**The Hunterian lectures on the evolution of the pelvic floor in the non-mammalian vertebrates and pronograde mammals : delivered before the Royal College of Surgeons of England on March 4th and 7th, 1910 / by R.H. Paramore.**

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*Delivered before the Royal College of Surgeons of England on*
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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. 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.

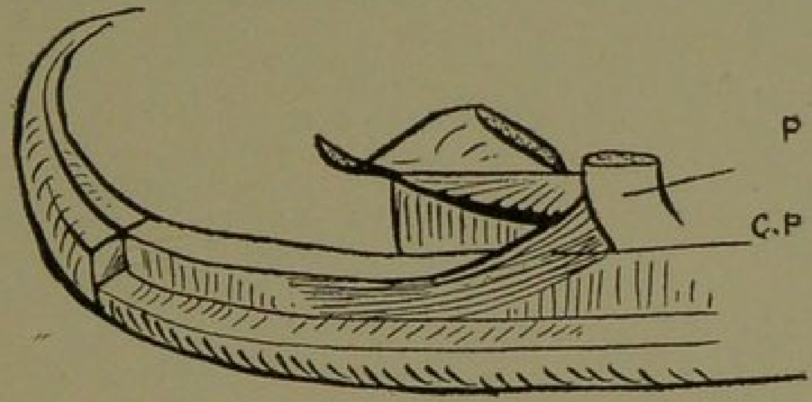
In Protopterus—one of the Dipnoi—the anatomical relations of the cloaca, and the parts immediately behind the pelvic plate, are similar to those found in Scyllium canicula, except that the transformation of the pelvic fins into slender cylindrical processes, and the displacement of the cloacal opening 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 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.

FIG. 1.



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

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

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* See Holl, p. 260, see reference 14

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 (Huxley[16]).† 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 dilatability 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.

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

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 (Wiedersheim[36]).

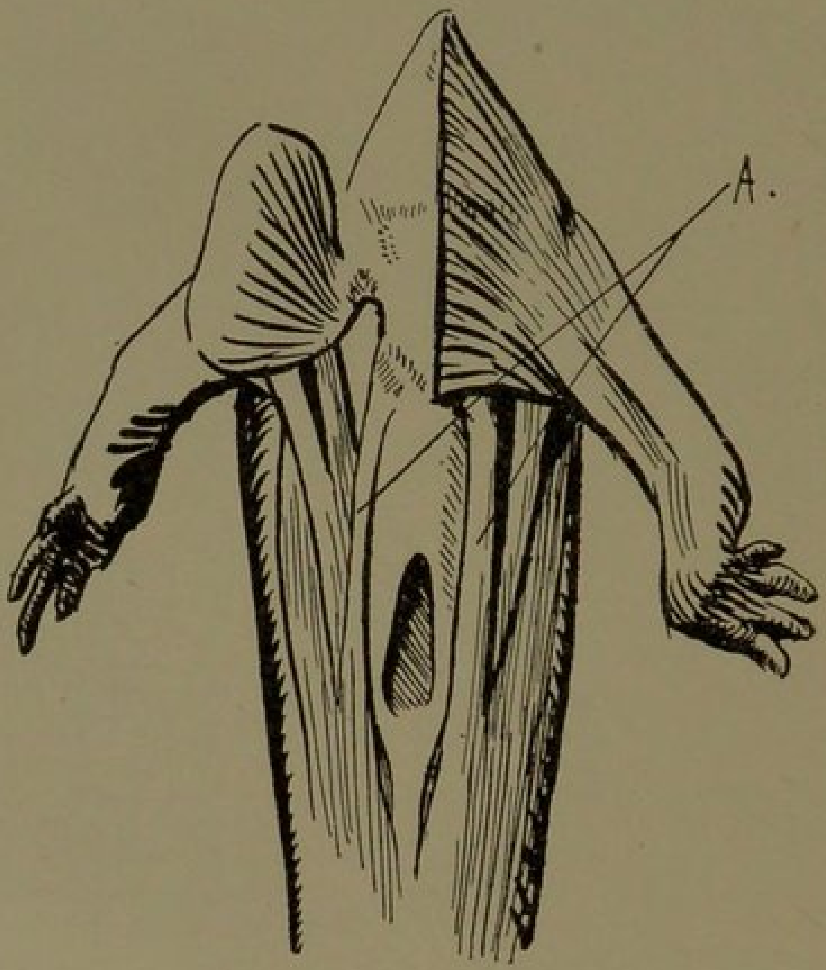
Such considerations as these seem to offer adequate explanations for the origin and the marked development in the fish of the caudo-pelvic strands on either side of the cloaca on the one hand and the oblique fibres in the ventral part of the lateral trunk musculature on the other, the essential function 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 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 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

FIG. 2.

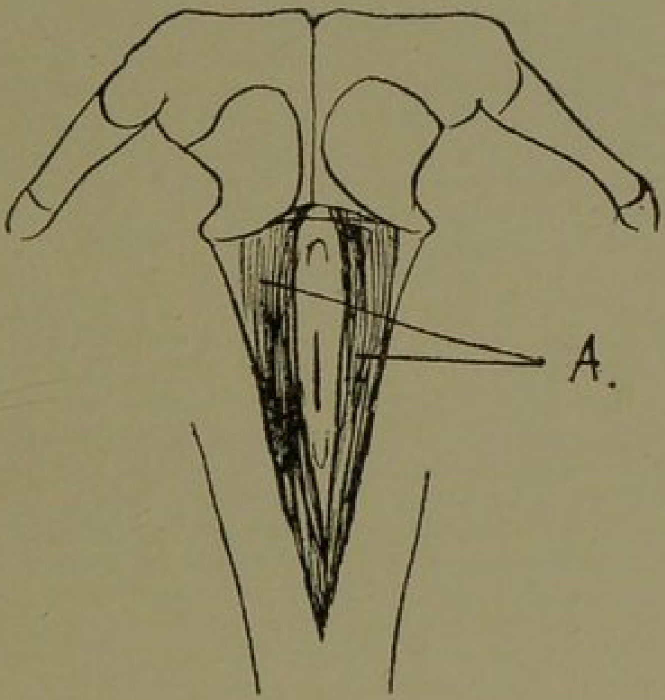


Dissection of Menobranchus, showing caudo-pelvic muscles A. The cloacal passage has been cut through on a plane with these muscles and the superficial parts have been removed.

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.

FIG. 3.



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

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 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.

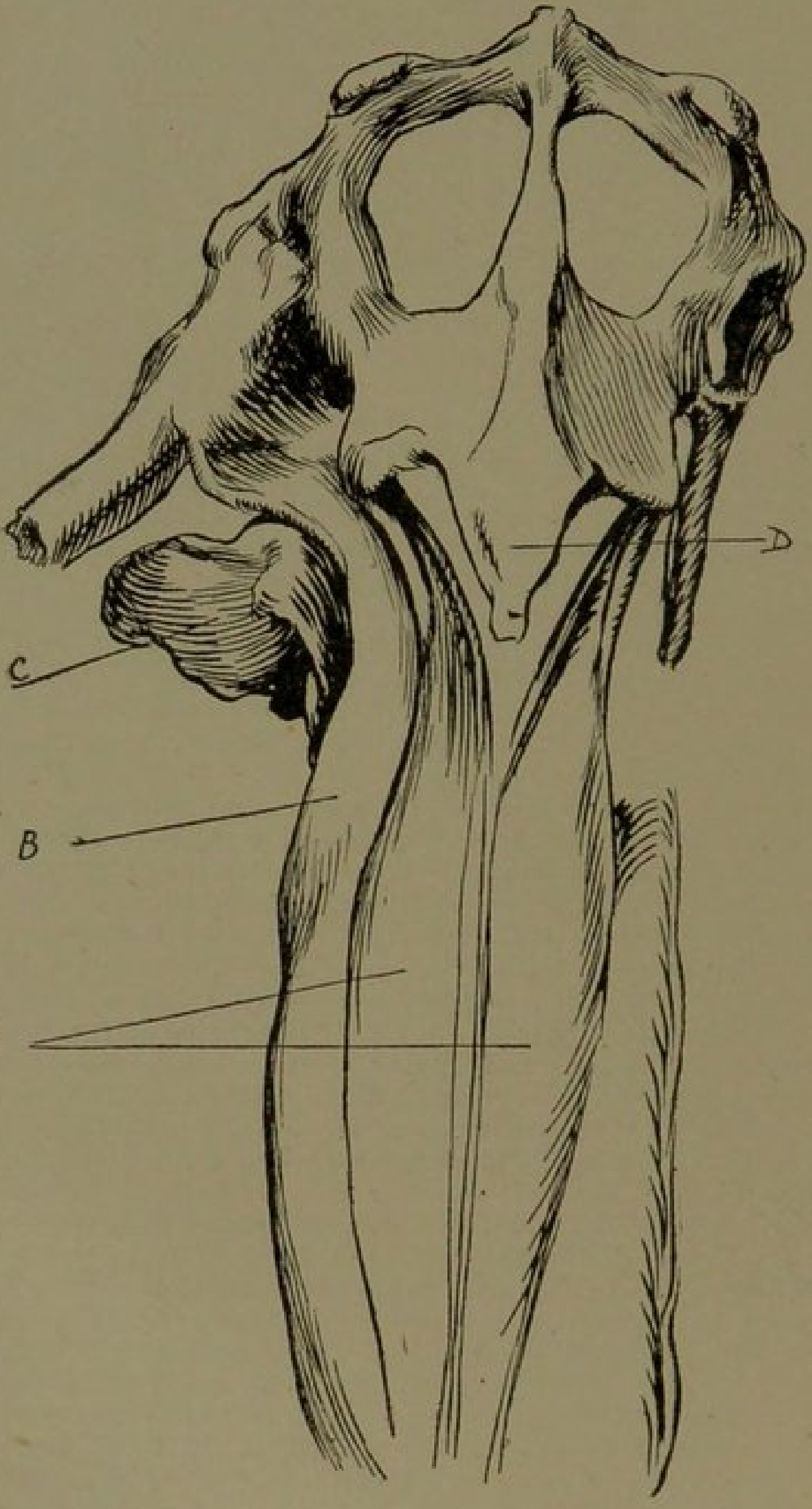
## REPTILES.

The condition found in reptiles is extremely interesting. At least two sacral vertebræ 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 sacroiliac 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 immoveably 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, 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.

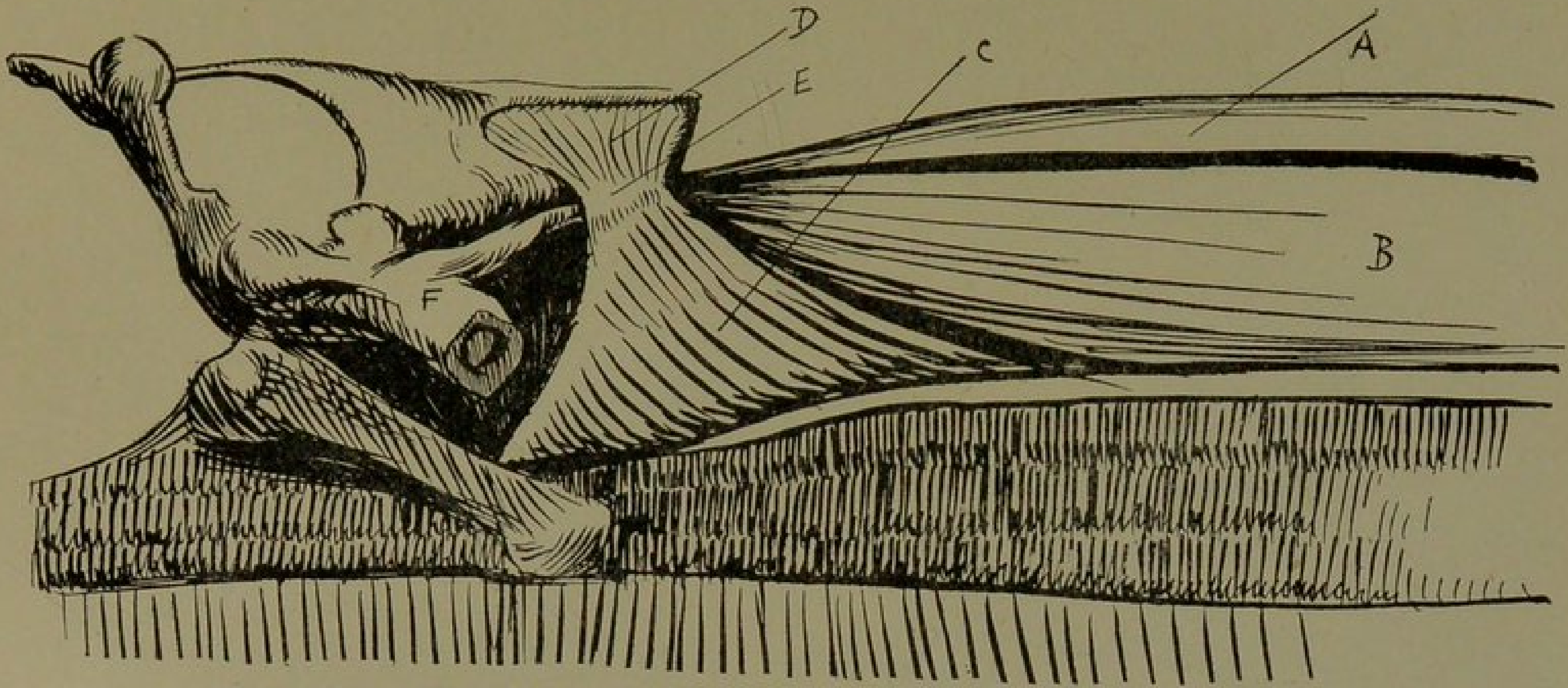
Filling up the big space between the spines of the chevron bones internally and the superficial tail musculature externally, and placed immediately dorsal to the belly of origin of the larger caudo-pelvic muscle which partially hides it from view, is the large caudo-femoral muscle (Figs. 4 and 5), the 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 hypo-ischium and passes outwards and upwards to be inserted

FIG. 4.



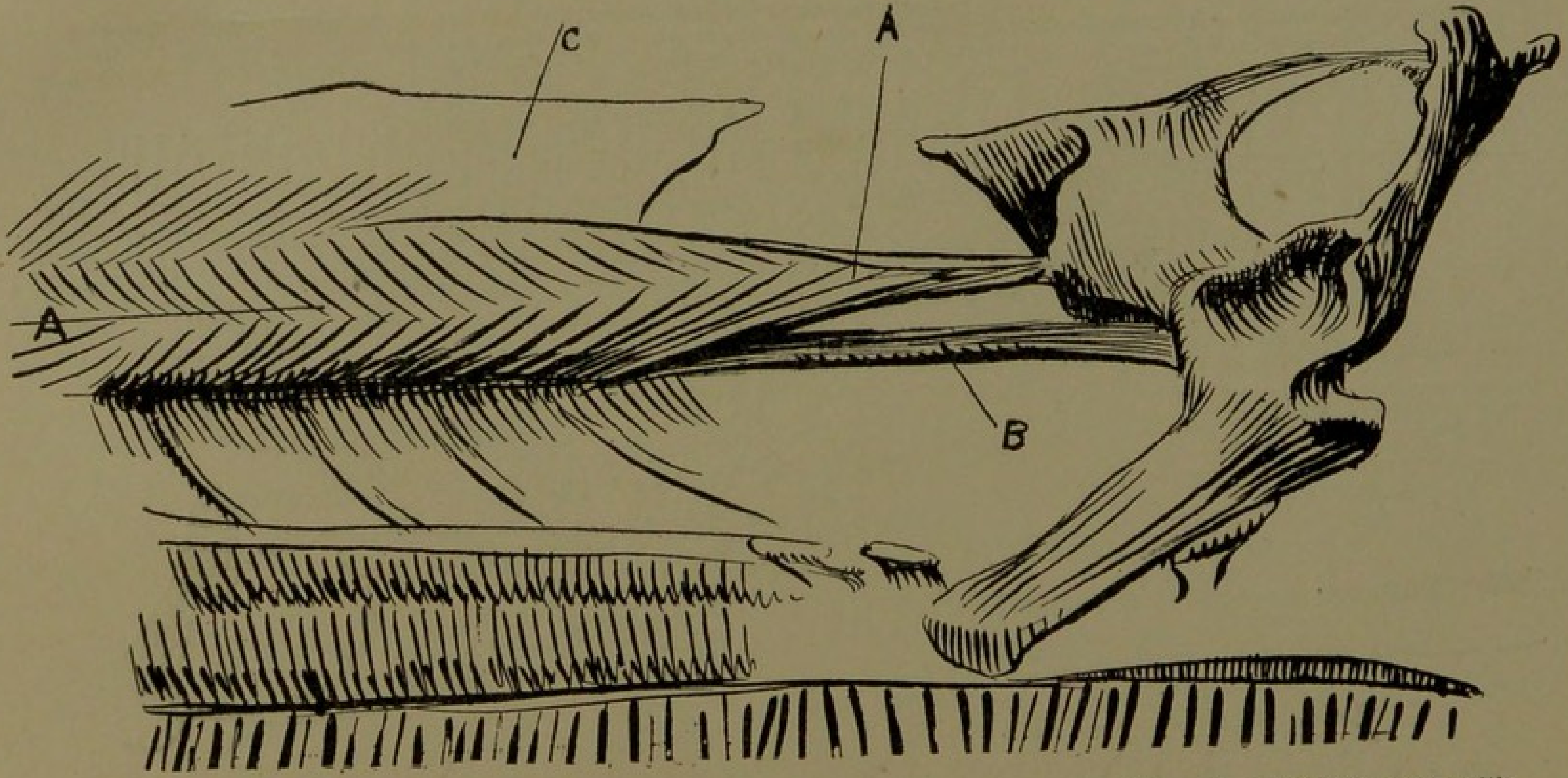
Ventral view of Iguana, showing pelvis. A, A, The large antero-posterior caudo-pelvic muscles. B, The caudo-femoral muscle of the right side attached to femur. C, The sling; the attachment of the sling to the hypo-ischium, D, has been cut through and turned outwards.

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.

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 cœlom, 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 and Amphibians extend throughout the cœlomic 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.

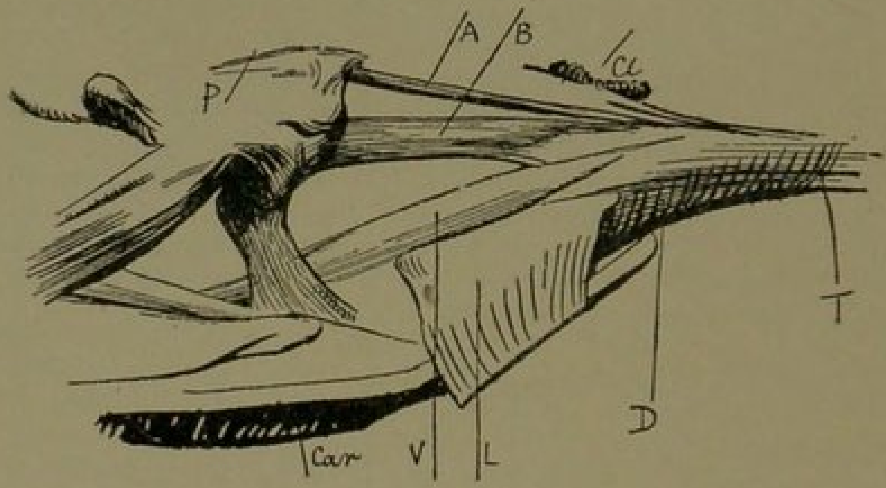
The condition in the Crocodile is essentially similar to that in Iguana. The caudo-pelvic muscles are present, but do not form such fleshy bellies as in Iguana; they appear rather as parts of the superficial tail musculature, the ventral fibres of which converge to be inserted by a small attachment into 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.

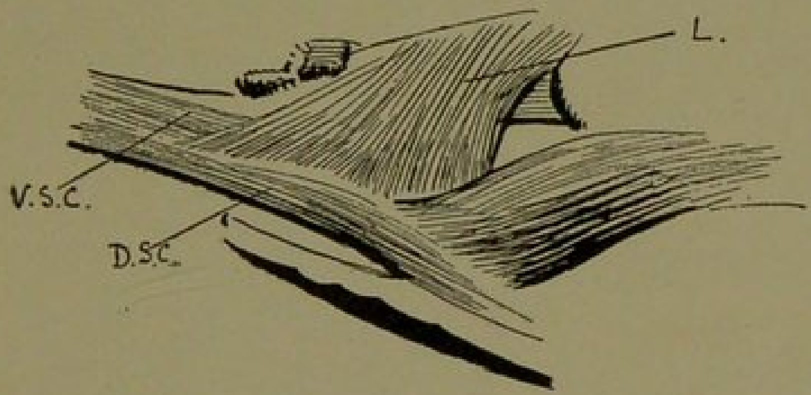
FIG. 7.



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.

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

FIG. 8.



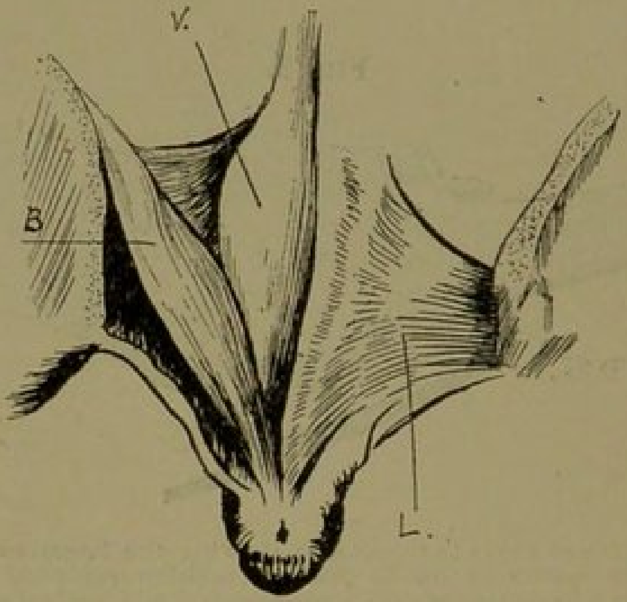
Dissection of Emys from left side showing the lateral caudo-pelvic muscle, L, in its natural position enclosing the cloaca, the antero-posterior caudo-pelvic and ventral sacro-coccygeal muscles. D.S.C., Dorsal sacro-coccygeus. V.S.C., Ventral sacro-coccygeus.

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

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.

from all the coccygeal vertebræ, 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 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 vertebræ; 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.*—Menobranchus lateralis, s. Necturus maculatus Salamander (*Salamandra maculosa*).

*Reptiles.*—Iguana, and several other lizards. Crocodile (*Crocodilus*). Tortoises (*Emys and Testudo*)

## LECTURE II.—PRONOGRADE MAMMALS.

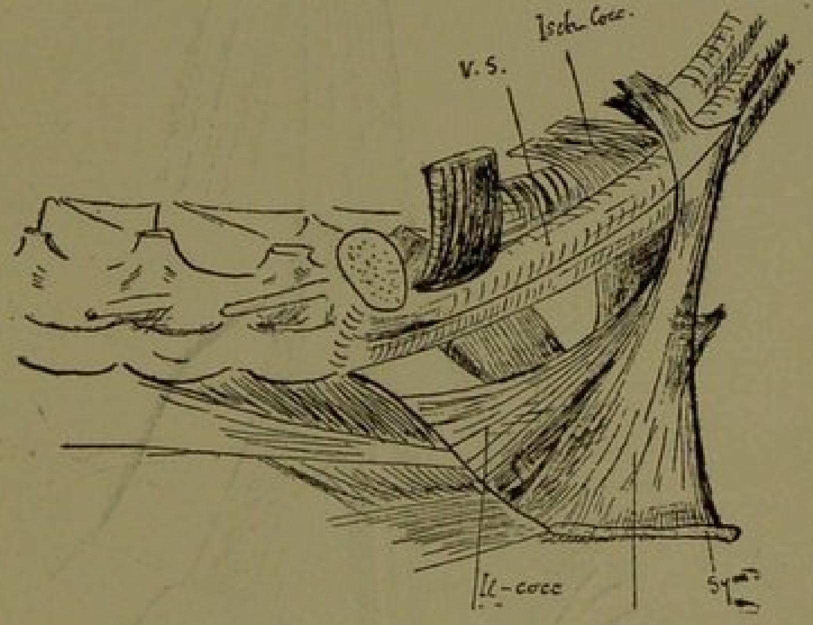
*Delivered on March 7th.*

### THE PELVIC FLOOR MUSCLES.

#### *In Carnivora and Pronograde Primates.*

MR. PRESIDENT, LADIES, AND GENTLEMEN,—In the great majority of terrestrial mammals the three pairs of muscles connecting the pelvis with the tail, and which we have hitherto spoken of as the antero-posterior and the lateral caudo-pelvic muscles, but which in mammals are known as the pubo-, ilio-, and ischio-coccygeus, are represented; and, with the tail and the superficial sphincteric layer, form an effective closure of the pelvis. In some, as the Carnivora and Pronograde Primates, these pelvic floor muscles exist as well-developed muscular sheets, disposed in two layers on each side of the pelvic cavity—an inner layer, consisting of the pubo- and ilio-coccygeus, which in man together form the levator ani muscle, and an outer, the ischio-coccygeus, representing the coccygeus of human anatomy. Of these the pubo-coccygeus and the ilio-coccygeus form a continuous sheet, the posterior margin of the one being contiguous with the anterior margin of the other, so that more or less difficulty may be experienced in differentiating the interval between them, and which is not always accurately defined by the passage of the obturator nerve (Fig. 10). The pelvic line of attachment extends along the internal aspect of the symphysis of the pubis in the whole of its extent, and along the ilio-pectineal line as far dorsally as the sacrum. From this wide origin the fibres converge as they pass upwards and backwards to reach the root of the tail, into the ventral mid-line of which they are inserted. At this insertion the ilio-coccygeus ends in a fascial strand, which is placed lateral to the pubo-coccygeus. Thus these two muscular sheets, one on each side, together form a funnel-shaped closure to the pelvis, which leads from the abdominal cavity to the perineal region, and which ends at the outlet as a vertical slit, formed by the most posterior fibres of the pubo-coccygei. At their origin and insertion these are attached to the mid-line, and thus are in apposition with each other, and in their course are only separated by the rectum and urogenital passages, which quit the pelvic cavity by passing between them (Fig. 11). To the outer side of this internal layer is the ischio-coccygeus, which also forms a conspicuous layer, the breadth of which varies in different species. It arises from the ischial spine and adjacent bone, and is inserted into the lateral aspect of the root of the tail, separated from the caudal attachment of the pubo- and ilio-coccygeus by the ventral sacro-coccygeus.

FIG. 10.



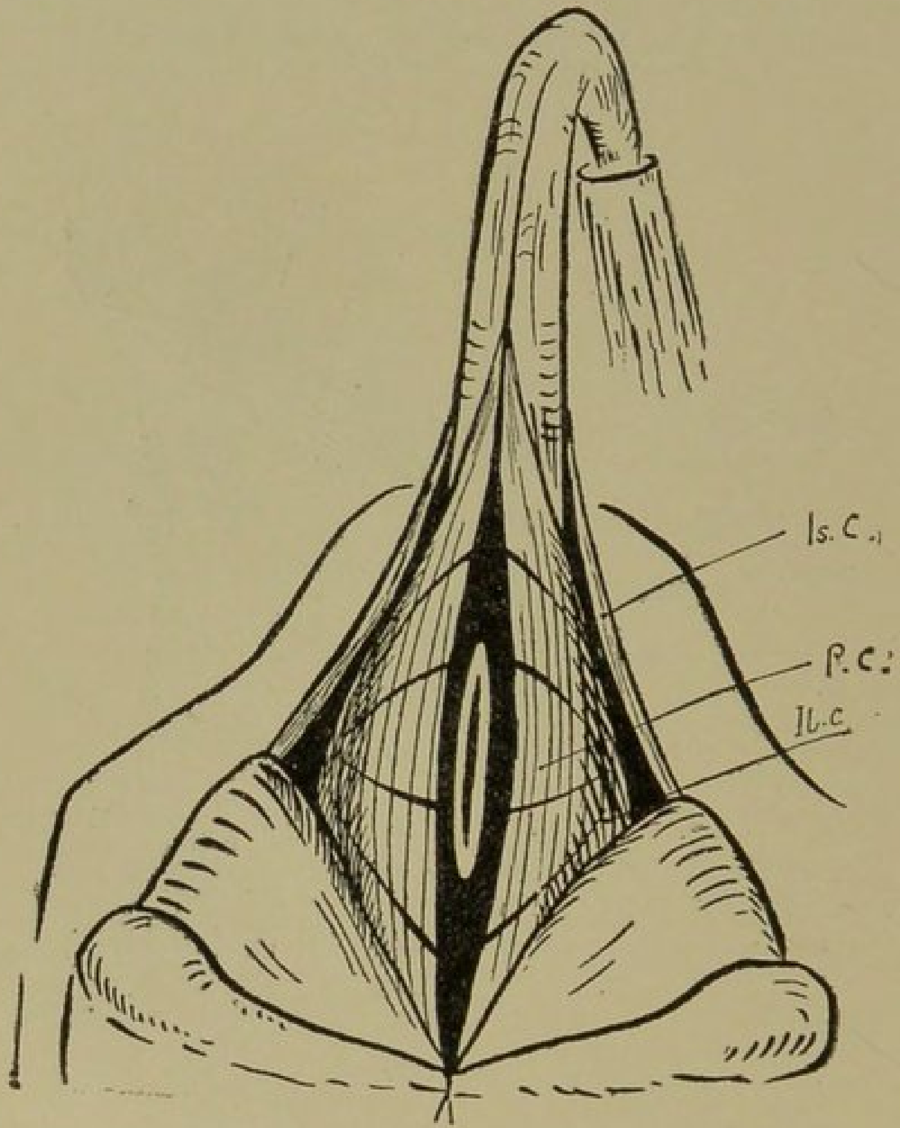
Dissection of the pelvis, showing pelvic floor muscles of a dog (fox-terrier) from within, about half life-size. P.C., Pubo-coccygeus muscle. Il.-cocc., Ilio-coccygeus muscle. Isch.-cocc., Ischio-coccygeus muscle. V.S., Ventral sacro-coccygeus muscle.

### *In Rodents.*

In the Rodents the pubo- and ilio-coccygeus are, as a rule, not well developed, and are not comparable to the homologous muscles in Carnivora and Primates. They exist as thin muscular sheets, which arise from the anterior part (only) of the symphysis pubis and the adjacent part of the antero-lateral pelvic wall (brim), and are inserted into the tail, not as a rule into the median line, at least not with that precision found in the Carnivora and Pronograde Primates, although some of their fibres may be traced into it, but usually ending in the fascia covering the ventral sacro-coccygeus, and more often towards its lateral aspect

(Fig. 12). In some species the ilio-coccygeus appears to be altogether absent, or, according to some, is incorporated with the distal part or border of the ischio-coccygeus, as in the rabbit (Fig. 13). In others, as the Squirrel, both the pubo- and ilio-coccygei are well developed.

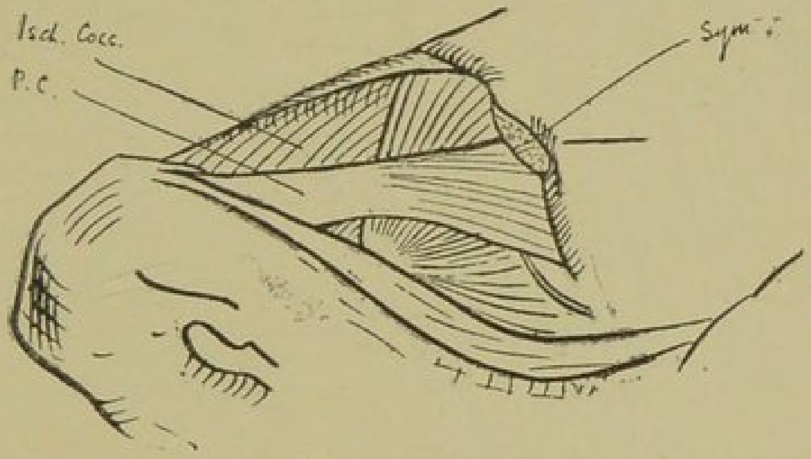
Fig. 11.



Dissection of the perineal region of the lynx, showing vertical slit formed by posterior margins of pubo-coccygei, through which the rectum alone is represented as passing. P.C., Pubo-coccygeus muscle. Il.-c., Ilio-coccygeus muscle. Is.-c., Ischio-coccygeus muscle.

The ischio-coccygeus in the Rodents is usually conspicuously present. It exists as a wide muscular sheet, as a rule quite distinct from the other muscles, and placed on their outer aspect. Often it is fan-shaped, as in the rabbit, arising from the ischial spine and passing inwards, its fibres radiating widely to be inserted into the proximal coccygeal vertebræ by an extensive insertion. In the tree-climbing and brush-tailed porcupines the muscle is remarkably developed. Its origin is not limited to the ischial spine, but it extends along the pelvic outlet, reaching almost to the symphysis. From these wide origins the fibres spread as they pass to the tail, forming thick and broad strata, clearly of considerable strength, and are inserted by still more extensive attachments. The pubo-coccygeus in each is an insignificant looking, thin sheet of muscle. An ilio-coccygeus cannot be distinguished.

FIG. 12.

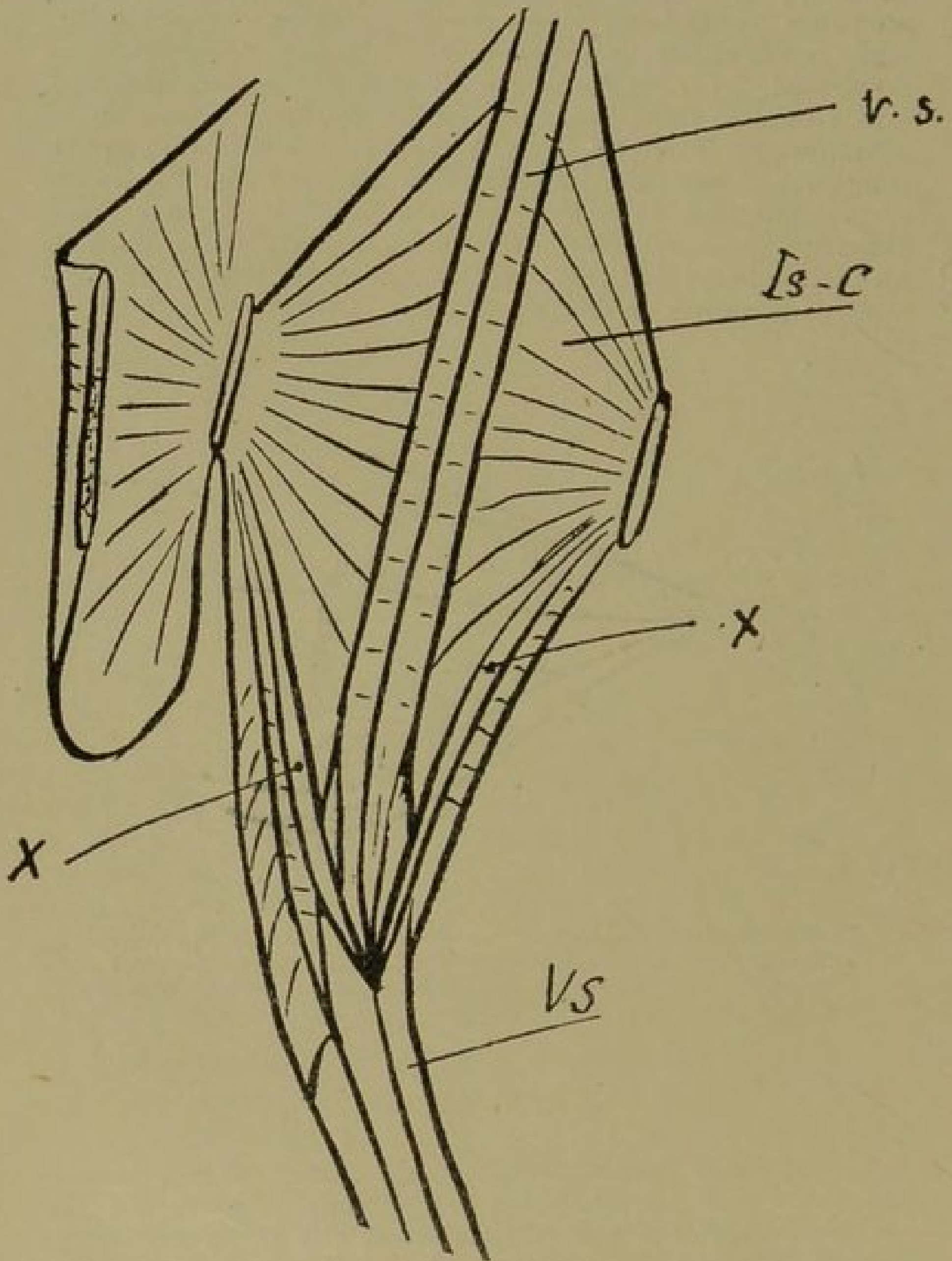


Dissection of the pelvis and pelvic floor muscles of the tree-climbing porcupine from within. P.C., the pubo-coccygeus muscle. Isch.-cocc., the ischio-coccygeus muscle. Sym., Symphysis pubis.

*In Ungulates.*

In yet other mammals—the large group of ungulates—the pubo- and ilio-coccygeus are entirely absent, and the ischio-coccygeus is the only muscle of the group occurring; but, unlike the muscle in the majority of the rodents, it does not form such an extensive sheet. In the horse (Fig. 18) it arises from the ischial spine by a fascial aponeurosis, and passes as a thick, strap-like muscle upwards, inwards, and slightly backwards, to be inserted into the root of the tail. The manner of its attachment in the horse is interesting, for at its insertion it splits into two laminæ; the outer, much the larger, passing upwards external to the ventral sacro-coccygeus, to be inserted by two slips into the transverse

FIG. 13.



Dissection of the pelvis of the rabbit. The symphysis has been divided, the right innominate bone turned outwards, and the left removed, leaving ischial spine. Life size. Is.-c., Ischio-coccygeus muscle. v.s., Ventral sacro-coccygeus muscle. x, So-called ilio-coccygeus muscle; this is inserted into mid-line of the tail, being thus separated from the caudal attachment of the ischio-coccygeus by the ventral sacro-coccygeus.

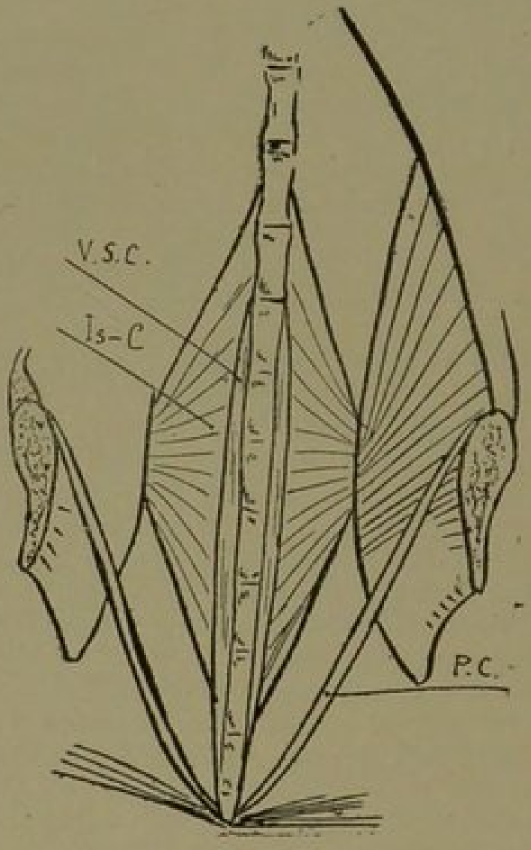
processes of the second and third coccygeal vertebræ; the median, or ventral lamina, smaller, passes inwards around the ventral sacro-coccygeus, and is inserted in the middle line into the fourth coccygeal vertebra. From the relation of these two parts of insertion to the ventral sacro-coccygeus we may perhaps speculate so far as to say that whilst the larger lateral insertion may be regarded as the ischio-coccygeus proper perhaps the ventral slip represents all that is left of a muscle, corresponding to the so-called ilio-coccygeus of the rabbit, which may have become fused with the ischio-coccygeus to a greater extent than it has done in that rodent, for in both its caudal attachment is separated from that of the ischio-coccygeus by the ventral sacro-coccygeus. In the Panolin Deer (Cervus Eldi) the disposition of the ischio-coccygeus is similar to that of the horse, except that no slip leaves the muscle to pass around the ventral sacro-coccygeus to be inserted into the median line.

### *In Hyrax.*

The condition in Hyrax is exceedingly interesting (Fig. 14). Although this species bears "a singular resemblance to the Rodents" (Beddard), from other anatomical peculiarities it is placed by zoologists amongst the Ungulates; and is indeed considered to be a survival from antiquity (Beddard). It has no free tail; and, as in the Rodents, the ischio-coccygeus is well-developed, and exists as a fan-shaped muscle arising from the ischial spine, its fibres spreading out as they pass inwards to be attached by a wide insertion into the remaining coccygeal vertebræ—thus forming, with these vertebræ and the muscle of the opposite side, a dorsal wall for the pelvic cavity. The ilio-coccygeus appears to be entirely absent; and in the specimens I examined I found no evidence of a muscle, situated along the posterior border of the ischio-coccygeus, corresponding to the so-called ilio-coccygeus of the rabbit or to the ventral slip found in the horse. A pubo-coccygeus, however, is present, and is represented by a narrow and slender band of muscle, which arises from the crest of the pubis, and is inserted into the distal extremity of the vertebral column.

If Hyrax is a representative of an ancient form of ungulate the presence of this diminutive yet plainly muscular pubo-coccygeus points to the existence of a similar muscle in the ancestors of the more common species of this order (ungulate), the earliest forms of which, according to Mr. Beddard, "are not by any means easily differentiated from the primitive carnivorous mammals of that date, the Creodonta." If, therefore, the present-day Ungulates and Carnivora have come from a common stock, it is plain that the pelvic floor muscles in each, presenting such marked differences as they do, have deviated, in the course of evolution, from a common plan; and we can only suppose the changes in structure of the closing apparatus of the pelvis which have ensued have been caused by changes in habits and environment of the ancestors of the several individuals of these orders. These we must endeavour to understand, so that we may be able to appreciate the factors which have determined the existence of such an efficient closure in the Carnivora, on the one hand, and, presumably, a less effective mechanism for the maintenance of an internal pressure in the Ungulates on the other: a study which will teach us the function of the pelvic floor musculature in each.

FIG. 14.



Dissection of the pelvis of the Hyrax. The symphysis has been divided and each innominate bone turned outwards. About double life size. P.C., Pubo-coccygeus muscle. Is.-c., Ischio-coccygeus muscle. V.S.C., Ventral sacro-coccygeus muscle.

## THE TAIL AND ITS MOVEMENT.

In the foregoing survey we have described the pelvic floor muscles as arising from the pelvis and being inserted into the coccygeal vertebræ; whereas in the fish, amphibians and reptiles, we spoke of the caudo-pelvic muscles as arising from the tail and being inserted into the pelvis. This change in description is due to the fact that in the non-mammalian vertebrates the tail, at least in its proximal part, is rigid in the dorso-ventral plane, and is only freely moveable from side to side; whilst the pelvis, such as it is, with some exceptions (e.g., Crocodile), is moveable antero-posteriorly upon the sacrum. But in the terrestrial mammals, the tail, when present, is moveable in all directions, whilst the pelvis has become fixed, and thus we speak of these muscles as arising from the pelvis in mammals, since this is their more fixed attachment. There is, however, this important point to notice, that whereas in tailed amphibians and reptiles (Lacertilia), the caudo-pelvic muscles are attached to the tail at some considerable distance from the pelvis, so that they are either in the same straight line, or very nearly in the same straight line, as the recti abdominis muscles, the pull of which upon the pelvis they are thus able to counteract; in the mammals—Carnivora and Primates especially—the attachments of these caudo-pelvic muscles to the tail have crept towards its root, so that instead of being approximately in the same straight line as the recti they are placed almost at a right angle to them. The fixation of the pelvis to the spine has done away with the necessity of the earlier position of these muscles and permitted the evolution of a freely mobile tail, whilst the forcible voluntary apposition of the tail root against the perineal region—forming the perineal shutter of Professor Arthur Keith—only became possible, or, at least, was best effected, as the laws of mechanics demonstrate, by such a recession. With this mobility the intrinsic muscles of the tail are correspondingly developed, and consist of four sets of muscles, arranged longitudinally about its skeleton, two dorsal and two ventral—each dorsal and each ventral set disposed symmetrically on either side of the dorso-ventral plane. They arise from the sacrum: the upper from its dorsal aspect, where they appear to be the continuations of the longissimus dorsi of each side; the lower, from its ventral aspect. These sacro-coccygei pass distally along the tail, and are usually segmented; numerous muscle bundles arise from each vertebra to be inserted into the next, and so on to the extreme tip. Sometimes the sacro-coccygei end in long and slender tendons, which pass to the several vertebræ, as in the Lemuroidæ and Kangaroos; but even in these cases distinct muscles arise from each vertebra to be inserted into the next vertebra, all along the tail skeleton. These muscles are clearly evident in the Horse, the Dog, and the Monkey (Semnopethicus entellus), and in all the tailed mammals I have dissected. In the proximal part of the tail the dorsal set are, as a rule, more conspicuous than the ventral, presumably because of the action of gravity and of the caudo-pelvic muscles, both of which they have to counteract. They are the true tail-moving muscles, and by various combinations cause the tail to move in any desired direction.

It has been assumed, stated, and is, perhaps, almost generally believed, that movement of the tail in tailed mammals depends upon the activity—besides other muscles, such as the sacro-coccygei—of the pubo- and ilio-coccygei, and of the ischio-coccygei, because these muscles arise from the pelvis and are attached to the tail; and on this assumption these muscles have been spoken of as "tail-moving" muscles, the pubo- and ilio-coccygei actually being called "flexors" and the ischio-coccygeus an "abductor." Further, the representation has been made that the prehensility of the tail in the case of the Tailed Apes and the rigidity of the tail in the case of the "Tripod" Kangaroo depend upon them. Whilst it is probably true that the contraction of the pelvic-floor muscles is increased when the tail is used as a prehensile organ, it seems rather strange to argue from this that they determine prehensility of the tail, for during any active movement whatever the contraction of the entire musculature of the body is increased in correspondence with the energy displayed in that movement. These pelvic-floor muscles are attached to the tail near its root, far away (two feet, Ateles †) from the distal, prehensile part, the grasping movement of which is, of course, effected by the intrinsic muscles. The representation that the pubo- and ilio-coccygei are responsible for this prehensility is all the more remarkable when it is known that only New World (American) monkeys, and not all these, display this faculty (Heilprin, Beddard, and others). Semnopithecus entellus, an Old World monkey, with a long and well-developed tail, has these pelvic-floor muscles extremely well developed, surely a remarkable condition of structure if these muscles determine prehensility of the tail; for in this monkey, as in all Old World monkeys, the tail is never prehensile.

As regards the statement that these pelvic-floor muscles are tail-moving muscles—that is, that they cause a movement of the tail, implying by that word what is generally understood—we may say that movement of the tail in the horse or in the cow is as free as, or is freer than, in the dog; and that the Ungulate has as much control of its movements as the Carnivora: but whereas the pubo- and ilio-coccygei are present in the latter (Carnivora), they are completely absent

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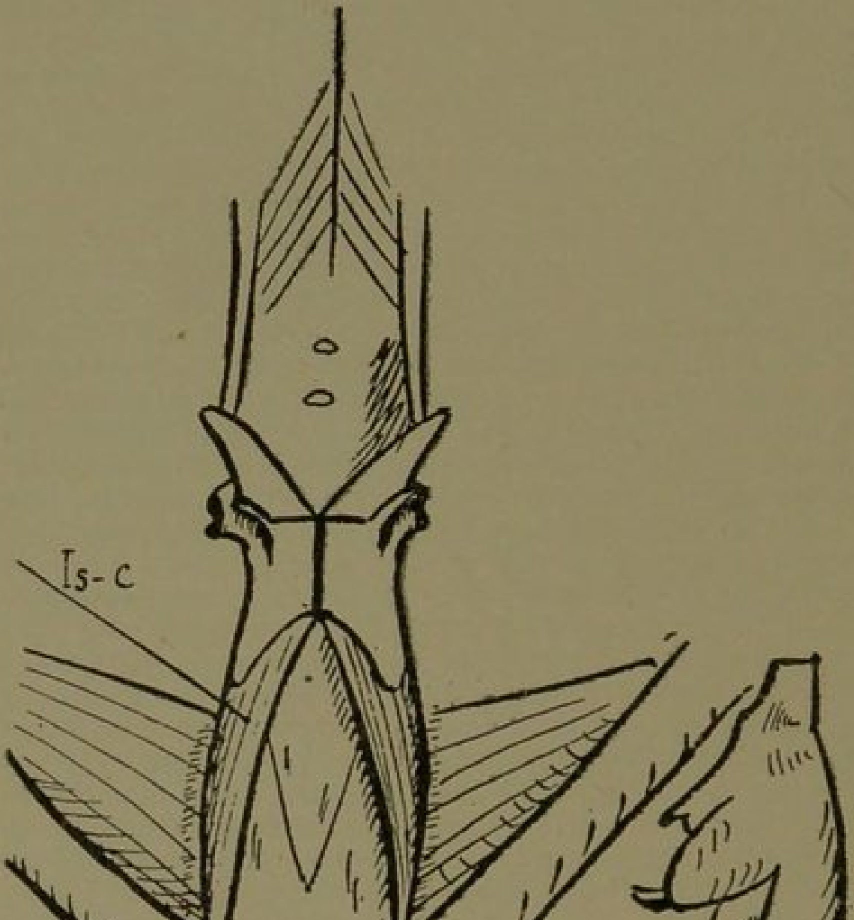
† See specimen in Zoological Society's Gardens.

in the former (Ungulate). It is therefore plain that efficient movement of the tail does not depend upon the contraction of the pubo- and ilio-coccygei since it takes place in their absence. Moreover, both Ungulates and Carnivora possess well-marked ischio-coccygei; but these can have no effect whatever over the distal and most mobile part of the tail. (Figs. 17 and 15.)

Yet the ischio-coccygeus is supposed to be the abductor of the tail, and is called the "abductor caudæ." This supposed function is deduced from the attachments of the muscle; and it is supposed that when one contracts, whilst the other is inhibited, the tail will be abducted. That such contraction on one side and relaxation on the other would result in abduction may be readily granted, although in many cases the line of traction is such that the tail would be pulled more downwards than to the side; but that such unilateral contraction takes place has not been shown to occur. In the first place the attachments of the muscle are no certain guide to its function. "It is impossible," says Dr. Pembrey,[27] "to analyse movement in the living by an examination of the points of origin and insertion of the different muscles acting upon the joints of dead subjects"—an opinion which is widely accepted. It is just as reasonable to suppose that the two muscles, one of each side, always act together; that they are synchronously and synergetically innervated, just as we believe the tranversalis abdominis of each side, and the two halves of the thoracic diaphragm are similarly innervated, as it is to take for granted that they invariably react apart, as is supposed. Abduction of the tail can as well be effected by the intrinsic muscles of the tail as its movements of flexion and extension. Indeed, the lateral extension of the ventral sacro-coccygeus on to the lateral pelvic wall in Myrmecophaga appears to be for this very purpose; for the tail, which is bilaterally compressed, has a much more extensive range of movement from side to side than dorso-ventrally, at any rate in its proximal part. At least it will be admitted that the ischio-coccygeus does not act as an abductor of the tail in Hyrax or in the Guinea-pig, in both of which it is conspicuously present; for in neither does a free tail exist. In these mammals, as in many others, Rodents especially, in which the pubo- and ilio-coccygei are not well developed, the ischio-coccygei, forming, with the interposed coccygeal vertebræ, a dorsal wall for the pelvic cavity, play a part in the maintenance of the pressure within; just as the transversalis and thoracic diaphragm play the chief part in the production of that pressure. This is supported by finding that in Ornithorhynchus (Fig. 15), in which, moreover, movement of the tail is more or less limited to the dorso-ventral plane, and in such Rodents as the Porcupines the ischio-coccygei have very extensive origins and insertions; in these species they plainly cause a similar occlusion of the pelvic outlet by an approximation of the root of the tail to the perineum, as is determined in other mammals by the pubo- and ilio-coccygei, for which end the muscle of each side of necessity must contract together. In

FIG. 15.

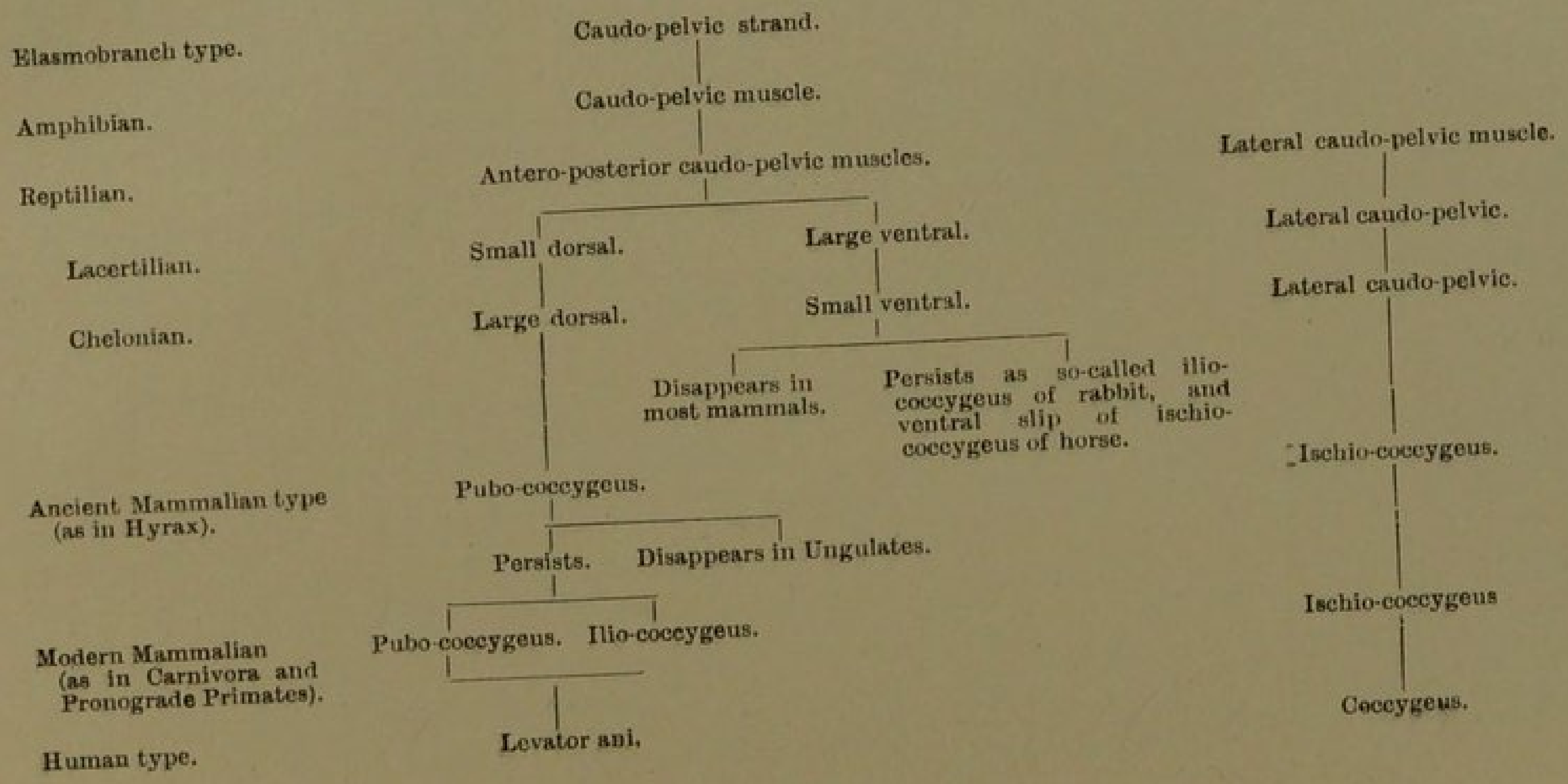


Dissection of posterior end of body of Ornithorhynchus, vertical view showing Is.c., the ischio-coccygeus muscle. Scale about life-size.

the Carnivora and Pronograde Primates the ischio-coccygei are auxiliaries to the same end; and whilst it cannot be denied that they may act individually as abductors—for the negative requires to be shown as well as the positive—there is very good ground for the opinion that this abduction is but a secondary, unimportant, and perhaps not actually occurring function.

In this place may be completed what is to be said concerning the fallacious assumption that the function of the pelvic floor muscles is to move the tail. From this assumption it is argued that because these muscles in tailed mammals are tail-moving, when the tail degenerates these muscles, too, must degenerate, just as the muscles of a limb atrophy when the joint they should move becomes ankylosed. Since, therefore, in man the tail has degenerated, it is further argued that the homologues of these tail-moving muscles, such as they are, which he may possess, have also degenerated; that they are indeed but vestigial structures. The argument is sound but the premises are false. That the argument is sound is shown by the fact that the representatives in man of the true tail-moving muscles of tailed mammals have in him, with the loss of his tail, verily degenerated; but they are not the pelvic floor muscles, they are the sacro-coccygei; for the former, although they have undergone considerable changes, are still remarkably developed. That the function of the pelvic floor muscles is not to move the tail *per se* is shown by their evolution in the fish, amphibians and reptiles (lizards and crocodiles), which are not able to flex the tail; in these they serve to fix the pelvis, and to play a part in the production and maintenance of a frequently recurring increased visceral pressure. That they play the same part in mammals is not hard to divine, and is a sufficient reason for the discovery that, in spite of a degenerate tail, in man they still function. In tailed mammals, however, they do this in one of two ways, either by drawing the root of the tail against the perineum, or else, when the tail is maintained extended by the dorsal sacro-coccygei, by a simultaneous increase in their contraction. These actions are comparable to a backward displacement or fixation of the pelvis in the fish, amphibians and reptiles; but it would surely be a misnomer to call the caudo-pelvic muscles in these vertebrates "pelvis-moving" muscles; and similarly, to describe the muscles in mammals which cause this movement of the root of the tail as tail-moving muscles, whilst true in the narrow sense that their activity may cause, and does cause, a movement of the root of the tail, is, in the wider sense, anything but a true representation of the conditions which actually exist. It is, indeed, to this faulty application of words that the erroneous conclusion has been come to that the pubo-, ilio-, and ischio-coccygei in man have degenerated past functioning because his tail has disappeared.

## THE HOMOLOGY OF THE CAUDO-PELVIC MUSCLES.—*Phylogeny of Pelvic Floor Muscles.*



## THE HOMOLOGY OF THE CAUDO-PELVIC MUSCLES.

That the antero-posterior and the lateral caudo-pelvic muscles in reptiles are homologous with the pubo- and ilio-coccygei and the ischio-coccygei of mammals is, of course, difficult, or perhaps impossible, to prove. No one, however, can examine the muscles which close the pelvic outlet in such reptiles as Iguana, Emys, and Testudo, and in such mammals as the Dog, Rabbit, Kangaroo, the Monotremes, and Hyrax, and fail to notice the remarkable correspondence which occurs in their attachments, and especially in their relations to such other muscles as in mammals are known as the pyriformis, the obturator internus, and the ventral sacro-coccygeus.

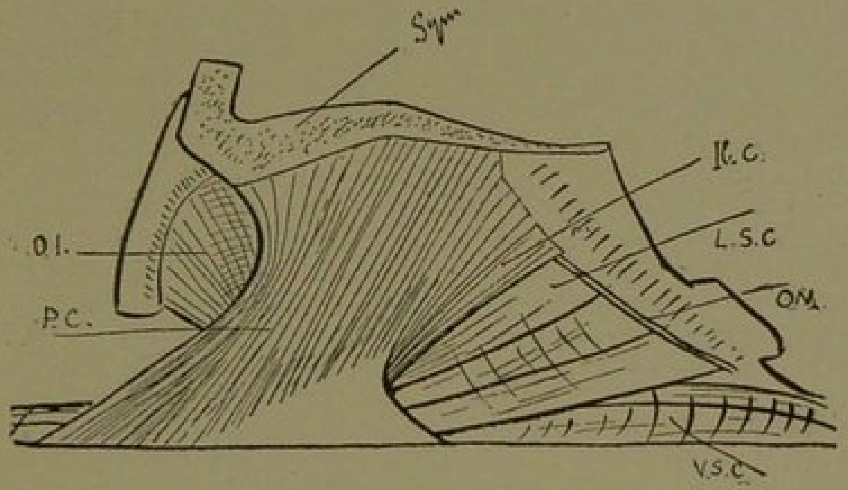
There can be little doubt that the caudo-pelvic muscles in Menobranchus and Salamander maculosa, and the antero-posterior caudo-pelvic muscles in Iguana and Emys, are all homologous; but whilst in the former (amphibians) these consist of a single belly on each side, in the latter a differentiation into two distinct muscles has occurred. The more dorsal of these in Iguana is much the smaller, and appears, from the resemblance of the other much larger muscle to the caudo-pelvic muscle of amphibians, to be a new element segmented off from it. In Emys, this new muscle has become much larger; but instead of passing obliquely forwards and outwards it passes directly forwards to be inserted into the pelvic brim (pubis), passing above the ventral part of the pelvis and above the muscle arising from this part, which appears to be the homologue of the obturator internus, and which in Iguana similarly separates the two antero-posterior caudo-pelvic muscles at their insertions. It seems as though the necessity for a more efficient closing apparatus for the pelvis in Emys has caused the pelvic attachments of both the antero-posterior muscles to shift from their lateral position in Iguana to the more median position in Emys; and that whilst the more dorsal and smaller muscle in Iguana has crept inwards along the pubic bone—i.e., pelvic inlet—the more ventral and larger muscle in Iguana has crept inwards along the pelvic outlet, the two being thus separated by the (?) obturator internus, the presence of which perhaps determined the direction adopted by each. With the transposition inwards, a change in size has occurred: the former muscle, small in Iguana becoming larger in Emys; and the latter, conspicuous in Iguana becoming quite diminutive in Emys. In Testudo, this small ventral caudo-pelvic muscle of Emys has disappeared entirely, and the other antero-posterior caudo-pelvic muscle—much enlarged—is the only one present. From a comparison of this antero-posterior caudo-pelvic muscle of Testudo with the similarly disposed pubo-coccygeus of Hyrax, it seems fairly clear that the two muscles are homologous. If this be so, we must regard the pubo-coccygeus of Hyrax as representing an ancient type of the mammalian pubo-coccygeus, which, on the one hand, has developed into the more extensive muscle of Carnivora, and on the other, has suffered suppression as in the Ungulates.

It has been supposed that the pubo- and ilio-coccygeus have evolved by a lateral extension of the fibres of origin of a primitive flexor muscle of the tail, placed along the ventral surface of the sacrum and coccygeal vertebræ; and that these crept along the lateral pelvic wall towards the pubic symphysis, so that, according to this conception, the pubic fibres, presumably, are the last instead of being the first, as the condition in the Tortoise teaches, to appear. If the pubo-coccygeus itself has arisen from the antero-posterior caudo-pelvic muscles of reptiles and amphibia, it clearly cannot have arisen from a ventral sacro-coccygeus, because the ventral sacro-coccygeus does not occur in the amphibia and Lizards and Crocodiles, and only first appears in the tortoise as the tail became moveable dorso-ventrally.

That a lateral extension of the ventral sacro-coccygeus on to the adjoining pelvic wall may occur, however, is shown by its having happened in the Kangaroo and Myrmecophaga—the condition in which two species has been advanced as representing an intermediate stage in the evolution of the pubo- and ilio-coccygeus from the primitive sacro-coccygeus. But this lateral extension of the ventral-sacro-coccygeus, which in the Wallaby (Fig. 16) consists of numerous muscular bellies all ending in long tendons (in my specimen 17 at least on each side) seems to be easily and sufficiently explained by the large development of the muscle necessary in the Kangaroo for the fixation of the tail which is used as a support for the body, the lateral parts of the muscle, owing to the relatively small size of the pelvic cavity and narrowness of the sacrum, having been crowded on to the lateral pelvic wall (ilium and ischium)—an extension which is readily intelligible. It is obvious that in virtue of this lateral extension the muscle can more efficiently fix the tail upon the pelvis and give it rigidity, just as the similar lateral extension in Myrmecophaga allows this part to act to the best advantage as an abductor of the tail.

That the lateral extension of the ventral sacro-coccygeus on to the lateral pelvic wall in the Kangaroo and in Myrmecophaga is not an intermediate stage in the evolution of the ilio-coccygeus in these animals is further shown by the fact that the anterior fibres of the pubo-coccygeus in both species are more obliquely placed than the posterior, and towards their caudal attachment overlap the posterior fibres, so that at their insertion they are placed laterally to them—just as in the Carnivora the ilio-coccygeus at its caudal attachment overlaps and lies lateral to the attachment of the pubo-coccygeus. Indeed, it seems that these anterior fibres really represent the beginnings of the ilio-coccygeus, which apparently has no homologue amongst the non-mammalian caudo-pelvic muscles—that is to say, that the ilio-coccygeus arises as a part segmented off from the more primitive mammalian pubo-coccygeus, the fibres of which, as they grow dorsally along the lateral pelvic wall, creep laterally rather than mesially to the obturator nerve—which may explain the fact that often this nerve pierces either the pubo- or the ilio-coccygeus (Holl), rather than passes through the interval between them. This hypothesis is supported by the fact that these muscles are always closely connected together, in many cases their complete separation being artificial; and, further, that in many rodents in which the pubo-coccygeus is relatively insignificant an ilio-coccygeus is apparently completely absent (as in Porcupine).

Fig. 16.



Dissection of the pelvis and pelvic floor muscles of a Wallaby. The vertebræ are not shown. Rather less than half size. Sym., Symphysis. O.I., Obturator internus muscle. P.C., Pubo-coccygeus muscle. Il.C., Ilio-coccygeus muscle. L.S.C., Iliac origin of the ventral sacro-coccygeus muscle. V.S.C., Sacral origin of the same. O.N., Obturator nerve.

The proximal part of the ventral sacro-coccygeus, by flexing the root of the tail, may act as an accessory to the pelvic floor muscles; and this may explain its existence in the short-tailed Echidna and in the tailless Guinea-pig and Hyrax, but compared with the pubo- and ilio-coccygeus it is clearly at a disadvantage for such a purpose because of the more ventral attachment to the pelvic brim of these muscles.

That the lateral caudo-pelvic muscle of reptiles (Tortoise) and the ischio-coccygeus of mammals are homologous is not unlikely, for each arises from the lateral aspect of the tail, immediately dorsal to the ventral sacro-coccygeus, both in the tortoise and mammal. It is, however, impossible to trace the transition of these muscles from the reptilian to the mammalian plan since the material is not forthcoming, but it is known that the ischial symphysis separates, and thus we may suppose that as it does so the muscles inserted medianly into it become displaced laterally with each half. In the Monotremes this separation of the ischial symphysis is not complete, and in Ornithorhynchus the pelvic attachment of the ischio-coccygeus reaches ventrally quite up to, or almost up to, the symphysis, a condition which closely resembles the pelvic attachment of the lateral caudo-pelvic muscle in Testudo. (Compare Fig. 9, Lecture I., and Fig. 15, Lecture II.) As flexion of the tail root became possible the sphincteric mechanism effected by the two lateral caudo-pelvic muscles in the reptiles was no longer so necessary, and thus their median ventral insertions were allowed to diverge, but instead they served as a powerful means of approximating the root of the tail to the pelvic outlet, and this explains their marked development in the monotremes, marsupials, and rodents. All these changes, presumably, were caused by the necessity for the frequent occurrence of considerable variations of the internal pressure, which are greatest in mammals of all vertebrates because of the presence of the thoracic diaphragm, to which pressure conditions alone can be attributed the extension of the ischio-coccygei anteriorly and their retention in such tailless species as Hyrax and the Guinea-pig.

Further support of the hypothesis that the lateral caudo-pelvic muscle and the ischio-coccygeus are homologous is afforded by the presence of the so-called ilio-coccygeus in the rabbit, for this muscle is intimately associated with the ischio-coccygeus at its origin from the ischium, and part of it is inserted into the mid-line of the tail and is thus separated from the ischio-coccygeus by the ventral sacro-coccygeus. If we can imagine the ischial attachments of the muscles of each side in the rabbit displaced ventrally and inwards around the pelvic outlet so as to meet in a median ventral symphysis, and if the caudal attachments of the muscles were displaced distally along the tail into the reptilian position, we should have the condition in Emys exactly reproduced, the so-called ilio-coccygeus of the rabbit corresponding in position to the small ventral antero-posterior caudo-pelvic muscle of Emys and the ischio-coccygeus to the lateral caudo-pelvic muscle; for the relation of the two muscles to each other in Emys at their insertion into the ischial symphysis is very intimate, and is exactly comparable to the relation of the two muscles at their origin from the ischium in the rabbit. Lartschneider[21] has stated that this so-called ilio-coccygeus of the rabbit is a part of the ventral sacro-coccygeus, which he supposes has deviated laterally from its original median position on to the ischium, from which in other (and past) species it crept up the lateral pelvic wall to ultimately reach the brim and so to become the ilio-coccygeus of mammals; but he brings forward no reason to show why it should have done so, and the only evidence he adduces in support of his statement is the fact of the lateral deviation of the ventral sacro-coccygeus in Myrmecophaga and the Kangaroo, which he says represents intermediate stages in this transition, but which we have already seen can be otherwise explained. Others have assumed that this so-called ilio-coccygeus of the rabbit has descended from the pelvic brim from a supposed primary lateral extension of the sacro-coccygeus, comparable to the descent of the muscle which has occurred in man; but this seems to me to be fallacious, for there is no evidence that the factors which have caused the descent of the ilio-coccygeus in man—factors which are dependent upon the assumption of the erect posture—have existed in the rabbit. The condition in Emys seems to be the key to the understanding of these muscles, and, if so, demonstrates that the so-called ilio-coccygeus in the rabbit is homologous with the small ventral antero-posterior caudo-pelvic muscle of Emys and not homologous with the ilio-coccygeus of Carnivora and of other Rodents (as the Squirrel), and that the lateral caudo-pelvic muscle of Reptiles and the ischio-coccygeus of mammals are homologous.

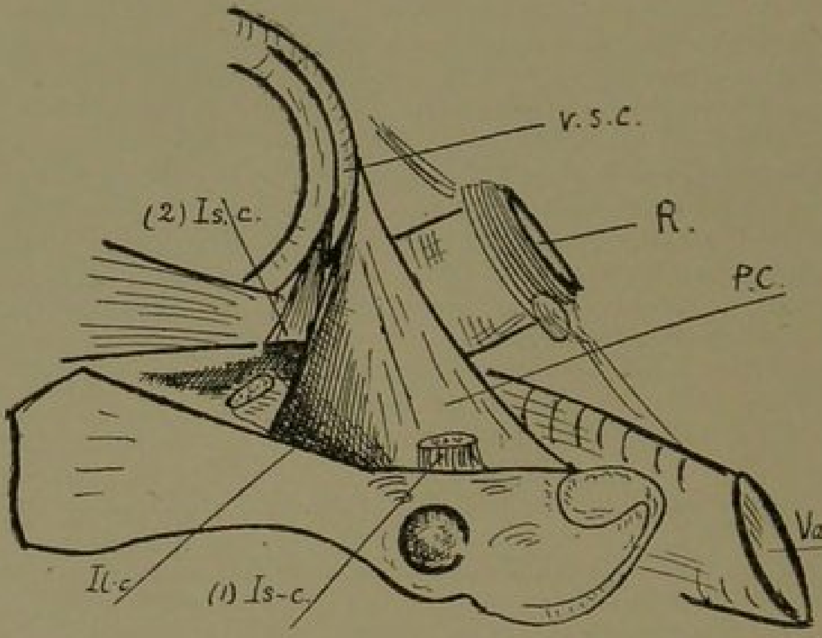
## THE SPHINCTERIC LAYER.

The superficial sphincteric layer of muscles, guarding the anal and urogenital orifices, is universally present in mammals; but presents wide variations in development and extent in different orders. As a rule, we may say that in those animals in which the closure of the pelvis is efficiently effected by the pubo-, ilio-, and ischio-coccygei, the sphincters exist, usually well developed, but merely as closing mechanisms for the orifices they surround; whilst in others, in which the pelvic floor muscles are either not so well developed or not so efficient, the superficial muscular layer not only forms sphincters for the orifices but in many cases, gaining extensive attachments to the pelvic outlet, plays a part in the maintenance of the internal visceral pressure. Thus in the Carnivora and Pronograde Primates the sphincters are well developed; but, often—as in the dog (Fig. 17)—are placed some considerable distance beyond the slit-like orifice formed by the posterior fibres of the pubo-coccygei (Lartschneider), and thus there is no connexion between them.

In the Rodents, in which the pubo-coccygei are not so well developed as in Carnivora, the superficial sphincteric layer is much more marked; especially in those species in which the ischio-coccygei do not compensate sufficiently to take their place. In the Rabbit and Guinea-pig, for instance, this superficial layer is conspicuously present.

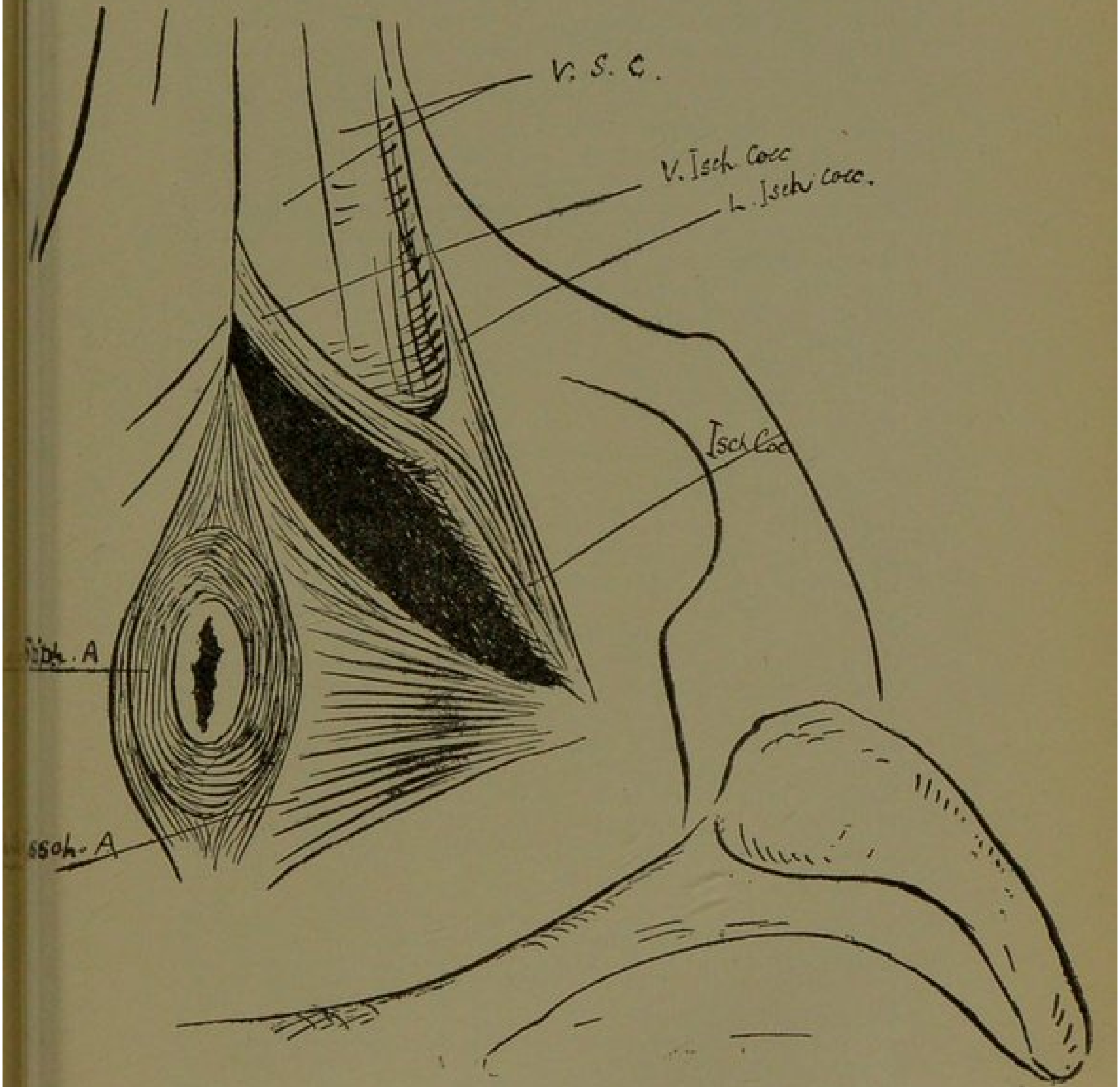
In the Ungulates, with the complete absence of the pubo- and ilio-coccygei, we find not only the sphincteric muscles remarkably developed, but also an ischio-anal muscle present which is almost as well developed as the ischio-coccygeus itself (Fig. 18). This muscle arises from the region of the ischial spine and is inserted into the terminal part of the rectum, in close association with the external sphincter muscle ; some of its fibres, with some of the external sphincter muscle, are inserted into the tail ; and others pass ventrally to the perineal region. According to Professor P. Thompson,[34] the ischio-anal represents a greatly developed transversus perinei muscle, and has evolved from the primitive sphincter of the cloaca. The ischio-anal of each side and the external sphincter ani together form a powerful tripartite musculature by means of which the internal pressure is safeguarded even in the absence of the pubo- and ilio-coccygei.

FIG. 17.



Dissection of the pelvis and pelvic floor muscles of a dog (fox terrier) from without. About half life-size. P.C., Pubo-coccygeus muscle. Il.-c., Ilio-coccygeus muscle, Is.-c., the ischio-coccygeus, cut through (1) the lower part, (2) the upper part. V.S.C., Ventral sacro-coccygeus muscle. R, Rectum surrounded by sphincter. Va, Vagina.

FIG. 18.



Dissection of the perineal region of a horse. About half life size. v.s.c., Ventral sacro-coccygeus muscles. Isch. Cocc., Ischio-coccygeus muscle, L.Isch.Cocc. and V.Isch.Cocc. being the lateral lamina and ventral slip. Isch.A, Ischio-anal muscle. Sph.A, Sphincter ani.

### *In Aquatic Mammals.*

The sphincteric muscles are also well developed in marine mammals (Whales, Dolphins and Seals, &c.)—a condition which contrasts with their absence in non-mammalian aquatic vertebrates, and is apparently correlated with the terrestrial type of respiration and circulation, and the presence of a thoracic diaphragm. It is clear the pressure within the thorax must be less than the pressure outside the animal exerted by the medium (water) by which it is surrounded, for its lungs are of delicate structure and their blood capillaries thin-walled, so that if the air were maintained within the chest by an occlusion of the glottis only, and subjected to the pressure exerted on the rest of the viscera by the medium from without, as obtains in non-mammalian aquatic vertebrates, an obstruction to the circulation of the blood through the lungs would certainly result with consequent asphyxia.[‡] This excessive pressure is prevented by the bony walls of the thorax and by its musculatures, of which the thoracic diaphragm plays a conspicuous part, for it has, so to speak, to prevent the weight of the water bearing upon the abdomen from being transmitted by the visceral mass to the thoracic viscera and from causing an obliteration of the lung capillaries. This it does by its tonic contraction, in correspondence with which we find the diaphragm in these aquatic mammals exceedingly well developed, the central tendon itself being replaced by muscular tissue. Since, however, this visceral mass is permeated by a vascular system in free communication with the thoracic viscera, it is plain the weight of the water without and the increased contraction of the diaphragm within will tend to drive the blood from the abdomen into the thorax, because the pressure there is less, which would result in a congestion of the lungs. This is prevented by the development of that part of the diaphragm immediately surrounding the passage of the inferior vena

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[‡] The essential difference between the mammalian and those non-mammalian aquatic vertebrates which possess lungs—i.e., from Dipnoi upwards—is that whilst the blood flowing to the heart can only reach the aorta by passing through the lungs in mammals, owing to the fact that the right side of the heart does not communicate with the left side because of the growth of the interventricular septum and to the fact that the primitive efferent vessel has been completely divided into the pulmonary artery and aorta, in the non-mammalian vertebrates, this condition of the heart not having been reached, there is a free way for venous blood to the primitive aorta, so that only a portion of it passes through the lungs, whilst its adequate oxidation is provided by the possession either of internal or external gills, to which the blood passes by branches which arise from the aorta. This mechanism of respiration is not necessary in the terrestrial, non-mammalian vertebrate, because, presumably, the pressure exerted on the lung capillaries by the medium (air) is much less in these than in aquatic ones in which the pressure is sufficient to necessitate another kind of breathing (ext. gills), because in them no muscular diaphragm is present to relieve by its contraction the lung capillaries from this obliterating pressure.

cava into a definite sphincter-like mechanism, which by its contraction regulates the amount of blood entering the chest from the abdomen and causes a damming up of the blood within the abdomen, as is shown by the development of huge venous sacs within the liver. This sphincteric action upon the inferior vena cava and the pressure exerted by the rest of the diaphragm upon the abdominal contents is therefore very considerable, and must be at least equal to that exerted upon the animal from without. Thus the pressure conditions prevailing within the abdomen of marine mammals approach those occurring in terrestrial mammals—in which the pressure within the abdomen, except perhaps during recumbency and sleep, is always greater than the pressure without (atmospheric pressure)—and during such active expiratory acts as spouting is probably considerably increased. These considerations seem to explain the reason for the existence of the sphincter muscles in aquatic mammals; they are well marked in the Whale (Struthers[32]), and in the Dolphin are connected with the rudimentary pelvis by muscles similar to the ischio-anal muscles of Ungulates.[35]

This sphincteric condition of the diaphragm upon the inferior vena cava, and the presence of the large blood sacs in the liver of the Walrus, have already been described by Mr. Burne, and are beautifully shown in a specimen taken from a seal, which is preserved in the Museum of the Royal College of Surgeons of England and which the same author recently exhibited before the Zoological Society (Fig. 19). The existence of these remarkable modifications of structure can only be explained by the aquatic habits of these animals; and they bring home to us the important and far-reaching influence which the pressure conditions within the abdomen exercise, for in these animals one of its effects at least is gross and obvious.

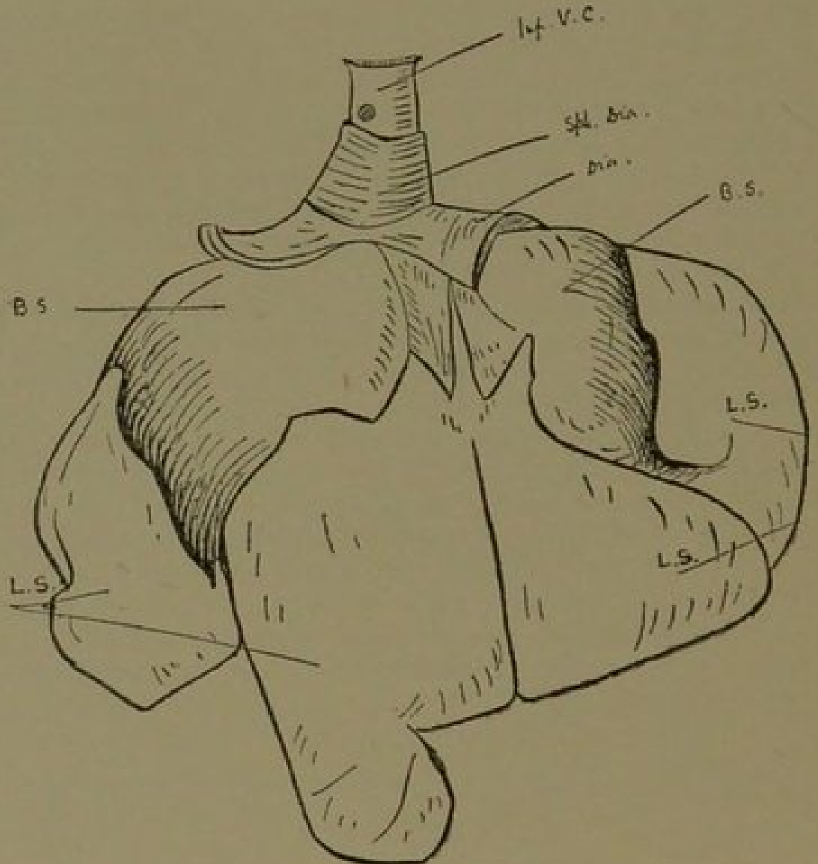
## THE FACTORS AT PLAY IN THE EVOLUTION OF THE PELVIC FLOOR.

If now we come to ask ourselves how it is these different orders of mammals present such striking differences as regards the structure of the closing apparatus of their pelves, in all of which an efficient closure exists, the various conditions at first sight seem inexplicable. Yet a certain order obtains, so that by an examination of a dissected pelvis it is possible to say from what sort of animal it came. And if we turn our eyes from the specimens before us to the natural history of the individuals to which they belong, we find corresponding and remarkable differences—differences which are specific and vital, upon which the preservation of the individual species depends.

Let us consider the Ungulates and Carnivora, and ask ourselves, How do they compare with each other? and, How being neighbours, living side by side, do they manage to exist?

The Ungulates are vegetarians: this is such a distinguishing feature that they are called "Herbivora." They are ill-adapted for attacking, for striking, for killing, for devouring other animals, for the simple reason that these accomplishments form no necessary part of their being, and because of their comparative defencelessness they usually roam in herds or else seek security in solitary and often mountainous places. What means of attack they possess is for the purpose of defence, for the preservation of themselves and their young in times of great peril, or is but the outcome of pure savagery, and is never for the obtaining of food. In the other the essential characteristic is that they are

FIG. 19.



Diagrammatic representation of liver of the seal. Inf. V.C., Inferior vena cava. Sph. Dia., Part of the diaphragm surrounding the inferior vena cava transformed into a sphincter muscle. Dia., Thoracic diaphragm. B.S., Blood sacs, overlapped by L.S., Liver substance.

flesh eaters; this is so significant of them that they are called "Carnivora." The ancestors of the former obtained their food from the succulent vegetation of primeval forests (cf. Tapirs) and subsequently by grazing on prairies (cf. Horses); the ancestors of the latter, by preying upon other animals, of which the most suitable as victims, because of their comparative defencelessness, were the ancestors of the present-day Ungulates (and Rodents). Thus it was determined the former should be hunted because the latter became hunters and preyed upon them. The preservation of the former from their flesh-eating opponents could only be effected by escape, and this necessitated the individuals should be capable of rapid and prolonged flight, to which their whole structure is splendidly adapted. Thus they came to use their limbs for progression only, which have become proportionately longer, so that they could cover the ground more rapidly, and unnecessary parts, such as (the possession of) several digits, necessary for clawing or grasping, have been suppressed. They acquired an easy and unobstructed respiration, essential for speed, conditioned by a wide larynx (Sir Lauder Brunton[§]), an easily expanding thorax, and by a continual avoidance of all movements, such as striking, which by determining a marked increase of pressure within the abdominal cavity necessitates a holding of the breath. Thus their power of vocalisation is poor, for it is impossible to utter loud and continuous sound without a considerable and correspondingly prolonged increase of intra-abdomino-pelvic pressure, which implies a fixation of the abdomen as well as of the thorax, and the necessity to do this frequently and efficiently is conditioned by the possession of good musculatures enclosing the visceral mass. The horse indeed neighs, but rarely; the bull bellows, but infrequently. These are curious sounds, apparently not easily produced, and perhaps their peculiarity depends upon this difficulty; they are scarcely comparable to those omitted by the Carnivora (cf. Dog[‖]), which in this way intimidate their prey (or their opponents), and thus gain an easier victory; but the Ungulates require no such means to be successful in obtaining food.

These underlying necessities of their existence were not required only occasionally but constantly; upon them the preservation of the species depended. The necessity for an

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[§] "In animals whose motions are chiefly those of running we find the ventricular bands (of the larynx) absent, or slightly developed. But in animals where the anterior extremities are used for striking, hugging, or climbing the vocal cords are strongly developed."—Valvular Action of Larynx, Journal of Anatomy and Physiology, vol. xvii., 1882-83, by Sir Lauder Brunton and Professor J. Theodore Cash.

[‖] The loud, disturbing bark of the dog is a good example. In this case inspection shows how the impulse accompanying each bark is reflected against the perineal region—an observation for which I am indebted to Dr. James Collier.

internal pressure as low as possible—that is, as low as consistent with the general metabolism of the animal—and an ever-readiness for flight lead to the suppression of the primitive pubo-coccygei present in their earliest ancestors (cf. Hyrax), and explains the undeveloped state of their larynx, just as their constant vigilance and the necessity for an extensive field of vision determined the aperture of their pupil to become a horizontal slit so that they might view the whole horizon simultaneously. This suppression of the pubo-coccygei permitted an easy defæcation and allowed the act to take place without the interruption of their locomotion, defæcation occurring in them as well trotting as standing still, for the absence of these muscles permitted it to occur without straining—that is, without an increase of visceral pressure, to procure which the crouching attitude is so necessary in Carnivora and the Primates.

Yet the pressure within required for an adequate circulation and expiration is provided for by several devices. Thus, the pelvis of these animals, in relation to the abdomino-pelvic cavity, is very highly placed, being situated almost at its summit, and is very obliquely inclined, so that its outlet looks much more upwards than backwards. Their bodies are nearly always maintained with the long axis horizontal ; they never crouch or sit, and if they rear they do so but rarely, and only momentarily. Thus there is not the same necessity for such a closure of the pelvis as occurs in Carnivora ; for they avoid those postures of the body, for the maintenance of which a considerable increase of internal pressure is essential. Their abdominal viscera are supported by the well-developed abdominal wall musculature, which slopes downwards and forwards from the pelvis towards the diaphragm, upon the tonic contraction of both of which the internal pressure conditions depend. These musculatures control their respiration : inspiration being effected by the posterior recession of the diaphragm, and a corresponding displacement of the abdominal viscera and protrusion of the belly wall ; whilst expiration is determined by the lessened contraction of the diaphragm and a replacement of the viscera by the abdominal wall (Keith). Thus the thoracic diaphragm and abdominal wall musculatures react against the weight of the viscera ; and when the pressure within becomes of necessity higher than usual, e.g., during coughing, the pressure impulses which are transmitted upwards and backwards to the pelvis are prevented from escaping by the closing mechanism provided by the high development of the superficial perineal musculature.

The preservation of the Carnivora, on the other hand, depended on their devouring prey, and was only possible by successful stalking and slaughter. Stalking required cunning, and thus the higher psychical centres were stirred to greater activity ; slaughter necessitated the use of the fore-limbs for striking purposes, and this in turn a fixation not only of the thorax but of the whole body. The necessity to hold the breath entailed by such fixation called the muscles constricting the glottis into greater prominence; the simultaneous necessity to convert the soft and supple abdomen into a comparatively rigid mass determined the further development of the pubo- and ilio-coccygei, the presence of which allowed a powerful and efficient vocalisation, and eventually permitted the assumption of the erect posture.

Can there be any doubt that the function of the caudo-pelvic muscles, which first definitely appeared in the Amphibia in association with the necessity for an increased visceral pressure, which evolved further during the Reptilian Era for the same end, and which in Carnivora have continued to evolve in association with the development of the fore-limb for striking purposes, and that of the larynx for powerful vocalisation, is really a pressure one, and that it reacts in association with the abdominal wall musculature and the thoracic diaphragm to this end? If this be so, the absence of the pubo- and ilio-coccygei in Ungulates is explained.

## GEOLOGICAL RECORD AND CONCLUSION.

In support of such a conception of the evolution of the Ungulates is the remarkable richness of the geological record in the case of the ancestry of the horse. Not only is it known that the horse—like all the mammalia (Beddard)—evolved from small forms, but that it evolved from animals with five digits, and that these in the course of evolution have been suppressed. That this suppression has occurred as the result of change of habit is shown by the fact that in the early stages it was more advanced in the hind foot than in the fore, such as we can readily imagine to have been caused by the hind foot giving up grasping or clawing movements at an earlier period than the fore-foot. Thus in Eohippus the fore-foot had four digits, with a vestige of the first, whilst the hind foot had only three; it stood 11 inches in height at the shoulder and was more like a carnivorous animal than an ungulate (Lull). Owing to the increasing adaptation to speed—which like all changes was but slow—"after vast ages," the suppression of the extra digit of the fore-foot was effected, and from that time the retrogression in each has been the same. "Still," writes Lull, "it is curious to note that, among living horses, in instances of reversion to ancestral conditions, the fore-foot is more apt to exhibit well-developed atavistic toes, showing that in it the reminiscent tendencies are stronger." In connexion with this it is interesting to discover that in the Tapir, "the most ancient of existing forms referable to the Perissodactyla Order" (Beddard), the fore-foot has four digits, but the hind-foot only three. We have but the bones, and often but few of these, from which to gain an idea of the skeleton of past forms; but as the skeleton and the musculature—indeed the whole structure—go hand in hand, it is not difficult or unreasonable to suppose that changes in the soft parts were similarly affected.

The same examination and arguments may be applied to other orders of animals. In the case of the Rodents, to which Hyrax is so similar, we may suppose they escaped destruction by hiding, rather than fleeing, and to this end learnt to burrow. Such activity in them as in the Ungulates was not so necessary, perhaps explaining their small size; but it is significant to find that in those that are hunted, such as the rabbit and the hare, the pubo-coccygeus is only feebly developed or not to be found. In them, as in the Ungulates, the pelvic outlet is secured by the superficial sphincteric layer of muscle. Similarly, in the Guinea-pig the pubo-coccygeus is only present as a fine membranous-looking muscular sheet. Yet in others, which have taken to climbing, as the Squirrel, the pubo-coccygeus and ilio-coccygeus are almost as well developed as in Carnivora. So animal after animal can be instanced, showing the response of the pelvic-floor muscles to form an adequate closing apparatus for the pelvis, sufficient for the maintenance of the internal pressure conditions of the particular animal—conditions which vary from time to time and depend on many factors, all of which themselves depend on the habits and mode of life of that animal. Thus the caudo-pelvic muscles of pronograde mammals, like those of the non-mammalian vertebrates, exist for one end—namely, a pressure effect, for they form an integral part of the internal pressure-regulating mechanism; and thus, in a most beautiful way, is exhibited a principle, universal throughout the vertebrates and dominating their lives, a principle becoming ever more dominant as we ascend the series, and which, had we time to consider it, we should find had reached its climax in man.

It is now my pleasing duty to acknowledge my obligations. I have to thank the Museum Committee of this College for permission to work in the Research Laboratories here and for material; I am indebted to Professor Keith for much personal kindness, help, and encouragement with the work; also to Mr. Burne, especially for drawing my attention to the structural conditions in the viscera of aquatic mammals; to Mr. Beddard, F.R.S., Prosector to the Zoological Society, for material; and finally, Ladies and Gentlemen, I have to thank you for your kind attention.

### List of Animals Dissected for Lecture II.

*Carnivora and Pronograde Primates.*—Dog (*Canis familiaris*). Lynx (*Felis lynx*). Civet (*Viverra civetta*). Seal (*Phoca vitulina*). Monkeys (*Semnopithecus entellus* and *Macacus sp.*).

*Rodents.*—Porcupine, tree-climbing (*Erethizon dorsatum*); brush-tailed (*Atherura africana*). Rabbit (*Lepus cuniculus*). Guinea-pig (*Cavia porcellus*). Hare (*Lepus europaeus*). Squirrel (*Sciurus ludovicianus*). Coypu Rat (*Myopotamus coypus*).

*Ungulates.*—Horse (*Equus caballus*). Panolin Deer (*Cervus eldi*). Hyrax (*Procavia*).

*Marsupialia.*—Wallaby (*Macropus bennettii*).

*Edentata.*—Great Ant-eater (*Myrmecophaga jubata*).

*Monotremes.*—Ornithorhynchus (*Ornithorhynchus anatinus*). Echidna (*Tachyglossus aculeatus*).

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