The Hunterian Lectures

ON

THE EVOLUTION OF THE PELVIC FLOOR IN THE NON-MAMMALIAN VERTEBRATES AND PRONOGRADE MAMMALS.

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LECTURE I.—NON-MAMMALIAN VERTEBRATES.

Delivered on March 4th.

INTRODUCTION.

MR. PRESIDENT, LADIES, AND GENTLEMEN,—In order to appreciate the significance of the pelvic floor musculature in man it has seemed necessary to me to investigate the several homologous anatomical conditions existing in the main types of the primary groups of the vertebrates, and to inquire into the manner in which anatomical structure has reacted to a modification of external environmental forces, in order that the internal visceral requirements of the individual, in spite of such change, might still continue to be satisfactorily met.

It may be thought that such an investigation, however interesting, is almost superfluous, and that an examination of the pelvic floor in the dissecting-room would suffice to explain how it acts in the living. Anyone who thinks so should look into the literature of the subject, and he will find that paper after paper has appeared, founded on an anatomical basis, but leading to no definite, clear, irresistibly convincing conception of the function of this musculature. According to Sappey, of all the muscles in the body the levator ani has been the most studied but is the least understood. No one would be content with the result of dissection to come to a conclusion concerning the functions of an organ, such as the liver, although such dissection will show that it receives all the blood from the intestine, and must therefore in some way be intimately related to the assimilation of food. It is only by experiment in the living that the functions of the liver have been disclosed, and it is only in a similar way that the functions of the pelvic floor can be revealed. Physiological experiment has, indeed, shown that by appropriate stimulation a living muscle fibre becomes shorter, and that by such contraction is capable of doing work, of moving limbs, &c.; but such inquiry will not demonstrate the reason of its activity in the body, although it shows the manner of it. It is only by such investigations as those instituted by Professor C. S. Sherrington with such brilliant and revolutionary results that the functions of various muscle groups concerned in the causation of various definite limb movements are becoming to be understood. It may be possible that such laboratory experiments, if arranged to demonstrate the functions of the levator ani, will solve the riddle of its existence; but such experiments can only be successful when the conditions calling the function of the muscle into play are provided, and this provision depends on considerable knowledge, which appears at present to be scarcely forthcoming. It is not, therefore, to the result of some such experiment I ask your attention, for none, as far as I know, has been performed. There is another, perhaps surer, way of studying the subject, and that is the investigation of the results obtained in that huge physiological laboratory, which is coextensive with the domain of Nature, and in which experiments have been in progress ever since life began. For Nature, by endowing the individual with the power of adaptation to new surroundings, which such individual may have been coerced to enter, as the result of some geologic disaster or climatic change, or from persecution of companions, or hunger, or from other causes, has permitted adaptive alterations in structure to occur—which we believe are necessarily correlated with the forces that caused them—so that the individual, in spite of that change, might continue to exist.

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That is to say, Nature has allowed a series of physiological experiments to be made, the results of which lie buried in the bodies of the present-day survival of types, more or less unaltered, of those passed individuals.

It may be supposed that such results throw but little light on the condition in man; but when we remember that the mechanism of life in all is similar, and that it depends on identical essentials, the application of such experiments must be admitted. The vertebrates are not only built on one plan, but the physiological mechanism of the living cells of which they are composed, which constitutes their life, is identical. The necessity for oxygen, the necessity for food, the necessity for reproduction, is the same in each. By altering the means by which these necessities have had to be obtained, a corresponding alteration in structure has been brought about, and thus the survival of the species safeguarded. It is this structural change, in so far as it concerns the pelvic floor, that we have to study. But this by itself can be of little service; to understand the structure in any type we must at the same time consider, as far as we are able, the conditions of the physiological experiment in question, whereby the particular variety of structure has been brought about.

FISHES.

A pelvic floor can scarcely be said to exist in the fish, for the pelvis is rudimentary. In the dog-fish (Fig. 1) the pelvic girdle is represented merely by a transverse bar of cartilage placed just in front of the cloaca. It is unconnected with the vertebral column except by means of that part of the lateral trunk musculature which extends forwards from the tail into the body, and which, as it passes over the pelvic bar, sends a good strand of its lowermost fibres to be inserted into its upper lateral part. This strand of fibres, which forms part of the ventral tail musculature, from which it cannot be differentiated, is directed from behind forwards to the pelvic bar and may be called the *caudo-pelvic strand*. Behind the cloaca it abuts upon the median line and is in apposition with the similar strand of the opposite side. As these two strands are traced forwards to reach the pelvic bar they diverge to allow the cloaca to pass between them, which they thus embrace. So, if a pelvic floor can be described in the dog-fish, it is evidently formed by the innermost margins and adjacent parts of the caudal extensions of the lateral trunk musculatures, which I have ventured to call the caudo-pelvic strands.

This lateral trunk musculature of the fish forms the most conspicuous part of its body. That part of it which forms the musculature of the tail passes in an uninterrupted way to the skull. In the dog-fish it consists of fibres horizontally placed, and is easily divided into two parts—a dorsal and a ventral—by the well-marked lateral line. In front of the pelvic bar, however, the lower part of the ventral musculature, that which encloses the body cavity, is formed of a thin sheet, the fibres of which are obliquely placed. These arise from the connective tissue enclosing the lower longitudinal fibres and pass obliquely downwards and forwards towards the median ventral line. But the fibres which arise from the anterior border of the pelvic bar pass directly forwards. There is no line of demarcation between the oblique fibres and the median longitudinal ones, but the former merge imperceptibly into the latter. The oblique fibres correspond to the internal oblique and the median longitudinal to the recti abdominis muscles of higher vertebrates.

In Protopterus—one of the Dipnoi—the anatomical relations of the cloaca, and the parts immediately behind the pelvic plate, are similar to those found in Scyllium canicula, except that the transformation of the pelvic fins into slender cylindrical processes, and the displacement of the cloacal opening from the median line to the left side, cause corresponding differences. The caudo-pelvic strand of muscle fibres is present on each side. They arise as oblique fibres from the ventral axial skeleton of the tail, and they pass downwards and outwards and forwards, and then inwards to become attached to the pelvic plate and the median line. Anterior to the pelvic plate, they are continuous with a layer of oblique fibres, which passes downwards and forwards, similar to that in the dog-fish, and which takes part in the formation of the ventral body wall. But besides this internal oblique layer, another layer of oblique fibres, directed downwards and backwards—i.e., caudalwards—exists in Protopterus; so that in this vertebrate the abdominal wall consists of two distinct layers, easily distinguished from

each other by the different directions of their fibres, the superficial corresponding to the external oblique of higher vertebrates. A comparison of the ventral abdominal wall of *Protopterus* with that of the dogfish also shows that the former is not only relatively, but absolutely, thicker than that found in the latter, so that there is not only a structural change in the obliquity of muscle fibres, but also an absolute addition. These external oblique fibres reach as high up as the lateral line from which they arise, and are inserted into the median ventral line; they also extend as oblique fibres into the tail.

It is to be noticed in *Protopterus* that the fibres of the dorsal part of the lateral trunk musculature are also oblique, not longitudinal as in the dog-fish, their direction being exactly the opposite of those of the external layer of the ventral part. Since the paired fins in *Protopterus*, on account of their cylindrical form, can scarcely have much, or any, effect in controlling ascent or descent whilst swimming, whatever the cause of the appearance of the external oblique muscles of the ventral wall may be, it seems as though the oblique disposition of the dorsal fibres may have arisen to counteract the effect of the former, and by variations of contraction in each to enable the fish to change its course whilst swimming either obliquely upwards or downwards.

A muscular diaphragm, corresponding to the thoracic diaphragm of mammals, does not exist in the fish; but the region containing the heart is cut off from the rest of the body cavity by the septum transversum.

The cloaca in the fish does not appear to possess a sphincter muscle. Neither in the dog-fish (Fig. 1) and

FIG. 1.

Dissection of cloacal region of the Dogfish. About half life size.
P, Pelvic bar bisected and turned outwards. C.P., Caudopelvic strand.

Protopterus, nor in the mackerel and herring have I been able to find one. In the former, the caudo-pelvic strands with the pelvic bar or plate appear to serve as a closing apparatus; whilst in the latter, a distinct muscle bundle arises from the median dense tissue and tips of ventral spines immediately behind the cloaca, and passes forwards, one on each side of it, along the median ventral line of the fish. In front of the cloaca these two muscle bundles are united together by connective tissue and on contraction cause a bilateral compression of the cloaca.* But no ring-like muscle exists. It would seem, indeed, that a closure of the cloaca by means of a special sphincter muscle is not so necessary for the fish as it is for terrestrial animals; for fish live in a medium—water—the specific gravity of which is not very different from that of their bodies, and the pressure exerted by this medium on all sides of the animal will tend of itself to prevent an extrusion of any part from within, such as excrement or ova. Their shape, and the compactness of their viscera, are sufficient evidence of this pressure; which varies, of course, with the depth of the fish from the surface, and may be very considerable. In vertebrates, however, which live on the land, and whose bodies, therefore, are surrounded by a medium of a greatly diminished specific gravity, quite different conditions exist; for the medium cannot, because of this physical difference, have the same effect on the contents of the cloaca, around the orifice of which in the great majority of terrestrial vertebrates, a distinct sphincter muscle is to be seen.

When, however, in the dog-fish an escape of visceral contents becomes a necessity, it is plain the pressure bearing upon the cloaca from without, and which opposes such escape, can only be overcome by an increased pressure within—i.e.,

an increased visceral pressure; for the contents of the viscera can only be expelled by means of a pressure effect, in which the pressure within the oviduct, for instance, becomes greater than that of the medium by which the fish is surrounded. This, in the case of the ejection of excrement, may be met by the contraction of the gut musculature; but such ejection will be more effectual if the body-wall musculature surrounding the viscera, responding by an increased contraction, increases the pressure to which they are already subjected. That such increased visceral pressure, brought about by contraction of the body-wall musculature, is a real factor will, I think, be admitted when it is remembered that the size of the ova passed, at least in the dog-fish, is very considerable (Huxley¹⁵).† This seems to explain the existence of the oblique fibres in the ventral wall of the dog-fish; for their direction is such that their contraction will determine an increase of pressure towards the cloaca. Such an end as the voluntary increase of visceral pressure, by the increased contraction of the enclosing musculature, would be impossible, or difficult to achieve, or, at least, it would not be so efficiently performed, were all the fibres of the trunk placed longitudinally. The fixation posteriorly of the pelvic bar, which is effected by the caudo-pelvic strands, and the limitation of the size and dilatibility of the cloaca, which this fixation causes, may also be a factor, necessitating an increased visceral pressure during the passage of ova; and this is in keeping with the fact that in many of the higher animals, including man, a similar difficulty occurs, constantly during parturition, and commonly during defæcation, and which is certainly not due to the medium in which these animals dwell, but to a very different cause.

In *Protopterus*, an increased visceral pressure is also necessary during aerial respiration for expiration. It is plain before a fresh supply of air can be taken that the volume of the lungs must be somewhat reduced. This can only be accomplished by a compression of the viscera amidst which the lungs lie, and is produced by the pressure of the medium about the animal, and supplemented by the increased contraction of the enclosing musculatures. In *Ceratodus*, a dipnoi, which is entirely aquatic, and which only occasionally rises to the surface to breathe—i.e., to swallow air, its blood being oxidised, as in the majority of fish, by means of the well-developed internal gills—the pressure of the water without will probably suffice to effect expiration, when the sphincter of the glottis is relaxed. But when the water drains away from the swampy places in which *Protopterus* lives, and exposes it to air, and during its long æstivation this force exerted by the water is lost; thus it necessarily follows that the contraction of the enclosing muscles must be increased to obtain the same result as before.

Although the increased thickness of the musculatures enclosing the visceral mass in *Protopterus* may perhaps be explained by the greater activity necessitated by wriggling movements in partially inspissated mud, the development of an additional muscle layer of oblique fibres, passing downwards and caudalwards seems to have been caused by such a necessity as that of a frequently recurring forced expiration; for the direction of their fibres is such that their contraction will determine an increase of pressure towards the pharynx.

In support of this, we find that whilst in *Ceratodus* the lung exists as a large unpaired sac, in *Protopterus* the lungs are paired, their structure much more sacculated and more lung-like, the internal gills have partially atrophied, and the heart has evolved further; and side by side with these visceral changes and different habits, that the ventral wall musculature in *Ceratodus* shows no trace of the second external oblique layer, which is so conspicuous in *Protopterus* (Wiedersheim³⁶).

Such considerations as these seem to offer adequate explanations for the origin and the marked development in the fish of the caudo-pelvic strands on either side of the cloaca on the one hand and the oblique fibres in the ventral part of the lateral trunk musculature on the other, the essential function of which evidently is to effect an increase of the internal visceral pressure.

AMPHIBIA.

In the amphibia development has proceeded further. A great change has taken place in the pelvis, in that a bony process, the ilium, already present as an outgrowth in some

* See Holl, p. 260, see reference 14.

† The superior figures relate to the Bibliography which will be printed at the end of Lecture II.

of the fishes (as in *Chimaera monstrosa*: Wiedersheim), has grown dorsally on each side from the pelvic plate, passing upwards in the tissues of the lateral trunk wall towards the spine. In some species, as in the Salamander, this ilium has reached and has become attached to the rib of the single sacral vertebra by an articulation, which allows a to-and-fro movement of the pelvis upon the spine; but in others, as in *Menobranchus*, this upgrowth has remained incomplete, so that the pelvis is freely moveable. It is significant to notice of these two species, whilst the adult form of the Salamander lives entirely on the land and does not possess gills, *Menobranchus* is wholly aquatic and large external gills are conspicuously present.

Next, dissection shows the existence of a pair of muscles arising from the ventral part of the tail skeleton in the middle line, at some distance from the pelvis, diverging as they pass forwards, one on each side of the cloaca, to be inserted into the posterior edge of the pelvic plate (ischia). (Figs. 2 and 3.) We have here, indeed, the caudo-pelvic strands of the dog-fish, segmented off from the lateral trunk musculature, and in Salamander, forming distinct and individual muscles. But in *Menobranchus*, whilst these muscles are as distinctly defined anteriorly as they are in Salamander, posteriorly they merge into the ventral tail musculature and thus appear to be continuations of it. Anteriorly these muscles are so placed that their surfaces look upwards and downwards, and their edges laterally, the median borders being only separated from each other by a small interval. As each muscle is traced distally it becomes

FIG. 2.

Dissection of *Menobranchus*, showing caudo-pelvic muscles A. The cloacal passage has been cut through on a plane with these muscles and the superficial parts have been removed.

twisted on its long axis, so that its superior surface becomes internal, and it thus presents a broad surface to the cloacal passage as it passes by it; at its origin from the tail it is vertically placed, and is contiguous with its fellow of the opposite side.

The abdominal wall in *Menobranchus* consists, besides the recti, of three distinct layers: an external, the fibres of which pass downwards and backwards or caudalwards; a middle, the fibres of which pass downwards and forwards; whilst the fibres of the innermost layer pass almost directly downwards and inwards, forming the transversalis, which is first met with in the tailed amphibians. It is interesting to notice that the direction of the fibres of the dorsal part of the trunk musculature (that dorsal to the lateral line) is also oblique, the fibres passing downwards and forwards as in *Protopterus*. In the Salamander the external and internal oblique muscles are well developed, but an inner layer of transverse fibres, corresponding to the transversalis, does not exist. Recti abdominis are present.

In neither *Menobranchus* nor in *Salamander maculosus* have I been able to discover a sphincter cloacæ. Since the *Menobranchus* is entirely aquatic, the absence of such a sphincter may be more easily understood. Its absence in the purely terrestrial Salamander seems to find an explanation in the well-developed caudo-pelvic muscles. Since these arise from the median line of the tail, and are inserted into the pelvic plate in such a fashion that their inner borders almost reach the middle line, when they synchronously contract, the pelvis being fixed by the recti, they will exert a bilateral compression of the cloaca, and apparently this is sufficient to effectually occlude its passage.

A survey of the conditions found in *Menobranchus* and the *Salamander maculosus* seems to show that the evolutionary advance trended towards the fixation of the pelvis to the

FIG. 3.

Dissection of *Salamander maculosus* to show A, caudo-pelvic muscles.

vertebral column, and that this is associated with greater variations of internal pressure, due to an increase in general activity. The change in the method of respiration, compared with that of the Dipnoi, is not very great. When this is carried out by means of the lungs, the air is forced into them by an act similar to that of swallowing; whilst expiration is effected by an increase of the contraction of the abdominal wall musculature—i.e., by an increase of the internal visceral pressure. Since the recti abdominis and external obliques are attached to the pelvis, their contraction can only become efficient by a fixation of this structure. This fixation was primarily attained by the development of the caudo-pelvic muscles, which thus anchored the pelvis posteriorly. These muscles are relatively of considerable length, and pass caudally from the pelvis almost in the same straight line as the recti abdominis, and thus are admirably adapted to resist a displacement of the pelvis forwards which contraction of the recti tends to bring about. Moreover, since these muscles are attached to the pelvis as broad horizontal bands abutting upon the median line, besides fixing the pelvis, they also prevent the escape of pressure impulses posteriorly; and further, by resisting these impulses, tend to increase the pressure effect. The frequent occurrence of these variations in internal pressure, not only necessary for expiration but also incidental to general activity, and of importance as an accessory circulatory mechanism, is also associated with the further development of the abdominal wall musculature and with the evolution of the caudo-pelvic muscles. Indeed, the correlation of these two factors—the need for an increased visceral pressure on the one hand, and for efficient enclosing muscular walls on the other—is such—the former being so plainly dependent on the latter—that they take on the forms of cause and effect.

REPTILES.

The condition found in reptiles is extremely interesting. At least two sacral vertebrae are present, which are either ankylosed or bound together by fibrous tissue, whilst the fibro-cartilage which connects the ends of their ribs and forms a single broad area for the attachment of the ilium

further restricts any movement between them. This sacro-iliac articulation is placed behind the acetabular joint and may permit a certain amount of a to-and-fro movement of the pelvis on the spine, as in Iguana and Emys, or the pelvis may be immovably fixed to the spine, as in the Crocodile. The pelvis is completed inferiorly by the junction of the pubic and ischial bones which may form a single median symphysis.

In Iguana the caudo-pelvic muscles are conspicuously present (Fig. 4), but instead of a single muscle two are found on each side, one being much larger than the other (Fig. 6). The larger caudo-pelvic muscles are of considerable length and are superficially placed, one on each side of the cloaca,

FIG. 4.

Ventral view of Iguana, showing pelvis. A, A, The large antero-posterior caudo-pelvic muscles. B, The caudo-femoral muscle of the right side attached to femur. C, The sling; the attachment of the sling to the hypischium, D, has been cut through and turned outwards.

behind which their median borders are in apposition, where they arise from the tail by an extensive origin. Traced forwards they rapidly diminish in size and give rise to a tendon which is inserted into a bony protuberance on the ventro-lateral aspect of the pelvis. The much smaller and much shorter caudo-pelvic muscle is placed on the inner and deep side of the larger muscle, which thus hides it from view. It arises from the fascial septum in the angle between the diverging larger caudo-pelvic muscles immediately behind the cloaca, and passes forwards and outwards, crossing the dorsal (deep) surface of the larger muscle, to be inserted into the ventro-lateral aspect of the pelvis, immediately behind the posterior lip of the acetabulum, on a more dorsal plane and more laterally to the insertion of the larger (caudo-pelvic) muscle. The larger and smaller caudo-pelvic muscles

are quite distinct from each other, and at their insertions are separated by an interval; but they are so closely related that it seems not unlikely they are differentiated parts segmented off from a single parent muscle.

Filling up the big space between the spines of the chevron bones internally and the superficial tail musculature externally, and placed immediately dorsal to the belly of origin of the larger caudo-pelvic muscle which partially hides it from view, is the large caudo-femoral muscle (Figs. 4 and 5), the origin of which reaches anteriorly the caudal limit of the pelvis, and here suddenly passes outwards over a sling to reach and be attached to the upper part of the femur. This sling (Fig. 5), over which the caudo-femoral muscle passes, is formed by a tendon interposed between two muscles—a dorsal and a ventral. The dorsal muscle—which, from its similarity to a muscle found in the Tortoise (Emys) may be called the *lateral caudo-pelvic muscle*—arises from the transverse processes of the anterior caudal vertebræ; its posterior fibres pass downwards and forwards, but its anterior fibres, which form much the thicker part, pass almost directly downwards to end in the short flat tendon forming the sling referred to. The other muscle, which serves to keep this tendon in place, arises from the hypischium and passes outwards and upwards to be inserted into the tendon. Besides retaining the upper part of the caudo-femoral muscle in place, this mechanism, with that of the opposite side, is also capable of exerting a bi-lateral compression upon the pelvic continuation of the body cavity and the cloaca, which is very evident on dissection.

The body wall musculature, in which ribs are embedded, consists, besides the recti, of three layers—the external and internal oblique and transversalis muscle. The ribs pass obliquely downwards and backwards in a series almost as far as the pelvis, the last two or three being short; anteriorly their ventral ends are united to a sternum, but posteriorly they lie freely in the ventral part of the flank musculature. The transversalis muscle exists as a continuous layer placed between the pelvis and the anterior limit of the thorax. It covers the internal aspects of the ribs, ventral to their angles from which it arises, and its fibres pass transversely to the ventral mid-line, thus crossing the ribs obliquely. In the abdomen its relations are similar to the corresponding mammalian muscle. On the dorsal wall of the thorax internally a muscle is present on each side, which arises from the vertebral column and passes obliquely outwards and forwards to be inserted into the ribs at their angles by slips which interdigitate with the slips of attachment of the transversalis, and which gradually become shorter and shorter as the neck is reached (vertebro-costalis). The heart is shut off from the peritoneal cavity by the pericardium and a fibrous septum which may contain muscular tissue, but the lungs lie freely in the dorsal and anterior part of the coelom, their basal parts related on each side to the liver and stomach, their upper (apical) parts passing forwards on each side of the heart towards the neck. A muscular diaphragm separating the thorax from the abdomen is not present.

A comparison of the anatomical conditions of such a reptile as Iguana (which is more or less typical, at least of the lacertilia) with that of the terrestrial amphibians, such as Salamander maculosa, coupled with a comparison of their habits and mode of life, shows that the advance in structure, which is self-evident, is due to an increase in general activity and to a change in respiration which is correlated with this advance. Owing to the presence of ribs inspiration is effected by a bilateral expansion of the fore part of the trunk (thorax), by which mechanism a much larger quantity of air is caused to enter and distend the lungs than would be possible by the amphibian force-pump action of the mouth and pharyngeal floor alone. That expiration is a muscular act is shown by the existence of the well-marked intra-thoracic muscles (transversalis and vertebro-costal muscles), the function of which plainly is to determine an increase of intra-thoracic pressure, and by causing a diminution of the thorax to result in the ejection of the respired air from the lungs. To this end they are aided by the abdominal wall musculature, which clearly participates in expiration; for unless the visceral pressure in the abdominal region were increased during expiration, increase in the thoracic pressure would as easily cause a displacement of the lungs posteriorly into the abdomen as it would cause the ejection of air anteriorly, and thus be only partially effective. Indeed, as we ascend the vertebrate series we find the lungs, which in the Dipnoi

FIG. 5.

Dissection of Iguana from right side showing A, large antero-posterior caudo-pelvic muscle; B, caudo-femoral muscle and sling in position. The sling consists of a dorsal muscle, C, lateral caudo-pelvic muscle, and a ventral muscle, D, arising from hypo-ischium, and an interposed tendon, E. F, Femur with attachment of caudo-femoral muscle.

FIG. 6.

Dissection of Iguana from the left side. The sheet of superficial tail musculature, C, has been cut through and turned upwards with the large antero-posterior caudo-pelvic muscle, A, to which C is attached, by which means the small antero-posterior caudo-pelvic muscle, B, is displayed. The lateral caudo-pelvic muscle, the caudo-femoral muscle, and the femur have been removed.

FIG. 7.

Dissection of Emys from right side. P, Pelvis. Cl, Cloaca. T, Tail. A, Small ventral antero-posterior caudo-pelvic muscle (attached to pelvic outlet ischium). B, Large dorsal antero-posterior caudo-pelvic muscle (entering pelvis to be attached to pelvic inlet?). L, Lateral caudo-pelvic muscle cut through at the ventral attachment and turned outward. V, Ventral sacro-coccygeus. D, Dorsal sacro-coccygeus muscle. Car, Carapace.

FIG. 8.

Dissection of Emys from left side showing the lateral caudo-pelvic muscle, L, in its natural position enclosing the cloaca, the antero-posterior caudo-pelvic and ventral sacro-coccygeal muscles. D.S.C., Dorsal sacro-coccygeus. V.S.C., Ventral sacro-coccygeus.

and Amphibians extend throughout the coelomic cavity, are bodily compressed more and more anteriorly, until finally they become entirely thoracic organs. This change in position, presumably, is to be attributed to the aspiration of the thorax during the reptilian inspiration and to the increasing activity of the abdominal wall during expiration, which, on account of the greater quantity of air inspired, is necessarily amplified in Reptiles, and is therefore of greater intensity than in the terrestrial amphibians—that is to say, greater increments of internal pressure occur during expiration. Similar increase of the internal pressure also occurs during all active movements; for the more intense these become, the more necessary is it for the body wall muscles to contract and give the trunk a certain rigidity; and even during rest they are maintained in tone, and probably play an important part in keeping up a certain amount of pressure upon the splanchnic venous system, and thus serve as an accessory circulatory mechanism. In accordance with this need for an increased internal pressure, varying from time to time with the requirements of the moment and the movement of the animal, we find not only a well-developed abdominal wall and a pelvis structurally much stronger and more firmly attached to the sacrum than in the amphibia, but also a more efficient closure of the pelvic outlet assured by the conspicuous lateral caudo-pelvic muscles, which compress the post-pelvic part of the body cavity and the cloacal passage from side to side. The antero-posterior caudo-pelvic muscles in Iguana clearly serve as a fixatory apparatus for the pelvis and thus form the structural basis for the effectiveness of the contraction of the body wall muscles, a fact which demonstrates the necessity for a tail rigid in the dorso-ventral plane, at least in its proximal part. These antero-posterior caudo-pelvic muscles can scarcely exert much or any pressure upon the cloaca, except perhaps when this is distended by the passage of visceral contents, for their insertion into the pelvis (in Iguana) is lateral and not median. The cloaca, however, is well guarded by the two bow- or crescent-shaped muscles, disposed transversely, the one in front, the other behind; these together form an efficient sphincter for its orifice, which opens on the surface as a transverse slit.

The condition in the Crocodile is essentially similar to that in Iguana. The caudo-pelvic muscles are present, but do not form such fleshy bellies as in Iguana; they appear rather as parts of the superficial tail musculature, the ventral fibres of which converge to be inserted by a small attachment into the pelvis (ischium) much nearer the middle line than in Iguana. Moreover, only one caudo-pelvic muscle is present on each side, a muscle corresponding to the smaller caudo-pelvic muscle of Iguana not being found. They are entirely muscular, and the cloaca passes to the surface between them. They cover an enormous caudo-femoral muscle, which passes outwards over a sling to reach the femur as in Iguana. This sling arises by means of a fascia from the lateral aspect of the proximal part of the tail; it gives rise to muscle fibres, most of which are inserted into the distal extremity of the ischial symphysis, in close relation with, and immediately ventral to, the attachment of the caudo-pelvic muscle; whilst others are inserted into a raphe which extends from the symphysis to the anterior part of the cloaca, which opens as a longitudinal slit just behind the symphysis.

Since the Crocodile presents a more advanced structure than in Iguana—in that the interventricular septum (of the heart) is complete, whilst in other reptiles it remains incomplete—it may be questioned how it is that the caudo pelvic muscles are less differentiated and less prominent than in Iguana. The answer seems to be that their function in part has disappeared, since the pelvis in the Crocodile is completely ankylosed to the spine, whilst in Iguana it is still mobile to some extent. Thus they are no longer required for its fixation, and presumably only exist to prevent the escape of pressure impulses from the pelvis. Moreover, they are attached to the pelvis much nearer the middle line than in Iguana, and they therefore exert more influence over the cloaca, which, however, is provided with sphincter muscles. To this end they are aided by the lateral caudo-pelvic muscles, which correspond with the similar muscles in Iguana.

The condition in the Tortoise is somewhat different from that in Iguana, owing to the fact that the body is encased in a

shell, the ventral part of which—the plastron—is united on each side in the region of the “bridge” to the dorsal part—the carapace—either by ligament, as in *Emys*, or by a suture, as in *Testudo*, in which, therefore, it is immoveable except for a transverse hinge in its posterior lobe. Elsewhere, the plastron and carapace are united by muscles and the thick leathery skin. The pelvis in each of these species is freely moveable, forwards and backwards, upon the carapace, to which it is attached by the ilia by a hinge joint, its ventral part being free from the plastron.

In *Emys*—the European Pond Tortoise—the tail is short and slender. Caudo-pelvic muscles are present and, as in Iguana, consist of two distinct muscles on each side (Fig. 7). The more ventral, which in *Emys* is much the smaller, arises from the mid-line of the tail just behind the cloaca; as it passes forwards it is closely applied to the lateral wall of the cloaca, and is inserted into the posterior margin of the pelvis (ischium) as a flattened horizontal band, its median fibres reaching the middle line and thus adjoining those of the corresponding muscle of the other side. The more dorsal caudo-pelvic muscle, much larger, consists of a thick fleshy band, which arises from the mid-line of the tail in front of the smaller muscle. It passes forwards, its broad surface closely applied to the cloaca, at a higher level than the smaller muscle, and, disappearing into the pelvis, is inserted as a horizontal band into the pubic bone, just in front of the obturator foramen, its insertion extending from just outside the median line to the lower part of the ilium.

On each side of the root of the tail, arising from its lateral aspect, is a sheet of muscle—the lateral caudo-pelvic muscle—the fibres of which pass downwards and forwards and are inserted into the ischial symphysis and into a median raphe which extends distally from this to the anterior limit of the cloaca (Fig. 8). With the similar muscle of the opposite side it encloses the cloacal passage, and covers in the antero-posterior caudo-pelvic muscles, to expose which the lateral caudo-pelvic muscle has to be divided and turned outwards. When this is done the ventral sacro-coccygeus of that side is also disclosed. This arises within the pelvis from the ventral aspect of the carapace; it abuts upon the middle line, its median surface being in apposition with that of the muscle of the opposite side. It passes distally, dorsal to the cloaca and to the outer side of the caudal attachment of the antero-posterior caudo-pelvic muscles, along the ventral aspect of the tail. Laterally, it is related to the lateral caudo-pelvic muscle. Thus the ventral sacro-coccygeus separates the origin of the lateral caudo-pelvic muscle from the origin of the antero-posterior caudo-pelvic muscles—a significant relation in view of the fact that in tail-bearing mammals, such as the dog, the ventral sacro-coccygeus separates the caudal attachment of the ischio-coccygeus from the caudal attachment of those caudo-pelvic muscles which in the mammal are known as the pubo-coccygeus and the ilio-coccygeus. In the Tortoise a dorsal sacro-coccygeus is also present on each side. It arises from the ventral aspect of the carapace, posterior to the pelvis, and passes along the tail, one on each side, dorsal to the origin of the lateral caudo-pelvic muscle; just as the dorsal sacro-coccygeus in the dog, for instance, similarly passes dorsal to the caudal attachment of the ischio-coccygeus in that animal.

In *Testudo* the tail is shorter but stouter than in *Emys*, ceasing just beyond the posterior limit of the cloacal aperture. Instead of two antero-posterior caudo-pelvic muscles on each side, only one is present, which, from its attachments, evidently corresponds with the more dorsal muscle in *Emys* (Fig. 9). It is a broad, stout, muscular band, and arises from the tail dorsal to the cloaca and anterior to its aperture; as it passes forwards its broad surface is closely applied to the cloacal passage; reaching the pelvis it disappears within and is inserted into the pubic bone in front of the obturator foramen, its innermost fibres reaching the mid-line. Posteriorly, it is related to the caudal attachment of the ventral sacro-coccygeus, the majority of its fibres passing internal to that muscle.

The lateral caudo-pelvic muscle is a broad sheet, much more extensive than in *Emys*. It arises by a wide origin from all the coccygeal vertebrae, anteriorly from the ventral mid-line, but posteriorly from the transverse processes. From this extensive origin the fibres converge towards the

ischial symphysis, the majority being inserted into it posteriorly by muscle; anteriorly, the attachment of the muscle is continued by an aponeurosis which reaches half way along the pubo-ischial symphysis.

It is unnecessary to go into detail in considering the mode of life of these interesting animals. Just as in Iguana, the necessity for an increased visceral pressure is clearly evident in the Tortoise, in which the act of expiration is performed by the contraction of the body wall musculature. Indeed, the complete surrounding of the visceral mass by muscular sheets and dermal bones, and the complete enclosure of the cloacal passage and occlusion of the pelvic outlet by the muscles attached thereto, leave no doubt in the mind that the mechanism necessary for causing a marked and repeatedly recurring increased visceral pressure is adequately, indeed abundantly, provided for. Whilst the antero-posterior caudo-pelvic muscles, in virtue of the fact that they arise and are inserted into or near the mid-line of the body, can cause a bilateral compression of the cloaca by their simultaneous contraction, the pelvis being fixed (by the body wall muscles), this is also provided for by the remarkable development of the lateral caudo-pelvic muscles, which completely

FIG. 9.

Dissection of *Testudo*, ventral view. The pubo-ischial symphysis has been divided, and each half of the pelvis widely separated. B, Antero-posterior caudo-pelvic muscle attached to pubis (pelvic inlet). V, Ventral sacro-coccygeus muscle. Both these muscles have been removed on the left side so as to completely display L, the lateral caudo-pelvic muscle.

enclose the cloacal passage as it passes from the pelvic cavity to its exit. This post-pelvic mechanism is sufficient, as an inspection of the dissected animal will convince one, to completely obstruct the escape of pressure impulses caused by a contraction of the body muscles, and by this obstruction to add to the pressure effect. In this connexion it is interesting to reflect upon the increased perfection of the pelvic closing apparatus, which has occurred in *Testudo*, for it is significant to find that whilst *Emys* is aquatic *Testudo* is a terrestrial tortoise, and again the influence of the medium is felt. Whilst the small, more ventral, caudo-pelvic muscle in *Emys*—in which species it is already a diminutive muscle—has disappeared in *Testudo*, the other antero-posterior caudo-pelvic muscle (pubo-coccygeus) is much increased; but besides, the lateral caudo-pelvic muscle has greatly developed and ensures more than ever a protection against the escape of pressure impulses from within.

Flexion of tail.—It may be supposed that the antero-posterior caudo-pelvic muscles (pubo-coccygei) of the Tortoise function solely as flexors of the tail; but in face of the shortness of the stumpy tail of *Testudo*, already flexed by its skeleton so that it cannot be extended, and the comparatively enormous development of its muscles, this can scarcely be maintained. That the muscle may cause a greater flexion of the tail in *Testudo* than exists during rest is very probable; indeed, by such increased flexion the pelvic outlet may be efficiently occluded—a use the tail is put to in mammals. According to Gadow, Tortoises use their tails for digging holes in the ground into which they lay their eggs. The caudo-pelvic muscles (pubo-coccygei) probably are useful for this and thus act as flexors, since they are attached to the less proximal rather than to the more proximal caudal

vertebrae; but, associated with the flexibility of the tail, it is significant to find a pair of new muscles has arisen in the Tortoise—the ventral sacro-coccygei. These, which are not present in the Lacertilia, Crocodilia, nor in Salamander maculosa, presumably are the real tail flexors, for both in *Emys* and *Testudo* they are larger than the pubo-coccygei—and in *Testudo* considerably larger—and, moreover, they pass distally into the tail beyond the attachment of the pubo-coccygei.

Even though it be admitted that the caudo-pelvic muscles may function as flexors of the tail in the Tortoise it is clearly impossible for them to do so in the Lacertilia and Crocodilia, for whilst the tail in all these can be bent laterally with ease and efficiently, in none does flexion, at least of its proximal part, occur—the body is so little elevated from the ground by the shortness of the legs and the tail is so long that this is obvious. The great movement of the tail in these reptiles (Lacertilia, &c.) is its abduction, caused by the conspicuously developed caudo-femoral muscles. In the Lizards it seems as though a tail, rigid in the dorso-ventral plane in its proximal part, is a necessity to allow varying pressure conditions to be produced within the body cavity by giving a firm and fixed origin upon which the caudo-pelvic muscles can contract and thus fix the moveable (reptilian) pelvis. But when the fixation of the pelvis to the vertebral column had occurred the necessity for a rigid tail disappeared, and thus in mammals especially the tail is markedly flexible. In the Tortoise the tail is also flexible, and further, in *Emys* and in *Testudo* the pelvis is moveable forwards and backwards upon the carapace. But here we have different conditions, for the production of the variations of visceral pressure, and their purposeful application, do not depend upon fixation of the pelvis, either directly to the spine or indirectly by means of a rigid tail. But besides the contraction of the muscles enclosing the visceral mass (transversalis abdominis, which is attached to the pubic bone), the production of an increased visceral pressure is facilitated by the presence of the plastron. Contraction of the transversalis plus contraction of the collective caudo-pelvic muscles will cause an increase of visceral pressure; this will be transmitted forwards towards the anterior limit of this muscular sheet, and will then impinge directly upon the central part of the plastron, against which the visceral mass abuts without the intervention of muscular tissue; and this, being maintained in position by its bony fixation, or by the muscles passing between it and the carapace, will prevent the escape here of pressure and thus lead to the effectiveness of the movement in question.

The existence of the plastron in *Emys* and *Testudo* has obviated the necessity for a fixation of the pelvis, for it prevents a spherical form of the visceral mass being caused by the contraction of the inner body musculature and the rotation forwards of the pelvis which the slender and flexible tail of *Emys* could scarcely prevent. Thus, in these species of Tortoise we have simultaneously a flexible tail and a moveable pelvis, a combination which, as far as I know, exists in no other species of vertebrate.

In conclusion, then, we may say that a study of the anatomical conditions found in the fish, amphibia, and reptiles shows the increasing need for the production of a varying internal visceral pressure, necessary not only for the functioning of the posterior end of the body, but also for the repeatedly recurring act of expiration, and which plays a part of an important accessory circulatory mechanism, and, moreover, occurs incidentally during activity. This necessity has been met by the gradual evolution of the pelvis and of the muscles enclosing the visceral mass, of which muscles those occluding the pelvic outlet plainly form an integral part. The development and segmentation of the antero-posterior and lateral caudo-pelvic muscles is to be attributed to this necessity, for we can only regard their existence as a structural means to meet this demand for an internal pressure—that is to say, they exist for a pressure effect.

LIST OF ANIMALS DISSECTED FOR LECTURE I.

- Fish.*—Dog-fish (*Scyllium canicula*). Mackerel (*Scomber scombrus*). Herring (*Clupea harrengus*).
Dipnoi.—Mud-fish (*Protopterus annectens*).
Amphibia.—Menobranchius lateralis, s. Necturus maculatus. Salamander (*Salamandra maculosa*).
Reptiles.—Iguana, and several other lizards. Crocodile (*Crocodilus*). Tortoises (*Emys* and *Testudo*).