

# Article XV.—CROCODILIAN PELVIC MUSCLES AND THEIR AVIAN AND REPTILIAN HOMOLOGUES

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PLATES XIX TO XXV

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## INTRODUCTION

The pelvic musculature of the Crocodilia is of especial interest because of its bearing on the evolution of the "Archosauria." The structure of the pelvis is one of the most characteristic features of this great reptilian group, which includes the dinosaurian orders and the flying reptiles amongst others, and from which the birds are descended. Von Huene (1908) and Gregory and Camp (1918) have attempted to use the crocodilian musculature in the restoration of that of the dinosaurs. Their efforts have been hindered because of our inadequate knowledge of the anatomy of the pelvic region in these, the only living Archosauria.

Following Buttmann (1826), Stamnius (1854), Gorski (1854), Houghton (1865 and 1868), and Hair (1868), Gadow (1882) has given a description of the crocodilian pelvic musculature which has found wide acceptance. But, while it is accurate in its description, its value is lessened by the fact that it is inadequately illustrated, rendering it difficult of comprehension to those who are not familiar with the material, and more especially because of the fact that the muscles described are often obviously non-homologous with those in more typical reptiles to which the same names are applied.

The purpose of the present paper is to give a restudy of crocodilian pelvic musculature, with more adequate illustration and with a critical discussion of the homologies of the muscles concerned with those of typical reptiles (lizards and *Sphenodon*) and of birds. The system of reptilian muscle nomenclature used by the writer in a previous paper (1922) and founded mainly upon that of Gadow is followed.

From the fact that Gadow's homologies are disputed in many cases it might be inferred that I am attempting to question the value of Gadow's paper of 1882. Nothing, however, would be further from the truth, as should be obvious from the fact that in this and previous papers I have used Gadow's work as a foundation. But in attempting, as Gadow did, to homologize for the first time the pelvic muscles of all the Reptilia, it is only natural that a certain amount of error should have crept in.

In the discussion of innervations, the division into crural, obturator and sacral regions, previously adopted by the writer (1922) is followed.

The illustrations are from dissections of a young specimen of *Alligator mississippiensis*.

The antero-ventral bone of the girdle is called the pubis in this paper; its homologies are not discussed.

I wish to acknowledge my indebtedness in many ways to Dr. W. K. Gregory, at whose suggestion this work was undertaken. Dr. J. P. Chapin loaned the writer his sketches of a dissection of the pelvic region of the ostrich, which were very useful in the consideration of bird musculature. Dr. G. K. Noble, Curator of Herpetology, kindly furnished me with material for dissection.

#### DESCRIPTION OF CROCODILIAN PELVIC MUSCLES

##### DORSAL MUSCLE MASS: DORSALIS TRUNCI, DORSALIS CAUDÆ

The dorsal musculature, into the subdivisions of which it is unnecessary to enquire for our purposes, runs posteriorly above the lumbar transverse processes and then, after finding surfaces of insertion and origin on the dorsal surfaces of the sacral vertebræ and the inner dorsal portion of the ilium, continues posteriorly without interruption as the dorsalis caudæ between spines and transverse processes of the caudal vertebræ.

ANTERIOR VENTRAL MUSCULATURE (Plates XIX, XX, XXII).—The three lateral members of this series all take origin dorsally from the lumbo-dorsal fascia, which arises from the surface of the dorsal musculature and from the tips of the transverse processes of the lumbar vertebræ. Posteriorly, the fascia finds attachment to the anterior spine of the ilium. Below this, it passes over the surface of the "quadratus lumborum" (pubo-ischio-femoralis internus, *partim*), to which it is closely adherent, without the formation of a distinct ilio-pubic ligament; some of the fibers of the underlying muscle attach to the inner surface of the fascia.

### OBLIQUUS ABDOMINIS EXTERNUS

Obliquus descendens, Buttmann; obliquus externus abdominis, Gorski; obliquus externus, Stannius, Hair, and Maurer; and obliquus abdominis externus, Gadow.

The two portions of the muscle are not well separated in the lumbar region. The fibers arise from the lumbo-dorsal fascia and run postero-ventrally to insert (1) by a tendon which reaches the anterior edge of the acetabulum beneath the ambiens; (2) into the posterior dorsal end of the last abdominal rib, whence the origin is continued into a strong tendon which passes to the external edge of the pubis; (3) by an aponeurosis which lies over the main portion of the rectus but beneath the trunco-caudalis portion.

These relations correspond in general with the usual reptilian arrangement; the first-mentioned insertion appears to correspond with the usual insertion into the process lateralis pubis, the second with the insertion into the pubo-ischiadic ligament.

### OBLIQUUS ABDOMINIS INTERNUS

Obliquus internus, Buttmann, Stannius, and Hair; obliquus abdominis internus, Gadow; and intercostalis internus, abdominal part, Maurer.

The muscle arises dorsally from the fascia lumbo-dorsalis and runs ventro-anteriorly to insert into the posterior true ribs and the anterior abdominal ribs.

### TRANSVERSUS ABDOMINIS

Transversus abdominis, Buttmann and Gadow; transversalis, Hair; and transversus, Stannius and Maurer.

Arises from the deep surface of the lumbo-dorsal fascia and runs ventrally, inserting on the deep surface of the rectus.

### RECTUS ABDOMINIS

Rectus abdominis and pyramidalis, Buttmann, Stannius, Gorski, and Hair; and rectus abdominis, Gadow and Maurer.

The main portion of the rectus passes backwards as a strong muscular mass, with the abdominal ribs interrupting its external portion, while the internal portion is without interruption in the abdominal region. Both parts insert on to the last abdominal rib, none of the fibres attaching directly to the pelvis, such attachment being afforded only by the fact that this rib is attached to the pubis by membranous tissue ventrally and by a strong tendon laterally. Externally, the rectus is covered by the aponeurosis of the obliquus externus and by that special

portion of the muscle about to be described. Internally, it is in relation to the transversus.

In addition, there is a posterior portion of the rectus called *trunco-caudalis* by Maurer and considered by Gadow as a *rectus lateralis* and *ventralis*, *partim*. This arises in several layers from the surface of the principal portion of the rectus and the *obliquus externus*, from the posterior edge of the last abdominal rib, and from the anterior end of the membranous anterior continuation of the pubic surface. The deeper portion of these fibers inserts on to the posterior edge of the pubis, the more superficial portion passes on caudally over the ventral surface of *ischio-caudalis*, on to which it inserts.

As stated by Maurer, the *rectus internus* of Gadow is merely that portion of the *rectus* proper which is not interrupted by the abdominal ribs.

#### ILIO-ISCHIO-CAUDALIS

Plates XIX, XX, XXII, XXIII

No name, p. 13 (*partim*), Buttmann; *ischiococcygeus*, Stannius, and Gorski; *ilio-ischio-coccygeus*, Hair; and *ilio-ischio-caudalis*, Gadow.

This muscle occupies the ventral half of the tail on either side, between the transverse processes and the mid-line ventrally. Anteriorly, it is split by the *coccygeo-femoral* muscles into two portions, one attaching to the posterior edge of the ilium at the level of the transverse processes, and the other inserting at the postero-external angle of the ischium. Near the pelvis are fibers which run nearly at a right angle to the general course of the muscle (*transversus perinei*). Ventrally, these fibers form two bundles, one inserting into the sphincter cloacæ, the other inserting on to the ischium. The anterior border of these muscles corresponds in position to the lacertilian *ilio-ischiadic* ligament; one head of the *flexor tibialis internus* arises from it.

#### EXTENSOR FEMORIS

Plates XIX to XXII

##### (a.) Ilio-tibialis

*Rectus femoris*, *vastus externus* and *semi-membranosus*, Buttmann; "streck-muskelmasse," 1-2 heads + *flexores abductores* (*partim*), Stannius; *sartorius*, tensor *fasciæ-latæ* and *glutæus maximus* (*partim*), Gorski; *gluteus maximus*, tensor *fasciæ femoris* and *biceps* (*partim*), Hair; *sartorius* (in *Alligator*) or *gluteus minimus* (in *Crocodilus*), *gluteus maximus*, and *agitator caudæ*, Haughton; and *extensor ilio-tibialis* (two parts) and *biceps* (*partim*), Gadow.

The long iliac portion of the main extensor mass of the thigh. It arises by three heads, all tendinous, from the dorsal edge of the iliac

blade. The smallest head arises from the region near the anterior spine and, passing underneath the smaller portion of the ambiens, ends on the surface of the femoro-tibialis. The next posterior, the largest of the three, has a line of origin from a large part of the dorsal edge of the iliac blade, and blends with the tendon of the femoro-tibialis near the knee. The third and most posterior head arises behind and dorsal to the ilio-fibularis (in the sense used here) and proximal to the knee joins the common extensor tendon but also sends a tendon distally and externally to join that of the ambiens.

Gadow, following earlier writers, homologizes the third head with a portion of the ilio-fibularis (biceps). But it arises external (dorsal) to the true biceps muscle, almost in continuity with the main portion of ilio-tibialis and its insertion is definitely a part of that of the extensor mass. It seems obviously merely a portion of the ilio-tibialis, which has become separated from that muscle, as has the small anterior slip.

The muscle has a double (crural and sacral) innervation, the line of division passing through the middle head.

#### (b.) Ambiens

Vastus internus and gracilis, Buttmann; "streckmuskelmasse," 3+4 heads, Stannius; "oberflächliche strecher" and rectus femoris, Gorski; rectus femoris and sartorius, Hair; rectus femoris and tensor vaginæ femoris (*Alligator*) or sartorius (*Crocodilus*), Haughton; and ambiens, Gadow.

This muscle consists of two quite distinct elements. The larger head arises at the junction, anteriorly, of the ilium and the pre-acetabular ramus of the ischium or the cartilage which precedes it. Near the knee, besides joining in part with the common extensor tendon, it forms a remarkable rounded tendon which passes through the extensor tendon, across the knee, to the external surface of the leg, where it joins the external head of the gastrocnemius. The small head arises from the base of the pubis and, passing laterally, unites with the ilio-tibialis just beyond the middle of the thigh.

#### (c.) Femoro-tibialis

Cruralis, Buttmann; cruræus and vasti, Stannius, Hair, and Haughton; cruralis and vasti, Gorski; and femoro-tibialis, Gadow.

This arises fleshily from the greater part of the shaft of the femur and inserts, together with the ilio-tibialis, into a tendon which reaches the head of the tibia. The internal head has much the same relations as the femoro-tibialis of lizards and *Sphenodon*, being bounded by the adductors antero-ventrally, the ilio-femoralis posteriorly (externally) and the

pubo-ischio femoralis internus proximally. In the Crocodilia, however, an additional external head is found, which passes between the ilio-femoralis and the adductors on the posterior (external) aspect of the bone.

#### ILIO-FIBULARIS

Semitendinous, Buttmann; flexores abductores (*partim*), Stannius; glutæus maximus (*partim*, *p*) Gorski; biceps (*partim*), Haughton; biceps, Hair; and ilio-fibularis (*partim*), Gadow.

This muscle arises from the external surface of the ilium, slightly ventral to the ilio-tibialis and appearing at its origin between the main and posterior heads of that muscle. It inserts into the head of the fibula and is connected with the external head of the gastrocnemius as well.

Previous writers also homologize the posterior head of ilio-tibialis with this muscle. This question has been discussed above.

#### PUBO-ISCHIO-FEMORALIS INTERNUS

##### Plates XIX to XXII

Psoas major and iliacus internus, Buttmann and Gorski; abductor femoris + iliacus internus, Stannius; psoas magnus and iliacus, Haughton; adductor femoris (psoas) and iliacus, Hair; and quadratus lumborum and pubo-ischio-femoralis internus, part III, Gadow.

This muscle is in two parts. One (Gadow's "quadratus lumborum") arises from the bodies and under surfaces of the transverse processes of the six lumbar vertebræ and passes backward to insert by a broad tendon on the dorsal surface of the proximal portion of the femur; the tendon is partially interrupted by the proximal part of the area of origin of the femoro-tibialis internus. The second and more ventral part arises from the internal surface of the ilium and ischium dorsally and the ventral portions of the sacral ribs, and runs out anteriorly beneath the preceding part to insert fleshily on to the femur antero-ventrally to the area of insertion of the more dorsal portion. The innervation of both parts is crural.

Gadow homologizes the dorsal portion, apparently because of its lumbar origin, with the quadratus lumborum, an axial muscle. Its insertion is proximal to that of the femoro-tibialis on the dorsal surface of the femur and corresponds to that of one of the two portions of the more typical pubo-ischio-femoralis internus (Romer, 1923). It appears to be that muscle mass, the origin of which has moved dorsally and anteriorly in correlation with the changed type of locomotion found in the Archosauria.

The remaining portion of the pubo-ischio-femoralis internus, as defined in this paper, is Gadow's part III. His parts I and II are considered under pubo-ischio-femoralis externus.

The insertion of the ventral portion of the pubo-ischio-femoralis internus is that of the more anterior part of the pubo-ischio-femoralis internus of lizards and *Sphenodon*, that is, antero-ventral to femoro-tibialis, antero-dorsal and proximal to the adductor(s), dorsal to the coccygeo-femorales, and antero-distal to the insertion of the other portion of the same muscle. The shifting posteriorly of the insertion of pubo-ischio-femoralis externus on the ventral surface gives the only difference in the relations of the insertion.

### ILIO-FEMORALIS

#### Plates XIX to XXII

Quadratus femoris, Buttman; glutæus medius, Gorski, Houghton, and Hair; glutæus, Stannius; obturateur externe, chef iliaque, Sabatier; and caudi-ilio-femoralis, Gadow.

The ilio-femoralis arises from a large expanse of the ilium above and behind the acetabulum, beneath the ilio-tibialis and anterior to the coccygeo-femoralis brevis and ilio-fibularis. It inserts on to the external (posterior) edge of the femur, between internal and external heads of the femoro-tibialis for the greater part of the length of the shaft. Its innervation is characteristically double, crural and sacral.

It is closely comparable with the typical reptilian ilio-femoralis, differing only in the fact that the presence of the external head of femoro-tibialis in the Crocodilia has changed its posterior relations at its insertion. Gadow calls it "caudi-ilio-femoralis" (coccygeo-femoralis brevis); but it is quite distinct from that muscle, which Gadow includes under coccygo-femoralis longus ("caudi-femoralis").

### ISCHIO-TROCHANTERICUS

#### Plates XX to XXII

Pectinæ inferiores (*partim*), Buttman; gemellus, Stannius and Hair; *h*, part of "auswärtsroller des Oberschenkels," Gorski; and obturator externus (*Alligator*) or quadratus femoris (*Crocodilus*), Houghton; and pubo-ischio-femoralis posterior (*partim*), Gadow.

A small muscle arising from the posterior portion of the inner surface of the ischium and running up and out to insert tendinously at the outer dorsal edge of the femur near the head. An ischiatic innervation. It is comparable to the typical reptilian muscle. Gadow homologizes it correctly but includes with it the posterior adductor, which arises from the outer surface of the ischium in the same region.

LONG FLEXORS TO LOWER LEG: PUBO-ISCHIO-TIBIALIS, FLEXOR  
TIBIALIS INTERNUS, FLEXOR TIBIALIS EXTERNUS

Plates XIX, XXII, XXIII

Triceps flexor cruris and sartorius, Buttmann; "flexores des unterschenkels" (two groups), Stannius; gracilis, semimembranosus, semitendinosus, Gorski and Hair; gracilis, semimembranosus, third or long adductor, extensor femoris caudali accessorius (Crocodile) or Nos. 18 and 22 (Alligator), Haughton; and flexor tibialis internus, flexor tibialis externus, Gadow.

This group, in the alligator, consists of six muscles which unite at their insertion into two groups of three each. We shall consider these groups in turn and then discuss their homologies.

EXTERNAL GROUP.—This has three heads as follows.

(1.) A slip arising from the anterior edge of the main blade of the ischium just below the acetabulum. It passes laterally anterior to pubo-ischio-femoralis externus III but posterior to adductor I and joins the other two components proximal to the knee.

(2.) A small slip which arises from the external ventral posterior portion of the ischiadic blade, near the insertion of ischio-caudalis, and unites with the third part half-way to knee.

(3.) A large belly from the posterior angle of the iliac blade just ventral to the flexor tibialis externus. It passes out and ventrally unites with 2 and then with 1. The common tendon passes to the internal side of the knee to insert into the tibia internal to all the lower leg flexors. The first two are innervated by the obturator nerve, the third is innervated by the ischiadic plexus.

These three muscles are all considered by Gadow as constituting part of the flexor tibialis internus (Theil I, 1, 2, and 3). But if we compare with the lacertilian condition, we find there an outer group of flexors, usually arising in three parts and inserting close together on the internal (anterior) side of the tibia, medial to all the flexor mass of the lower leg (the third member of the group tends to insert more proximally) (Romer, 1922, p. 570). These muscles include the pubo-ischio-tibialis and two portions of the flexor tibialis internus. The two portions of the flexor tibialis internus associated with this group arise from the posterior portion of the ischium near the tubercle and from the ligamentum ilio-ischiadicum. This agrees well with the two more posterior portions of the crocodilian triad, except that the third member of the latter (Gadow's I, 3) arises from the ilium at the upper end of the ligament instead of the ligament itself. But the anterior part, instead of arising as does the pubo-ischio-tibialis of the lizard from the whole ventral expanse of the girdle, is confined, in the Crocodilia, to a narrow area at the anterior edge



of the ischium. This muscle (Gadow's I, 1) is then in all probability the pubo-ischio-tibialis, which, owing to the great change in the pubo-ischiadic plate, has had its area of origin greatly diminished.

Gadow, although finally deciding that the pubo-ischio-tibialis was not represented in the Crocodilia, suggests in a footnote (p. 404) that two parts of his "Theil I, 1 and 2" might be homologized with pubo-ischio-tibialis. The innervations do not stand in the way of the suggested homologies; both pubo-ischio-tibialis and flexor tibialis internus in the Lacertilia have a double (obturator and ischiadic) innervation.

We may reasonably conclude then that the superficial medially inserting triad of flexors in the Crocodilia is composed of a reduced pubo-ischio-tibialis and two heads of flexor tibialis internus.

INTERNAL GROUP.—This likewise consists of three muscles, Gadow's flexor tibialis internus II and III and his flexor tibialis externus. As Gadow has shown (1882, fig. 50), they have a common insertion by a double tendon, of which one part reaches the tibia between the two heads of the gastrocnemius and the other runs along the external head of that muscle, with which it unites near the foot.

The most ventral and anterior of the three heads (Gadow's flexor tibialis internus III) arises from the posterior margin of the ischium behind the posterior portion of the adductor and proximal to the area of origin of that muscle. The next (Gadow's flexor tibialis internus II) arises from the fascia at the anterior edge of the ilio-ischio-caudalis from the position of the lacertilian ilio-ischiadic ligament. The third, a large head (flexor tibialis externus) arises tendinously from the posterior end of the dorsal edge of the iliac blade, just above the iliac head of flexor tibialis internus.

The iliac portion is certainly the lacertilian flexor tibialis externus, the latter, however, usually arising a bit more ventrally from the ilio-ischiadic ligament. The two remaining heads may be homologized, although perhaps not exactly, with the usual single belly of flexor tibialis internus associated with the deep flexors in lizards and *Sphenodon*. The lacertilian head arises from the ilio-ischiadic ligament in the position of one of the two heads under consideration; the other crocodilian head arises from the ischium, ventral to the position of the usual lacertilian head.

The innervations of this group are sacral in character. This and the fact that all the origins are posteriorly placed, precludes any attempt to homologize one of these heads with the lizard or *Sphenodon* pubo-tibialis, which has an anterior origin and apparently an obturator innervation.

The pubo-tibialis, which forms one of the deep triad in more typical reptiles, has been lost in the Crocodilia.

The chief differences between the long flexors of the lizards and the Crocodilia are that in the latter the pubo-tibialis has been lost, the pubo-ischio-tibialis reduced, and with the loss of the ilio-ischiadic ligament the flexors originating from it have removed their origins to the adjacent bones (except for one small slip).

#### ADDUCTOR FEMORIS

Plates XIX, XXII, XXIII

Adductores, Buttmann; adductores, primus + secundus, Stannius and Hair; adductores, longus + magnus, Gorski; adductores, brevis + magnus (Alligator), first + second (Crocodile), Haughton; and ischio-femoralis + pubo-ischio-femoralis posterior (*partim*), Gadow.

This consists of two parts, both arising from the outer side of the ischium but separated by part III of pubo-ischio-femoralis externus. The two converge to a long and narrow area of insertion on the ventral side of the femur, comparable to that of typical reptiles, except that the presence of an external head of femoro-tibialis separates it from the ilio-femoralis. The double (obturator and sacral) innervation of the lacertilian muscle is repeated in the more posterior of the two heads.

Gadow correctly homologizes the anterior head with the "ischio-femoralis" (adductor) of other reptiles, but he includes the posterior head with the ischio-trochantericus, calling the two muscles pubo-ischio-femoralis posterior.

The division into two parts and the fleshy origins are in marked contrast to the usual reptilian condition.

#### PUBO-ISCHIO-FEMORALIS EXTERNUS

Plates XIX, XXIII

Pectinei superiores et inferiores (*partim*), Buttmann; obturator internus + obturator externus + quadratus femoris, Stannius and Hair; pectinei + adductor brevis, Gorski; pectineus + marsupiales, Haughton; obturateur externe, chef pubien + chef ischiatique + pectiné ou pubien interne, Sabatier; and pubo-ischio-femoralis externus + pubo-ischio-femoralis internus, I + II, Gadow.

This consists of three main portions arising (1) from the dorsal (internal) surface of the pubis and the adjacent edge of the last abdominal rib; (2) from the external (ventral) surface of the pubis and the membrane between it and the last abdominal rib; (3) from the outer surface of the ischium between the two heads of the adductor femoris. With the first two are associated shorter and smaller heads arising beneath them

from the proximal portion of either surface of the pubis. With the third is associated a small head separated from it at its origin by the anterior head of the adductor femoris and the pubo-ischio-tibialis.

All these portions unite in a tendinous insertion at the posterior ventral edge of the femur close to the head.

This disposition is in marked contrast to the pubo-ischio-femoralis externus of lizards and *Sphenodon*. Part I, as here described, arises from the dorsal or internal surface of the pubis; and consequently Gadow homologizes it with part of pubo-ischio-femoralis internus, although its obturator innervation and its insertion show that this is impossible. Further, the usual origin of the muscle from the outer surface is in one solid mass, as contrasted with two widely separated surfaces in the Crocodilia.

#### COCYGEO-FEMORALIS BREVIS

##### Plates XIX, XXIII

Obturator-internus, Buttmann; pyriformis, Stannius; "auswärtsroller des Oberschenkels" (*partim*), Gorski; quadratus femoris (Alligator), obturator externus (Crocodile), Haughton; pyriformis + glutæus minimus, Hair; and caudi-femoralis (*partim*), Gadow.

This muscle arises from the last sacral and first caudal vertebræ and passes outward beneath the posterior end of the ilium. Here it receives another slip from the posterior edge of that bone and then inserts on to the femur dorsal to the insertion of the coccygeo-femoralis longus.

Gadow calls this muscle caudi-ilio-femoralis in other reptiles but applies this name to the ilio-femoralis of the Crocodilia, where the coccygeo-femoralis brevis is considered as part of the following muscle.

#### COCYGEO-FEMORALIS LONGUS

Pyriformis, Buttmann; subcaudalis, Stannius; "femoro-péroneo-coccygien Cuv.," Gorski; extensor femoris caudalis, Haughton; femoro-perineo-coccygius, Hair; and caudi-femoralis (*partim*), Gadow.

This arises from the bodies and lower sides of the transverse processes of the caudal vertebræ, approximately the third to the fifteenth. It runs forward, constantly increasing in size and covered by the ilio-ischio-caudalis, to end in a thick tendon which inserts into the "fourth trochanter" of the femur. From the side of this tendon another extends, deeply placed at right angle to the knee region, where it inserts ventrally into the fibula. This is similar to the lacertilian muscle.

As noted above, Gadow includes coccygeo-femoralis brevis with this muscle.

TABLE OF SYNONYMY  
Gadow (1882) and The Present Paper

GADOW, 1882	ROMER, 1923
Axial Muscles	
“Rückenmuskeln”	Dorsalis trunci, Dorsalis caudæ
Obliquus abdominis externus	Obliquus abdominis externus
Obliquus abdominis internus	Obliquus abdominis internus
Transversus abdominis	Transversus abdominis
Rectus abdominis	Rectus abdominis
Ilio-ischio-caudalis	Ilio-ischio-caudalis
Dorsal Group	
Extensor ilio-tibialis, Part II	Ilio-tibialis, Part I
Extensor ilio-tibialis, Part I	Ilio-tibialis, Part II
Ilio-fibularis, Part II	Ilio-tibialis, Part III
Ambiens, Part I	Ambiens, Part I
Ambiens, Part II	Ambiens, Part II
Femoro-tibialis, inner head	Femoro-tibialis internus
Femoro-tibialis, outer head	Femoro-tibialis externus
Ilio fibularis, Part I	Ilio-fibularis
Pubo-ischio-femoralis internus, Part III	Pubo-ischio-femoralis internus, Part I
Quadratus lumborum	Pubo-ischio-femoralis internus, Part II
Caudi-ilio-femoralis	Ilio-femoralis
Pubo-ischio-femoralis posterior ( <i>partim</i> )	Ischio-trochantericus
Ventral Group	
Flexor tibialis internus I, 1	Pubo-ischio-tibialis
Flexor tibialis internus I, 2	Flexor tibialis internus Part I
Flexor tibialis internus I, 3	Flexor tibialis internus Part II
Flexor tibialis internus, III	Flexor tibialis internus Part III
Flexor tibialis internus, II	Flexor tibialis internus Part IV
Flexor tibialis externus	Flexor tibialis externus
Pubo-ischio-femoralis	Adductor femoris, Part I
Pubo-ischio-femoralis posterior ( <i>partim</i> )	Adductor femoris, Part II
Pubo-ischio-femoralis internus, Parts I and II	Pubo-ischio-femoralis externus, Part I
Pubo-ischio-femoralis externus, Part I	Pubo-ischio-femoralis externus, Part II
Pubo-ischio-femoralis externus, Part II	Pubo-ischio-femoralis externus, Part III
Coccygeo-femoral Muscles	
Caudi-femoralis, Part I	Coccygeo-femoralis longus
Caudi-femoralis, Part II	Coccygeo-femoralis brevis

## COMPARISON OF AVIAN AND REPTILIAN PELVIC MUSCLES

Following the name of each reptilian muscle its probable avian homologues are discussed. For the purposes of this paper the nomenclature of Gadow and Selenka in Bronn's 'Thierreich' (1891) has been adopted for bird muscles and the reader is referred to that volume for detailed descriptions and for illustrations.

## AXIAL MUSCLES

The dorsal (spinal) muscle mass is completely interrupted by the sacrum, as contrasted with the reptilian condition. This has separated off the caudal portion as the levator coccygeus, connecting the posterior end of the ilium with the remaining caudal vertebræ.

The abdominal muscles are the same, although the modifications in the pelvic girdle have necessarily modified their attachments. The obliquus externus inserts on to the whole anterior edge of the pubis. The origin of the obliquus internus usually is from the preacetabular portion of the ilium, then bridging over the gap below, to the middle portion of the anterior edge of the pubis. The origin of the transversus likewise bridges over the gap between the preacetabular portion of the ilium and the anterior edge of the pubis. The rectus inserts on to the distal halves of the pubes. The differences in the pelvic relations are clearly associated with the forward growth of the ilium and the backward turning of the pubis. It will be noted that the iliac attachments are ventral to the whole group of anterior muscles running from the ilium to the femur. The reptilian obliqui and transversus form a bridge posteriorly over the region of exit of pubo-ischio-femoralis internus from the internal aspect of the girdle. Since this muscle now arises from the ilium, the need for such an interruption in the attachments of the lateral muscles has been done away with.

The ilio-coccygeus from the ilium to the tail and the depressor caudæ from the last sacral vertebra along the ventral side of the transverse processes of the tail vertebræ, represent a reduced ilio-caudalis. The pubo-coccygei represent the ischio-caudalis. The more internal of the two, from its position between the obturator and the transversus, appears to represent the deep portion of the ventral caudal musculature, which is generally reduced in the Reptilia. The transverso-analis represents the transversus perineus of reptiles in a somewhat variable fashion.

## TRICEPS

We may consider in order (a) ilio-tibialis, (b) ambiens, and (c) femoro-tibialis.

**ILIO-TIBIALIS.**—As homologues of this muscle may be considered the ilio-tibialis internus s. “sartorius” and ilio-tibialis, the latter usually divided into anterior, median and posterior parts. They are dorsal in origin and gain insertion into the tibia either directly or through the intervention of the patella or the patellar ligament, with the femoro-tibialis. The “sartorius” and anterior portion of the ilio-tibialis proper are innervated from the crural plexus, the posterior portion from the sacral plexus. This double innervation is similar to that of reptiles. The ilio-tibialis is often two-headed in the lizards; the triple ilio-tibialis of the Crocodilia is, however, closer to the bird condition. That the “sartorius” is essentially part of this group is indicated by the fact that it is often more or less fused with the ilio-tibialis anterior. The origins are similar in character to the reptilian, in general from the dorsal border of the ilium, mostly tendinously posteriorly, and more fleshily in the case of the “sartorius.”

The “sartorius” is not, of course, the mammalian muscle of that name (which is the sauropsid ambiens) nor can it equal the reptilian pubo-tibialis, which is a ventral muscle (Romer, 1922, p. 563).

**AMBIENS.**—This muscle, running from the region of the pubic spine and terminating in a tendon which crosses the knee joint to the outer side to end in relation with the lower leg musculature, is indisputably the muscle of the same name in reptiles and resembles strikingly the main portion of the alligator ambiens. It leaves the girdle ventral to the pubo-ischio-femoralis internus as in reptiles. There is, in general, no representative of the smaller portion of the crocodilian ambiens. In many higher birds the muscle is lost or seen reduced, and showing a probable secondary return to the original condition in a closer union with the main elements of the ilio-tibialis.

**FEMORO-TIBIALIS.**—The femoro-tibialis is in two main portions, which seem to be essentially similar to the internal and external portions of the same muscle in Crocodilia. But because the ilio-femoralis is restricted to the proximal part of the femur, the division into two portions is not so clear; further, the great growth of the muscle, with a subdivision into numerous heads and a tendency to push the area of insertion towards the acetabulum wherever possible, makes the homologies of the smaller subdivisions difficult and unprofitable.

#### ILIO-FIBULARIS

It arises from the dorsal edge of the postacetabular ilium, usually covered by the ilio-tibialis, and running through a peculiar “tendon sling” attached to the femur and the external head of the gastrocnemius, inserts

on to the fibula. The area of origin postero-dorsally and its position slightly deeper than the ilio-tibialis are reminiscent of the Reptilia. The insertion internal to a portion of the gastrocnemius is in contrast to the usual reptilian condition; but in the Crocodilia it is in intimate relation with the outer (femoral) head of the gastrocnemius; out of this connection may have arisen its changed insertion and the new tendon arrangement, which is connected with the external head of the gastrocnemius. Gadow notes that in *Struthio* the ilio-fibularis has a tendinous connection with gastrocnemius.

#### PUBO-ISCHIO-FEMORALIS INTERNUS

We have noted that in the Crocodilia this muscle is entirely antero-dorsal in origin as contrasted with the primitive reptilian condition. I purpose to homologize with this muscle the bird muscles with an origin in a similar region; although this region, instead of being a bare expanse along the lumbar vertebræ, is now covered by an anterior extension of the ilium (Romer, 1923). These muscles include the ilio-trochanterici and ilio-femoralis internus. The insertion of these muscles is in general divisible into two regions, one more postero-dorsal, comparable to the "quadratus lumborum" insertion, and another more anterior and ventral, corresponding to the "p. i. f. i. Part III" insertion.

Gadow (1880) at first reached the same conclusion, but later (1891) modified his views, stating that of this group only the ilio-femoralis internus belonged to the pubo-ischio-femoralis internus (quadratus lumborum) and that the ilio-trochanterici are derived from the ilio-femoralis (together with the ilio-femoralis externus). The only reason advanced for this conclusion is that in a few cases the ilio-trochanterici have a slight innervation from the sacral plexus, which is not typically the case with pubo-ischio-femoralis internus; a double innervation from both crural and sacral plexes is typical of the ilio-femoralis. But, as he notes, this innervation is infrequent and of slight extent; the division between the two plexi is often through the ilio-femoralis externus, giving that muscle in itself the characteristics of the reptilian ilio-femoralis. Further, it seems probable that ilio-femoralis and pubo-ischio-femoralis internus are differentiations from a primitively single muscle mass (Romer, 1922, p. 565), with a double innervation; it is not improbable that in the ancestors of the birds the separation between the two muscles corresponded very nearly to the division between the two plexes, and that slight variations would cause the sacral innervation to cross the division into the pubo-ischio-femoralis internus or the contrary (as in most reptiles).

## ILIO-FEMORALIS

It is agreed that the avian ilio-femoralis externus is derived from the reptilian ilio-femoralis and, if the above reasoning holds, it is the only muscle so derived. It has an innervation which is often purely sacral but sometimes crural as well, the latter more closely resembling the typical reptilian condition. It runs rather straight out from the ilium to the postero-external region of the femur, contrasting with the more antero-posterior course of the ilio-trochanterici. But its insertion does not extend so far down the femur and hence it does not differentiate internal and external heads of the femoro-tibialis so markedly as its reptilian predecessor. It is smaller than the reptilian muscle but like it arises from a surface above the acetabulum, covered by the ilio-tibialis.

## ISCHIO-TROCHANTERICUS

There seems no doubt that this muscle has given rise to the ischio-femoralis of the birds. This is a deep muscle, inserting, as in reptiles, near the head of the femur and arising posteriorly in the region of the ischium. In Reptilia the origin is from the inner surface of the ischium but the great change this bone has undergone in the evolution of the birds has caused its origin to be from the outer surface and often on to the membrane covering the area between ischium and pubis.

## LONG FLEXORS: PUBO-TIBIALIS, PUBO-ISCHIO-TIBIALIS, FLEXOR TIBIALIS INTERNUS, AND FLEXOR TIBIALIS EXTERNUS

There has been great reduction in this group; there are usually but two muscles which can be assigned to it, as contrasted with the half-dozen or so common among reptiles.

The more posterior and dorsal of the two is the caud-ilio-flexorius, which arises from the dorsal edge of the posterior portion of the ilium and from the anterior caudal vertebræ, and inserts (1) by an accessory muscle into the distal part of the shaft of the femur; (2) into the tibia and internal head of the gastrocnemius. Gadow seems correct in homologizing this with the flexor tibialis externus of reptiles; there are, however, points of difference. An iliac origin for this muscle is found in the Crocodilia at least, and through the ilio-ischiadic ligament in many lizards; the caudal extension of the origin is probably secondary, although *Sphenodon* furnishes a parallel.

The insertion into tibia and gastrocnemius is typically reptilian. The "accessory" muscle, which binds it to the femur, is very peculiar. Gadow suggests that this is a partial retention of a primitive insertion



running the whole way from trochanters to tibia; but there is no indication of such a muscle in any reptile. It seems more probable that, as certain of his figures suggest, the muscle is a slip separated from the gastrocnemius (Gadow, 1891, Plate XIII b, figs. 2, 5, 6). It would thus be, as Gadow admits it appears to be, an origin rather than an insertion.

The other avian member of this group is the ischio-flexorius. This arises usually from the ischium and sometimes to a slight extent from the pubis, and inserts into the tibia between the heads of the gastrocnemius.

Gadow seems correct in homologizing it with some portion of the flexor tibialis internus. It has an ischiadic innervation, which makes a homology with the pubo-tibialis or anterior part of pubo-ischio-tibialis impossible. Its area of insertion is in contrast with pubo-ischio-tibialis and the more external portions of flexor tibialis internus and in agreement with the deeper portion or portions of the latter muscle. This is strengthened by its frequent association with the caud-ilio-flexorius and gastrocnemius, paralleling the association of the deep part of flexor tibialis internus with flexor tibialis externus and gastrocnemius in reptiles. Its closest homologue in reptiles would be some such slip as the third portion of flexor tibialis internus in the Crocodilia.

#### ADDUCTOR FEMORIS

This is represented by the pubo-ischio-femoralis. This arises from the pubo-ischium by two heads, which insert close to one another on a line extending most of the length of the femur to the internal condyles.

The Crocodilia have also two parallel heads, although the more antero-ventral one does not, as in birds, extend on to the pubis as well as the ischium. The avian muscles have an obturator innervation; the obturator innervates the anterior and part of the posterior adductor of the Crocodilia.

Gadow would homologize this muscle with part of pubo-ischio-femoralis externus; but the insertion is in marked contrast with that of the reptilian muscle mentioned, and in perfect agreement with that of the adductor.

#### PUBO-ISCHIO-FEMORALIS EXTERNUS

The obturator and accessory obturator muscles represent this muscle, in part at least, in birds, as Gadow states. Their proximal insertion and obturator innervation agree with this. Apparently in correlation with the backwardly directed position of the pubis, the muscle is no

TABLE OF MUSCULAR HOMOLOGIES BETWEEN TYPICAL REPTILES,  
CROCODYLIANS, AND BIRDS

TYPICAL REPTILES	CROCODYLIA	BIRDS
Dorsalis trunci including longissimus dorsi, ilio-costalis, dorsalis caudæ	The Same	Dorso-spinal muscles, including longissimus dorsi, ilio-costalis, levator coccygeus.
Obliquus abdominis externus	Obliquus abdominis externus	Obliquus abdominis externus
Obliquus abdominis internus	Obliquus abdominis internus	Obliquus abdominis internus
Transversus abdominis	Transversus abdominis	Transversus abdominis
Rectus abdominis	Rectus abdominis	Rectus abdominis
Ilio-caudalis	Ilio-caudalis	Ilio-coccygeus and depressor coccygeus
+	+	+
Ischio-caudalis	Ischio-caudalis	Pubi-coccygeus
Ilio-tibialis (one or two parts), <i>crur + sac</i>	Ilio-tibialis I, <i>crur</i>  Ilio-tibialis II, <i>crur + sac</i> Ilio tibialis III, <i>sac</i>	Ilio-tibialis internus ("sartorius," <i>crur</i> ) Ilio-tibialis (often 3 heads), <i>crur + sac</i>
Ambiens, <i>crur</i> .	Ambiens I, <i>crur</i> Ambiens II, <i>crur</i>	Ambiens, <i>crur</i>
Femoro-tibialis, <i>crur</i>	Femoro-tibialis internus, <i>crur</i> Femoro-tibialis externus, <i>crur</i>	Femoro-tibialis (several divisions), <i>crur</i>
Ilio-fibularis, <i>sac</i>	Ilio-fibularis, <i>sac</i>	Ilio-fibularis, <i>sac</i>
Pubo-ischio-femoralis internus, <i>crur</i>	Pubo-ischio-femoralis internus I, <i>crur</i> Pubo-ischio-femoralis internus II, <i>crur</i>	Ilio-trochanterici + Ilio-femoralis internus, <i>crur (+ sac)</i>
Ilio-femoralis, <i>crur + sac</i>	Ilio-femoralis, <i>crur + sac</i>	Ilio-femoralis externus, <i>sac (+ crur)</i>
Ischio-trochantericus, <i>sac</i>	Ischio-trochantericus, <i>sac</i>	Ischio-femoralis, <i>sac</i>
Pubo-tibialis, <i>obt</i>	.....	.....
Pubo-ischio-tibialis, <i>obt + sac</i>	Pubo-ischio-tibialis (reduced), <i>obt</i>	.....
Flexor tibialis internus, <i>obt + sac</i>	Flexor tibialis internus (4 parts), <i>obt + sac</i>	Ischio-flexorius (deep), <i>sac</i>
Flexor tibialis externus, <i>sac</i>	Flexor tibialis externus, <i>sac</i>	Caud-ilio-flexorius, <i>sac</i>
Adductor femoris, <i>obt + sac</i>	Adductor femoris (2 parts), <i>obt + sac</i>	Pubo-ischio-femoralis (2 parts), <i>obt</i>
Pubo-ischio-femoralis externus, <i>obt + sac</i>	Pubo-ischio-femoralis externus (3 main parts), <i>obt</i>	Obturator + accessory obturators, <i>obt</i>
Coccygeo-femoralis longus +	Coccygeo-femoralis longus +	Caud-ilio-femoralis
Coccygeo-femoralis brevis	Coccygeo-femoralis brevis	

longer found on the outer surface of the pubis and ischium, but on the inner surface, where the apposition of the two bones has imprisoned it. Near the proximal foramen, where it escapes to the exterior, are found variable small accessory muscles.

#### COCYGEO-FEMORALIS

Caud-ilio-femoralis in birds. Its areas of origin are exceedingly variable but generally include one from the tail vertebræ and one from the ilium below the ilio-fibularis. The former is the primitive area of origin of the two reptilian muscles; in the Crocodylia the coccygeo-femoralis brevis has a slight area of origin from the external surface of the ilium, of which the bird iliac origin seems an expansion. The femoral insertion is not such a definite one as is usual in reptiles, nor is there the typical reptilian tendon from the longer of the muscles to the knee region; possibly the association of the muscle with the "accessory semi-tendinosus" of *Rhea* and *Dromæus* may be reminiscent of this.

#### DISTINCTIVE FEATURES OF ARCHOSAURIAN PELVIC MUSCULATURE

From the features which the Crocodylia and birds possess in common, in contrast to the more typical Reptilia, we may deduce a number of features which were probably possessed by the common archosaurian stock.

1.—There was a general tendency for a fragmentation of muscles, both living groups possessing at least half a dozen additional heads not separated out in typical reptiles. This is apparently associated with a greater diversity of limb movements.

2.—The ilio-tibialis, primitively in one, or at the most two, heads, split into three in the Crocodylia and usually into four in birds.

3.—The ambiens tendon crossing the knee was developed.

4.—The femoro-tibialis acquired an additional external head.

5.—The pubo-ischio-femoralis internus moved dorsally at its origin.

6.—The long flexors tended to become concentrated posteriorly, with the reduction (Crocodylia) or loss (birds) of pubo-ischio-tibialis, and the loss in both of pubo-tibialis.

7.—The adductor femoris divided into two portions.

8.—The caudi-femoralis brevis acquired an iliac head.

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## TABLE OF ABBREVIATIONS

## Plates XIX to XXV

ad. 1, 2	adductor femoris, parts 1 and 2
amb. 1, 2	ambiens, parts 1 and 2
c. f. b.	coccygeo-femoralis brevis
c. f. l	" " longus
fem. tib. ext.	femoro-tibialis externus
fem. tib. int.	" " internus
fl. tb. ext.	flexor tibialis externus
fl. tb. int. 1, 2, 3, 4	" " internus, parts 1-4
il. fem.	ilio-femoralis
il. fib.	ilio-fibularis
il. is. c.	ilio-ischio-caudalis
il. tib. 1, 2, 3	ilio-tibialis, parts 1-3
is. tr.	ischio-trochantericus
o. a. e.	obliquus abdominis externus
o. a. i.	" " internus
p. i. f. e 1, 2, 3	pubo-ischio-femoralis externus parts 1-3
p. i. f. i 1, 2	pubo-ischio-femoralis internus parts 1, 2
p. i. t.	pubo-ischio-tibialis
r. abd.	rectus abdominis
tr. abd.	transversus abdominis
tr. per.	transversus perinei

**PLATES XIX to XXV**

**PLATE XIX**

**Fig. 1.** Lateral view of pelvic region; the limb is shown as if cut half-way down the femur. (All views are of the right side.)

**Fig. 2.** The same, with a portion of the superficial musculature removed.

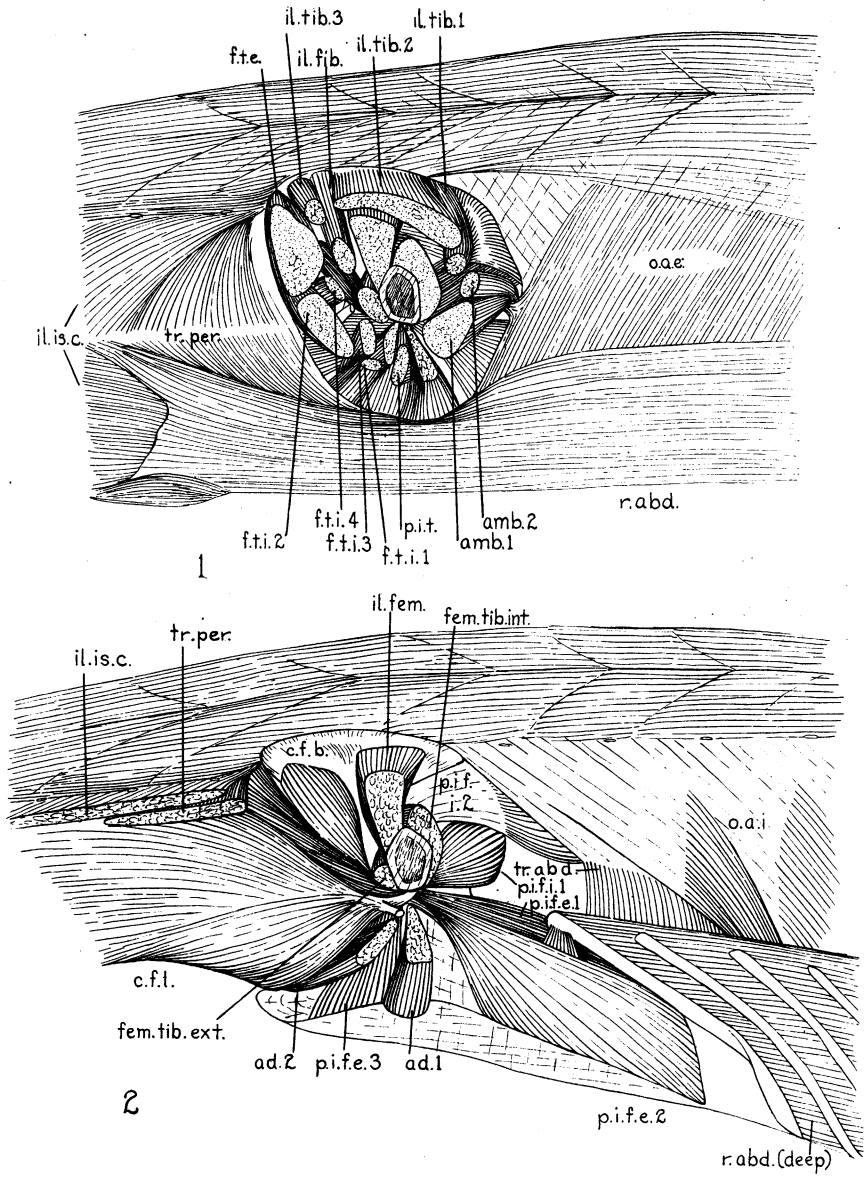
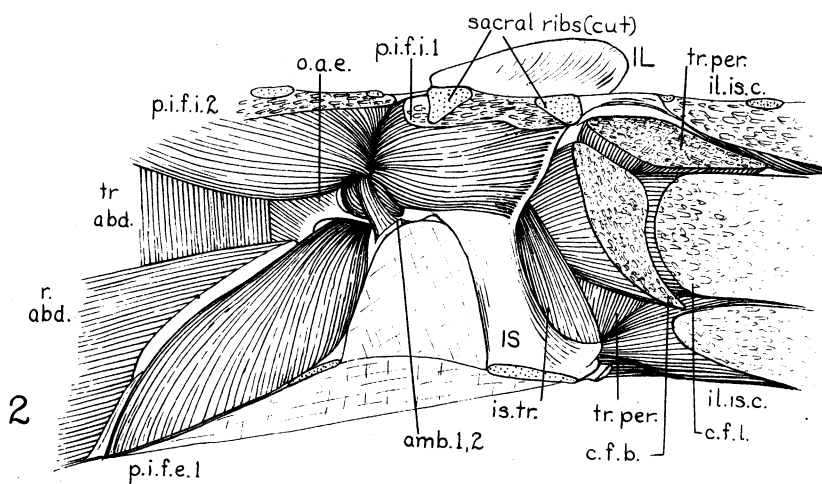
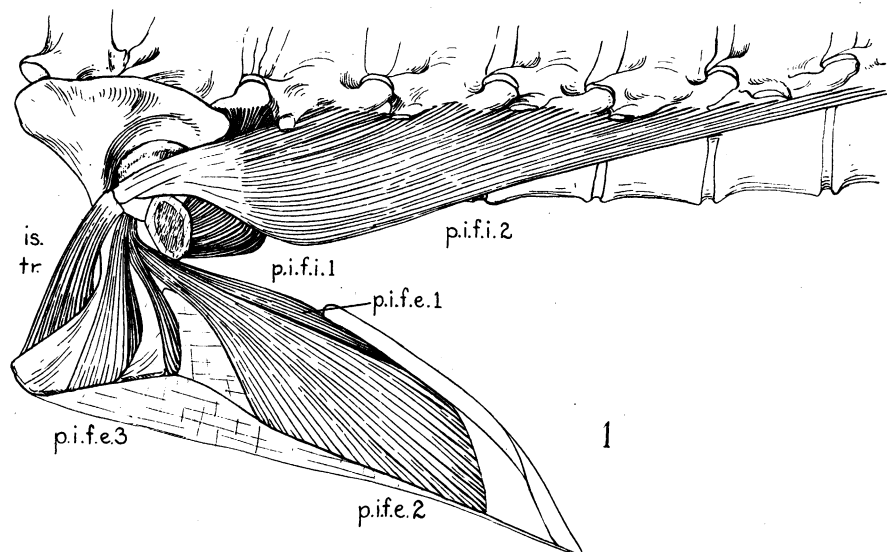


PLATE XX

Fig. 1. Lateral view of the deep musculature of the pelvic region, with most of the muscles shown in Plate XIX removed.

Fig. 2. Inner aspect, through the mid-line ventrally and cut through the sacral ribs dorsally. The dorsalis trunci+caudæ have been removed.

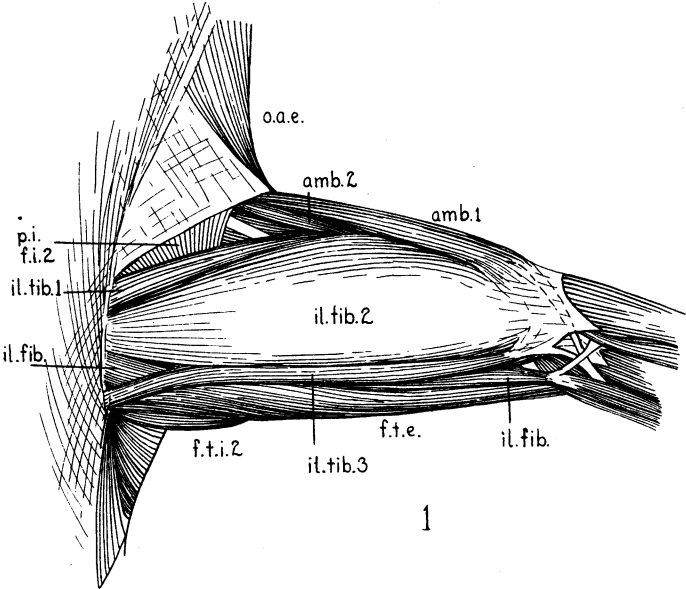




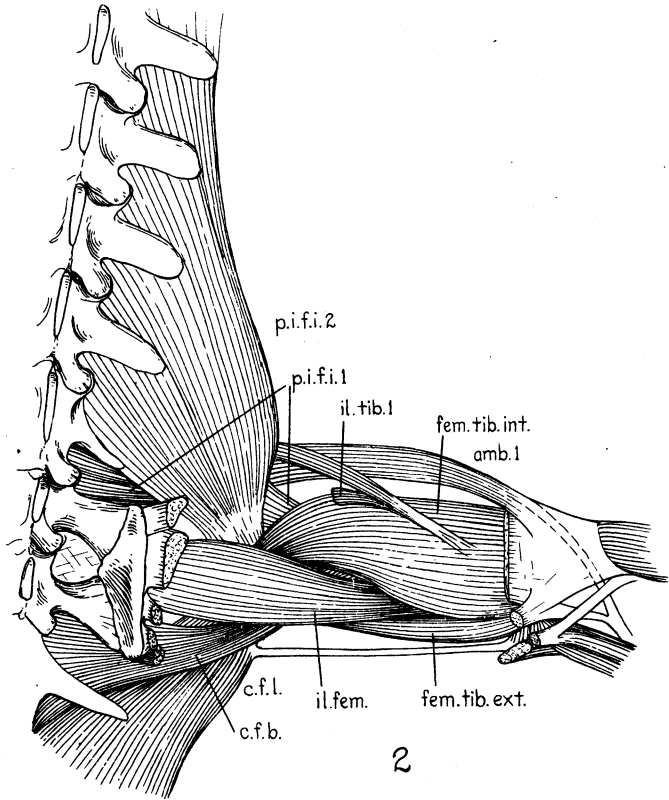
**PLATE XXI**

**Fig. 1.** Superficial dorsal view.

**Fig. 2.** Deeper view of the dorsal musculature.



1



2

**PLATE XXII**

**Fig. 1.** Dorsal view of pelvic region, with the spinal column and ribs removed, to show the deep musculature.

**Fig. 2.** Superficial ventral view.

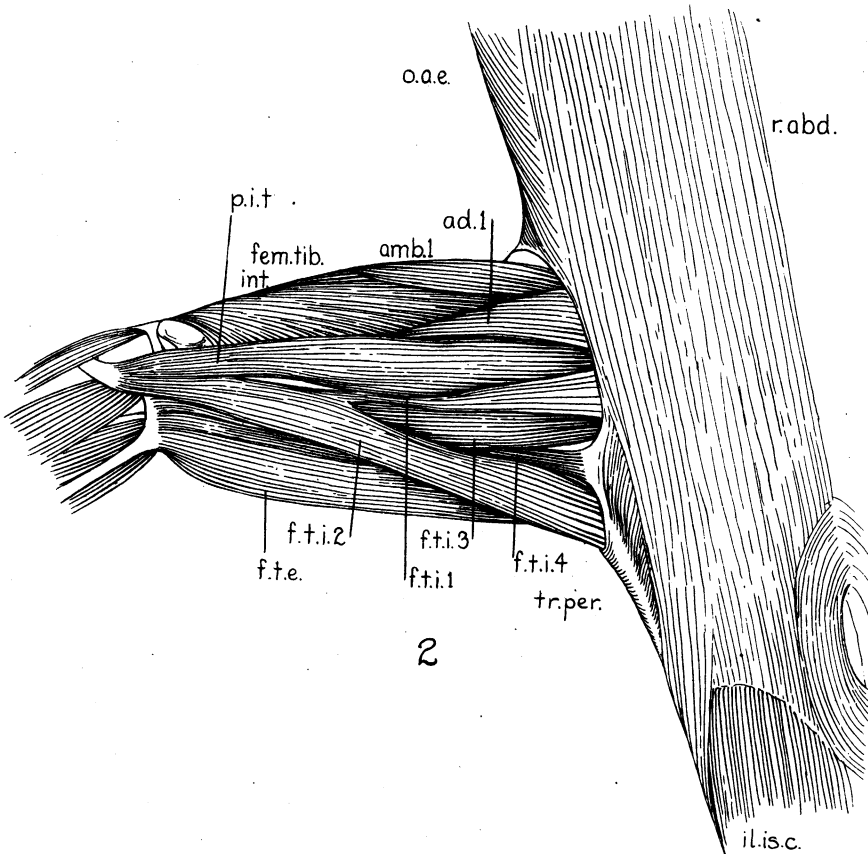
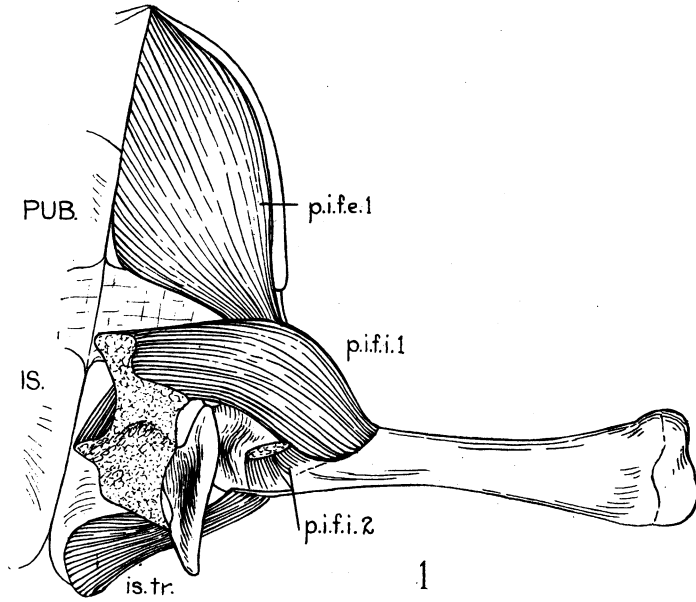
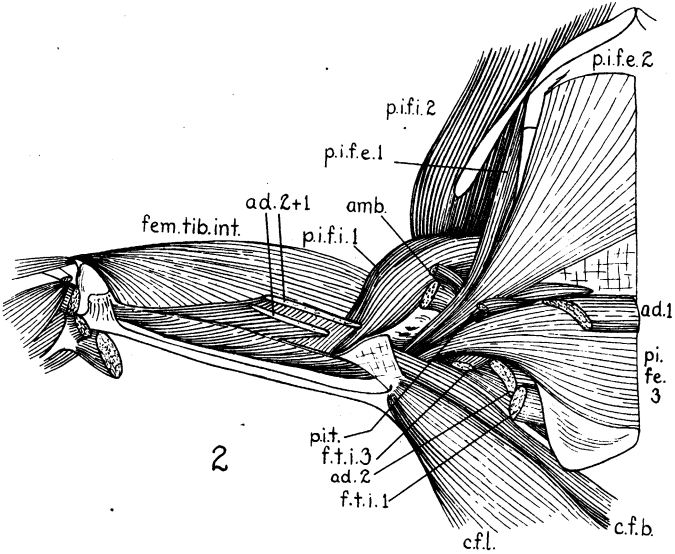
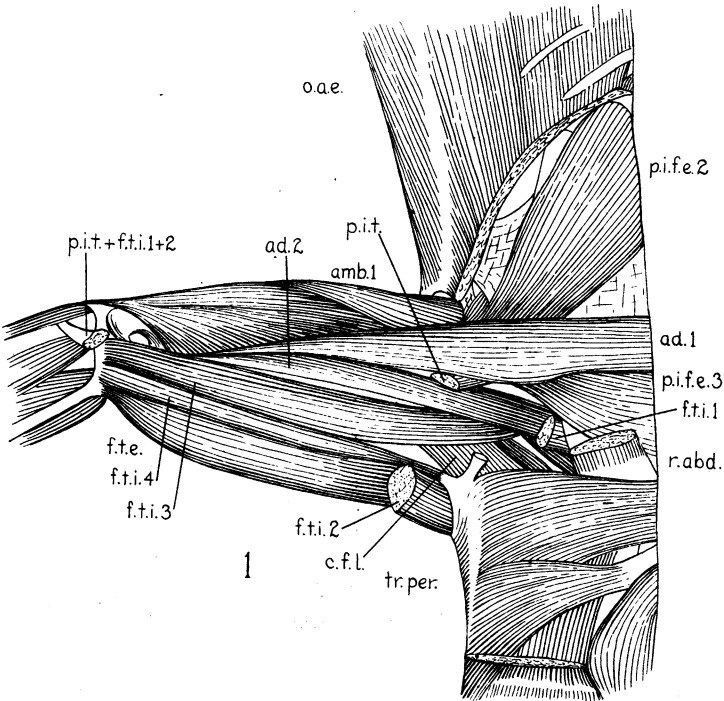


PLATE XXIII

Fig. 1. Ventral view, with a portion of the axial musculature and the long flexors cut.

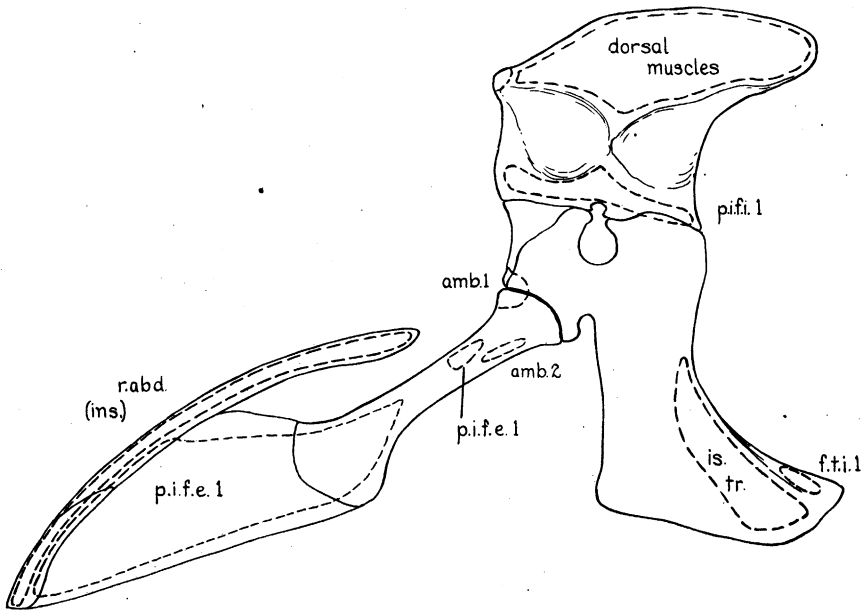
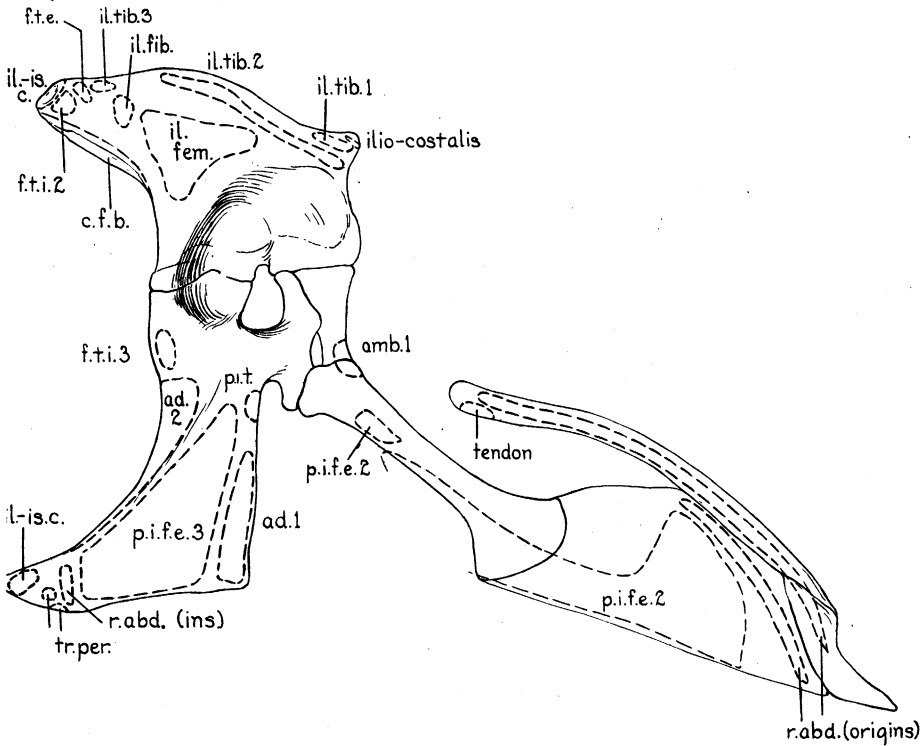
Fig. 2. Deep ventral view.



**PLATE XXIV**

**Outer and inner surfaces of pelvic girdle, showing muscle attachments.**





**PLATE XXV**

**Dorsal, anterior, ventral and posterior aspects of the femur, showing muscular attachments.**

