ON THE 'LEVATOR ANI' OR ISCHIO-ANAL MUSCLE OF UNGULATES, WITH SPECIAL REFERENCE TO ITS MORPHOLOGY. By Peter Thompson, M.B., Ch.B., Senior Demonstrator of Anatomy in the Owens College, Manchester.¹

THE object of this communication is to show that the so-called levator ani of ungulates is an entirely different structure from the muscle bearing the same name in man and anthropoid apes. In point of fact, the levator ani does not exist in ungulates, and the muscle so designated should be called, as indeed it is by veterinarians, the ischio-anal muscle.

As long ago as 1845, Straus-Durckheim pointed out that the levator ani of man corresponded to two tail muscles present in carnivores, viz., the ilio-caudal or ilio-coccygeus, and the pubocaudal or pubo-coccygeus, and considerable additions to our knowledge of the anatomy and morphology of the caudal muscles have subsequently resulted from the observations of Eggeling on marsupials, of Kollmann on tailed apes and anthropoids, of Lartschneider on carnivores and primates, and of Holl on the muscles of the pelvic outlet in man.

The levator ani, as it exists in man and some primates, is not present in lower mammals, though the homologous muscles can usually be recognised without difficulty. In most cases where observers refer to the levatores ani in lower mammals, the descriptions given, except perhaps in ungulates, are those of two muscles which pass to the tail without coming into direct connection with the rectum. Take, for example, the descriptive accounts by Ellenberger and Baum of the levator ani in the dog, and by Miller in the seal. In them we find details of two muscles whose origin from the pelvic wall and insertion into the caudal vertebræ leave no doubt as to their real nature.

Clearly then, two muscles in lower mammals, the ilio-coccygeus and pubo-coccygeus, correspond to the levator ani in man. They are attached to the inner aspect of the lateral wall

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of the pelvis, the ilio-cocygeus to the neighbourhood of the ilio-pectineal line or immediately below it, the pubo-cocygeus to the back of the pubis, and each is inserted into the proximal caudal vertebræ. At the most, any action which they exert on the rectum is limited to lateral compression, and is quite secondary to that of moving the tail. Both the ilio-cocygeus

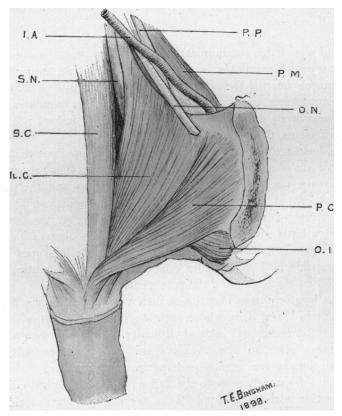


Fig. 1.—Flexor muscles of the tail in a monkey (Macacus rhesus), left side from within; P.P., psoas parvus; P.M., psoas magnus; O.N., obturator nerve; P.C., pubo-coccygeus; O.I., obturator internus; h.C., ilio-coccygeus; S.C., sacro-coccygeus; S.N., sacral nerves; I.A., iliac artery.

and pubo-coccygeus are the result of a lateral extension on to the side wall of the pelvis from a single powerful flexor of the tail situated on the ventral aspect of the sacral and caudal vertebræ. In the majority of mammals, the ilio-coccygeus and pubo-coccygeus are similarly arranged. Even in man, in whom, in consequence of the retrogression of the caudal vertebræ and the assumption of the erect posture, the greatest modifications are evident, the primitive arrangement of two muscles passing from the side wall of the pelvis to the rudimentary coccyx is retained to a remarkable extent (fig. 3). In man, however, they are modified to effect the more efficient closure of the pelvic outlet, and to support the superimposed viscera. It is interesting to find that some anatomists recommend the discontinuance of the name 'levator ani' entirely, and the substitution of the terms 'ilio-coccygeus' and 'pubo-coccygeus.'

In ungulates, however, this general arrangement is not adhered to. From dissections of the camel, cow, bull, mare, and stallion, I have satisfied myself, so far at least as these animals are concerned, that neither the ilio-coccygeus nor the pubococcygeus are present; and inasmuch as the levator ani is admittedly only a specially modified form of these muscles, it is obvious that there is no morphological equivalent of the levator ani in the ungulates referred to.

In the camel, which may be taken as a type, there are two muscles which arise in close apposition from the internal surface of the ischium, but they are morphologically distinct from both the ilio- and pubo-coccygei. One, arising close to the spine and passing to be inserted into the caudal vertebræ, is dorsal in position, the other, arising close to the thyroid foramen, is ventral; the ventral muscle passes along the lateral aspect of the rectum, to terminate in short tendinous fibres in its walls near the anus. At its insertion the fibres intermingle with the deeper layers of the external sphincter ani, and none are attached to the caudal vertebræ.

There can be no doubt that the dorsal muscle is the ischiococygeus or abductor caudæ, but the significance of the ventral muscle, which, from its attachments, is well named ischio-anal, seems to have been misunderstood. By most observers it is regarded as corresponding to the levator ani, and if this is so, the question naturally arises,—To which of the flexor tail muscles does it correspond, the ilio-coccygeus or pubo-coccygeus, or does it represent both?

Apparently, observers do not agree upon this point. Holl, who has found a similar disposition of the two corresponding muscles in the horse and roebuck, is of opinion that the dorsal

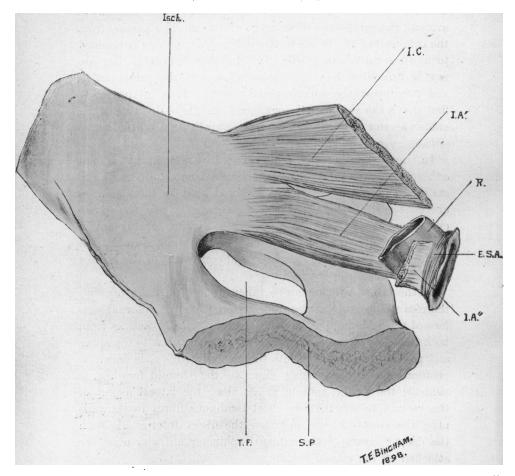


Fig. 2.—Ischio-anal and coccygeus muscles in the camel (Camelus dromedarius). Isch., ischium; I.C., ischio-coccygeus passing to be inserted into the caudal vertebræ; I.A'. and I.A"., ischio-anal muscles of the two sides; R., rectum; E.S.A., external sphincter ani; S.P., symphysis pubis; T.F., thyroid foramen.

muscle is the ilio-coccygeus, and the ventral muscle the pubococcygeus. He thinks this view is not unlikely, because in the rabbit and guinea-pig the origin of the ilio-coccygeus is transferred to the mesial surface of the ischium, in the region of the spine. It may be pointed out, however, that the descent of the attachments of the flexores caudæ on the lateral pelvic wall does not appear to influence their insertion into the caudal vertebræ. In the rabbit, guinea-pig, and even in man, although the transference of the pelvic attachment has undoubtedly taken place, the connection of the muscles with the vertebral column is still retained.

Lartschneider, after examining the horse and stag, came to the conclusion that the dorsal muscle was the ischio-coccygeus, and that the ventral muscle was the homologue of the pubo-coccygeus of the rabbit and edentates. But Holl has shown that what Lartschneider regarded as the pubo-coccygeus in the rabbit was a part of the sphincter cloacæ. Lartschneider commenced with this observation in tracing the phylogenetic history of the pubo-coccygeus, and he believed that the pubo-coccygeus of edentates, and indeed of mammals generally, was derived, like the sphincter cloacæ, from the great skin muscle (M. cutaneus maximus). Holl has shown that this view is untenable, and that the pubo-coccygeus of the rabbit and edentates is, like the corresponding muscle in other mammals, an extension of the tail musculature.

Lastly, Paulet, writing on the comparative anatomy of the perineum, states that the ischio-anal muscle in the stag is homologous with the levator ani of man, but that they differ in form. He regards the ischio-anal muscle as corresponding only to a limited part of the levator ani, viz., to that which remains if the fibres arising from the pubis and obturator fascia be removed. It is noteworthy that Paulet, whilst holding this view, was struck with the close resemblance of the ischio-anal muscle in the stag, cow, and horse.

Thus, whilst Holl, Lartschneider, and Paulet disagree as to the precise homologies of the ilio- and pubo-coccygei, and differ particularly as regards the extent to which they are represented in the 'levator ani' of the ungulates examined by them, they are apparently in accord in stating that the "levator ani" represents one or other of the two flexor tail muscles, either wholly or in part. A careful consideration of (1) the attachments and (2) the nerve-supply has convinced me that this view is probably incorrect.

There is no resemblance between the attachments of the pubococcygeus of other mammals and the ischio-anal muscles of ungu-No fibres of the latter arise from the pubis, and none pass to the caudal vertebræ. I have examined specimens of monotremes, marsupials, carnivores, rodents, insectivores, and primates, and in all the pubo-coccygeus never failed to exhibit in some degree its primitive attachments. Invariably the muscle took origin either from the back of the symphysis, from the body of the pubis, or from the horizontal ramus of the pubis. Similarly, with regard to its insertion, fibres could always be traced either to the bodies or transverse processes of the proximal caudal vertebræ. Nevertheless, Lartschneider, whilst admitting that no fibres are attached to the vertebral column, believes that the ischio-anal muscle represents the pubo-coccygeus of edentates, marsupials, carnivores, and primates, and that its peculiarities depend on the size of the body and the mode of nutrition of the animal.

It should be mentioned here, that in the cow some of the fibres of the ischio-anal muscle do not pass into the walls of the rectum, but unite with the fascia of the tail. Lartschneider has noted a similar arrangement in the stag and horse. I shall refer to the significance of these fibres subsequently.

Again, with reference to the possible correspondence of the ischio-anal muscle to the ilio-coccygeus. The latter muscle is always inserted into the caudal vertebræ. As to its origin, it must be admitted that this does not always take place from the ilium. The attachment may descend on the side wall of the pelvis, and the muscle then arises from the ischium as in the rabbit and guinea-pig, according to Holl, or from the fascia obturatoria as in man.

From the attachments, therefore, we may reasonably conclude that the ischio-anal muscle of ungulates corresponds neither to the pubo-coccygeus nor to the ilio-coccygeus of other mammals. Moreover, its direct connection with the rectum suggests that it should be included with the external sphincter ani in the group of extrinsic rectal muscles.

The considerations of nerve-supply lend additional support to this conclusion. The importance of including the nerve-supply of a muscle in the consideration of morphological questions is recognised by all observers. Quite recently, Dr Mall, in a paper on the "Development of the Ventral Abdominal Walls in Man," says on this subject, "that the studies in comparative anatomy by Gegenbaur, Huxley, and Kollmann have proved almost beyond doubt that nerve and muscle are associated with each other in the earliest stages of development, and that comparison of muscles can be made satisfactorily only when their nervesupply is included." According to his views, "the history of a muscle is indicated by its nerve, and in studying the development of a muscle our main guide is its nerve." On the other hand, Professor Cunningham has shown that nerve-supply "is not an absolutely infallible guide."

As already mentioned, the ilio- and pubo-coccygei are simply differentiated parts of a single powerful tail muscle, which we may now refer to as the sacro-coccygeus, situated on the ventral aspect of the sacral and caudal vertebræ, and it is particularly interesting and significant to note that in monotremes and some marsupials, the three muscles are not distinct from one another. Whilst, however, there is no clear separation of the three constituent elements, they are easily recognisable, and the whole group appears as a flat muscular sheet passing from the side wall of the pelvis to the tail. This continuous sheet receives a continuous nerve-supply. The sacro-coccygeus is innervated by twigs from the sacral plexus, and the laterally extended differentiations of ilio-coccygeus and pubo-coccygeus respectively carry with them their nerve-supply from the same source. This holds good also in those animals in which the individual muscles of the group are more or less completely separated from each other. I have, indeed, found no exception in the animals I have had the opportunity of dissecting, but I note that Leche describes the ilio-coccygeus in chrysochloris as being supplied by a branch of the oburator nerve.

The levator ani in man receives its nerve-supply partly direct from the fourth sacral, and the branches from this source enter the muscle on its pelvic surface. In addition, branches from the internal pudic are also distributed to it, and these pierce its external surface. This variation from the primitive type may perhaps be looked upon as an example of transference of nerve fibres from a familiar to an unfamiliar route. The transfer-

ence becomes intelligible if we remember that the internal pudic supplies the group of muscles derived from the primitive sphincter cloacæ, and that, as a result of the formation of a pelvic floor, two muscular layers have been brought into close apposition, viz., one consisting of modified caudal muscles—the levator ani, the other, the superficial perineal muscles. We have here an excellent illustration of what has been described as "the struggle for supremacy between two contiguous nerves supplying contiguous groups of muscles." 1

In ungulates, the ischio-anal muscle is apparently always supplied by branches from the internal pudic nerve. Apart from my own observations, which support this statement, I find that Chauveau describes the ischio-anal muscle in solipeds as supplied by the pudic nerve, and A. M. Paterson and R. C. Dun have recently described the levator ani in the Indian elephant as receiving its innervation from the same source. In all the ungulates I examined, I failed to find any nerves passing direct from the sacral plexus to the ischio-anal muscle, and this attracted my attention the more since in other mammals, in which the ilio- and pubo-coccygei were present, nerve fibres from the sacral plexus direct were invariably found. On the other hand, a number of branches proceeded from the internal pudic nerve, and these supplied not only the ischio-anal muscle, but also the external sphincter ani.

The nerve associated with the primitive sphincter cloacæ is the internal pudic, and all the muscles which are differentiated from it derive their nerve-supply from the same source. And although, as illustrated by the innervation of the human levator`ani, there is a tendency for the nerve to overstep its original limits and extend its territory, these invasions must be regarded as secondary, and they need not obscure the primitive arrangement.

The conclusion arrived at from a consideration of the muscular attachments—that the ischio-anal muscle corresponds neither to the ilio-coccygeus nor the pubo-coccygeus of other mammals—is thus supported by the further consideration of the nerve-supply of these muscles, and the fact that the ischio-anal muscle is innervated solely from the internal pudic affords

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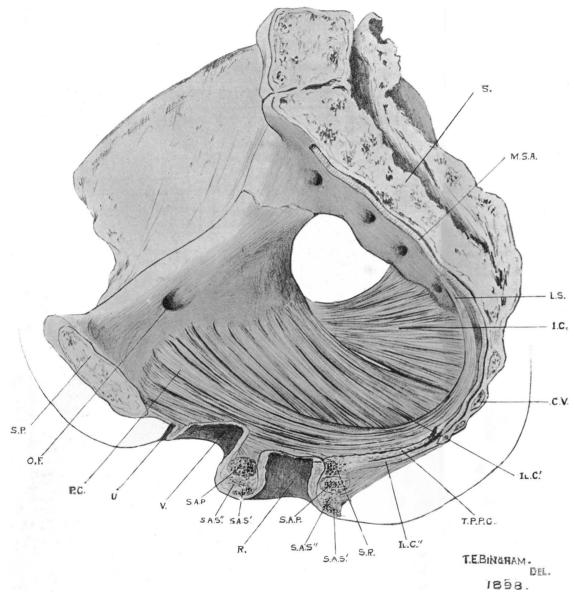


FIG. 3.—Sagittal section of the pelvis to show the pelvic diaphragm and external sphincter ani. S., sacrum; M.S.A., middle sacral artery; L.S., ligamentum sacro-coccygeum anterius; I.C., coccygeus; C.V., coccygeal vertebræ; IL.C'., ilio-coccygeus; T.P.P.C., tendinous aponeurosis of pubo-coccygeus; IL.C''., raphé formed by ilio-coccygei; S.R., sphincter recti; S.A.S'., S.A.S''., sphincter ani externus subcutaneus and superficialis; S.A.P., sphincter ani externus profundus; R., rectum; V., vagina; U., urethra; P.C., pubo-coccygeus; O.F. obturator canal; S.P., symphysis pubis.

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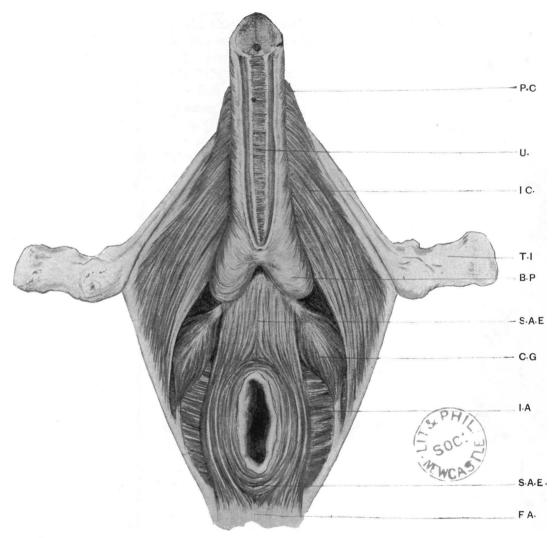


Fig. 4.—Perineal muscles of the camel (Camelus dromedarius). P.C., pubo-cavernosus or levator penis; U., layer of muscular fibres under urethra; I.C., ischio-cavernosus; T.I., tuber ischii; B.P., bulb of penis; S.A.E., sphincter ani externus; C.G., Cowper's gland; I.A., ischio-anal muscle; S.A.E'., circular fibres of sphincter ani externus; F.A., fibrous aponeurosis by which the sphincter ani externus is attached to the tail.

additional evidence that this muscle should be associated with the anal sphincter and the other superficial muscles of the pelvic outlet.

I therefore venture to suggest that the ischio-anal muscle is not a tail muscle like the ilio-coccygeus and pubo-coccygeus, and that it cannot be regarded as homologous to them or to the modified levator ani. Its connections and nerve-supply show that it is probably derived from the primitive sphincter cloace, like the bulbo- and ischio-cavernosi. It has not, however, like these muscles, become attached to the circumference of the pelvic outlet, but has passed within its margin to the neighbourhood of the spine of the ischium, possibly, and at any rate the more easily, in consequence of the absence of the ilio- and pubo-coccygei muscles.

The connections between it and the other superficial perineal muscles are very intimate, and at once suggest a common origin. In the camel this is especially evident. The external sphincter ani encircles the posterior part of the rectum, and passes below into the bulbo-cavernosus. At the lateral margin of the continuous muscular mass two muscles are found on each side. Of these, one situated at the root of the penis is the ischio-cavernosus; the other, situated at the side of the rectum, is the ischio-anal muscle, and this extends upwards into the pelvic cavity, to be attached to the side wall, near the spine of the ischium.

The insertion of the fibres of the ischio-anal muscle into the fascia of the tail in the cow, stag, and horse finds an explanation if this view of the origin of the muscle be accepted. We know that the sphincter cloacæ is primarily attached to the under surface of the tail, and the caudal attachment is retained in ungulates, not only by the external sphincter ani, but also by the ischio-anal muscle.

The development of the ischio-anal muscle, and the peculiar course of its fibres, may possibly be explained by the behaviour of the rectum during defectation. The muscle is specially developed in those animals in which protrusion of the rectal mucous membrane occurs during the expulsion of the fæces, and the function of the muscle is clearly to pull the anus forwards, and retract the protruded mucous membrane after the rectal

contents have been expelled. Hence the name 'retractor ani' which has, not inappropriately, been applied to it. Professor Sir William Turner has described the retractores ani in the dolphin, and remarks that from "the presence of this pair of muscles it is probable that the dolphin, like the horse, protrudes the anal mucous membrane in the act of defecation, and the functions of these muscles is to retract it on completion of the act." Now, the attachments of the retractor ani in the dolphin closely resemble those of the ischio-anal or retractor ani in ungulates. In the former, the muscle arises from the pelvic bone, and ends in the muscular mass of the sphincter. Lartschneider regards the muscle in question in ungulates as a true levator ani, i.e., a sling muscle of the rectum, but with this I cannot agree.

Since, then, the ilio- and pubo-coccygei muscles are apparently not represented at all in ungulates, one may in conclusion ask, What has determined their absence? To this question I am not at present prepared to give any definite answer. It may be due to the skeletal peculiarities, to the size of the body, or to the mode of nutrition. We know that in the herbivora the capacity of the intestinal canal assumes considerable proportions, and that this is largely dependent on the nature of the aliment. food contains a small proportion of nutritive elements, enclosed in an abundant matrix, so that they are compelled to ingest large quantities at short intervals. As the gastric and intestinal parts of the alimentary canal have been so profoundly modified to meet these special demands, there seems no reason why the modifications should not have extended to the rectum and the muscles in relation with it, though it is difficult to see why suppression of certain of the caudal muscles should have resulted.

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