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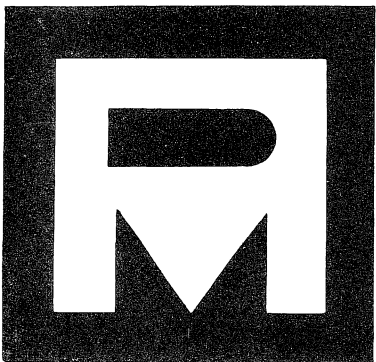
POSTILLA
PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 131.

15 MAY 1969

THE PELVIC MUSCULATURE
OF THE DINOSAUR HYPSI-
LOPHODON (REPTILIA:
ORNITHISCHIA)

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POSTILLA

Published by the Peabody Museum of Natural History, Yale University

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Editors: Jeanne E. Remington and Nancy A. Ahlstrom

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THE PELVIC MUSCULATURE OF THE DINOSAUR HYSILOPHODON (REPTILIA: ORNITHISCHIA)

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ABSTRACT

Evidence is provided to show that: 1) the prepubic process, diagnostic of an ornithischian, did not provide the main support for the abdomen; 2) the abdomen was large and extended ventral to the pelvic girdle with a strong *M. rectus abdominis* that was not functionally replaced by the lateral abdominal muscles; 3) either the *M. pubo-tibialis* or the ventral part of the *M. pubo-ischio-femoralis internus* originated on the lateral surface of the prepubic process. An important femoral protractor, the anterior part of the *M. pubo-ischio-femoralis externus*, had to be functionally replaced before the pubis changed position to lie close to the ischium in ornithischians and birds. This was accomplished by the development of a long anterior process to the ilium with the differentiation of a large *M. ilio-tibialis 1*. The lateral curvature of the anterior process of the ilium enabled it to clear the adjacent ribs and improved the mechanical position of part of the *M. dorsalis trunci*, the *M. ilio-tibialis 1* and the dorsal part of the *M. pubo-ischio-femoralis internus*. A third dorsal muscle to the femur, the *M. ilio-trochantericus*, was differentiated in *Hypsilophodon*. The well-developed depression at the base of the fourth trochanter was the main insertion area of the *M. caudifemoralis longus*. The large size of the fourth trochanter of the ornithopod femur lengthened the moment arm of the *M. caudifemoralis brevis* during the initial part of femoral retraction; its pendant form resulted from stresses imposed by part of the *M. gastrocnemius* which originated on the tendon connecting the trochanter to the fibula.

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INTRODUCTION

The first study of the pelvic musculature of an ornithopod dinosaur was by Dollo (1883) who discussed the muscles inserting on the femoral trochanters of *Iguanodon*. Subsequently Dollo (1888) suggested that the "trochanter creté" of *Iguanodon* was primitive for ornithopods. He regarded the pendant trochanter of *Hypsilophodon* and *Camptosaurus* as a secondary development but Nopcsa (1905), on the basis of the primitive nature of *Hypsilophodon*, argued that the reverse was the case. Gregory (1919 and in Romer, 1927b) made the first attempt to locate the area of attachment of all the pelvic muscles. Romer contributed several papers on the pelvic musculature of dinosaurs and related forms: 1923a (dinosaurs and birds), 1923b (alligator), 1923c (saurischian dinosaurs) and 1927a (chick). These studies were followed (1927b) by a detailed discussion of the pelvic muscles of ornithischians with a reconstruction of the pelvic musculature of the hypsilophodont *Thescelosaurus*. The pelvic musculature of the ceratopsian *Chasmosaurus* (Russell, 1935) and the hadrosaur *Anatosaurus* (Lull & Wright, 1942) has been briefly described but in both instances Romer's interpretations were followed. Janensch (1955) discussed the attachment areas in the region of the fourth trochanter of the femur of the hypsilophodont *Dysalotosaurus*.

Marsh (1878), using material of *Dryosaurus* (= *Laosaurus*) *altus* (YPM 1876), first showed that the complete ornithischian pubis consisted of an anteriorly directed prepubic process and a postpubic rod that lies close to the ischium. However, the presence of the latter was originally demonstrated by Huxley (1870) using a specimen of *Hypsilophodon* [BM(NH) 28707]. Although Dollo (1888), Nopcsa (1905), Romer (1927b) and Janensch (1955) referred to *Hypsilophodon*, the material has not been studied in detail with reference to the pelvic musculature. Most of the material is in the British Museum (Natural History), London and includes several articulated specimens, details of which are given in Galton (in press). The good specimens consisted of blocks with only some of the bone(s) exposed (see Hulke, 1882). I have prepared most of these in acetic acid so that the bones are completely free of matrix. Among these specimens is BM(NH) R193 (Figs. 4, 6-11, 13, 15) consisting of a pelvic region and partial

hind limb. The figure of the pubis and ischium of *Hypsilophodon* given by Romer (1927b, fig. 7), was based mainly on the figure of this specimen given by Hulke (1882, pl. 66). The surface of the bones of the pelvic girdle and femur of this specimen is very well preserved so that the boundaries of several areas of muscle attachment can be located. These areas were identified using for the main part the descriptions and the reconstruction of the pelvic musculature of *Thescelosaurus* given by Romer (1927b) and information from living forms. In the process it was possible to compare the areas in these two genera that both belong to the family Hypsilophodontidae (for diagnosis see Romer, 1956). It also became apparent that there were several problems that needed discussion. These, together with certain functional considerations, are dealt with in the second half of this paper (see below, p. 21).

PELVIC MUSCLES OF THE ALLIGATOR AND BIRDS

The reconstruction of the musculature of an extinct form should agree as far as possible with the musculature in the closest living relatives. Dinosaurs are classified in the subclass Archosauria, the only living order of which is the Crocodylia. Birds are archosaurian derivatives and, because the pubis lies close to the ischium, are particularly relevant to the musculature of any ornithischian. Consequently a brief summary of the pelvic musculature of the alligator and birds is given below. The following classification of the pelvic muscles of reptiles and birds has been adapted from Romer (1923b, 1927a, b, 1962).

Axial muscles

A. Dorsal

M. dorsalis trunci and caudae

B. Ventral

M. obliquus abdominis externus and internus,

M. transversus abdominis, M. rectus abdominis

M. ilio-caudalis and M. ischio-caudalis

Appendicular Muscles

A. Dorsal

- i) To the lower leg
 - a) *M. triceps femoris* — *M. ilio-tibialis* (including *sartorius* of birds), *M. ambiens* and *M. femoro-tibialis*
 - b) *M. ilio-fibularis*
- ii) To the femur
 - a) *M. pubo-ischio-femoralis internus* of reptiles, *M. ilio-femoralis internus* of birds
 - b) *M. ilio-femoralis* of reptiles, *M. ilio-femoralis externus* and *M. ilio-trochantericus* of birds

B. Ventral

- i) To the lower leg
 - a) *M. pubo-tibialis*
 - b) *M. pubo-ischio-tibialis*
 - c) *M. flexor tibialis internus* of reptiles, *M. ischio-flexorius* of birds
 - d) *M. flexor tibialis externus* of reptiles, *M. caudo-ilio-flexorius* of birds
- ii) To the femur
 - a) *M. caudi-femoralis longus* and *brevis* of reptiles, *M. caudo-ilio-femoralis* of birds
 - b) *M. adductor femoralis* of reptiles, *M. pubo-ischio-femoralis* of birds
 - c) *M. pubo-ischio-femoralis externus* of reptiles, *M. obturator internus* of birds
 - d) *M. ischio-trochantericus* of reptiles, *M. ischio-femoralis* of birds

In the following summary, unless indicated otherwise, information concerning the pelvic muscles of the alligator was taken from Romer (1923b) and for birds from Romer (1923b, 1927a, b). The areas of attachment and the lines of action of the individual muscles are shown for the alligator in Figures 1 and 2 and for an eight day old chick in Figure 3.

Dorsal Axial Musculature

The dorsal axial muscles in the alligator, lizards and *Sphenodon* lie lateral to the neural arches and dorsal to the transverse processes of the dorsal and caudal vertebrae. The *M. dorsalis trunci* has areas of insertion and the *M. dorsalis caudae* areas of origin on the inner surface of the dorsal part of the ilium. Further subdivision of this musculature is unnecessary in the present connection. The *M. dorsalis trunci* and *caudae* are completely separated by the ilia in birds.

Ventral Axial Musculature

In the alligator anteriorly the three lateral muscles originate from the lumbodorsal fascia. This fascia attaches to the surface of the *M. dorsalis trunci*, the tips of the transverse processes, the tip of the anterior process of the ilium and the surface of the *M. pubo-ischio-femoralis internus*. The *M. obliquus abdominis externus* passes posteroventrally and it has three insertion areas: by a tendon to the anterior edge of the acetabulum below the *M. ambiens*; on the posterodorsal end of the last abdominal rib, which is connected to the external edge of the pubis by a tendon; and on an aponeurosis lying above the main part of the *M. rectus abdominis*. The first insertion corresponds to the one on the lateral process of the pubis and the second to that on the pubo-ischiadic ligament in lizards (Snyder, 1954, fig. 21) and *Sphenodon* (Gregory & Camp, 1918, pl. 45, fig. A²). The *M. obliquus abdominis internus* passes anteroventrally to insert on the posterior long rib and the anterior abdominal ribs. The *M. transversus abdominis* is the deepest muscle and it passes ventrally to insert on the deep surface of the *M. rectus abdominis*.

The three lateral abdominal muscles are slightly different in birds (George & Berger, 1966). The *M. obliquus abdominis externus* originates on the costal margin of the sternum and a midline raphe anteriorly or a fleshy contact with the muscle of the other side. It passes dorsally and slightly anteriorly or posteriorly depending on the genus to insert on an aponeurosis on the lateral surface of the ribs and on the ventral edge of the anterior part of the pubis. The *M. obliquus abdominis internus* originates from the last rib, passes posterodorsally and inserts by an aponeurosis on the distal third to two-thirds of the pubis. The origin of

the *M. transversus abdominis* forms a ventral midline raphe that extends from the posterior margin of the sternum to the interpubic ligament. It inserts on the medial surface of the last two or three ribs and by an aponeurosis and/or by fleshy fibers on the ventral margin of the pubis. In ratites all three muscles insert on the whole of the ventral edge of the pubis (Gadow, 1880).

The *M. rectus abdominis* is large in the alligator as is the case in *Sphenodon* and lizards. It originates from the posterior edge of the sternum and the distal part of the long ribs. The more lateral part is interrupted by the gastralia and inserts on the last gastralia, which is connected to the pubis by membranous tissue ventrally and by a strong tendon laterally. The deeper fibers of the more medial part insert on the posterior edge of the pubis while the rest insert on the ventral surface of the *M. ischio-caudalis*. The *M. rectus abdominis* in birds originates from the posterior margin of the sternum and the last sternal rib; it inserts by an aponeurosis on the posterior part of the pubis and the interpubic ligament (George & Berger, 1966). In ratites the *M. rectus abdominis* inserts on the distal part of the pubis (Gadow, 1880).

Posteriorly the *M. ilio-caudalis* and *M. ischio-caudalis* (= *M. ilio-ischio-caudalis*; Romer, 1923b) are separated by the *M. caudifemoralis* in the alligator. The more dorsal *M. ilio-caudalis* originates on part of the dorsal edge of the ilium and inserts on the undersides of the transverse processes and centra of the caudal vertebrae. The *M. ischio-caudalis* originates on the posteroexternal angle of the ischium and inserts on the haemal arches of the tail. There are four posteroventral axial muscles in birds that control the movements of the very short tail. The details (George & Berger, 1966, p. 282), are unimportant because they are not relevant to the muscles in ornithischians.

Appendicular Muscles

The *M. triceps femoris* consists of three parts:

M. ilio-tibialis. This muscle originates along most of the dorsal margin of the ilium and is divided into two parts in lizards, three in crocodiles and five in birds. All these origins are tendinous except the most anterior one in birds which is fleshy. The insertion in all forms joins the tendon of the *M. femoro-tibialis* on the cnemial crest of the tibia.

M. ambiens in reptiles and birds has a tendinous origin just anterior to the acetabulum close to the ilio-pubic boundary and inserts on the tendon attaching to the cnemial crest. A second tendon crosses the knee to the fibular side in crocodiles and birds to join the external head of the *M. gastrocnemius*.

M. femoro-tibialis has a fleshy origin from much of the femoral shaft. In the alligator there are two parts but in birds there are several additional small heads. The tendinous insertion is on the cnemial crest of the tibia.

M. ilio-fibularis. This muscle in crocodiles and birds has a large fleshy origin on the postacetabular part of the ilium and is overlain by the *M. pubo-tibialis*. It inserts on the fibula and also on the external head of the *M. gastrocnemius*.

There are two dorsal muscles inserting on the femur in modern reptiles. The *M. ilio-femoralis* originates on the outer surface of the ilium and inserts on the posterior surface of the femoral shaft. The two parts of the *M. pubo-ischio-femoralis internus* primitively originate on the medial surface of the pubis. In the alligator they have a more dorsal origin. The main part originates on the ventral surfaces of the transverse processes of the last six dorsal vertebrae; it inserts on the dorsal surface of the proximal part of the femur. The more ventral part originates on the internal surface of the ilium and ischium and the ventral surfaces of the sacral ribs and passes ventrally to insert more anteroventrally on the femur.

There are three dorsal muscles inserting on the femur in birds that all originate on the outer surface of the ilium. The homologues of the two reptilian muscles are the *M. ilio-femoralis externus* and the more anterior *M. ilio-femoralis internus*. The muscle in between is the *M. ilio-trochantericus* that inserts in part on the greater trochanter.

The *M. pubo-tibialis* of primitive reptiles is lost in crocodiles and birds. The *M. pubo-ischio-tibialis* of lizards is a large ventral muscle (Snyder, 1954). It is reduced to a slip that originates on the lateral surface of the ischium below the acetabulum in the alligator. It is lost in birds.

The *M. flexor-tibialis internus* has three heads in the alligator. The first originates on the medial surface of the ischium near the posteroventral corner, the second on the outer surface postero-

ventral to the acetabulum and the third is on the posterior corner of the ilium. These three heads have a double tendon, one part inserting on the medial surface of the tibia and the other passing along the external head of the *M. gastrocnemius*. The only part in birds is the *M. ischio-flexorius*.

The *M. flexor-tibialis externus* arises from the posterior angle of the ilium in the alligator and from the tail in birds (*M. caudo-ilio-flexorius*). It inserts on the medial aspect of the head of the tibia.

The *M. caudi-femoralis brevis* originates on the posteroventral edge of the ilium and the sides of the centra of the last sacral and the first caudal vertebra in the alligator. It inserts on the dorsal surface of the fourth trochanter of the femur. The iliac portion is more important in birds.

The *M. caudi-femoralis longus* originates on the sides of the centra and the ventral surface of the transverse processes of caudal vertebrae 3 to 15 in the alligator. The thick tendon inserting on the fourth trochanter is connected to the head of the fibula by a thin tendon that is also present in lizards and birds.

M. adductor femoris has two heads that originate on the outer surface of the ischium. These two heads are separated by a portion of the *M. pubo-ischio-femoralis externus* in the alligator but not in birds. The insertion is a long and narrow area on the ventral side of the femur.

M. pubo-ischio-femoralis externus has three heads in the alligator. The first is on the ventrolateral surface of the pubis, the second on the dorsomedial surface of the pubis and the third on the outer surface of the ischium. The common tendon inserts on the posteroventral edge of the femur close to its head. This muscle has only one head in birds, the *M. obturator internus*, which originates on the ventral edge of the ischium and the dorsal edge of the pubis.

M. ischio-trochantericus of alligators is a small muscle which originates on the posterior part of the inner surface of the ischium. Its tendinous insertion is on the outer dorsal edge of the femur close to its head. This muscle originates on the outer surface of the distal part of the ischium and neighboring pelvic bones in birds.

THE PROBABLE AREAS OF ORIGIN AND INSERTION OF THE PELVIC MUSCLES IN HYSILOPHODON

Romer (1927b) discussed the probable attachment areas of each pelvic muscle in ornithischians and gave a detailed reconstruction of these muscles for *Thescelosaurus* (Figs. 5, 16). His study has been used to interpret certain well-defined surface markings on BM(NH) R193 (Figs. 6-11, 13, 15), a specimen of *Hypsilophodon* that has an extremely well-preserved ilium, ischium, pubis and femur. The following section provides a summary of the evidence shown by this specimen but the reasons for certain of the interpretations are discussed in later sections. Data for other ornithischians are taken from Romer (1927b) unless otherwise indicated. Romer (1927b) applied avian names to several of the muscles of ornithischians. However, as ornithischians are reptiles I have not followed this practice unless there is good evidence that the muscle in *Hypsilophodon* resembled that of birds. When Romer (1927b) used the avian term this is given in parenthesis after the appropriate section heading (see also the classification of muscles given on p. 5).

A. AXIAL MUSCULATURE

Only the more superficial part of the dorsal axial musculature attached to the ilium (Figs. 4, 6). Part of the M. dorsalis trunci probably inserted on the medial surface of the anterior process, which is strengthened by a couple of longitudinal ridges. The square and rugose posterior edge of the ilium probably provided an area of origin for part of the M. dorsalis caudae.

The reconstruction of the ventral axial muscles anterior to the pelvic girdle must be rather tentative but I consider that the following is a reasonable approximation. The M. obliquus abdominis internus probably originated from the posterior edge of the sternum and by a midline raphe or a fleshy contact with the muscle of the other side. This muscle passed laterally and posterodorsally to insert on a dorsal fascia, similar to that in the alligator, and on the pubis. The M. transversus abdominis originated from a midline raphe and passed dorsolaterally to insert on the dorsal fascia and on the pubis. The M. obliquus abdominis externus originated from a midline raphe and from the lateral edge of the M. rectus abdominis and passed laterally and anterodorsally to

insert on the pubis and on the dorsal fascia. The *M. rectus abdominis* originated from the posterior edge of the sternum and inserted on the distal part of the pubis and on the expanded distal end of the ischium.

The three lateral abdominal muscles probably inserted on the ventral edge of the pubis, as in birds. The insertion of the *M. obliquus abdominis externus* may have been restricted to the more anterior part of the pubis and that of the *pars internus* to the more posterior part as is the case in carinate birds (George & Berger, 1966). It would appear more likely that both these muscles, like the *M. transversus abdominis*, inserted along the whole of the ventral edge of the pubis (Fig. 6) as is the case in ratites (Gadow, 1880). It is possible that more distally the area of insertion of these three muscles was on the adjacent surface of the ischium. The problem of the abdominal musculature is discussed on page 21.

B. APPENDICULAR MUSCULATURE

The functional grouping of the limb muscles of *Hypsilophodon* is simplified because the action of the hind limbs was mainly anteroposterior.

1. Muscles that Extended the Tibia.

The three parts of the *M. triceps femoris* provided much of the propulsive force. The more anterior portion of the *M. ilio-tibialis* also raised the leg during forward movement and effected minor adduction and abduction. The insertion of all parts was presumably a tendinous one onto the cnemial crest of the tibia.

a) *M. ilio-tibialis*. This originated on the dorsal margin of the ilium. The dorsal edge of the ilium in lateral view (Fig. 6) has a definite bevel running from the posterior corner onto the anterior process. The complete bevel is visible in BM(NH) R196 and that part of it present in BM(NH) R193 has well-marked muscle scars. A separate portion, the *M. ilio-tibialis* 1 (the sartorius) was probably differentiated on the anterior process of the ilium as in birds. The posterior boundary of this portion is indicated by a rugose line running across the process in hadrosaurs and *Thescelosaurus* (Fig. 5); this is not present in *Hypsilophodon*.

b) *M. ambiens*. The origin on the pubis seems to be just anterior to the acetabulum. Romer (1927b) showed that this region varies in *Thescelosaurus* because a distinct bump is preserved in the type (Gilmore, 1915, fig. 17) that is lacking on specimens at the American Museum of Natural History. *Hypsilophodon* specimens BM(NH) R193, R195 and R196 show muscle scars on the dorsolateral edge of the prepubic process close to the acetabular region (Figs. 4, 6, 7) in the same position as the bump in *Thescelosaurus*. The main insertion was presumably on the cnemial crest of the tibia but, as in crocodiles and birds, there may also have been a tendon that crossed to the fibular side of the leg to insert on the external head of the *M. gastrocnemius*.

c) *M. femoro-tibialis*. Unlike the other two divisions of the *M. triceps femoris* there was no possibility of the *M. femoro-tibialis* functioning to protract the femur. Among archosaurs there was a general tendency for the *M. femoro-tibialis* to enlarge its area of insertion (Romer, 1923b, c; 1927b) so that it covered much of the femoral surface. Concerning *Thescelosaurus*, Romer (1927b, p. 261) wrote that "the femoro-tibialis origin, as is usually the case, is not well defined, but apparently includes a main area lying on the dorsal (anterior) surfaces of the femur, bounded externally by a ridge extending down from the 'lesser trochanter'. Probably a head originated on the ventral (posterior) surface external to the ridge, while a third (not seen in the figures) extended around the internal margin towards the ventral surface interior and anterior to the coccygeo-femoral insertion." These three divisions are referred to below as *M. femoro-tibialis* 1, 3 and 2 respectively and their areas of origin are clearly seen in the femur of *Hypsilophodon*, BM(NH) R193 (Figs. 8-10). It should be noted that the ridge below the lesser trochanter in *Thescelosaurus* is not equivalent to the groove in this position in *Hypsilophodon* but corresponds to the more posteriorly placed ridge.

M. femoro-tibialis 1. The area of insertion of this muscle is delimited by two longitudinal features on the femur. At the base of the lesser trochanter there is a well-defined shallow groove (Fig. 10C), with surface markings, which becomes wider close to the broken end of the bone. On the outer surface there is a strong and curved ridge (Figs. 8A, 9A, 10B) which commences level with the top of the fourth trochanter. Distally this ridge

curves inward and widens to form a flat area with surface striations (Figs. 8A, 9A, 10A, B). The area bounded by these two features is convex and its anterior limit is marked by a series of rugose markings, which extend from the base of the lesser trochanter to the flatter area at the end of the ridge. There are few surface markings on this area but distally there is a diagonal system of low parallel ridges and grooves (Figs. 8A, 9A).

M. femoro-tibialis 2. The insertion area of this muscle is convex and is mainly bounded by the M. femoro-tibialis 1 and 3. The proximal extent of this muscle is not certain. There are some rugose markings, situated at the level of the lower part of the depression at the base of the fourth trochanter, which may mark the proximal limit (Figs. 8B, 9B, 10C, D). Alternatively, this muscle may have extended medial to the depression toward the base of the lesser trochanter.

M. femoro-tibialis 3. The area of insertion of this muscle is bounded externally by the sharp ridge mentioned above. Internally the proximal boundary is a faint line, formed by a series of small depressions, that extends from the proximal end of the ridge onto the base of the fourth trochanter. More distally on the trochanter this boundary continues as a rugose ridge (Figs. 8A, 9A, 10A) and then by an edge formed by the thickening of the trochanter (Fig. 10B). Distal to the trochanter the internal boundary is a line of small depressions extending from the distal end of the well-developed depression at the base of the fourth trochanter (Figs. 8B, 9B, 10D). The surface for the origin of this muscle is mostly concave but internally, in the region distal to the fourth trochanter, it is convex. A part of this muscle probably originated on the central area underneath the pendant part of the fourth trochanter (Figs. 8A, 9A, 10B) where there are surface markings.

d) M. pubo-tibialis. There is a well-defined area on the lateral surface of the prepubic process of *Hypsilophodon* on which the M. pubo-tibialis or the ventral part of the M. pubo-ischio-femoralis internus may have originated (see below, p. 28). The lateral area is best preserved in BM(NH) R193 (Figs. 4, 6, 7). The anterior part is also shown on BM(NH) R196 and the posterior part on BM(NH) R195 and R5829. The surface markings cease anteriorly close to the end of the process. Ventrally the area is delimited by a groove running along the corner of the process (Fig.

7). Posteriorly the surface of the prepubic process is concave, so that the area projects laterally (Fig. 11). Dorsally the markings continue to the rounded edge of the process. The surface markings are best developed posteriorly, where the area is wider, making an angle of about 45° to the long axis of the process (Figs. 6, 7). These same markings are present in BM(NH) R5829 but the area does not project laterally. Anteriorly, the area is narrower and the markings have no apparent direction. This part is the same in BM(NH) R196 where the markings stop a short distance from the end. If the M. pubo-tibialis was present, it would presumably have inserted on the medial surface of the tibial head.

The prepubic process of *Dryosaurus altus* (YPM 1876) has an area on the lateral surface similar to that in *Hypsilophodon*. Posteriorly the well-defined muscle scars are diagonally inclined and the area continues onto the dorsolaterally facing surface of the slightly flattened and expanded anterior part where the markings are longitudinal. The prepubic process of *Thescelosaurus* (AMNH 117) is similar to that of *Dryosaurus* but the posterior region is less well-defined and the markings less diagonally inclined. The markings on the prepubic process of most other ornithischians examined are, as Romer (1927b) noted, longitudinal striations. This is true for *Thescelosaurus neglectus* (NMC 8537, USNM 2210 and AMNH 6120), *Iguanodon atherfieldensis* [BM(NH) R5764] and the mounted skeletons of hadrosaurs and ceratopsians in the Peabody Museum of Yale University, United States National Museum, National Museum of Canada and the Royal Ontario Museum, Toronto. In some of the mounted hadrosaurs at the American Museum of Natural History (*Procheneosaurus*, AMNH 5461; *Saurolophus*, AMNH 5220; and *Corythosaurus*, AMNH 5240) the pattern is slightly different. In these specimens the striations radiate from the narrow part into the dorsoventrally expanded anterior part of the process. As a result the most dorsal and ventral striations are parallel to the appropriate edge of the process.

2. Muscles that Protracted the Femur.

a) M. ilio-femoralis(=M. ilio-femoralis externus; Romer, 1927b). Romer (1927b) concluded that the M. ilio-femoralis originated on the antitrochanter of the ilium of hadrosaurs. In

Thescelosaurus (Fig. 5) and *Hypsilophodon* (Fig. 6), in which the area of origin cannot be distinguished, the area shown on the ilium is comparable in position to that of the hadrosaurian antitrochanter. The insertion of the *M. ilio-femoralis* completely covered the lesser trochanter (Figs. 4, 10); it probably extended to the depression at the base on the anterior edge (Fig. 10C). This muscle helped to prevent disarticulation of the femur.

b) *M. pubo-ischio-femoralis internus*(=*M. ilio-femoralis internus*; Romer, 1927b). The ventral part of this muscle, rather than the *M. pubo-tibialis*, may have originated on the well-defined area on the lateral surface of the prepubic process (see p. 14, 28). A possible area of insertion for this part was on the femoral shaft proximal to the depression at the base of the fourth trochanter (Figs. 8B, 9B, 10D) and possibly also proximal to *M. femoro-tibialis 2*. On the ventral surface of the head and neck there is an area, with very strongly developed markings (Figs. 8B, 9B, 10C), which probably was not for this ventral part but for ligaments that held the head of the femur in the acetabulum.

3. Muscles that Flexed the Tibia.

a) *M. ilio-fibularis*. There is no indication of the area of origin of this muscle on the ilium in either *Thescelosaurus* or *Hypsilophodon*. Romer (1927b) concluded that it originated on the ilium posterior to the antitrochanter in hadrosaurs. The *M. ilio-fibularis* is shown in a comparable position in *Thescelosaurus* (Fig. 5) and *Hypsilophodon* (Fig. 6). The insertion was on the lateral surface of the fibula head. In BM(NH) R5830 there is a well-defined area with muscle scars on the posterior part of this surface which was probably for the *M. ilio-fibularis* (Fig. 4). This muscle, together with the other flexors, aided in retracting the femur.

b) *M. flexor-tibialis internus*(=*M. ischio-flexorius*; Romer, 1927b). Romer (1927b) showed that in *Thescelosaurus* the origin of this muscle was on a projection on the dorsal edge of the ischium just distal to the end of the obturator process (Fig. 5). There is no comparable projection in *Hypsilophodon* so its position in *Thescelosaurus* has been used in the reconstruction

(Fig. 6). A second head of the *M. flexor-tibialis internus* may have originated from the postacetabular part of the ilium as in the alligator but there is no evidence that this slip was present. The main insertion was presumably a tendinous one on the posterior part of the tibial head. A second tendon may have inserted on the external head of the *M. gastrocnemius* as in the alligator.

c) *M. flexor-tibialis externus*(=*M. ilio-flexorius*, Romer, 1927b). This muscle was probably present, but its area of origin has not been observed on the posterior part of the ilium of any ornithischian. The insertion was presumably on the posterior part of the tibial head.

d) *M. pubo-ischio-tibialis*. This muscle is reduced to a slip in the alligator and is lost in birds as was probably also the case in ornithischians.

4. Muscles that Retracted the Femur.

a) *M. pubo-ischio-femoralis internus*(=*M. ilio-femoralis internus*; Romer, 1927b). The more dorsal part of this muscle originated from the ventral surface of the transverse processes of the more posterior dorsal vertebrae. Romer (1927b) deduced that this muscle inserted on the greater trochanter in *Thescelosaurus* (Fig. 16). On the outer surface at the base of the greater trochanter in *Hypsilophodon*, there is a very prominent ridge that continues distally (Figs. 8A, 9A, 10B). Proximally, this ridge is sharp edged because it is the line of contact between two concave surfaces. More distally the anterior surface becomes convex and the posterior concave area cuts a distinct edge into this. The anterior concave area has strong longitudinal striations. The posterior area has only faint striations proximally but distally there are strongly developed and irregular markings on BM(NH) R193. In BM(NH) R2487 the posterior area is covered by longitudinal striations.

The two surfaces evidently formed an extension onto the shaft of the insertion area of two muscles that were attached to the greater trochanter. The *M. pubo-ischio-femoralis internus* probably inserted on the posterior area and the *M. ilio-trochantericus* on the anterior area (see p. 36).

b) *M. ilio-trochantericus*. The area of insertion of this muscle has just been discussed. Romer (1927b) deduced that in hadrosaurs the *M. ilio-trochantericus* originated from the lateral surface of the ilium anterior to the antitrochanter. The origin of this muscle is shown in a comparable position in *Thescelosaurus* (Fig. 5) and *Hypsilophodon* (Fig. 6). The *M. ilio-trochantericus* helped to prevent disarticulation of the femur.

c) *M. caudi-femoralis longus* and *brevis* (= *M. coccygeo-femoralis longus* and *brevis*; Romer, 1927b). The *M. caudi-femoralis longus* probably originated on the sides of the centra and the ventral surface of the transverse processes of the anterior third of the tail. Romer (1927b) pointed out that in many primitive ornithischians, including *Thescelosaurus*, the ilium has a broad *brevis* shelf from which the *M. caudi-femoralis brevis* originated. This muscle probably originated on the broad *brevis* shelf in *Hypsilophodon* (Figs. 4, 6) and, in addition, may have originated from the sides of the centra of the last sacral and the first caudal vertebra as in the alligator. Both of these muscles inserted on the fourth trochanter of the femur.

The outer surface of the fourth trochanter of *Hypsilophodon* continues the concave curve of the adjacent shaft (Fig. 10A). More distally on the outer surface there is a ridge extending to the tip of the trochanter (Figs. 8A, 9A, 10B). The position of this ridge relative to the distal edge of the trochanter varies—it is progressively farther away in the series BM(NH) R193, R195 and R196. Between this ridge and the dorsal edge there is a concave depression that proximally becomes indistinct as the ridge disappears. In BM(NH) R193 (Figs. 8A, 9A, 10A, B) this depression is rugose; it can be followed proximally where its boundary is formed by two series of small ridges that are parallel to the dorsal edge. The line of these ridges is continued onto the shaft of the femur as a faint line formed by a series of small depressions (Figs. 8A, 9A, 10A). In BM(NH) R195 there is a well-defined series of fine ridges running across this concave depression. In BM(NH) R196 the depression is less well defined and there are only faint insertion markings.

Distally the dorsal edge of the fourth trochanter is sharp because there is another concave area, with strongly developed insertion

markings, on the inner side of the pendant portion of the trochanter (Figs. 8B, 9B, 10D). Proximally the dorsal edge is thickened on this side to form a strong ridge with very well-developed but irregular insertion markings (Figs. 8B, 9B, 10D). Internal to this ridge there is a smooth concave area that widens out distally between the strongly concave area on the pendant part of the trochanter and the depression on the shaft of the femur (Figs. 8B, 9B, 10D).

In BM(NH) R193 (Figs. 8B, 9B, 10D), R195 and R2477a the depression at the base of the fourth trochanter is deep with a well-defined edge anteriorly and distally. Proximally the depression merges with the shaft surface and posteriorly it merges with the smooth concave area below the dorsal ridge. The whole of the surface of this depression is rough with extremely well-developed insertion markings. In BM(NH) R196, R5829 and R5830 there is a well-defined area, with irregular and strong insertion markings, in the same position on the shaft but forming only a slight depression. Distally this area is slightly higher than the adjacent part of the femoral shaft. The remaining boundaries of this area can only be distinguished by the presence of insertion markings.

I consider that the main insertion of the *M. caudi-femoralis longus* was on the medial depression and that the *pars brevis* inserted on the lateral surface of the fourth trochanter. The anterior limit of *M. caudi-femoralis brevis* is indicated by the line approximately parallel to the edge of the trochanter (Figs. 8A, 9A, 10A). Consequently the *pars brevis* inserted on a marginal zone on the lateral surface that extends the complete length of the trochanter. Proximally the *brevis* may have extended slightly onto the shaft but no boundary is visible. The *brevis* probably wrapped round the edge of the trochanter to insert on the medial surface of the strong ridge (Figs. 8B, 9B, 10D). The medial depression on the pendant part of the fourth trochanter was for a tendon which extended to the head of the fibula (Figs. 4, 8B, 9B, 10D). The lateral surface of the base of the *M. caudi-femoralis longus* was closely applied to the adjacent structures (Figs. 8B, 9B, 10D): the unoccupied medial surface of the trochanter, the surface of the tendon to the knee and the medial surface of the *brevis*. The fourth trochanter and the depression at its base is discussed on page 38.

d) *M. obturator internus* (= *M. pubo-ischio-femoralis externus*, anterior part). Romer (1927b) thought that the posterior part of the *M. pubo-ischio-femoralis externus* had been lost in ornithischians and that it was replaced by the anterior part, which originated from ligaments connecting the postpubic rod and the ischium. There is no evidence to show whether or not the posterior part was lost in ornithischians but it is reasonable to conclude that it was as is the case in birds. In *Hypsilophodon* the postpubic rod has a sharp upper edge on which the puboischiadic ligament could have attached. Specimen BM(NH) R193 has surface markings running below the dorsal edge and passing below the obturator foramen (Figs. 6, 7) that were probably for the puboischiadic ligaments. Romer (1927b) stated that there is no sure indication of the area of origin of the *M. obturator internus* on the ischium of *Thescelosaurus* but that in hadrosaurs there is a ridge running lengthwise that marks its dorsal border. In *Hypsilophodon* the ischium of BM(NH) R193 has on its outer surface a definite ridge running along just below the middle of the shaft which marks the dorsal limit of the *M. obturator internus* (Figs. 6, 7). The lateral surface of the obturator process probably formed another surface for the origin of this muscle but no definite boundaries can be seen in this region or along the length of the blade. Romer (1927b) did not find any indication of the insertion area; he noted that it is on the ventral surface of the head in living forms. The femur of BM(NH) R193 of *Hypsilophodon* (Fig. 10A) has a small, faint circular rugose area that was possibly the area of insertion for the tendon of this muscle.

e) *M. adductor femoralis*. Romer (1927b) placed the origin of the two heads of this muscle on the shaft region of the ischium in *Thescelosaurus* (Fig. 5) where there is a series of rugose markings between the origin areas of the *M. obturator internus* and the *M. ischio-trochantericus*. In *Hypsilophodon* there is a longitudinal depression on the shaft of the ischium [BM(NH) R193, Figs. 6, 7 and BM(NH) R195] bounded by a slight ridge dorsally and ventally. Romer (1927b) noted that the insertion of the *M. adductor femoralis* is sometimes shown by a slight indication on a line from the fourth trochanter towards the outer condyle. This has not been located on the femora of *Hypsilophodon* unless it is represented by an area on the posterolateral part of the shaft

in BM(NH) R193 (Figs. 8A, 9A, 10A, B). This area bears well-developed longitudinal striations and is separated by a sharp edge from the insertion area of *M. femoro-tibialis* 3.

f) *M. ischio-trochantericus*. In *Thescelosaurus* (Fig. 5) this muscle probably originated on the flattened upper surface internal to the dorsal edge of the ischium, which forms a prominent shelf below this muscle (Romer, 1927b). Romer noted that in all forms in which the position is determinable except *Camptosaurus* and *Protoiguanodon* there is no prominent shelf and the muscle originated from the outer surface. A rugose or ridged line running along most of the length of the ischium marks the ventral limit of this muscle in these forms.

In *Hypsilophodon* (Figs. 6, 7) the posterior part of the *M. ischio-trochantericus* probably originated on the flattened inner surface of the blade of the ischium as in *Thescelosaurus*. The dorsal margin of the shaft region does not form a distinct ledge and the muscle probably originated on its rounded margin, extending slightly onto the outer surface as far as the dorsal limit of the adductor muscles (Fig. 6). This dorsal margin shows very strongly developed markings in BM(NH) R195 and R196.

Romer (1927b) noted that the area of insertion of the *M. ischio-trochantericus* near the head of the femur is not visible. In his reconstruction of *Thescelosaurus* the insertion is shown very close to the head of the femur, behind the greater trochanter. In *Hypsilophodon* it probably inserted in the same region (Figs. 4, 8A, 9A, 10A).

DISCUSSION

Several problems of an interpretational or functional nature became apparent while trying to identify the areas of muscular attachment described in the above section. The conclusions relevant to the identification of attachment areas were included but the reasons still need to be considered.

A. THE PUBIS

1. The Ornithischian Pubis and Abdominal Support.

The ornithischian pelvic girdle has a characteristic tetradial form (Figs. 5, 6) with the pubis forming an anteriorly directed "prepubic process" and a posterior "postpubic rod". The prepubic

process is diagnostic of the order Ornithischia, one of the two orders of dinosaurs which were so successful during the Mesozoic era. The presence of a rod-like pubis close to the ischium occurs in only one other group, the Class Aves (Fig. 14D, E). Consequently it is important that the functional significance of the similarities and differences of the form of the pelvic girdle of ornithischians and birds be understood.

The prepubic process is generally regarded as a new structure with the postpubic rod as part of the normal reptilian pubis that, early in the history of the Ornithischia, came to lie close to the ischium. However, the postpubic rod had originally been regarded as a new development (Marsh, 1878, p. 451; more recently, Lebedinsky, 1913) but it is difficult to account for its development in terms of a muscle shifting its attachment area posteriorly. As Romer (1927b) maintained, a muscle involved in such a shift would probably have passed onto the adjacent anterior edge of the ischium. He thought it unlikely that a thin rod, lying close to the ischium, would have been formed because this is mechanically weaker. In addition, I consider that the implied evolutionary history of this "new" structure would be rather improbable because, after the lengthening of the rod until it was as long as the ischium in hypsilophodonts and camptosaurus, which on other characters are regarded as primitive Ornithopoda, it was then considerably shortened in the advanced Ornithopoda iguanodonts and hadrosaurs as well as in psittacosaurus and ceratopsians.

The pubis of birds has a postpubic rod similar to that of ornithischians and an anteriorly directly pectineal process (Figs. 3, 14D) for the *M. ambiens*. The pectineal process is best developed in ratites (Lebedinsky, 1914) but proportionally it is always minute in comparison with any prepubic process. The postpubic rod of birds clearly represents the original reptilian pubis because in the earliest bird known, the Jurassic *Archaeopteryx* (Fig. 14E), there is no pectineal process. In modern birds during embryonic development the pubis swings back to lie close to the ischium (Romer, 1927a). It seems likely, as Romer (1927b, 1956) believed, that the same thing occurred during the embryonic development of ornithischians.

In most reptiles the abdominal muscles insert on the anterior margin of the pubis and, if it is present, on the pubo-ischiadic ligament. As noted the postpubic rod probably represents the

original reptilian pubis that, during the evolution of the Ornithischia, changed position to lie close to the ischium. Romer (1927b) pointed out that this change would have resulted in longer abdominal muscles under heavy pressure and without adequate support. He accounted for the development of the prepubic process of ornithischians as an adaptation to offset this weakness. Romer considered that a structure comparable to the processus lateralis of the Lacertilia lengthened and took over most of the obliqui muscles and possibly part of the rectus abdominis muscle. According to Romer the main part of the pubis could change position only *after* it had been released from its role of supporting the abdominal muscles. Romer (1927b, p. 246) suggested that the rotation provided the obturator muscle with a more advantageous position. Romer cited several points that he thought tended to confirm that the ornithischian prepubic process provided the main support for the abdomen: the direction of the prepubic process; its form, which in many types is a long thin blade; and when present, the muscle markings, which are longitudinal striations. Further evidence was obtained from a mounted skeleton of *Triceratops* in which the prepubic process was orientated so that its anterior end was in the plane of the ribs (Fig. 12). Romer (1927b, p. 244) pointed out that on the posterior border of the adjacent long dorsal rib there are "indications of a muscular or ligamentous attachment of considerable strength which matched in size and position the end of the prepubic process. This quite definitely seems to show that abdominal support was a major, although perhaps not the sole function of the process." Later, in discussing the musculature of *Thescelosaurus*, he argued (p. 260) that the M. rectus abdominis was probably not of great strength, "as suggested by the lack of any well-marked area for its insertion", and that the obliqui muscles had taken over the great part of the abdominal support. Romer followed W. K. Gregory in considering that there was a considerable constriction of the waist region, with little more than a flap of skin below the girdle, so that the thighs were not restricted.

2. The Pubis in Birds.

The pubis of birds lies close to the ischium and there is no prepubic process to provide support of the abdomen. Romer (1927b, 1956) considered that a prepubic process was unneces-

sary because of the shortness of the abdomen and the large sternum, which extends almost to the pelvic region. As a result the abdominal muscles have only a comparatively small space to cross. This is certainly the case in carinate birds that are extremely specialized for flying, but not in the earliest known bird, the Jurassic *Archaeopteryx*. In *Archaeopteryx* the pubis is directed backward and there is neither an anterior prepubic process nor a pectineal process (Fig. 14E). The abdominal area with 12 dorsal vertebrae (Heilmann, 1926, fig. 23; and in Romer, 1966, fig. 253) is proportionally almost as extensive as in ornithischians, which have 15 dorsal vertebrae. The sternum of *Archaeopteryx* could not have provided much support for the abdomen because, although broad, it is very short (Beer, 1954). It is therefore apparent that the short abdomen and the large sternum of birds developed *after* the pubis had changed position and, as a result, these features cannot be cited to explain the absence of a prepubic process in birds. *Archaeopteryx*, however, had at least 9 to 10 pairs of gastralia (Heilmann, 1926, fig. 7) which would have provided accessory support for the abdominal muscles.

Archaeopteryx was about the size of a large pigeon, which may reduce its relevance to the present inquiry, but the size of the early ornithischians in which the pubis shift occurred is not known. Gastralia are primitively present in reptiles of all groups and their occurrence in *Sphenodon*, *Archaeopteryx*, crocodiles, phytosaurs, thecodonts and some saurischians strongly suggests that they were present in primitive ornithischians. They have been reported only from *Stegoceras* (Gilmore, 1924a), but these may have belonged to a saurischian dinosaur. It must be concluded that gastralia were either cartilaginous or absent in most ornithischians. The possible absence of gastralia in most ornithischians does not necessarily mean that the prepubic process was essential for abdominal support because gastralia are also absent in ratites. The sternum of ratites is small and the abdominal muscles span a distance that is comparable to that in an ornithischian of the same height (see figure *Struthio* in Gadow & Selenka, 1891, pl. 5, fig. 1 and *Dinornis* in Romer, 1966, fig. 257). There is no accessory support provided by gastralia, a large sternum or a prepubic process yet some moas reached a height of 10-11 feet (Romer, 1966). An ornithopod of this height would have been at least 20 feet long. In addition there is no accessory support

in any large mammal in which the ventral abdominal muscles are very long (see figures in Romer, 1966).

To summarize, *Archaeopteryx* shows that the pubis can lie close to the ischium without the development of a prepubic process, a large sternum or a short abdomen. Although gastralgia were probably present in early ornithischians, their absence would be no problem because the ventral abdominal muscles of ratites and large mammals can span long distances without any accessory support. Consequently I consider that the basic assumption made by Romer (1927b) is incorrect. The arguments used to show that the obliquii muscles had functionally replaced the *M. rectus abdominis* as the principal supporter of the abdomen. will now be considered.

3. The Abdominal Muscles.

The mounted skeleton of *Triceratops* cited by Romer (1927b) is shown in Figure 12 (see also Osborn, 1933, for other views; for another mount see Erickson, 1966). The presence of a strongly developed ligamentous or muscular connection between the last dorsal rib and the prepubic process would certainly have braced and strengthened the side wall of the abdominal cavity. The high position of this process in *Triceratops*, like that in other ornithischians must, however, have limited its effectiveness in providing the main supporting point for the abdomen. According to Romer (1927b, fig. 17) for *Thescelosaurus* the *M. obliquus abdominis* passed posterodorsally to insert on the anterior end of the prepubic process (Fig. 5). Consequently in *Triceratops* the posterior limit of the effective abdominal cavity is marked by the last long dorsal rib (Fig. 12). This would give a short abdominal cavity and, as Romer noted, little more than a flap of skin below the pelvic girdle. This is a rather strange condition for herbivorous animals which in many cases reached a considerable size. Herbivorous mammals are characterized by a barrel-like rib cage and a large abdominal cavity to contain the greatly elongated intestine required to digest plants. The rib cage of *Triceratops* is certainly barrel-like as shown in Figure 12, in Osborn (1933) and even more clearly in Erickson (1966, pls. 1, 2) where the ventral part of the rib cage has been restored. It would seem more logical and provide a larger abdominal cavity if the principal

muscles that supported the abdomen continued posteriorly and attached to the distal end of the ischium.

In marsupials there is a separate anterior part of the pubis, the epipubic bone, that is definitely important for abdominal support with the *M. obliquus abdominis internus* and *externus* inserting along its length (Elftman, 1929). In some marsupials, such as the wombat *Phascolomys* and especially the koala *Phascolartos* (Elftman, 1929, pls. 13, 14), the epipubic bone is very well developed and the abdomen large. In both these genera the epipubic bone is more ventrally directed so that the anterior end is proportionally much lower than that of the prepubic process of most ornithischians, e. g. *Hypsilophodon* (Fig. 4), *Thescelosaurus* (Fig. 5) and *Triceratops* (Fig. 12; for figures of other ornithischians see Colbert, 1961; Romer, 1966).

Romer (1927b) considered that the *M. rectus abdominis* was weak because there was no well-defined area for its insertion. In his reconstruction of *Thescelosaurus* Romer (1927b, fig. 16) showed the *M. rectus abdominis* attached only to the slender postpubic rod (Fig. 5). Although not specifically stated, it is apparent that Romer considered that the slender nature of the postpubic rod resulted from the reduction of the *M. rectus abdominis*. However, the slenderness may indicate that this muscle had transferred at least in part onto the ischium, a possibility that Romer (1927b, fig. 18) accepted for the *M. obturator internus*. Romer (1927b, p. 260) also noted that when the distal part of the pubis is lost, as in iguanodonts, hadrosaurs and ceratopsians, the *M. rectus abdominis* would have attached to the anterior border of the ischium below the termination of the pubis. Obviously such a transfer must have occurred *before* the postpubic rod could be lost so I consider that the *M. rectus abdominis* probably inserted on the ischium in hypsilophodonts and camptosaurus. The distal part of the ischium of *Hypsilophodon* (Fig. 13) and *Thescelosaurus* is expanded transversely. The anterior surface of the swollen distal end would have provided an adequate insertion area for a strong *M. rectus abdominis*. The adjacent part of the blade region probably formed an additional insertion area. This surface is covered by longitudinal striations in BM(NH) R193 and R5829 and it is unlikely that the *M. obturator internus* occupied the whole of this surface. I consider that the *M. rectus abdominis* of *Thescelosaurus* was not reduced and that it was a strong muscle that

provided an important role in supporting the large abdomen. In addition it would have provided a ventral tie that would have helped in maintaining the curvature of the dorsal vertebral series.

It should be noted that Romer (1927b, figs. 16, 17) showed only two abdominal muscles in *Thescelosaurus*: the M. rectus abdominis passing posteriorly to insert on the whole of the ventral edge of the pubis and the M. obliquus abdominis passing postero-dorsally to insert on the anterior end of the prepubic process (Fig. 5). He stressed that the former muscle had been functionally replaced by the latter but ventral to the pelvic girdle the reverse is the case with the M. rectus abdominis as the only muscle. The abdominal wall as reconstructed by Romer is rather unique and ill-adapted to support any viscera. In living amphibians, reptiles (except Chelonia), birds and mammals there is a ventral M. rectus abdominis and three lateral abdominal muscles that, though each is only a thin sheet, together form a strong abdominal wall as the fiber directions form a lattice work. Details of these muscles in the alligator and birds are given above (p. 7) and the reconstruction of these muscles in *Hypsilophodon* on page 11 and Figures 4 and 6.

From the similarity of the form of the postpubic rod the abdominal musculature of *Hypsilophodon* probably resembled that of birds rather than that of living reptiles. If the musculature resembled that of carinates (see p. 8 and George & Berger, 1966), then the M. obliquus abdominis externus probably inserted on the ventral surface of the prepubic process and the anterior part of the postpubic rod, the pars internus on the distal half of the postpubic rod and the M. transversus abdominis on all of the ventral edge of the pubis. With such an extensive abdomen it is more likely that the lateral abdominal muscles extended their area of insertion on the pubis so that they all inserted along the whole of the ventral edge of the pubis as in ratites (Gadow, 1880). In addition, it is possible that part of each muscle inserted on the laterally expanded distal part of the ischium. Consequently, I consider that the region below the pelvic girdle did not consist of "little more than a flap of skin." Even so, there was no problem as regards the free movement of the legs because the width of the sacrum, combined with the offset heads of the femora, provided plenty of space for a large and tapering abdominal cavity between the thighs. This is clearly shown in the posterior view of a mounted

skeleton of *Camptosaurus* (Gilmore, 1912, pl. 60) and in figures of *Triceratops* mounts (Osborn, 1933; Erickson, 1966). The potential strain on the abdominal muscles, due to the posterior position of the pubis, was probably compensated for by an increase in the strength of all the abdominal muscles including the *M. rectus abdominis*. Apparently in the ornithopods part of this muscle and possibly the lateral abdominal muscles transferred to the adjacent surface of the ischium and, as a result, the postpubic rod became reduced in thickness (*hypsilophodonts*, *camptosaurus*). Subsequently this transfer was completed and the distal part was lost in *iguanodonts*, *hadrosaurs*, *psittacosaurus* and *ceratopsians*. It should be noted that the postpubic rod is thick and about the same length as the ischium in *stegosaurs* (Gilmore, 1914). Romer (1927b, p. 251) stated that he could not explain "on functional grounds the peculiar construction of the ischium and postpubis in this group. The broad surface presented by the two bones affords a large external area of origin for the obturator. But this can be but a minor factor." The position in *stegosaurs* probably indicates that the abdominal muscles had not shifted their insertion to the ischium to such an extent as had occurred in ornithopods.

4. The Question of Muscle Attachment to the Lateral Surface of the Prepubic Process of *Hypsilophodon*.

Romer (1923b, 1927b) concluded that the abdominal muscles, the *M. ambiens* and the anterior part of the *M. pubo-ischio-femoralis externus* were the only muscles on the pubis of *saurischian* and *ornithischian* dinosaurs. These muscles, together with the *M. pubo-tibialis* and the *M. pubo-ischio-femoralis internus*, will be considered in this section in an attempt to determine which muscle was attached to the well-defined area on the lateral surface of the prepubic process of *Hypsilophodon* (see above p. 14 and Figs. 4, 6, 7).

a) An abdominal muscle.

As suggested above (p. 27) all three lateral abdominal muscles inserted on the ventral surface of the prepubic process. The orientation of the muscle scars on the posterior part of the lateral area of BM(NH) R193 and R5829 are at about 45° to the long axis of the prepubic process. This indicates that the muscle concerned

probably passed posteroventrally or anterodorsally. The *M. obliquus abdominis externus* may have had a posteroventral orientation so it could have occupied the lateral area. However, I think that this muscle was probably restricted to the ventral surface of the pubis. The extra insertion area for abdominal muscles on the prepubic process was probably a secondary result; certainly ratites and large herbivorous mammals manage to support their abdomen adequately without such a process.

In hypsilophodonts (Figs. 5, 6), *Psittacosaurus*, *Protoceratops* and *Leptoceratops* the prepubic process is rod-like (for figures of these and following genera, see Romer, 1927b, 1966; Colbert, 1961). In *Camptosaurus* and *Stegosaurus* the process is slightly expanded dorsoventrally. In *Iguanodon*, hadrosaurs and ceratopsians the anterior end is considerably expanded dorsoventrally, reaching its greatest extent in hadrosaurs and advanced ceratopsians (Fig. 12). Romer (1927b) correlated this with increased size and the resulting heavier strains on the obliquii muscles that supported the abdomen, because the expansion is in the plane of these muscles. However, this expansion may represent the increased size of a limb muscle, with particular emphasis on the longer fibers which originated on the more anterior part of the prepubic process. The ventral and the medial surfaces would still provide an insertion area for abdominal muscles. In most ornithischians where they are present the surface markings on the lateral surface of the prepubic process are longitudinal striations (see p. 15). Romer (1927b) cited this as evidence that the obliquii muscles inserted on this surface. However, in most of the ornithischians mentioned on page 15 the lateral surface of the anterior process of the ilium also has longitudinal striations. These were caused by the *M. ilio-tibialis* 1 and in hadrosaurs (Lull & Wright, 1942) and advanced ceratopsians (Fig. 12 and Lull, 1933) the prepubic process is similar but much larger than the anterior process of the ilium. The possibility that a limb muscle originated from the prepubic process must therefore be reconsidered.

b) *M. pubo-ischio-femoralis externus*.

In the alligator two heads of this muscle originate on the pubis and one on the ischium (Romer, 1923b); in saurischians probably one head was on each bone (Romer, 1923c). In birds there is no

posterior part but the anterior part of the *M. obturator internus* swings back with the pubis during embryonic development to become secondarily associated with the ischium (Romer, 1927a, b). This probably occurred in *Hypsilophodon* so that the *M. pubo-ischio-femoralis externus* originated from the postpubic rod and ischium as a *M. obturator internus*. As Romer (1927b) pointed out, this muscle would have had to follow a devious route from the prepubic process to reach its normal area of insertion on the posterior surface of the femur.

c) *M. ambiens*.

There are insertion markings on the dorsolateral edge of the prepubic process in *Hypsilophodon* close to the acetabular region in BM(NH) R193 (Figs. 4, 6, 7), R195 and R196. These markings, which are completely separate from the well-defined lateral area (Figs. 4, 6, 7), correspond quite closely to the position of the bump for the *M. ambiens* in *Thescelosaurus* (see p. 13). It is considered unlikely that the *M. ambiens* also originated from the well-defined area on the lateral surface of the prepubic process of *Hypsilophodon*. Romer (1927b) noted that such an anterior origin would give the *M. ambiens* a very open angle quite unlike that found in any other group; its usual archosaurian course across the knee would appear to be impractical without interference with the tendon of the *M. triceps femoris*.

d) *M. pubo-tibialis*.

This muscle is absent in crocodiles and birds so Romer (1927b) concluded that it was also absent in ornithischians but the presence of the prepubic process itself could also be denied on these same grounds. In lizards the *M. pubo-tibialis* originates between the *M. ambiens* and the *M. obliquii abdominis* which is on the *processus lateralis* (Snyder, 1954). The origin of the *M. pubo-tibialis* is also adjacent to that of the *M. ambiens* in *Sphenodon* (Gregory & Camp, 1918). If the *M. pubo-tibialis* originated on the lateral area of the prepubic process of *Hypsilophodon*, it would have had the same spatial relationships with the *M. ambiens* and *M. obliquii abdominis*. The *M. pubo-tibialis* of *Sphenodon* (and lizards) extends to the medioproximal prominence of the tibia (Gregory & Camp, 1918). In hadrosaurs and ceratopsians especially, the form

of the prepubic process resembles that of the anterior process of the ilium. It is possible that the *M. pubo-tibialis* originated on the prepubic process and inserted on the medial part of the tibial head while the *M. ilio-tibialis*, which originated more dorsally on the anterior process of the ilium, inserted on the cnemial crest (Fig. 4). Both muscles would have acted to raise the leg. This interpretation involves no change in muscle locations and, when the femur was no longer held laterally, the prepubic process was developed to give the *M. pubo-tibialis* a better leverage with an anteroposterior line of action. If the *M. pubo-tibialis* originated on the prepubic process of *Hypsilophodon*, then the absence of this process in birds could be related to the absence of a *M. pubo-tibialis*. However, the retention in *Hypsilophodon* of a muscle that has also been lost in crocodiles does pose certain problems. I consider that either this muscle or the one considered below probably originated on the lateral area of the prepubic process.

e) *M. pubo-ischio-femoralis internus*.

In its course from an origin on the centra of the posterior dorsal vertebrae to the greater trochanter of the femur this muscle passed dorsally, close to the prepubic process. Romer (1927b) stated that, despite this, it is improbable that it had any strong attachment to that element. There is a part of the *M. pubo-ischio-femoralis internus*, regarded by Romer (1927b) as a slip, that may have originated from the lateral area of the prepubic process. Romer (1927b, p. 255) noted that a part of the "ilio-femoralis internus may have followed the course normally taken by a portion of the primitive pubo-ischio-femoralis internus (and the ilio-femoralis of birds) and inserted farther down the femur towards the inner margin in the general position of the mammalian lesser trochanter. Rugosities for such an insertion have been located in specimens of *Corythosaurus*, *Triceratops*, and a few other forms, but they are generally rare and uniformly weak-appearing." The abdominal muscles inserted on the ventral surface of the prepubic process so in *Hypsilophodon* this ventral part would have passed laterally, from the dorsal centra over the prepubic process, and then ventrally to insert proximally on the shaft of the femur. This postulated course means that the ventral part of the *M. pubo-ischio-femoralis internus* wrapped around the prepubic process. It seems

more likely that it actually originated on the lateral area on the prepubic process (Figs. 4, 6, 7). The line of action of this ventral part would have been more anteroposterior if it originated on the prepubic process rather than on the centra of the posterior dorsal vertebrae. Such an origin might account for the orientation of the muscle scars on the posterior part of this lateral area. According to Romer (1927b) the muscle scars on the femur for the insertion of this ventral part are generally rare and uniformly weak. This does not necessarily prove that the muscle itself was weak as several undoubtedly powerful muscles originated from the ilium in *Hypsilophodon* but, apart from the *M. ilio-tibialis*, the areas on which these muscles originated cannot be identified. There is a large area on the anteromedial surface of the femur above the area for *M. femoro-tibialis* 2 (Figs. 8B, 9B, 10E) on which this ventral portion could have inserted by a large but fleshy attachment. Consequently, it is possible that the ventral part of the *M. pubo-ischio-femoralis internus* originated on the lateral area on the prepubic process of *Hypsilophodon*.

5. The Pelvic Girdle of Ornithischians and Birds.

The anterior process of the ilium in *Archaeopteryx* (Fig. 14 E) and primitive ornithischians (Fig. 14C) is proportionally much longer than it is in primitive saurischians (Figs. 14A, B) while in crocodiles it is practically nonexistent (Fig. 1). The *M. ilio-tibialis* 1 (*sartorius*) probably originated from the complete length of this process and was the principal long femoral protractor that inserted on the tibia and extended the knee (Fig. 4). As a result of the much longer anterior process of the ilium in ornithischians and birds, this muscle was much larger and had a better mechanical position than in saurischians. In *Archaeopteryx* the anterior process of the ilium is deep (Fig. 14E) and covers the centra of the adjacent lumbar vertebrae (Romer, 1966, fig. 253). As a result the *M. pubo-ischio-femoralis internus* of *Archaeopteryx* originated on the ilium as in modern birds. The ventral part of this muscle may have originated on the prepubic process of ornithischians, and, if this was the case, it would account for the absence of this process in birds (see above p. 16). This femoral protractor occupied a more lateral position in both *Archaeopteryx* and primitive ornithischians so that the line of action in both was fore

and aft rather than more obliquely as in crocodiles and saurischians. However, it is possible that the prepubic process was for the *M. pubo-tibialis*, a muscle lost in birds, which would have supplemented the action of the *M. ilio-tibialis 1* (see p. 14). This would also have been the case if the muscle on the prepubic process were the *M. ambiens* (see p. 13). Consequently the two femoral protractors in *Archaeopteryx* and primitive ornithischians probably occupied a position of better leverage than in saurischians and crocodiles. Saurischians probably possessed another anteriorly placed protractor, the *M. pubo-ischio-femoralis externus* (see Romer, 1923b, c), which originated from the pubis that was anteroventrally directed as in other reptiles (Fig. 14B). This muscle was probably large as in crocodiles (Figs. 1, 2) in which it is an important protractor of the femur.

It should be noted that when the pubis rotated backwards towards the ischium in birds and ornithischians the *M. pubo-ischio-femoralis externus* would have changed from a femoral protractor to a retractor. I suggest that the presumed greater development and improved mechanical position of the more anterodorsally situated protractors (the sartorius and possibly the ventral part of the *M. pubo-ischio-femoralis internus*) in *Archaeopteryx* and primitive ornithischians was necessary *before* the pubis could change position. Only when the *M. pubo-ischio-femoralis externus* was no longer essential as a femoral protractor could the pubis have come to lie close to the ischium.

As Romer (1927b) noted the pubis is directed ventrally rather than anteriorly in some primitive archosaurs. Thus in the thecodonts *Euparkeria* (Ewer, 1965), *Stagonolepis* (Walker, 1961) and *Saltoposuchus* the more distal part of the pubis is rod-like, ventrally directed and more or less perpendicular to the adjacent part of the vertebral column so the ventral part of the *M. pubo-ischio-femoralis internus* must have passed very close to the proximal part of the pubis to reach the femoral shaft. In the line of thecodonts leading to ornithischians, fibers of the ventral part of the *M. pubo-ischio-femoralis internus* probably attached to the proximal part of the pubis. The increased importance of these fibers with a more fore and aft action would have resulted in the formation of the prepubic process. When the *M. ilio-tibialis 1* and possibly the ventral part of the *M. pubo-ischio-femoralis internus* were adequately developed the *M. pubo-ischio-femoralis*

externus would no longer have been essential for protracting the femur. When this stage was reached, the pubis continued rotating backward to lie next to the ischium. In birds both muscles were on the ilium, but the result was the same with the pubis lying close to the ischium.

Depending on the degree of development of the *M. ilio-tibialis* 1 (as shown by the size of the anterior process of the ilium) it is possible that the prepubic process was quite small or even nonexistent when the pubis changed its position. In the latter case the attachment of the *M. pubo-ischio-femoralis internus* to the pubis would have occurred after this change occurred. I consider that the anterior process was probably quite long when the pubis rotated backward with quite a short prepubic process. If the muscle concerned was the *M. pubo-tibialis* then the prepubic process was probably moderately developed before the pubis changed position. It is probable that in ornithischians, as was certainly the case in birds, the development of a large anterior process of the ilium was the critical factor that enabled the pubis to lie close to the ischium.

The posterior position of the pubis in the ornithischian line would have provided a larger abdominal cavity which, as Nopcsa (1917) suggested, would be advantageous to an herbivorous animal. Romer (1927b) rejected this idea because it failed to explain why the same change occurred in birds. He related the backward shift of the pubis to a change in the position of the *M. pubo-ischio-femoralis externus* to form the *M. obturator internus*. However, this must have been a result rather than a cause. It is hard to visualize a selective force whose primary result was to convert a femoral protractor into a retractor. There would be a half-way stage when the muscle was neither but this would be no problem if other selective forces were acting. A backward extension of the effective abdominal cavity would also result in a posterior shift of the center of gravity nearer the acetabulum. This is advantageous to a bipedal animal and its importance was increased in birds in which, with the exception of *Archaeopteryx*, the tail is very short. The explanation may be even more general than this since in eutherian mammals, where the anterior part of the ilium is elongated, the anteroventral part of the pubis has been lost although it was present in earlier mammal-like reptiles. Consequently in these groups in which the femur moves anteroposteriorly

in a vertical plane the emphasis has been on the more anterodorsally situated protractors. Ornithischians achieved a less perfect mechanical system than birds or mammals because one of the protractors was still on the pubis. However, the prepubic process is more anterodorsal than the pubis of other reptiles.

In ornithischians the more posterior position of part of the pubis (postpubic rod) probably resulted in the transformation of the anterior part of the *M. pubo-ischio-femoralis externus* from a protractor to a retractor. This anterior part became a *M. obturator internus* and replaced the posterior part as Romer (1927b) noted. This change in position of the pubis also affected the abdominal muscles. The lateral abdominal muscles extended their insertion along the complete ventral edge of the pubis. The lengthened *M. rectus abdominis* became stronger and, as in the example of living reptiles (except chelonians), remained the principal supporting muscle of the abdomen. When the pubis reached a position close to the ischium the *M. rectus abdominis* and the other abdominal muscles probably transferred to the adjacent surface of the ischium to a variable degree (see above p. 28).

B. THE ANTERIOR PROCESS OF THE ILIUM

The anterior process of the ilium of *Hypsilophodon* curves out laterally (Fig. 15). This outward curvature is a general feature of the ilium of ornithischians, as can be seen from the comparative illustrations given by Romer (1927b, figs. 2-5). There are several functional reasons for this lateral curvature: a) the outward curvature resulted in the anterior process clearing the ribs of the adjacent dorsal vertebrae; b) by curving outward the anterior process presented a larger surface, set at an angle to the longitudinal axis, for the insertion of part of the *M. dorsalis trunci*, so that the lateral extent of this muscle was increased; c) the outward curvature would have given the *M. ilio-tibialis* (*sartorius*, Fig. 4) a slightly improved mechanical position, as its line of action would be more anteroposterior (Fig. 15); and d) the anterior process overhung the dorsal surface of the *M. pubo-ischio-femoralis internus* that passed from the centra of the lumbar vertebrae to the greater trochanter of the femur (Fig. 4). As a result the ventral surface of the anterior process

would have provided a potential surface of origin for this muscle. Such an origin probably did not occur in primitive ornithischians but, as Romer (1927b) suggested, it may have been important in many ceratopsians, stegosaurs and ankylosaurs.

C. THE FEMUR

1. The Greater Trochanter.

Romer correctly pointed out that the greater trochanter of saurischian (1923c) and ornithischian (1927b) femora is found almost precisely where the posteriorly inserting portion of the *M. pubo-ischio-femoralis internus* attached in primitive reptiles and crocodiles. Romer (1927b) concluded that in ornithischians the *M. pubo-ischio-femoralis internus* inserted on the greater trochanter, but he argued that the development of the antitrochanter on the ilium in hadrosaurs indicated that a second anterior femoral muscle had developed. This was the *M. ilio-trochantericus*, which probably originated on the surface of the ilium anterior to the antitrochanter in hadrosaurs. This origin closely resembles that of the *M. ilio-trochantericus* in birds, which inserts on the femur in a position similar to that of the greater trochanter of ornithischians. Thus it is reasonable to conclude that the hadrosaurian muscle inserted in the same region. Romer also (1927a, b) pointed out that the derivation and hence homology of the avian *M. ilio-trochantericus* is uncertain, because the evidence from development and comparative anatomy is inconclusive. The hadrosaurian muscle may have been derived from the *M. pubo-ischio-femoralis internus*, in which case an insertion on the greater trochanter would be expected. On the other hand, it might have been derived from the primitive *M. ilio-femoralis*, in which case an insertion on the lesser trochanter would be expected.

The ilium of hypsilophodonts does not provide any evidence concerning the differentiation of a *M. ilio-trochantericus*. Romer (1927b, p. 233) wrote that "from the point of view of the femur, however, a division into a more posterior *ilio-femoralis* and a more anterior *ilio-trochantericus* seems required (see Part V)." In Part V, when discussing the insertion of the *M. ilio-trochantericus*, Romer (1927b, p. 254) only said that the lesser trochanter,

“when well developed, points upwards and, in most positions of the limb, markedly backward, very nearly at right angles with the direction necessarily taken by most fibers of the ilio-trochantericus. It seems improbable that the ilio-trochantericus inserted on the lesser trochanter.” In his reconstruction of the musculature of *Thescelosaurus*, he showed the two muscles inserting on the greater trochanter (Fig. 16). The more posterior M. ilio-trochantericus is shown inserting on the fascia of the M. pubo-ischio-femoralis internus, the insertion of which covers the top of the greater trochanter. Romer (1927b) did not mention the presence of any insertion marks on the greater trochanter or in its immediate vicinity. Consequently, Romer did not provide any evidence to show that a M. ilio-trochantericus was differentiated in hypsilophodonts; the presence of this muscle was assumed by extrapolation from the ilium of hadrosaurs.

The lateral surface of the femoral shaft adjacent to the greater trochanter has two well-developed insertion areas that are separated by an “S” shaped ridge (Figs. 8A, 9A, 10B, see above, p. 17). This ridge was first figured by Hulke (1882, pl. 77) for BM(NH) R193 but its significance has not been commented upon. The ridge is present on all femora of *Hypsilophodon* in which this region is not damaged. This ridge is also visible on the femur of *Laosaurus minimus* (Gilmore, 1924b, pl. 2, fig. 4) and there are traces of it on the femur of *Dryosaurus altus* (YPM 1876). The origin of the M. pubo-ischio-femoralis internus was more anteriorly placed so it probably inserted on the anterior area while the M. ilio-trochantericus inserted on the posterior area (Figs. 4, 10B). The cleft between the proximal ends of the lesser and greater trochanters enabled the fascia of the M. pubo-ischio-femoralis internus to reach the inner area with less effect on the M. ilio-femoralis. This ridge at the base of the greater trochanter in *Hypsilophodon* supports Romer’s assumption that a M. ilio-trochantericus inserted on the greater trochanter of hypsilophodonts. It also supports his suggestion that this muscle in ornithischians was derived from the M. pubo-ischio-femoralis internus rather than from the primitive M. ilio-femoralis. Romer (1962, table 2) lists the avian M. ilio-trochantericus and M. ilio-femoralis internus as homologous to the reptilian M. ilio-femoralis. If this is correct then the M. ilio-trochantericus of ornithischians and birds may not be homologous.

2. The Fourth Trochanter.

Dollo (1883, 1888) first pointed out that the fourth trochanter was the area of insertion for the well-developed caudi-femoralis muscles. Romer (1927b) merely noted that the size of the fourth trochanter furnished a rough guide to the size of these muscles. In his reconstruction of *Thescelosaurus* he showed the M. caudi-femoralis brevis inserting on the proximal part of the trochanter (Fig. 16). The M. caudi-femoralis longus is shown inserting more distally with a tendon passing from the pendant end of the trochanter. The muscle to which this tendon runs is not labeled in Romer's figure but from his text it is clear that it was the M. gastrocnemius (1927b, p. 257). Romer labeled a second muscle as the M. gastrocnemius so he recognized two divisions of the M. gastrocnemius. This omission of a label in Romer's figure appears to have misled Janensch (1955) who discussed this "problem". Janensch postulated a tendon in *Dysalotosaurus* that extended from one division of the M. gastrocnemius to a distinct facet on the lateral face of the pendant end of the fourth trochanter. He reconstructed the M. caudi-femoralis longus insertion on both sides of the fourth trochanter, but noted that the more proximal insertion of the M. caudi-femoralis brevis could not be definitely placed. He also drew attention to the well-developed depression near the base of the fourth trochanter in *Dysalotosaurus* and *Hypsilophodon*.

a) Possible functions for the depression at the base of the fourth trochanter.

1) To house a mucous gland.

Janensch (1955) thought that the depression near the base of the fourth trochanter in *Dysalotosaurus* and *Hypsilophodon* was too deep and extensive to have been the insertion area of a muscle. He postulated that the depression was for a mucous gland though, as he noted, the presence of such a structure is difficult to prove in fossil material. Janensch did not suggest why a mucous gland should have been housed in a depression on the femoral shaft or what function it would have served. However, such a position is much too deep for a characteristically epidermal structure. The depression is quite deep in some femora of *Hypsilophodon*

but in others it is not (p. 19). In both types of femora an equivalent area is covered with surface markings of muscle attachments. Consequently this depression did not house a mucous gland but was the area of insertion of a muscle.

ii) Insertion area for part of the *M. pubo-ischio-femoralis internus*.

Janensch (1955) noted that on the femur of *Crocodylus niloticus*, dorsal to the wide depression on the fourth trochanter, there is another smaller depression that corresponds in position to the deep depression in *Dysalotosaurus*. He cited the figure of the alligator femur given by Romer (1923b, pl. 25) in which part of the *M. pubo-ischio-femoralis internus* is shown inserting on this region (Fig. 17). Romer (1927b) discussed this muscle (see above, p. 31) but, as Janensch (1955) noted, did not show it in the reconstruction of *Thescelosaurus*. Janensch considered that this muscle might have inserted on the deep depression on the femur of *Dysalotosaurus*.

iii) Insertion area for the *M. caudi-femoralis*.

The depression in *Hypsilophodon*, *Thescelosaurus* (Gilmore, 1915), *Camptosaurus leedsi* (Gilmore, 1909) and *Camptosaurus* (Gilmore, 1909), is partly on or close to the base of the fourth trochanter. This depression is further from the base in *Dryosaurus altus* (YPM 1876) and more markedly so in *Dysalotosaurus* where the depression is found quite anteriorly on the femoral shaft (see Janensch, 1955, pl. 15, fig. 2). Janensch (1955) recognized that the same muscle inserted on the depression is *Hypsilophodon*, *Camptosaurus* and *Dysalotosaurus* but, because it is separated by a wide space from the fourth trochanter in *Dysalotosaurus*, he considered that the depression was not for the *M. caudi-femoralis*. This depression is close to the fourth trochanter in *Iguanodon* (see Casier, 1960, pl. 10) and hadrosaurs (see Sternberg, 1924, pl. 4). I consider that the position of this depression in *Dryosaurus* and *Dysalotosaurus* is secondary and that it corresponds to the large depression at the base of the fourth trochanter on the alligator femur. Romer (1923b) showed the *M. caudi-femoralis longus* inserting on the depression at the base of the fourth trochanter in the alligator (Fig. 18). I checked the

insertion areas of the *M. caudi-femoralis longus* and *brevis* in a *Gavialis gangeticus*, the only crocodylian that was available. The adjacent parts of the *M. caudi-femoralis longus* and *brevis* are closely spaced and when they are parted the fourth trochanter is seen between them. The *M. caudi-femoralis longus* inserts on the anterior surface of the trochanter, with an especially strong insertion on the depression at its base. The *M. caudi-femoralis brevis* inserts on the posterior surface of the trochanter. Because of the different postures of these reptiles the medial view (Fig. 10D) of the femur corresponds to the anterior view in the gaval and alligator (Fig. 17). I consider that the *M. caudi-femoralis longus* inserted into this depression in *Hypsilophodon* and *Dysalotosaurus* as it does in modern Crocodylia. The areas of the femur of *Hypsilophodon* [BM(NH) R193, Figs. 4, 8, 9, 10] on which the *M. caudi-femoralis brevis* and *longus* and the tendon from the knee region attached are described on page 31.

b) The function of the fourth trochanter.

A large fourth trochanter is characteristic of many dinosaurs, especially those that are bipedal, and its size is generally considered to reflect the degree of development of the caudi-femoralis muscles (Romer, 1927b; Lull & Wright, 1942; Ostrom, 1964). In crocodiles the caudi-femoralis muscle, which is the principal retractor of the femur (Snyder, 1962), is a very large muscle (see Houghton, 1865, fig. 20) but the fourth trochanter is small (Fig. 17). However, the *pars longus*, which forms the major part of the caudi-femoralis muscle, inserts mainly on the depression at the base of the fourth trochanter. It is possible that the size of the fourth trochanter of dinosaurs reflects the degree of development of the *pars brevis* rather than that of the *longus* or the caudi-femoralis musculature as a whole. The areas of origin and insertion of the *M. caudi-femoralis brevis* and *longus* were presumably similar in all bipedal ornithischians and like those of the alligator. The area of origin of the *pars brevis* was close to the head of the femur while that of the *pars longus* extended some way down the tail. The *pars brevis* inserted at the same level as the *longus* so its line of action was at a smaller angle to the femoral shaft (Fig. 4) and, as a result, its moment arm relative to the head of the femur was much shorter. In addition,

when the femur was swung forward the moment arm of the pars brevis was shortened to a greater extent than that of the pars longus so it would have been reduced to zero sooner. Consequently the presence of a large fourth trochanter at right angles to the femoral shaft would have had a proportionally greater effect on the moment arm of the pars brevis. In normal positions of the femur the trochanter projected towards the area of origin of the pars longus and resulted in only a small increase in the moment arm of this part. Certainly an insertion on the depression on the femoral shaft would have been stronger than one on a projecting process. The moment arm of the pars longus of ornithopods is increased phylogenetically because the fourth trochanter is above the middle of the femur in hypsilophodonts, just below mid-femur length in camptosaurus and about two-thirds femur-length in iguanodonts and hadrosaurs. I consider that the function of the large fourth trochanter of dinosaurs was to increase the moment arm of the *M. caudi-femoralis brevis* during the initial part of femoral retraction. As the femur approached a vertical position the pars brevis became progressively less important while the moment arm of the pars brevis reached its maximum and its line of action became more perpendicular to the femoral shaft.

Nopcsa (1905) argued that the pendant fourth trochanter of hypsilophodonts and camptosaurus is primitive for ornithischians and that the "trochanter creté", considered by Dollo (1888) to be primitive, was a later development. However, Ostrom (personal communication) considers that the fourth trochanter of *Iguanodon* and hadrosaurs was also probably pendant. The functional significance of the pendant fourth trochanter is not certain. The space below the pendant part might have allowed a nerve, blood vessel or tendon to cross this part of the femur but there is no such structure in this region in crocodiles. In *Hypsilophodon* BM (NH) R193 (Figs. 8A, 9A, 10B) there are insertion markings on the distal surface, formed by the thick basal part of the trochanter, which were probably for part of *M. femoro-tibialis* 3 (see p. 14). Romer (1927b) noted that it is a general archosaurian tendency for the *M. femoro-tibialis* to increase in size. This origin on the fourth trochanter would have increased the moment arm of the fibers concerned, but I have not been able to find similar muscle scars on other ornithischian femora. I consider

it unlikely that the origin of part of the *M. pubo-tibialis* 3 was the primary reason for the pendant form of the trochanter. A tendon of the *M. caudi-femoralis longus* muscle probably originated from the pendant part of the trochanter (Fig. 4) and passed to the knee region as Dollo (1888) first suggested. This tendon presumably inserted on the posterior aspect of the fibula head as it does in crocodiles, lizards and *Sphenodon* (Romer, 1923b; Snyder, 1954). The pendant form of the fourth trochanter may reflect stresses transmitted by this tendon if, as was possibly the case, a head of the *M. gastrocnemius* originated from the distal part (Figs. 4, 16). The moment arm of this head, or rather the part that originated from the tendon, would have been increased slightly. Consequently the pendant nature of the fourth trochanter may reflect stresses from the distal part of the leg rather than from the caudi-femoralis muscles.

SUMMARY

The reconstruction of the pelvic musculature of *Thescelosaurus* by Romer (1927b), with certain modifications, adequately accounts for the surface markings on the very well preserved pelvic girdle and femur of *Hypsilophodon* BM(NH) R193. Using data from living forms and functional considerations it is possible to place different degrees of confidence on the various possibilities that have been discussed.

Because the prepubic process is characteristic of ornithischian dinosaurs, it is important that its functional significance be understood. The suggestion by Romer (1927a, b, 1956) that this process provided a base for the obliquii muscles, which he considered had taken over the support of the abdomen from the *M. rectus abdominis*, was very neat. This theory accounted for a unique structure in terms of a new function and, apparently, explained why this process was not developed in birds. Unfortunately *Archaeopteryx* and ratites show that it was possible to have a backwardly directed pubis with long ventral abdominal muscles not supported by either a large sternum or a prepubic process. The pubis of birds had changed position to lie close to the ischium before the very large sternum and the short abdomen were evolved. The position in birds, together with the dorsal position of the prepubic process and the probable presence of

gastralia in early ornithischians at least, indicates that the primary function of the prepubic process was not abdominal support. Any potential weakening of the abdomen that resulted from the changed position of the ornithischian pubis was probably compensated for by an increase in size of all the abdominal muscles. The three lateral abdominal muscles, the fiber directions of which formed a grid-like arrangement, probably extended their area of insertion along the ventral surface of the whole length of the pubis and, in addition, possibly on to the blade-like distal part of the ischium. The latter also provided an additional insertion area for the strong *M. rectus abdominis*. The degree of transfer of the abdominal muscles on to the ischium occurred to a varying extent in different groups of ornithischians (see above, p. 28). The abdomen of ornithischians was probably large as in ratites and herbivorous mammals and was not just a flap of skin below the pelvic girdle as Romer (1927b) suggested.

I consider it unlikely that the muscle on the lateral surface of the prepubic process was an abdominal muscle or the *M. ambiens* (p. 28). The similarity in form of the prepubic process to that of the anterior process of the ornithischian ilium and the position of the *M. pubo-tibialis* in *Sphenodon* suggest that this might be the muscle concerned. Birds lack this muscle which would account for the absence of a prepubic process in that group. The presence of the ventral part of the *M. pubo-ischio-femoralis internus* on the prepubic process would also explain the absence of this process in birds where this muscle is on the ilium (*M. ilio-femoralis internus*). The ventral part of this muscle probably originated on the prepubic process and did not wrap around the process as it would, if, as Romer (1927b) suggested, it originated on the centra of the dorsal vertebrae.

Although the postpubic rod of ornithischians probably represents the original reptilian pubis, as must be the case in birds, the functional reason for the change in position is not clear. Romer (1927b) suggested that it was related to a change in position of the anterior part of the *M. pubo-ischio-femoralis* which became the *M. obturator internus*. However, during the change in position of the pubis this muscle was converted from a femoral protractor into a retractor. I consider that the key factor in birds and ornithischians was the development of a very long anterior process to the ilium to provide a large *M. ilio-tibialis* 1. When the *M. ilio-*

tibialis 1 (possibly with the ventral part of the *M. pubo-ischio-femoralis externus* or the *M. pubo-tibialis* in ornithischians) was adequate for femoral protraction, then the anterior part of the *M. pubo-ischio-femoralis externus* would not have been required for protraction so the pubis could change its position. In ornithischians, birds and mammals emphasis was on the more anterodorsally situated femoral protractor with a more fore and aft line of action. The change in position of the ornithischian pubis would have enlarged the abdominal cavity which, as Nopcsa (1917) suggested, would have been an advantage to an herbivorous group. In addition, it would have shifted the center of gravity more posteriorly and this would have been an advantage to a bipedal animal.

The anterior process of the ilium curved laterally so that it cleared the adjacent ribs, provided both a larger area of insertion for part of the *M. dorsalis trunci* and a more fore and aft direction for the fibers of the *M. ilio-tibialis 1*. In addition the process overhung the *M. pubo-ischio-femoralis internus* and the ventral surface was an important area of origin for this muscle in stegosaurs, ankylosaurs and ceratopsians.

There are two distinct areas of muscle insertion near the base of the greater trochanter of the femora of *Hypsilophodon*. These indicate that a third dorsal muscle, analagous to the *M. ilio-trochantericus* of birds, was differentiated in hypsilophodonts as Romer (1927b) had postulated by extrapolation from the structure of the ilium in hadrosaurs. In some femora of *Hypsilophodon* the depression near the base of the fourth trochanter is well developed while in others it is not. In both cases the equivalent area has muscle insertion markings and, because the position of this depression is too deep for an epidermal structure, it is considered extremely unlikely that this depression housed a mucous gland as Janensch (1955) suggested. His second suggestion, that the depression was for the ventral part of the *M. pubo-ischio-femoralis internus*, is considered unlikely because this muscle in the alligator inserts on the shaft next to a comparable large depression. The *M. caudi-femoralis longus* inserts on the large depression in an alligator so it is reasonable to assume that this was also the case in *Hypsilophodon*. The degree of development of the fourth trochanter is probably not related to the size of the caudi-femoralis musculature as a whole. The function of the large

fourth trochanter of bipedal dinosaurs was to lengthen the moment arm of the *M. caudi-femoralis brevis* during the first part of femoral retraction. The pendant form of the fourth trochanter of ornithopods may reflect the stresses from part of the *M. gastrocnemius* that attached to the tendon connecting the trochanter to the fibula.

ACKNOWLEDGEMENTS

Much of this paper is based on work done at the Zoology Department, King's College, University of London, England, made possible by a three year Research Studentship from the Department of Scientific and Industrial Research (subsequently the Natural Environment Research Council). I am especially grateful to Dr. C. B. Cox for all his advice and interest during the course of this work and to the British Museum (Natural History) for permission to borrow their unique material of *Hypsilophodon* and prepare it in acetic acid. The final paper has been much improved thanks to the criticisms and suggestions of Dr. J. H. Ostrom of Yale University. The manuscript was also read by Dr. A. W. Crompton, Mr. F. A. Jenkins, Jr. and Mr. R. T. B. Bakker, all of Yale University; Dr. G. E. Erickson of Brown University, Providence, R.I., and Dr. D. A. Russell of the National Museum of Canada, Ottawa; all of whose comments were much appreciated.

I am very grateful to people in the various museums for their help while studying the material under their care as cited in the text: to Dr. A. J. Charig of the British Museum (Natural History); Dr. E. H. Colbert of the American Museum of Natural History, who also kindly supplied the original for Figure 12; Drs. A. W. Crompton and J. H. Ostrom of the Peabody Museum of Yale University; Dr. A. G. Edmund of the Royal Ontario Museum, Ontario and Dr. D. A. Russell of the National Museum of Canada. Last but not least, my thanks must go to Dr. A. S. Romer of the Museum of Comparative Zoology, Harvard University who, as must be rather obvious by now, provided most of the information upon which this paper is based.

ABBREVIATIONS

Unless indicated to the contrary all figures show bones from the left side; Figures 4, 6, 7-11 and 13 have been printed in reverse.

The museum names have been abbreviated as follows:

AMNH	American Museum of Natural History, New York.
BM(NH)	British Museum (Natural History), London.
NMC	National Museum of Canada, Ottawa.
USNM	United States National Museum, Washington, D.C.
YPM	Peabody Museum, Yale University, New Haven.

The structures indicated in Figures, 5, 10, 13 and 15 are as follows:

acet — acetabulum	obt proc — obturator process
ant proc — anterior process	po rod — postpubic rod
br sh — brevis shelf	pre proc — prepubic process
gr troc — greater trochanter	4th troc — fourth trochanter
les tro — lesser trochanter	

The muscles have been abbreviated as follows:

ACC	— M. accessory obturator
ADD	— M. adductor femoralis
AMB	— M. ambiens
CA-FEM BR	— M. caudi-femoralis brevis
CA-FEM L	— M. caudi-femoralis longus
CA-IL-F	— M. caudi-ilio-fibularis
DOR CA	— M. dorsalis caudae
DOR T	— M. dorsalis trunci
FEM-T 1, 2 & 3	— M. femoro-tibialis 1, 2 & 3
F T E	— M. flexor tibialis externus
F T I	— M. flexor tibialis internus
G	— M. gastrocnemius
IL-CAUD	— M. ilio-caudalis
IL-COST	— M. ilio-costalis
IL-FEM	— M. ilio-femoralis
IL-FEM EXT	— M. ilio-femoralis externus
IL-FEM INT	— M. ilio-femoralis internus

IL-FIB	— M. ilio-fibularis
IL-TIB 1 & 2	— M. ilio-tibialis 1 (sartorius) & 2
IL-TROC	— M. ilio-trochantericus
IS-CAUD	— M. ischio-caudalis
IS-FLEX	— M. ischio-flexorius
IS-TROC	— M. ischio-trochantericus
LIG	— ligaments for holding head in acetabulum
O A EXT	— M. obliquus abdominis externus
O A INT	— M. obliquus abdominis internus
OBL	— M. obliquus abdominis
OBT	— M. obturator internus (anterior part of P-I-F E)
P-I-F	— M. pubo-ischio-femoralis
P-I-F E	— M. pubo-ischio-femoralis externus
P-I-F INT 1	— dorsal part of M. pubo-ischio-femoralis internus
P-I-F INT 2	— ventral part of M. pubo-ischio-femoralis internus
P-TIB	— M. pubo-tibialis
R ABD	— M. rectus abdominis
TND	— tendon inserting on fibula
TR A	— M. transversus abdominis
TR P	— M. transversus perinei

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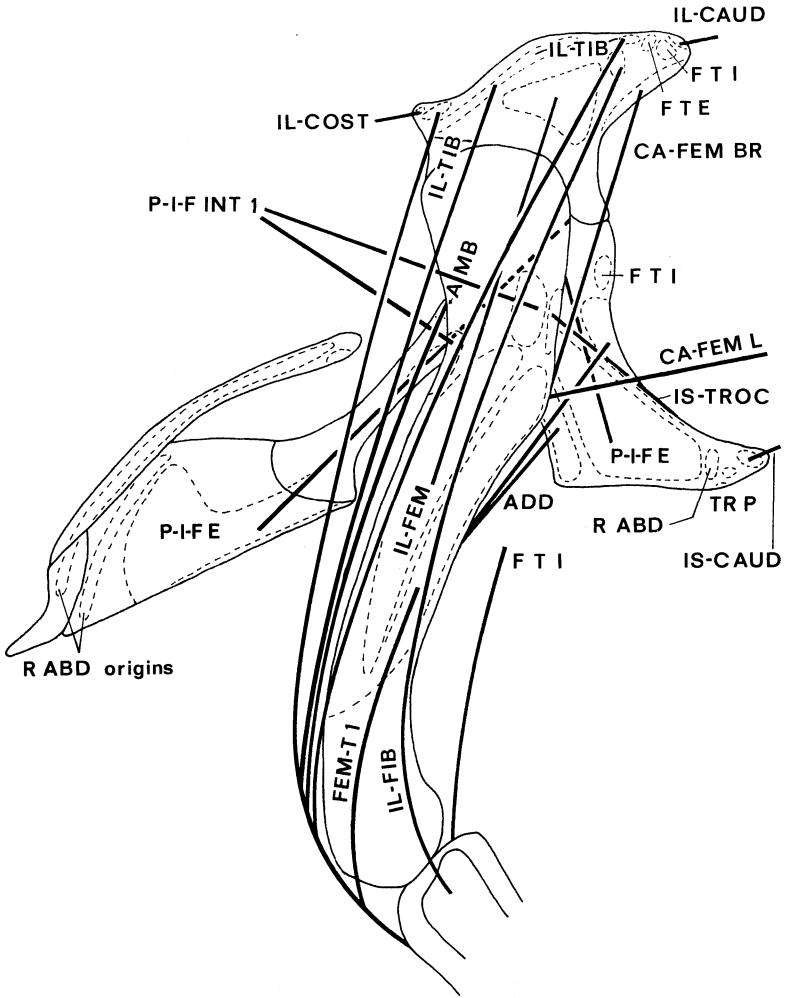


FIG. 1. Pelvic region of *Alligator mississippiensis* showing the areas of muscle attachment visible in lateral view and the lines of action of most of the muscles. Femur shown under the body in a position comparable to that of birds and dinosaurs. Data from Romer (1923b, pls. 19-25). Abbreviations on p. 46.

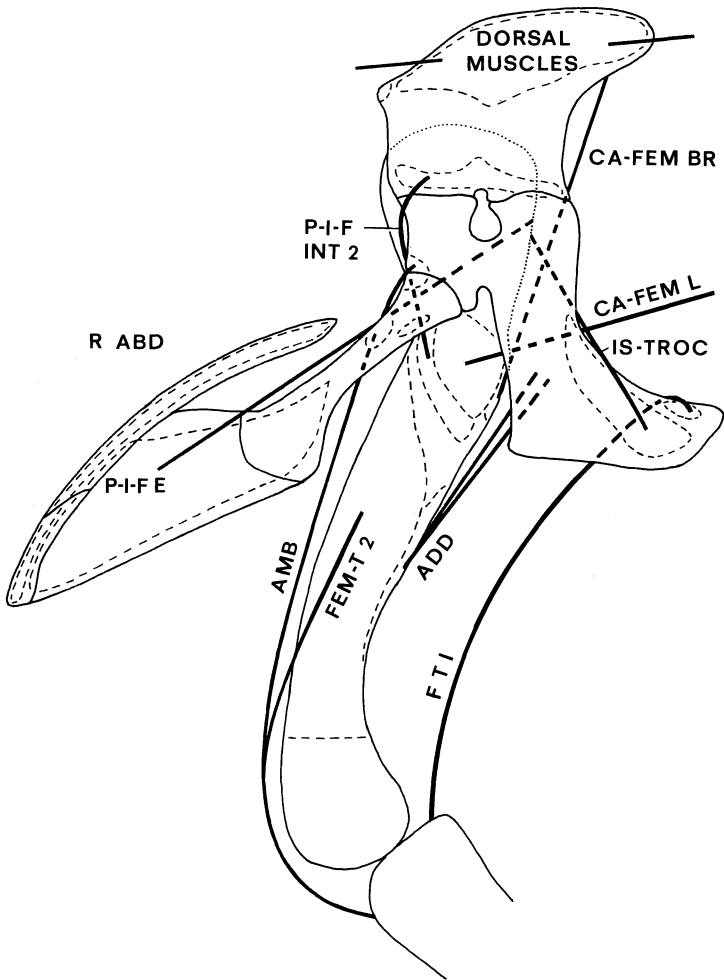


FIG. 2. Pelvic region of the alligator showing the line of action of the muscles whose area of attachment is visible in the medial view of the right side. Compare with Figure 1. Data from Romer (1923b, pls. 19-25). Abbreviations on p. 46.

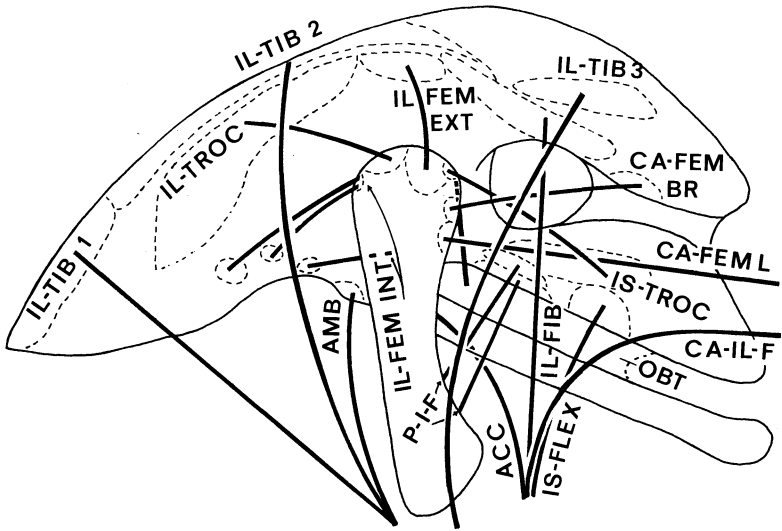


FIG. 3. Pelvic region of an eight day old chick to show attachment areas. Data from Romer (1927a, figs. 5, 5a, 5b; 1927b, fig. 1). Abbreviations on p. 46.

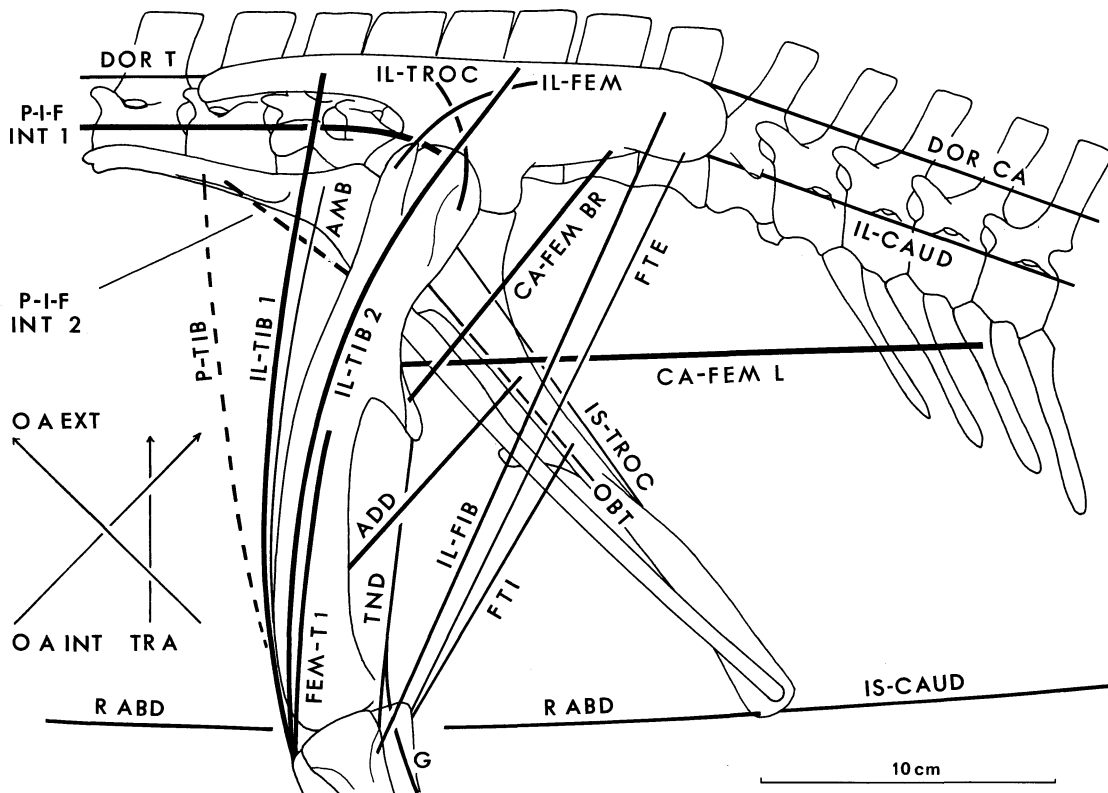


FIG. 4. Reconstruction of the pelvic region of *Hypsilophodon* showing the lines of action of the individual muscles. Data from BM(NH) R193, R196, R5830 and 28707. Abbreviations on p. 46.

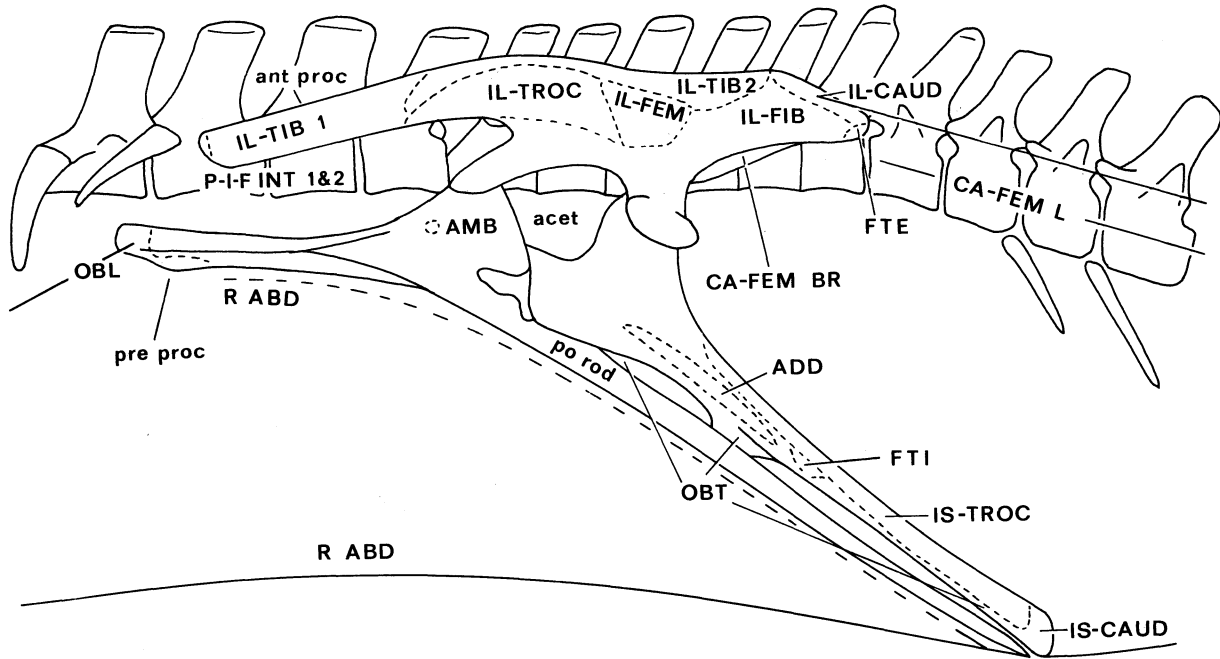


FIG. 5. Pelvic girdle of *Thescelosaurus* showing areas of attachment of pelvic muscles. Data from Romer (1927b, figs. 14-18). Abbreviations on p. 46.

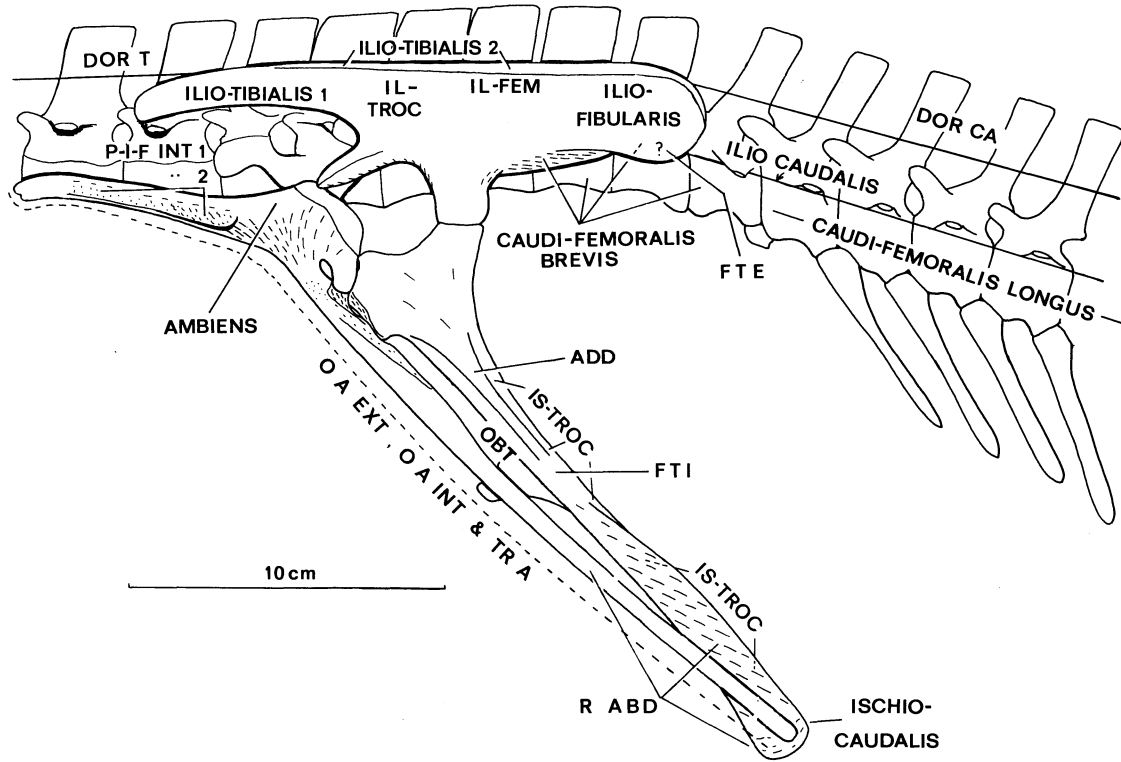


FIG. 6. Pelvic girdle of *Hysilophodon*, BM(NH) R193, showing the areas of attachment of the individual muscles. Data also from BM(NH) R196 and 28707. Abbreviations on p. 46.



FIG. 7. Pubis and ischium of *Hypsilophodon*, BM(NH) R193. Compare with Figure 6. The scale is 10 cm.

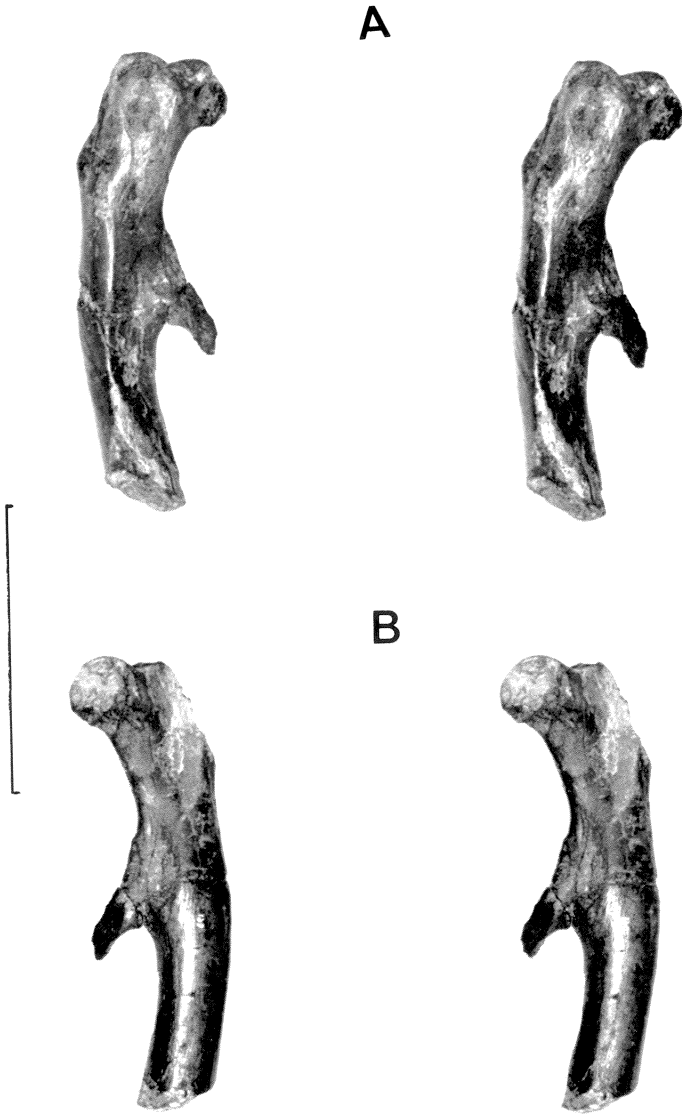


FIG. 8. Femur of *Hypsilophodon*, BM(NH) R193. A. Anteromedial view. B. Posterolateral view. Compare with Figure 9. The scale is 10 cm.

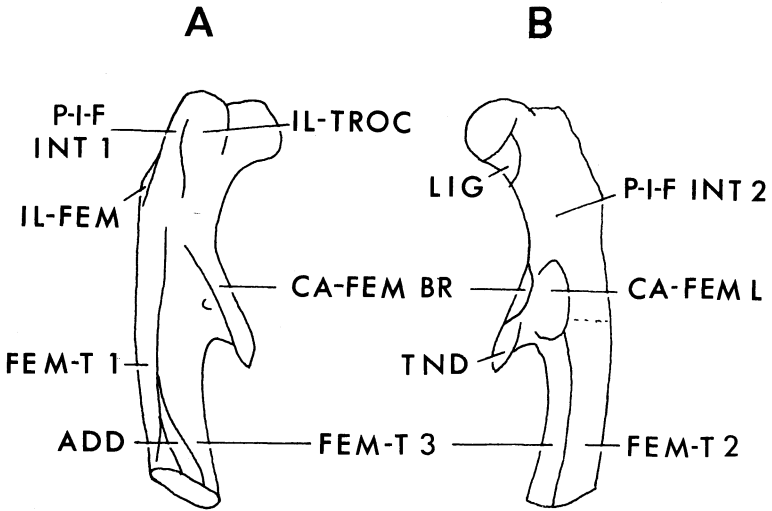


FIG. 9. Diagrams showing the attachment areas in the stereo-photographs of Figure 8, A and B. Abbreviations on p. 46.

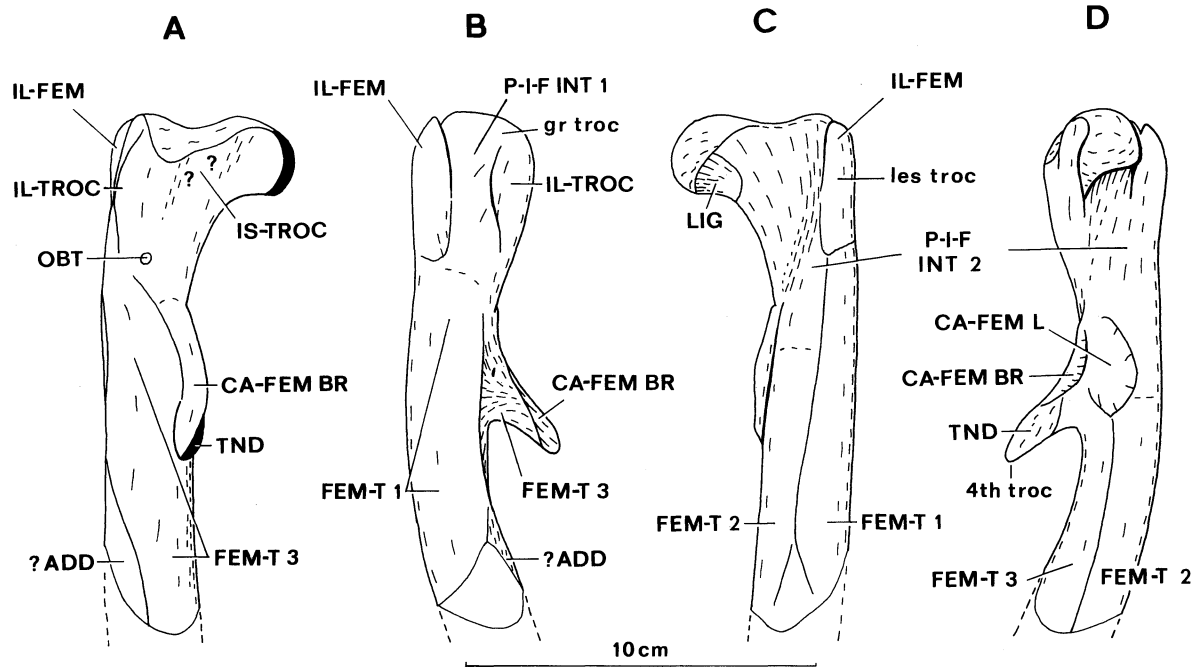


FIG. 10. Femur of *Hypsilophodon*, BM(NH) R193, showing the areas of attachment of the limb muscles. Data also from BM(NH) R196 and R5830. A. Posterior view, B. Lateral view, C. Anterior view, D. Medial view. Abbreviations on p. 46.

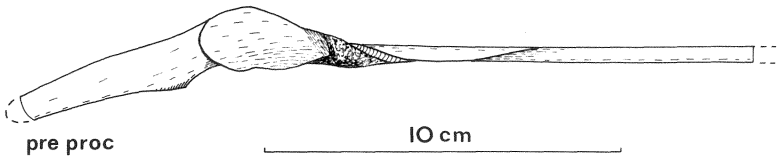


FIG. 11. Pubis of *Hypsilophodon* in dorsal view, BM(NH) R193.

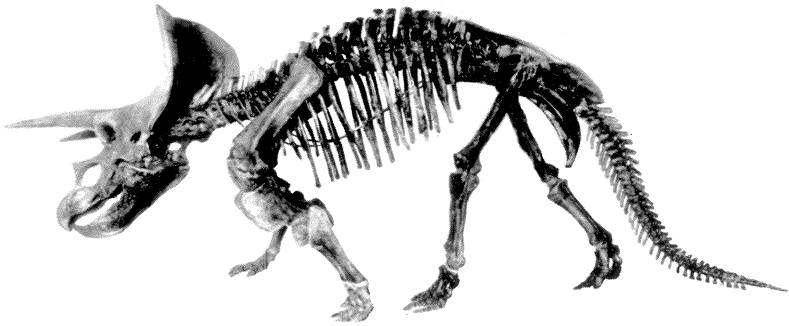


FIG. 12. Skeleton of *Triceratops* cf. *elatus*, AMNH 5116, 5033, 5039, 5095. Original about 20' or 6.2 meters. Courtesy of the American Museum of Natural History.



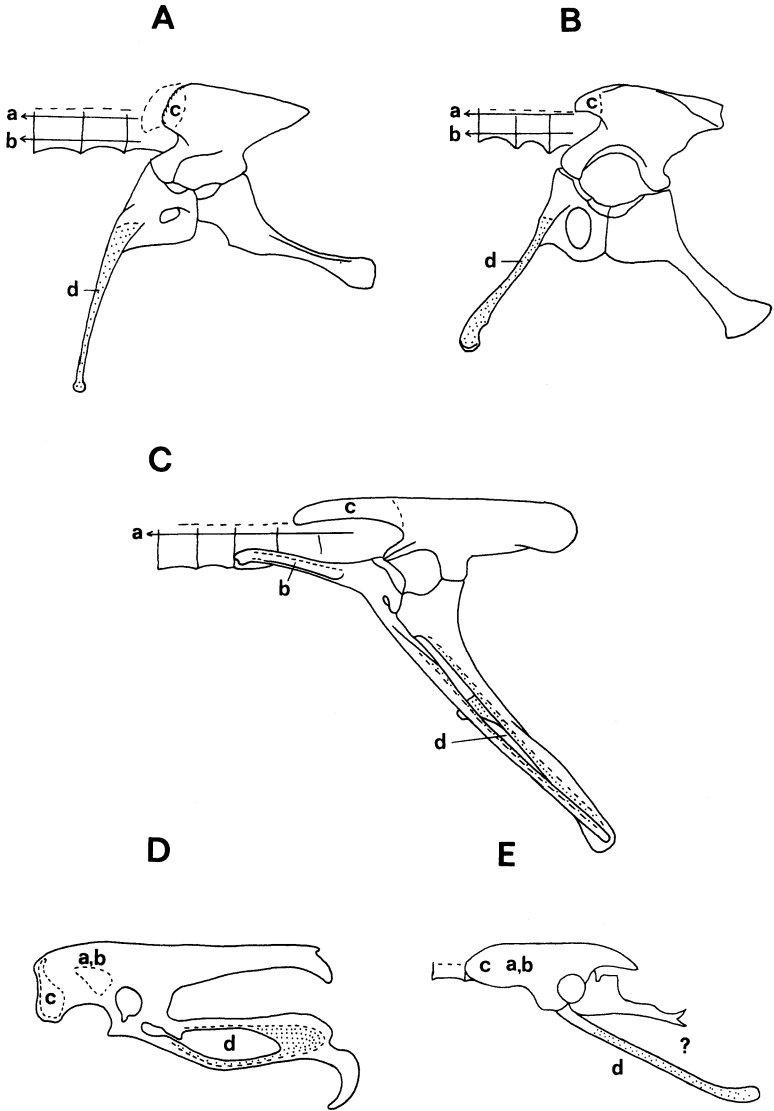
FIG. 13. Ischium of *Hypsilophodon* in ventral view, BM(NH) R193. Abbreviations on p. 46.

FIG. 14. Diagrams showing attachment areas of certain pelvic muscles in archosaurs.

- A *Ornithosuchus* — Saurischia — Carnosauria (after Walker, 1964). The dotted part of the ilium represents a cartilaginous extension whose precise size and outline cannot be determined. As shown, it resembles *Tyrannosaurus*.
- B *Plateosaurus* — Saurischia — Prosauropoda (after von Huene, 1926).
- C *Hypsilophodon* — Ornithischia — Ornithopoda.
- D *Struthio* — Aves — ratite (after Gregory & Camp, 1918, and Romer, 1923a).
- E *Archaeopteryx* — Aves (after Heilmann, 1926) The question mark indicates the possibility of a cartilaginous extension to the ischium but its form is not known.

Abbreviations used in this figure:

a. dorsal part of *M. pubo-ischio-femoralis internus*. b. ventral part of the *M. pubo-ischio-femoralis internus*. In D and E these two parts form the *M. ilio-femoralis internus*. c. *M. ilio-tibialis 1* (*sartorius*). d. anterior part of *M. pubo-ischio-femoralis externus*. In C-E this is the *M. obturator internus* that replaced the posterior part.



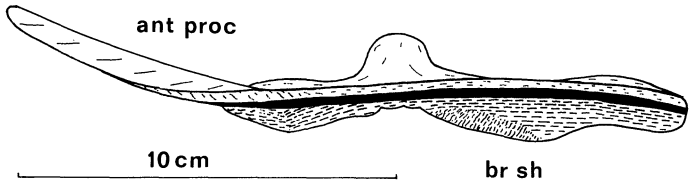


FIG. 15. Right ilium of *Hysilophodon*, BM(NH) R193. Dorsal view. Abbreviations on p. 46.

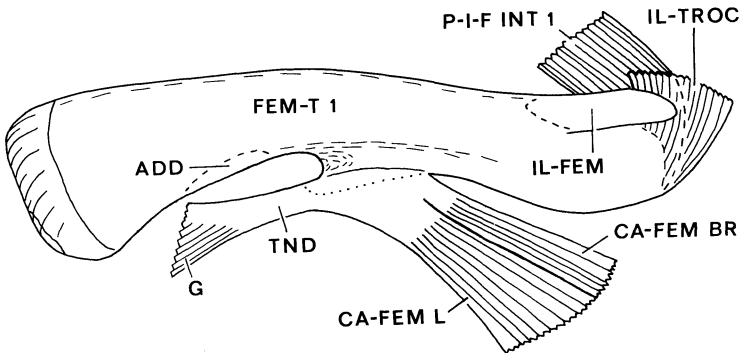


FIG. 16. Femur of *Thescelosaurus* showing areas of insertion of the pelvic muscles. Data from Romer (1927b, figs. 16-18). Abbreviations on p. 46.

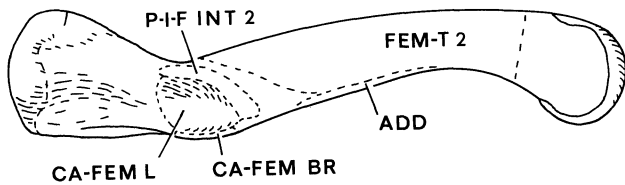


FIG. 17. Femur of *Alligator* showing areas of muscle attachment. Ventral view based on Romer (1923b, pl. 25). Abbreviations on p. 46.

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