bone, with the corresponding fin-ray, as consisting of a right and left actinapophysis mesially united—that is, to consider the right and left halves of which they consist in the young

I think also the view is somewhat too readily accepted, that these fins which I have named are to be regarded in the light of dermal appendages, and that the interspinous bones by which they are continued into the interior are either prolongations from the surface which have insinuated themselves between the deeper structures or are mere membrane-bones, whereby a cardinal distinction is implied between them and the neural and hæmal arches and other parts of the vertebral skeleton.

The ray-bones, it is true, are closely invested by the derma, though they are, at their roots at any rate, covered by the whole thickness of the derma and by areolar tissue as well as by muscular expansions. The superficial muscles of these ray-bones are expanded beneath the skin, and are closely connected with it; and the interspinous bones and their covering muscles are to a great extent separate from the lateral muscles of the trunk, and present the appearance of having been insinuated between them; and in raising the skin from the lateral muscles, the fin and its muscles are readily detached with the skin. Still, the tendinous terminations of the superficial fin-muscles are in some instances¹ inserted into the inter-muscular septa of the lateral trunk muscle, as well as into the skin; and the skin, as is well known, is closely connected with these septa, indeed they are continued into it. And, which is of more importance, the mesial membranous septa, above and below, in the plane of the neural and hæmal spines, are extended to the interspinous bones and establish a direct continuity between the spinous and the interspinous elements (fig. 1).

These membranous septa are of course in each case double, consisting of two planes which have met and coalesced in the middle line. The two planes, passing superiorly from the dorso-lateral and inferiorly from the ventro-lateral parts of

fish, as fundamental elements of opposite sides of the body." He draws an argument in favour of this view from the occurrence of double anal and caudal fins in monstrous fishes. *Anatomical Memoirs*, by Turner, II. 106.

Gegenbaur, *Grundzüge der Vergl. Anat.*, 675, remarks that the ossifications in the rays of unpaired fins commence in pairs and unite into single portions at a little distance from the base. This may be perceived in most fishes; and the two portions usually admit of being easily separated from one another in the whole length of the ray.

¹ *e.g.* the Sole. In the Perch a series of muscular bundles pass, on either side, from the edge of the lateral muscle, being extensions of the fibres of that muscle, to the joints between the fin-rays and the interspinous bones of the great dorsal fin.

the vertebral centres, and enclosing the neural and hæmal canals, extend to the upper and lower margins of the animal, and constitute the boundary lines between the parts formed in the ascending neural and the descending hæmal layers of the two sides. With lateral perforations for nerves and vessels and with lateral intermuscular processes they form, together with the notochord, the primitive skeleton, as instanced in the Lancelet. They give off laterally processes or sheets which form the intermuscular septa of the great lateral muscle; and at the parts where there are no fins (fig. 2) they give off, near the upper and lower edges of the body, oblique processes which enclose the supra- and infra-carinales muscles, while the septa themselves are continued, in the middle line, between the carinales of the two sides to the skin. The dorsal and anal fins occupy the place of the carinales. Accordingly a membranous process from each septum passes on either side of the fin and its muscles, separating it from the edges of the lateral muscle, while the septum itself is continued to, and blends with, the interspinales bones. This may be seen in the transverse sections, and is better seen by stripping off the muscles on the sides from the interspinous bones and the spines of the vertebræ, when both sets of bones will be found to be enclosed in, and connected with one another and with those in front and behind by, one continuous membranous sheet. The blood-vessels and nerves may at the same time be displayed passing on either side of this sheet, in each interval between the spinous processes, to the fin.

In a Pike about a foot long, from which the accompanying drawings were made, I found the large or distal ends of the interspinous bones, both neural and hæmal, composed of cartilage.

In the deeper parts of the mesial septum, above and below, at the lines of junction with, or giving off of, the transverse intermuscular septa, the neural and hæmal spines are formed; and deeper still, where the coalescence of the two sides of the septa is prevented by the presence of the neural and hæmal tubes, the neural arches are formed. In the abdominal part of the animal (fig. 3) the presence of the viscera causes the visceral or descending embryonic laminæ to take a wider sweep,

and prevents the juxtaposition of the laminæ of the two sides and, consequently, of their lining membranous plates which would have united to form the hæmal septum. The abdominal cavity may therefore be said to lie in this septum, and is commonly confluent with the hæmal canal, though not always or at all parts; that is to say, it separates or keeps asunder the two walls of the septum, not merely where they are membranous, but where the hæmal spines should be formed; and the ossifying bars, instead of coalescing as mesial hæmal spines, are lateralized as ribs. The separation generally extends through the hæmal arches as well as the spines, and lays the hæmal and abdominal cavities into one. It affects also the lowest part of the abdominal septum; for the lower margins of the lateral muscles are pressed asunder, and the interval between them is occupied, and the abdominal cavity is closed beneath by the infra-carinales muscles. The foremost interspinous bone, a little behind the anus, with its muscles, commonly closes the abdominal cavity in this direction, and in front of the anus the mesially arranged interspinous series is wanting.

At a variable point however, in front of the anus, usually near to it, are the ventral fins (fig. 3), two in number, one immediately on either side of the middle line, and they are often connected with each other in the middle line. They are quite symmetrical, forming a pair. Each is composed, like the constituents of the anal fin, of an internal portion, that is, a portion projecting inwards between the ventral margins of the lateral muscles of opposite sides, and which is often simple, dagger-shaped and strikingly reminds us of the interspinous bones of the anal fin, and of an external portion projecting beyond the level of the body and consisting of ray-bones with an envelope of skin. These ray-bones are jointed with the internal bones and moved upon them by simple muscles, much as are the rays upon the interspinous bones of the anal fin. Indeed, so close is the similarity, that if a single ventral fin (fig. 5) is held in front of the anal fin, we can scarcely avoid the conviction that it is a continuation of the same series; and, I think, there can be little doubt of this being the case: the chief difference being, that the ventral fin is double, that is, is composed of two symmetrical slightly lateralized portions, instead

of the two portions having coalesced and occupying a strictly median position. It is also more obliquely placed than the anal fin; though the obliquity is in the same direction, viz. slanting from before backwards and downwards. Both these points of difference are attributable to the presence of the abdominal viscera and cavity, which keep asunder the laminæ of the hæmal septum in the manner already mentioned, and cause the interspinous and muscular and ray elements of the fin to be developed on the sides of, instead of in, the mesial line. So that just as the fibrous septa and the ribs lining the abdominal cavity, serially considered, are the ununited lateral elements which in the caudal region combine to form the hæmal spines and the hæmal septum, so the ventral fins, serially considered, are the ununited elements which, behind the abdomen, combine to form the anal fin.

It may be observed that the ventral fins, whether they are placed just in front of the anus or more forwards, derive their nerves, just as do the components of the anal fin, from the ventral branches of the spinal nerves near which they lie.

The pelvic bones of the ventral-fin I regard, therefore, as the serial homologues of the interspinous bones of the anal-fin; each pelvic bone answering to one or more halves of interspinous bones which have been kept separate from those of the opposite side, while their deeper ends have been directed forwards, and their anterior edges inclined inwards towards the middle line. The effect of this has been to throw the hinder margin of the ray backward, and the surface, which in the primitive condition was internal, or opposed to that of the opposite side, backward and upward. Hence, to bring the ventral fins into a position corresponding with the elements of the anal fin, it is only necessary to turn the pelvic bones and the ray from their horizontal to a vertical position, bringing the anterior extremities of the pelvic bones upwards, and their inner edges forwards. The upper surfaces of the ray will now be turned towards each other, or thrown into contact, their inner edges will be directed forwards, and their hinder extremities will point downwards.

The pelvic bones covered by the fin muscles perforate the abdominal wall, their hinder parts, where articulated with the

fin-rays, being external and connected with the skin and the edge of the lateral muscle as well as with the carinales near the middle. In the greater part of their extent they are internal, forming part of the abdominal wall, and separated from the peritoneum only by the fibrous lining of the abdomen. This membrane invests the pelvic bones and muscles and contributes to hold them *in situ*. At the outer edge of the pelvis it divides into three strata, of which one passes externally between the pelvic muscles and the edge of the lateral muscle, and is connected with the skin: a second stratum passes upon the upper or deep surface of the fin, meeting its fellow of the opposite side, and so forming a continuous sheet which strengthens the part and prevents the protrusion of the viscera; while a third or middle stratum passes between the pelvic muscles to the outer edge of the pelvic bone and is blended with it, so establishing a direct continuity between this internal membranous sheet and the pelvic bone, like that which exists between the corresponding sheet in the caudal region and the interspinous bones.

It not unfrequently occurs that the pelvic bone of each side is not so simple as in the Pike, but, as in *Clarias anquillaris* (fig. 6), presents divisions, a broad portion passing inwards to meet its fellow of the opposite side, while a second portion passes forwards and inwards, and a third passes more directly forwards. These reminders of the pelvic bones of higher animals not improbably represent the incompletely united and diverging interspinous components of the pelvic bone.

The pectoral fins (fig. 4) are situated more laterally than the ventral, being placed at the retiring angle between the ventral and ventro-lateral portions of the great lateral muscle in front, whereas the ventral fins are placed on the mesial side of the ventral portion of the lateral muscle, with the exception of a bundle of the muscle, which, separating itself from the remainder, passes backwards, near the middle line, to the pelvic bone of each side, and lies internal to the projecting part of the fin. Still there seems no good reason to doubt the generally accepted view that the pectoral and ventral fins are serially homologous. If this is so, and the view I have taken of the relations of the ventral fin is correct, it follows that the pectoral

fins are also serially homologous with the anal fin, and the coracoids, like the pelvic bones, answer to the interspinous bones, or portions of them. I say 'or portions of them,' for a comparison of the parts in different fishes (fig. 7) suggests that the series of ossicles intervening between the coracoids and the rays—the brachials of Parker and the carpals of some anatomists—are segmented from the distal part of the interspinous element of which the coracoids form the chief part, and correspond therefore with the distal portions of the pelvic bones.

The collar-like series of bones (fig. 4), which extend from the upper and back of the cranium to the middle line beneath, enclosing the coracoids, lie immediately beneath the skin, yet are connected with the lateral muscle above and beneath, indeed beneath are to some extent imbedded in the ventral portion of that muscle. It is pretty certain that they do not correspond with the coracoids of higher animals, as supposed by Owen. Whether they really deserve the name clavicle which has, with more probability, been assigned to them by Gegenbaur and Parker, further observation must decide.

If the view which I have here given is correct, if the pectoral and ventral fins correspond with the limbs, including their girdles, in higher animals on the one hand, and with the components of the anal fin on the other, and if the osseous elements of that fin and of the pectoral and ventral fins are developed in extensions of the membranous lining of the visceral cavity, in which membrane the hæmal arches and the ribs are developed, it follows that the limb-girdles are in the same internal plane of the visceral wall with the ribs and hæmal arches. They are not hæmal arches or ribs, but formed on a level inferior to, or more marginal than, both. Hence they do not originate in the neighbourhood of the vertebral centres, or have, like the ribs, any direct relation to them, but originate in a more distant part of the visceral layer, and may or may not spread into contact with the vertebræ. The region in which they spring corresponds more nearly with that of the sternum and sternal ribs. Like the several fins of fishes, each is connected with the general muscular system of the animal and has, besides, its own independent muscles passing from segment to segment of the limb.

It follows, further, that each limb of the higher animals

corresponds with a lateral factor or factors of the mesial fin of the fish, and would, if development had proceeded in a similar manner, have united with its fellow into a mesial organ; but the limbs being produced only in the region of the trunk, the (theoretically) apposed surfaces—the palmar and plantar—have been kept apart, and have, as in the case of the lateral fins of the fish, been directed backwards. The direction however of the surfaces, in this instance, is dependent not so much on the inclination of the parts (the girdles) lying in the walls of the trunk, as on the rotation of the outlying parts upon the girdles (see p. 69).

It may be observed also that, according to this view, the median fins—dorsal and caudal, as well as anal—are a series of coalesced lateral limbs, and that on this ground the fish presents some claim to the title of ‘neuropod’ as well as of ‘hæmapod,’ which may, when our knowledge of the morphology of the two is more complete, prove to be an additional connecting link between the vertebrate and the invertebrate skeletons.

DESCRIPTION OF PLATE II.

Fig. 1. Transverse section through the tail of a Pike including the dorsal and anal fins: *a.* interspinous bones of the dorsal fin; *b.* interspinous bones of the anal fin. The muscles of the fins are seen on the sides of the interspinous bones. The four divisions of the lateral muscle with its intermuscular septa are seen.

Fig. 2. Transverse section through the hinder part of the abdomen of a Pike; *s. c.* supra-carinalis muscle; *i. c.* infra-carinalis muscle; *a. c.* abdominal cavity.

Fig. 3. Section through abdomen and pelvic bones (*p.*) of a Pike; these are surrounded by the muscles of the fin. The lateral muscles abut upon the fin muscles, but do not at this part extend to the pelvic bones.

Fig. 4. Section just behind the head of a Pike: *s. c.* supra-carinales muscles; *l., l., l.* lateral muscle; *p. t.* post-temporal bone; *s. cl.* supra-clavicle; *cl.* clavicle; *c.* coracoid with muscles of pectoral fin above and below. The fibres of the lateral muscle are seen to be inserted into the post-temporal and the clavicle.

Fig. 5. The skeleton of the ventral fin of a Pike.

Fig. 6. The skeleton of the ventral fins of *Clarias anquillaris*.

Fig. 7. The skeleton of the pectoral fin of a Pike.

Fig. 1.

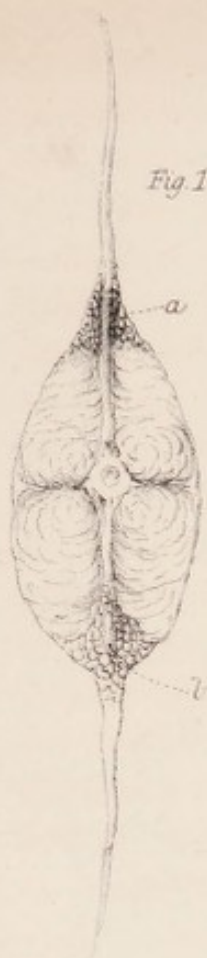


Fig. 2.

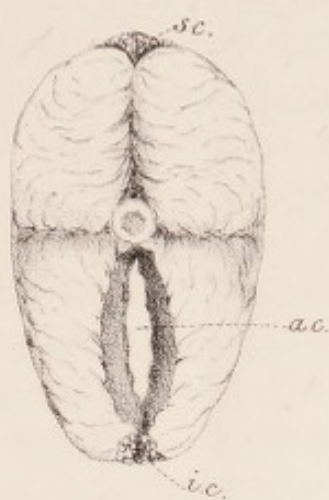


Fig. 3.

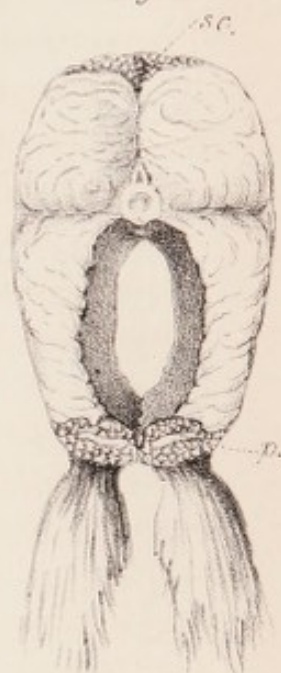


Fig. 4.



Fig. 5.



Fig. 6.

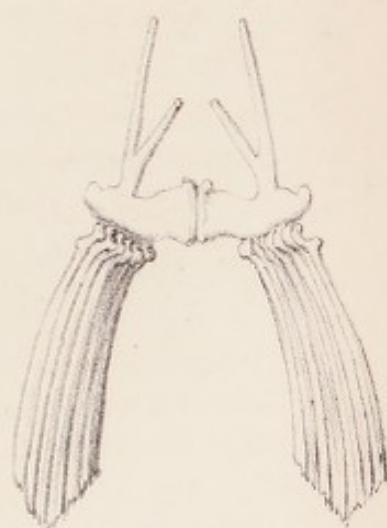


Fig. 7.

