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Article XIX.—THE PELVIC MUSCULATURE OF SAURISCHIAN DINOSAURS

By Alfred S. Romer

Von Huene in 1908 first attempted the restoration of the musculature of the pelvic region of the Saurischia. Gregory and Camp ten years later figured the pelvis of *Ornitholestes*, a member of this group, with a tentative localization of the muscular areas of origin. Subsequently, the dinosaurian pelvis was restudied by Dr. W. K. Gregory and a number of illustrations prepared. Through the kindness of Dr. Gregory, I am permitted to publish two of his figures relating to the Saurischia here (Fig. 1). They will be discussed in the body of this paper.

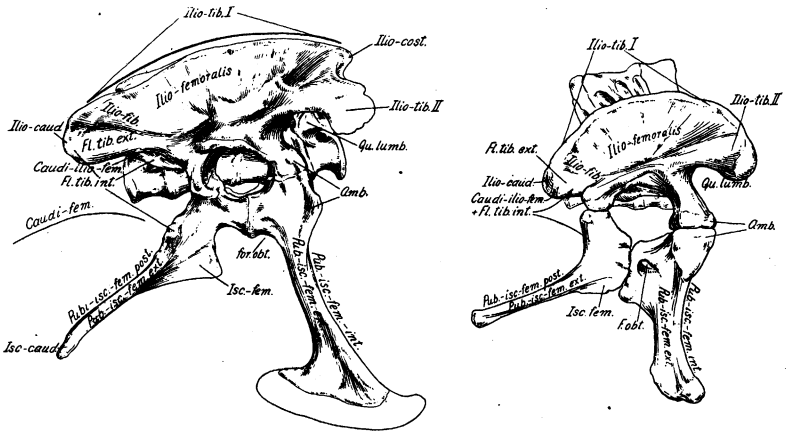

Fig. 1. Previously unpublished restorations of the pelvis in saurischian dinosaurs by Dr. W. K. Gregory. For explanation see text.

Lack of knowledge of the nature of the crocodilian musculature, however, handicapped these attempts to restore the dinosaur pelvis. In order to remove this obstacle the writer has made a study of the pelvic muscles of the Crocodilia, the results of which have recently appeared in this bulletin (1923*a*). The present paper is an attempt to apply the information gained to the musculature of the Saurischia. The nomenclature adopted in my previous paper will be followed here.

The ilium of the Saurischians presents few major difficulties; I have previously outlined its history (1923). The type of ilium present in the primitive forms from which the "Archosauria" have been derived is represented morphologically by such a reptile as *Dimetrodon* (Fig. 2).

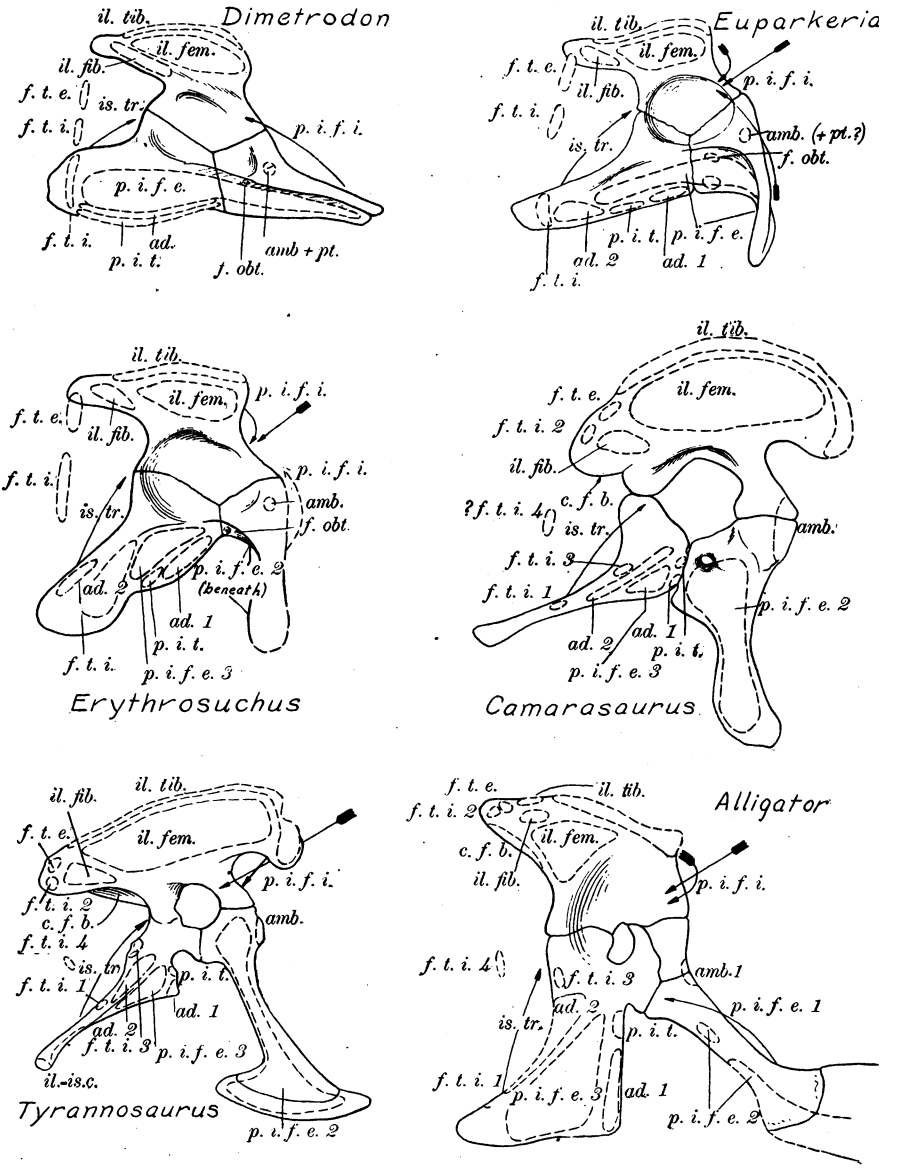

Fig. 2. The musculature of the pelvis in primitive reptiles, the primitive "Archosauria," *Alligator* and saurischian dinosaurs, to show especially the steps in the differentiation of the pubo-ischium.

Abbreviations: *ad.*, adductor; *amb.*, ambiens; *c.f.b.*, coccygeo-femoralis brevis; *c.f.l.*, coccygeo-femoralis longus; *f.obt.*, obturator foramen; *f.t.*, femoro-tibialis; *f.t.e.*, flexor tibialis externus; *f.t.i.*, flexor tibialis internus; *il. fem.*, ilio-femoralis; *il. fib.*, ilio-fibularis; *il.tib.*, ilio-tibialis; *is.tr.*, ischio-trochantericus; *p.i.f.e.*, pubo-ischio-femoralis externus; *p.i.f.i.*, pubo-ischio-femoralis internus; *p.t.* pubo-tibialis.

It had a broad outer surface extending little, if at all, anterior to the acetabulum. The greater part of this surface was utilized as an area of origin by the ilio-femoralis, while the ilio-tibialis arose tendinously from its dorsal edge. Near the posterior angle was the origin of the ilio-fibularis. The saurischian ilium is comparatively little modified. The external surface is carried forward a short distance without changing the muscular arrangements on its outer surface. This anterior prolongation arches over the pubo-ischio-femoralis internus, a small portion of which arises from the anterior edge of the ilium. Posteriorly, in the Saurischia, portions of the long flexors have gained attachment to the bone, as discussed below. Ventro-posteriorly, the coccygeo-femoralis brevis had an area of origin.

In primitive reptiles (Romer, 1922, p. 578) such as *Dimetrodon*, the pubo-ischium was a solid plate, broken only by the foramen for the obturator nerve, with a continuous ventral symphysis extending in an almost straight line antero-posteriorly. Three principal muscle groups arose from the outer surface of the plate. Externally were the long flexors to the lower leg (pubo-ischio-tibialis, flexor tibialis internus, flexor tibialis externus). Deep to these lay the adductor, running to the distal part of the femur. Still deeper lay the pubo-ischio-femoralis externus, attaching to the proximal part of the femur. That portion of the pubis close to the acetabulum gave origin to the ambiens (a member of the quadriceps group) and to the pubo-tibialis (an anterior member of the long flexor series). Internally the pubis was covered by the pubo-ischio-femoralis internus, which ran up and back to emerge on to the thigh above the ambiens. The ischio-trochantericus took origin from the inner surface of the ischium.

The three chief muscle groups arising from the outer surface of the plate have been greatly modified in the "Archosauria," as known in the Crocodilia and as deduced from the dinosaur pelvis. These changes appear to be correlated with changes in the position of the femur.

In the primitive reptiles, the femur was extended very nearly straight out from the acetabulum in a horizontal direction. The three muscle masses of the plate acted upon it in a plane passing nearly vertically through its long axis, as diagrammatically represented in figure 3.

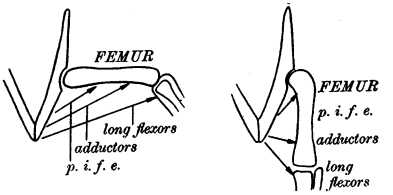

Fig. 3. Diagram to show effects upon the muscles of the pubo-ischium of the change in the femur from the primitive (left) to the archosaurian position (right).

In the "Archosauria," with a higher type of locomotion, the femur (1) has been turned inward anteriorly so as to bring its shaft to a position nearly parallel to the long axis of the body and (2) has, in consequence of the bipedal character of primitive saurischians, been carried downwards and backwards so that, if the primitive plate-like pubo-ischium had been retained, the femur would lie very close to the plate.

The results of such a position on the musculature of the pubo-ischium are obvious from the diagram on the right in figure 3. The long flexors and adductors would be excessively shortened and rendered of little value, especially if situated near the middle of the plate. To correct this, a movement of the areas of origin upwards might be deduced. Further, the main pull of these muscles is now a backward one; a backward migration or a disappearance of anterior portions of these muscles might be expected.

With regard to pubo-ischio-femoralis externus, no movement to a more dorsal position is possible. It is clear, however, that the middle portion of the muscle is at a disadvantage as compared with its anterior and posterior extremities, and the development of anterior and posterior heads of the muscle and the disappearance of the middle portion might perhaps be suggested.

The development of this series of modifications is shown, somewhat diagrammatically, in figure 2. *Dimetrodon* shows the primitive condition; the alligator and sauropod and theropod dinosaurs show the end forms. In the dinosaurs, the muscle areas can be located with almost the same degree of accuracy as in *Alligator*, except that I am unable to locate exactly the origins of pubo-ischio-tibialis and adductor 1 in the theropods. *Euparkeria* and *Erythrosuchus* from the figures of Broom (1906, 1913) are introduced to show the steps by which the changes have taken place, although I am unable to locate exact muscle areas on these forms.

It will be noted that the main change in the form of the pelvis has been a "buckling" of the pubo-ischium, by which the ventral border has been changed from a straight line to an irregular crescent, convex above. Thus the middle part of the pubo-ischium, functionally of the least value, has disappeared.

The apparent "fenestra" caused by this is not at all homologous with the obturator fenestra of other modern reptiles or the obturator foramen of mammals. These openings are essentially a fenestration within the primitive plate, centering about the pubo-ischio-femoralis externus (obturator externus); the line of the symphysis is ventral to the fenestra. In the "Archosauria," on the other hand, the symphysis

turns dorsally as the "buckling" takes place and is continuous in such a form as *Erythrosuchus;* the apparent "fenestra" is ventral to the symphysis. Later, apparently in connection with the strengthening of the sacrum, the primitive symphysis is interrupted and confined to separate pubic and ischiadic surfaces. Hence the ventral edge of the pubis and ischium of the Crocodilia and Saurischia may be considered as the equivalent of the primitive symphysis. Parallels to the obturator fenestra may be sought in excavations in the surface of the ischium in the part of that bone serving as an area of origin for pubo-ischio-femoralis 3 (as in *Ornitholestes*).

If we take a line from the distal end of the ischium to the distal end of the pubis as marking the ventral line of the body, it will be seen that in the saurischian dinosaurs, the muscles of the ischium as a whole are located farther dorsally than in primitive forms or even in the Crocodilia. If the lower half of the saurischian ischium were removed, the remaining triangular area would be almost exactly comparable to the whole of the ischium in the Crocodilia. Such a dorsal movement, as has been noted previously, might be expected in bipedal forms, or those whose ancestors were bipedal.

The pubis of primitive reptiles seems homologous with that of such primitive archosaurians as *Euparkeria* and *Erythrosuchus*. These in turn are similar to the sauropods as regards the pubis; while the theropods have merely carried the reduction farther and eliminated the obturator foramen. In the Crocodilia, further reduction has caused the exclusion of the bone from the acetabulum. But this reduced crocodilian pubis can apparently be carried back through a series showing slight morphological changes to that of the primitive reptiles.

Von Huene (1908) states that the much smaller number of muscles attached to the crocodilian pubis, as compared with that of other living reptiles, tends to show that the crocodilian bone is not the true pubis. But the reasons for a reduction in muscle on the pubis are apparent. In typical reptiles six appendicular muscles may take origin from the pubis: pubo-ischio-femoralis internus, pubo-ischio-femoralis externus, ambiens, pubo-tibialis, adductor and pubo-ischio-tibialis. Of these, the pubo-ischio-femoralis internus has shifted dorsally, as I have explained elsewhere (1923, 1923*a*), the pubo-tibialis has been lost, and the adductor and pubo-ischio-tibialis have shifted (as expected) posteriorly. This leaves the ambiens and pubo-ischio-femoralis externus as the only possible muscles which might be expected on the pubis in the Crocodilia; and it is these two muscles which are found on the bone commonly called by that name.

The rearrangement of the musculature may now be considered in detail.

The long flexors, as I have termed them, consist essentially of two sets in a primitive reptile. (1) An outer group, made of pubo-ischio-tibialis, from the ventral edge of the pubo-ischium, and a portion or portions of the flexor tibialis internus originating from the region near the posterior ventral angle of the ischium or the lower end of the ilio-ischiadic ligament. (2) An inner group, consisting of pubo-tibialis, from the pubis near the acetabulum, of a portion of flexor tibialis internus from the region mentioned above, and of the flexor tibialis externus, from the ilio-ischiadic ligament dorsal to the last mentioned.

These muscles have, for the most part, moved posteriorly or dorsally as expected. Pubo-ischio-tibialis, one of the most anterior members of this group, has been reduced, confined posteriorly to the ischium and, further, has moved dorsally to a position just below the acetabulum on the anterior edge of the ischium. In doing this it has not only entered between the two main heads of pubo-ischio-femoralis externus but, as its course shows, has broken in on to the ischium so as to separate the two heads of the adductor. One portion of flexor tibialis internus (1) is in its primitive position in the alligator; but in the Saurischia its origin is only about halfway down the posterior edge of the ischium. A second portion of flexor tibialis internus (2) has moved dorsally and gained an origin from the ilium.

Of the deeper set, the most anterior member, the pubo-tibialis, has disappeared entirely. The remaining members of the group are posterior and dorsal in position, flexor tibialis internus 3 having migrated up along the posterior margin of the ischium, part 4 having migrated up along the ilio-ischiadic ligament (in the Crocodilia at least; its existence in the Saurischia cannot, of course, be proved) and flexor tibialis externus having moved dorsally to the ilium.

The adductor musculature has also moved somewhat posteriorly and dorsally. It is divided into two portions, both arising from the ischium and not at all from the pubis. In the dinosaurs, the small size of the part of the ischium devoted to appendicular muscles has brought the adductors halfway from the original ventral line to the acetabulum. This is not true of the Crocodilia; but even here, by the division into two parts, both (especially the posterior) have pushed upwards on either side of pubo-ischio femoralis externus 3 so that they extend some distance dorsally along either edge of the ischium.

Pubo-ischio-femoralis externus, as has been mentioned above, cannot move dorsally. Its differentiation has consisted in a division into

two main portions, part 2 from the outer surface of the pubis, and part 3 from the outer surface of the ischium.

In addition, the Crocodilia possess an additional head (part 1) from the inner surface of the pubis, emerging (in contradistinction to pubo-ischio-femoralis internus) below, rather than above, the ambiens, and joining part 2, of which it is a derivative. This muscle is not found in other living reptiles; and it was apparently also absent in primitive forms. The region through which it passes from the internal to the external surface of the pubis is usually occupied by the insertion of the rectus in modern reptiles. In the Crocodilia, the rectus inserts mainly into the strong last abdominal rib and this leaves the edge of the pubis free for the passage of the muscle. Its existence depends then upon the presence of a strong abdominal rib paralleling the pubis. As far as I know, this condition is not found in the Saurischians. For example, a specimen of *Struthiomimus* in this museum has a well-preserved "abdominal basket," extending to the pelvis; but there is no noticeable strengthening posteriorly. In default of such evidence it seems probable that pubo-ischio-femoralis 1 of the Crocodilia was not present in the Saurischia.

As I have shown previously, the pubo-ischio-femoralis internus has retreated from the interior of the pubic region in the "Archosauria."

The ambiens remained in position near its primitive place of origin from the pubis near the acetabulum. The ischio-trochantericus also appears to have been unchanged. The coccygeo-femoral muscles appear to have been well developed. The "fourth trochanter" for the insertion of coccygeo-femoralis longus on to the femur is well marked. There is an excavation beneath the posterior end of the ilium for the origin of part of coccygeo-femoralis brevis.

In a number of cases areas of origin from the pubis and ischium are absolutely determinable in saurischian dinosaurs; and in every case they agree closely with the conditions found in the Crocodilia. The tendinous origin of flexor tibialis internus 3 is seen on almost every theropod pelvis; it was apparently a large muscle. That of flexor tibialis externus 1 is shown on several specimens. These two origins are also to be observed on a specimen of *Diplodocus* in this museum. In *Tyrannosaurus* an outward curving of the antero-ventral corner of the ischium is comparable to the region from which adductor 1 arises in the alligator. And in a mounted specimen of *Tyrannosaurus* the origin of pubo-ischio-tibialis may be seen. With these landmarks the areas of origin of pubo-ischio-femoralis externus 3 and adductor 2 may be determined with reasonable

accuracy. A tuberosity on the pubis (or pubis and ilium) is usually present and indicates the site of the ambiens.

In figures 4–8 a restoration of the pelvic musculature of *Tyrannosaurus* has been attempted. It is, of course, impossible to be sure of a number of points, such as the subdivisions of the ilio-tibialis or ambiens or the arrangement of the tendons at the knee. Where there has been doubt the crocodilian arrangement has been followed as being the most probable in

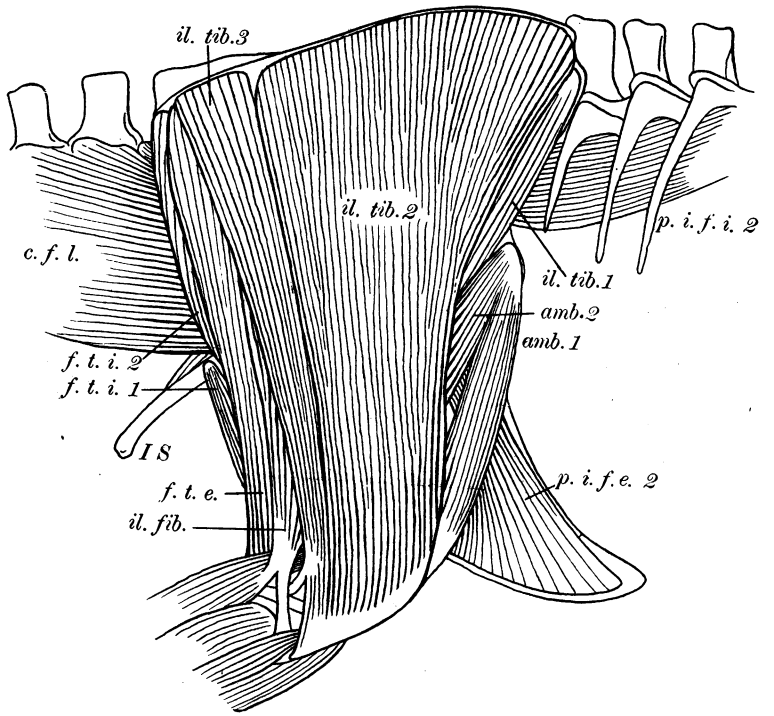

Fig. 4. Lateral view of pelvic region of *Tyrannosaurus* (right side) with the appendicular muscles restored. For abbreviations, see Fig. 2.

view of the close similarity in all known points. The muscles were restored in clay on a reduced model of the pelvic region. In the figures the axial musculature has been omitted to avoid too great a complexity. Its relations to the girdle are simple.

The dorsal musculature was primitively continuous, universally attaching itself to the inner surface of the ilium above the ribs and to the anterior (ilio-costalis) and posterior margins of this bone. This was true

of the sauropods and some theropods, as *Ornitholestes*. In *Tyrannosaurus* the two ilia are applied to the spines, separating caudal and trunk portions. Huge rugose surfaces on the posterior end of the ilium of *Brontosaurus* and *Tyrannosaurus* and surfaces on a line with these on the transverse processes of the caudal vertebræ indicate strong ligaments running longitudinally in this region and separating the dorsal tail

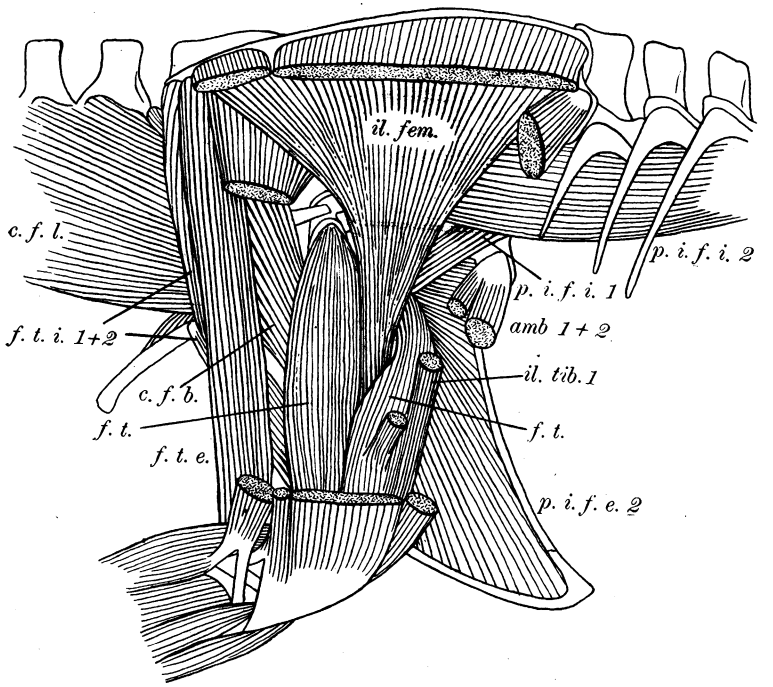

Fig. 5. Same as Fig. 4, but ilio-tibialis, ambiens and ilio-fibularis have been cut.

musculature (dorsalis caudæ) from the ventral (ilio-ischio-caudalis). The ilio-caudalis undoubtedly attached to the lower edge of this ligament and perhaps along its lower margin reached the ilium.

Antero-ventrally, the rectus attached to the extremity of the pubis, or rather its cartilaginous extension, and probably, as mentioned above, to the anterior edge of the body of the pubis. The obliquus externus probably attached tendinously in the neighborhood of the ambiens, as is usually the case in reptiles, and (through its connection with the rectus) to the pubis. Postero-ventrally, the ischio-caudalis arose from the distal portion of the ischium, as did undoubtedly part of the cloacal musculature.

A number of criticisms may be made of the restorations of the musculature of Triassic dinosaurs by Von Huene (1908); as I have mentioned most of these are due to our inadequate knowledge of the Crocodilia. On the ilium (p. 291) no origin is afforded for ilio-tibialis (except as we consider ilio-fibularis 1 as part of this muscle). Ilio-fibularis was probably farther posterior and ventral. Ilio-femoralis (externus) was prob-

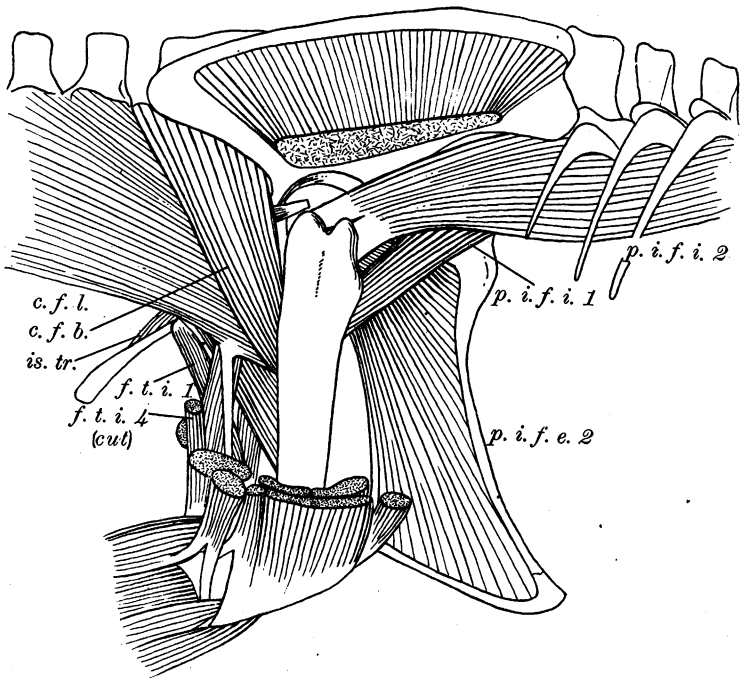

Fig. 6. Same as Fig. 5, with ilio-femoralis, flexor tibialis externus, flexor tibialis 2, and femoro-tibialis removed.

ably larger. On the pubis (p. 292) the "pubo-tibialis" insertion may have been either for part of ambiens or a tendon of the obliquus: there is no pubo-tibialis in the Crocodilia nor in birds. In regard to the ischium (p. 293) there is never, of course, any origin of the extensor ilio-tibialis from this bone. Pubo-ischio-femoralis externus (3) and ischio-femoralis (adductor 1) are correctly placed. Flexor tibialis internus 2 is incorrectly located, and locations for pubo-ischio-tibialis and flexor tibialis internus 1 and 3 of the writer are not indicated. Pubo-ischio-femoralis posterior, if equivalent to the writer's ischio-trochantericus,

should be on the upper internal instead of the ventral external portion of the bone. The ischio-caudalis should be restricted to the distal portion of the bone.

The femur (p. 295). The ilio-femoralis (externus), "quadratus lumborum," and pubo-ischio-femoralis posterior are shown attaching to the greater trochanter. The first is undoubtedly correct. "Quadratus

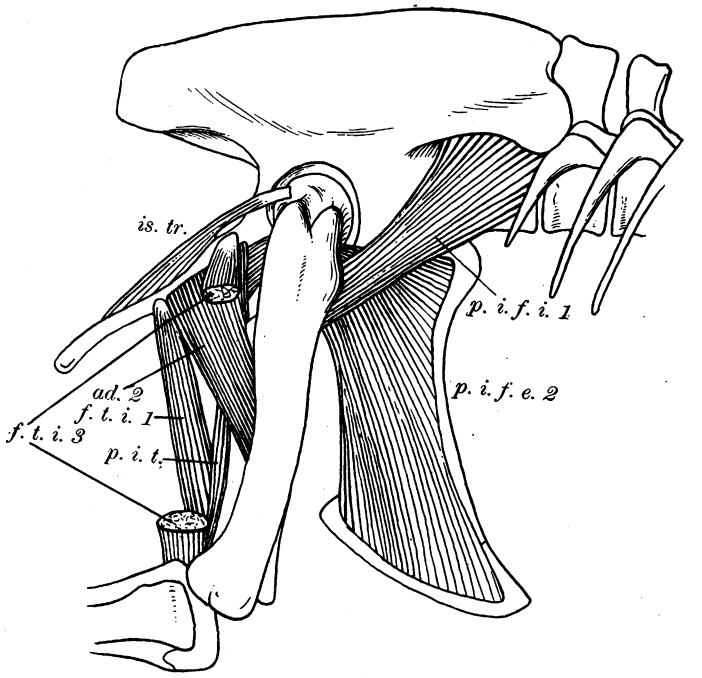

Fig. 7. Same as Fig. 6, with the coccygeo-femoralis, pubo-ischio-femoralis internus 2 and flexor tibialis internus 3 cut.

lumborum" (pubo-ischio-femoralis internus 2) runs beneath the ilio-femoralis in a direction opposite to that of the red arrow and probably inserted about, but not on, the trochanter. Caudo-ilio-femoralis (coccygeo-femoralis brevis) inserted more ventrally, about in the position of Von Huene's pubo-ischio-femoralis internus 3. The area occupied by femora-tibialis, to judge by either Crocodilia or birds, was much greater. I know of no part of pubo-ischio-femoralis internus likely to insert so far proximally as that shown in figure *b*. Of the muscles shown inserting on the fourth trochanter, probably only caudo-femoralis (coccygeo-

femoralis internus longus) should be placed there. The pubo-ischio-femoralis externus and that portion of pubo-ischio-femoralis which equals ischio-trochantericus inserted proximally to this trochanter. The adductors (ischio-femoralis and pubo-ischio-femoralis posterior in part) inserted about in the area marked "pubo-ischio-femoralis posterior zum Teil."

Most of the modifications of the tentative restoration of *Ornitholestes* by Gregory and Camp (1918), which might be suggested, are merely ones of nomenclature.

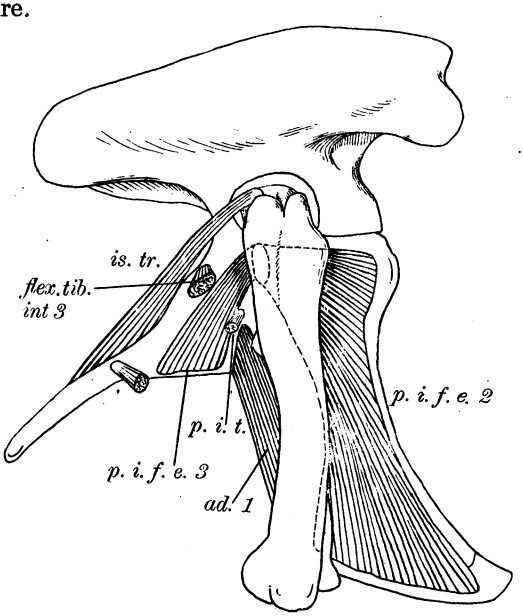

Fig. 8. Same as Fig. 7, from which adductor 2, the remaining flexors and pubo-ischio-femoralis internus 1 have been removed.

The question as to whether pubo-ischio-trochantericus internus (= pubo ischio-femoralis externus 1 of the Crocodilia) extended down the inner side of the pubis has been discussed above. "Adductor longus" = pubo-ischio-tibialis. The ridge below it was probably occupied by adductor 1. The space labeled ischio-femoralis was occupied by pubo-ischio-femoralis 3 and this probably extended anteriorly to include the excavation in the ischium, which is thus (as explained above) a close parallel to the "obturator fenestra." The posterior area marked pubo-ischio-femoralis externus is that for adductor femoris 2, except that the latter muscle probably did not extend so far distally. No area is marked

off for flexor tibialis internus 1. It seems probable that ilio-femoralis extended farther posteriorly.

Few criticisms may be made of the later restorations by Dr. Gregory shown in figure 1. Ilio-tibialis, ilio-femoralis, ilio-fibularis, flexor tibialis externus, caudi-ilio-femoralis (=coccygeo-femoralis brevis), "quadratus lumborum" (=pubo-ischio-femoralis internus), ambiens, the pubic head of pubo-ischio-femoralis externus, pubo-ischio-femoralis posterior (=ischio-trochantericus), and the iliac and one ischiadic head of flexor tibialis internus, I believe to be all correctly located. The question as to an internal pubic muscle has been mentioned previously. Adductor 2 probably occupied the proximal part of the area given the ischiadic head of pubo-ischio-femoralis externus. That muscle occupied most of the flat surface marked ischio-femoralis, the ischio-femoralis (adductor 1) lying slightly more anteriorly. Pubo-ischio-tibialis and flexor tibialis internus 1 are not located; the head of the latter muscle shown arising from beneath the posterior part of the ilium is probably incorrect.

SUMMARY

The evolution of the pelvis of saurischian dinosaurs is discussed. The marked change in the pubo-ischium is attributed to the changed position of the femur, which has resulted in a shifting of many muscles posteriorly and dorsally. The similarity of the saurischian musculature to that of the Crocodilia is pointed out. A restoration of the pelvic musculature of *Tyrannosaurus* is attempted.

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