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PELVIC AND HINDLIMB MUSCULATURE OF ARCHOSAURIAN REPTILES

City University of New York PH.D. 1981

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PELVIC AND HINDLIMB MUSCULATURE OF ARCHOSAURIAN REPTILES

by

SAMUEL F. TARSITANO

A dissertation submitted to the Graduate Faculty in
Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy, The City
University of New York.

1981

Samuel Tarsitano

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

PELVIC AND HINDLIMB MUSCULATURE OF ARCHOSAURIAN REPTILES

by

Samuel F. Tarsitano

Advisor: Professor Max K. Hecht

This study presents for the first time a comparison of hindlimb myology of eusuchian crocodilians. From this study I will demonstrate that there is a crocodilian plan of musculature, and that the muscular variability found in birds is not characteristic of the Eusuchia. The minor differences in hindlimb morphology between the subfamilies of the Eusuchia are also illustrated for the first time. Within this study is a description of the pelvic and hindlimb musculature of *Gavialis gangeticus* a form previously undescribed. The hindlimb musculature of *Gavialis* was found to be different from all other crocodilians in its adductor musculature.

In addition, The muscle scar anatomy of fossil gavials allows for its identification and separation from other crocodilians. The adductor muscle scar data provides the necessary information for this identification. Thus gavials can be identified in the fossil record using fragmentary specimens whose femora are preserved. In this study I have added to the description of the pelvic and hindlimb musculature of Alligator and other crocodilians. I have traced tendons of each muscle to their insertion points. In most instances this information is not available in the previous studies by Romer, (1923a) and Gadow, (1882a,b). This study also contains a detailed description of the shank musculature as well as those pelvic muscles which traverse the tarsal joint.

My analysis of fossil theropods is based on the data I have collected on crocodilians and birds. The study of any fossil must include if possible a study of that particular fossil's closest living relatives. The extant material provides the data base from which the fossil can be examined. Without such studies the interpretation of the morphology of fossils becomes arbitrary and subject to the prejudices of each researcher. A case in point is the restoration of the hindlimb musculature of theropod dinosaurs. For each restoration there appears new combination and placements of muscles. This is clearly illustrated in the comparative

section of each muscle description. My study identifies each scar on the hindlimb and pelvic bones of theropod dinosaurs. The muscle scars were identified on the basis of crocodilian and avian musculature. Finally a new stance for theropod dinosaurs is introduced based on a functional analysis of their reconstructed musculature and osteology.

ACKNOWLEDGEMENTS

I wish to extend my sincere gratitude to the following people whose help was invaluable in the preparation and completion of this dissertation. First and foremost I thank Dr. Max K. Hecht for his unfailing support, advice and guidance throughout the course of this study. He also provided me with the fossil and living material upon which this work is based. Dr. Stanley Salthe critically read the manuscript, gave freely of his time and knowledge, and supported my efforts throughout the research period. Dr. Giles T. MacIntyre provided me with many helpful suggestions, served as a source of knowledge and critically read the manuscript. Dr. James Mellett advised me on the functional aspects of my study and offered helpful suggestions concerning the illustrations. Dr. Nicholas Hotton III generously gave of his time and provided pertinent data concerning the hip joint morphology of archosaurs. Thanks also to Dr. Paul Maderson who contributed information and insight into the problems of homology. Dr. Samuel McDowell critically read the manuscript and I thank him for our many informative discussions. Dr. John Ostrom made available specimens for study. My thanks to Matthew Hecht who supplied numerous photographs of living and fossil archosaurs. Finally I thank Kathryn Tarsitano for the preparation and typing of the manuscript.

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PELVIC AND HINDLIMB MUSCULATURE OF ARCHOSAURIAN REPTILES

INTRODUCTION

The basis of comparative anatomy is the study of structures varying among taxa. One of the goals of comparative anatomy is the determination of homologous structures or the study of morphoclines. It is in the determination of the polarity of morphoclines that we can obtain data on the relationships of taxa. The study of the reptilian pelvic and hindlimb musculature in the tradition of Gadow (1882a,b) and Romer (1923a,b) allows us to form the data base from which these studies can be performed. Furthermore, we can test the predictive qualities of this comparative study in an attempt to reconstruct the musculature of extinct relatives of the living forms. If our transformation series are analyzed properly, the anatomical analysis of living forms and reconstructions of fossils should produce a concordant set of functional and phylogenetic interpretations. It is this latter hypothesis that I attempt to examine.

The restoration of the musculature and the interpretation of the stance and gait of fossil vertebrates depends on the determination of homologous muscle morphologies between the fossil taxon and its closest living relatives. A case in point is the restoration of the pelvic and hindlimb musculature of the theropod dinosaur, Tyrannosaurus rex. The reconstruction of not only the musculature but also the stance and gait of Tyrannosaurus depends upon the muscle homologies between birds and crocodilians, the closest living relatives of theropod dinosaurs. The question of homology has been dealt with by Gadow (1882b), Romer (1923a,b), Vaughn (1956), Ellsworth (1974) and Lance-Jones (1979). There remains unresolved two fundamental questions: 1) the variation of the pelvic and hindlimb musculature among crocodilians, and 2) the reliability of muscle scars as indicators of muscle position and size. This study was undertaken to resolve these questions, to examine their bearing on current controversies regarding homologies and to use [illegible] sources as a data base to provide a more rigorously controlled reconstruction of the locomotor function of predaceous dinosaurs.

Musculature has been used by both biologists and paleontologists in the determination of phylogenetic relationships. In birds the jaw, wing, syringeal and pelvic musculature have been used taxonomically

(Hudson, 1937, 1948; George and Berger, 1966). Musculature has not been used taxonomically within the Crocodilia because of the limited number of studies (Gadow, 1882a,b; Romer, 1923a; Schaeffer, 1941; and Brinkman, 1980) which included only two genera, *Alligator* and *Caiman*. For the remaining archosaurians muscle reconstructions and muscle scars have been used. Ostrom (1976) has used musculature in relating theropod dinosaurs to birds while Walker (1972, 1977) has used the same musculature in relating birds to certain fossil crocodilians.

Muscle scar anatomy has been used in the restoration of the pelvic musculature of extinct archosaurs. An early restoration of theropod musculature was attempted by Heune (1908). This restoration was later criticized by Romer (1923b) who restored the hindlimb musculature of *Tyrannosaurus rex*. According to Romer (1923b), the restoration by Heune (1908) was inaccurate, since it was accomplished without the aid of detailed knowledge of the *Alligator* hindlimb morphology (although the work of Gadow,1882a,b, on the pelvic musculature of *Alligator* was available). Other restorations of saurischian dinosaur pelvic musculature were attempted by Gregory and Camp (1918) and more recently Russell (1972), Charig (1972), and Walker (1977). In addition, partial and complete restorations of hindlimb musculature of ornithischian dinosaurs were introduced by Heune (1908), Romer (1927) and Galton (1969).

If the major aspects of the hindlimb musculature can be restored (based on distinct muscle scars), then it may be possible to test whether one posture is more probable than another or eliminate postures which do not correspond to the osteology and myology of the fossil. Furthermore, a study of the osteology and muscle scar anatomy might reveal different or similar methods of locomotion within the Theropoda. Thus, a study of the method of bipedal progression of theropods should be of systematic value in determining the intra-relationships within the theropods.

Since only two archosaurian groups survive today, the Crocodilia and Aves, a basic knowledge of their musculature is essential in understanding and reconstructing fossil archosaurian groups. It is unknown whether or not muscle scars can provide reliable data as to the presence or absence of muscles in fossil and living archosaurs. Bird musculature is fairly well known and is known to vary, both inter- and intraspecifically (George and Berger, 1966). In contrast, the pelvic and hindlimb musculature of many species of crocodilians is poorly known and largely undescribed.

Thus, until this study it was unknown whether the variability found in birds exists for crocodilians.

There have been numerous restorations of theropod dinosaurs since their discovery in the latter part of the nineteenth century. The reconstruction which has served as a model for many of these restorations was presented by Osborn in 1906. This reconstruction of the theropod dinosaur, Tyrannosaurus rex (AMNH 973 and 5866) was perhaps patterned after the early restorations of Anchisaurus colurus Marsh in 1893. The restorations of Marsh and Osborn, in which the vertebral column is positioned at an angle of approximately 45 degrees above the horizontal plane, is considered the traditional posture for carnosaurs, many coelurosaurs and supposed bipedal pseudosuchian thecodonts. (Osborn, 1917; Walker, 1964). In addition, many ornithopod dinosaurs were also given a posture similiar to the Tyrannosaurus restoration of Osborn, (Gilmore, 1909, 1920; Hooley, 1925; Lull and Wright, 1942 and Brown and Schlaikjer, 1943). Thus the restoration of Osborn had great influence on the later reconstructions of bipedal dinosaurs.

In recent years, new reconstructions of bipedal dinosaurs have been presented by Ostrom (1969, 1976a,b; 1978) Russell (1970, 1972), Newman (1970), Bakker (1975), Walker (1977) and Battaglia (1979). New restorations of ornithopod ornithischian dinosaurs have also been presented by Galton (1969) and Thulborn (1972). All of the recent restorations of theropod dinosaurs have apparently been patterned after ratite birds. That is, the vertebral column including the pelvis is held strictly parallel to the ground with the cervical vertebrae angled at about ninety degrees to the dorsal vertebrae. In order to maintain the head at a horizontal level another ninety degree bend occurs between the atlas and skull.

There are apparently two reasons for the new restorations of theropod dinosaurs. They are: 1) a reinterpretation of the morphology and 2) a reconsideration of the phylogenetic relationships of theropod dinosaurs. Newman (1970), Russell, (1972) and Walker, (1964, 1977), based their new restorations on new interpretations of the morphology. Newman (1970) re-examined the osteology of *Tyrannosaurus rex*, in particular, the joint surfaces of the hindlimb. Russell (1972) interpreted the muscle scars of *Ornithomimus* from which he restored the pelvic musculature. Walker (1977) also re-examined the muscle scars of theropod dinosaurs, restoring the pelvic musculature. Ostrom (1969), Bakker (1975) and Battaglia (1979) have also given theropod dinosaurs a "ratite" stance similar to

Struthio. Ostrom's reasoning is twofold. In addition to his osteological studies of theropod dinosaurs, Ostrom's phylogenetic conclusion that birds are the descendants or the sister group of theropods (Ostrom 1975a, 1975b, 1976a, 1976b, and 1979) has influenced his restoration of both *Deinonychus antirrhopus* YPM 5206 (Ostrom 1969 and 1976) and *Compsognathus longipes* BSP 563 Wagner (Ostrom 1978). The belief that birds are derived from endothermic dinosaurs are the chief reasons for the restorations of Bakker (1975) and Battaglia (1979). In all of these restorations the vertebral column is horizontal. The restorations of Bakker (1975) and Battaglia (1979) have added feathers to the integument of theropods even though there has never been any physical evidence found to support this belief.

Thus there are now two published postures for theropod dinosaurs: the traditional stance of Marsh (1893) and Osborn (1906) and the recent restorations giving theropods a "ratite" stance. Early restorations of theropod hindlimb musculature were presented by Heune (1908), Gregory and Camp (1918) and Romer (1923b). All of these restorations were based on the interpretation of muscle scars. Romer (1923b) interpreted the muscle scars of *Tyrannosaurus* based on his comparison of the pelvic musculature of *Alligator mississippiensis*

(Romer, 1923a). Another restoration of the hindlimb musculature of theropods was attempted by Colbert (1964). His restoration was a reiteration of the Romer restoration.

The recent restorations by Russell (1972) and Walker (1977) are not only different from those of Gregory and Camp (1918) and Romer (1923b), but are also different from each other. The Russell restoration was based on crocodilian musculature (Russell, 1972). The Walker (1977) restoration was patterned on both crocodilian and lacertilian musculature.

There are a number of reasons for the different reconstructions of theropod musculature. First, pelvic muscle scars may vary from one theropod to another. This would mean that the hindlimb musculature of theropods is not uniform thoughout the taxon. Second, that phylogenetic interpretion of the relationships of theropods may influence the restoration of theropod musculature. Third, that specimens of theropods that are used for restorations may not be well enough preserved for this work. This would lead to arbitrary assignments of muscles. Fourth, that muscle scars may represent combinations of muscles which are unknown in extant taxa or combinations of known taxa. For example, some muscles may follow a crocodilian pattern while others might follow an avian pattern. Finally, it may be impossible to restore the musculature of a fossil animal, due to lack of muscle scars on the bones.

The different restorations of musculature and interpretations of the joint surfaces may be the cause of the different theropod postures. The hypothesis that birds are the descendants of theropod dinosaurs has been investigated by Tarsitano and Hecht (1980). Their conclusions based on a cladistic analysis of theropod, crocodilian and avian morphology has cast serious doubt as to the avian relationships of theropod dinosaurs. As far as posture is concerned, it is the musculature and osteology which must be interpreted. Phylogenetic relationships may act as a check on the morphological analysis but cannot form the basis of such an analysis.

Methodology

A detailed analysis of crocodilian musculature and its intraordinal variation is presented in Table I. and a comparison with birds is outlined. This comparative study of intraordinal variation among crocodilians and comparisons with the surviving

Table I

Muscle	Alligatorinae	Crocodylinae	Thoracosaurinae	Gavialidae	Aves
Adductor femoris part one	origin: anterior margin ischium	same	same	origin-expanded to medial surface of ischium	similar
Adductor femoris part two	insertion with part one on adductor ridge	same as in Alligatorinae	same as in Alligatorinae	both heads insert into pit below fourth troc.	similar
Ischio-trochantericus	same	same	same	same	similar-larger
Coccygeo-femoralis brevis and longus	same	same	same	same	insertion shifted to lateral surface - no fourth troc.
Femoro-tibialis externus	same	same	same	same	same
Femoro-tibialis internus	same	same	same	same	same but termed the medius; avian internus absent in Crocodilia

Table I

Muscle	Alligatorinae	Crocodylinae	Thoracosaurinae	Gavialidae	Aves
Ilio-tibialis	same	same	same	same	similar
Ilio-fibularis	same	same	same	same	larger with biceps loop
Ilio-femoralis	same	same	same	same	similar
Flexor-tibialis externus	same	same	same	same	similar
Flexor-tibialis internus	same	same	same	same	similar-only two parts
Pubo-ischio-femoralis internus	same	same	same	same	similar origin-part two diff.
Pubo-ischio-femoralis externus	same	same	same	same	similar even with pubic rotation
Pubo-ischio tibialis	same	same	same	same	absent
Ambiens One	same	same	same	same	similar but shortened
Ambiens Two	reduced:inserts midway on ilio-tibialis three	larger:inserts into extensor tendon of knee	same as Crocodylinae	same as Crocodylinae	absent

out-groups, the birds, provides the data base from which fossil archosaurs can be examined. Without this data base the reconstructions of archosaurian musculature can become arbitrary.

Comparisons of archosaurian musculature with that of lepidosaurian musculature such as Sphenodon (Byerly, 1925) and lizards (Schaeffer, 1941; Romer, 1942; Snyder, 1954; Rewcastle, 1977; and Brinkman, 1980), have not been considered in this work because of the obviously large osteological and muscular differences. For these reasons it is impractical to consider lacertilian morphology at this time.

In order for reconstructed musculature based on muscle scar evidence to be employed as a taxonomic tool or as an aid in the restoration of fossil archosaurians, it must first be ascertained whether the other living archosaurian group, the Crocodilia, varies in its pelvic and hindlimb musculature. Once the limits of variation are known then it may be possible to restore the pelvic musculature of well preserved archosaurs based on the presence and disposition of muscle scars preserved on their bones.

The reliability of muscle scar evidence can be tested by dissecting various species of crocodilians from the existing subfamilies. Knowledge of the musculature along with any intra- or interspecific variations would be an invaluable aid in the identification of muscle scars as well as a taxonomic tool in phylogenetic studies of the living Crocodilia. The anatomical studies of Gadow, (1882a,b,), Romer, (1923a), Brinkman(In Press),Hudson, (1937, 1948), George and Berger, (1966), McGowen, (1979) and my own dissections are essential for comparisons and interpretations within the Archosauria. The comparisons of birds and crocodilians can best be made with the well preserved specimens of the fossil archosaurian group, Theropoda.

In the study of the hindlimb musculature, I have dissected the following members of the Crocodilia:

Suborder Eusuchia
  Family Crocodylidae
    Subfamily Alligatorinae Kalin, 1940
    Alligator mississippiensis Daudin, 1801
    Alligator sinensis Fauvel, 1879
    Caiman crocodilius Linne,1758
    Paleosuchus palpebrosus Cuvier, 1807
    Subfamily Crocodilinae Cuvier, 1807
    Crocodylus johnsoni Kreffi, 1873
    Osteolaemus tetraspis Cope, 1860
    Crocodylus porosus Schneider, 1801

    Subfamily Thoracosaurinae Nopcsa, 1928
    Tomistoma schlegelii Muller, 1846

Subfamily Gavialinae Nopcsa, 1923

Gavialis gangeticus Gmelin, 1789

The pelvic musculature is similar in the forms listed above. There are, however, some differences between the subfamilies. For convenience I have briefly described these differences in Table 1. The formal description of the general pelvic and hindlimb musculature of crocodilians is presented in the text.

From the Table 1 it is evident that the major elements of the crocodilian pelvic and hindlimb musculature are uniform. Thus it can be stated that there is a crocodilian plan of pelvic musculature. In fact, as will become evident from this paper, this plan extends into the Saurischia as well.

In studying the hindlimb musculature of the Crocodilia I have dissected both sides of three specimens of *Alligator mississippiensis*; two specimens of *Caiman crocodilius*, *Osteolaemus tetraspis*, *Gavialis gangeticus*; one specimen of *Alligator sinensis*, *Paleosuchus palpebrosus*, *Crocodylus johnsoni*, *Crocodylus porosus* and *Tomistoma schlegelii*. In this study I have found no variation in the contralateral musculature of each specimen nor among members of the same species. Furthermore, members of the same subfamily did not vary in their pelvic and hindlimb musculature. There are consistant although minor differences between the subfamilies. In addition, the subfamily Gavialinae displayed major differences in the adductor musculature not found in any other crocodilian.

The following study is my account of the pelvic and hindlimb musculature of crocodilians and other archosaurs. The reconstruction of the musculature of fossil archosaurs was based on the positions of muscle scars on the skeleton. My diagrams of crocodilian musculature were made with the connective tissue removed. Thus, in order to understand the true relationships of one muscle to another, I refer the reader to Romer (1923a).

Since bird musculature varies throughout the class it would be unwise to compare just one species of bird to theropods. I therefore refer the reader to George and Berger (1966) and Hudson (1937) for additional descriptions and diagrams of avian hindlimb musculature.

It should be noted that homologizing muscles between crocodilians, birds and theropods was done on the basis of origin and insertion since no muscles are preserved in fossil theropods. These homologies follow those determined by Romer (1923a). An out group comparison (not included here) was made with the hindlimb musculature of lizards (Snyder, 1954) to determine whether muscle scars could represent muscles not found in crocodilians or birds. No muscle scars were found that did not fit either the alligator or avian pattern.

THE PELVIC AND HINDLIMB MUSCULATURE OF THE ARCHOSAURIA

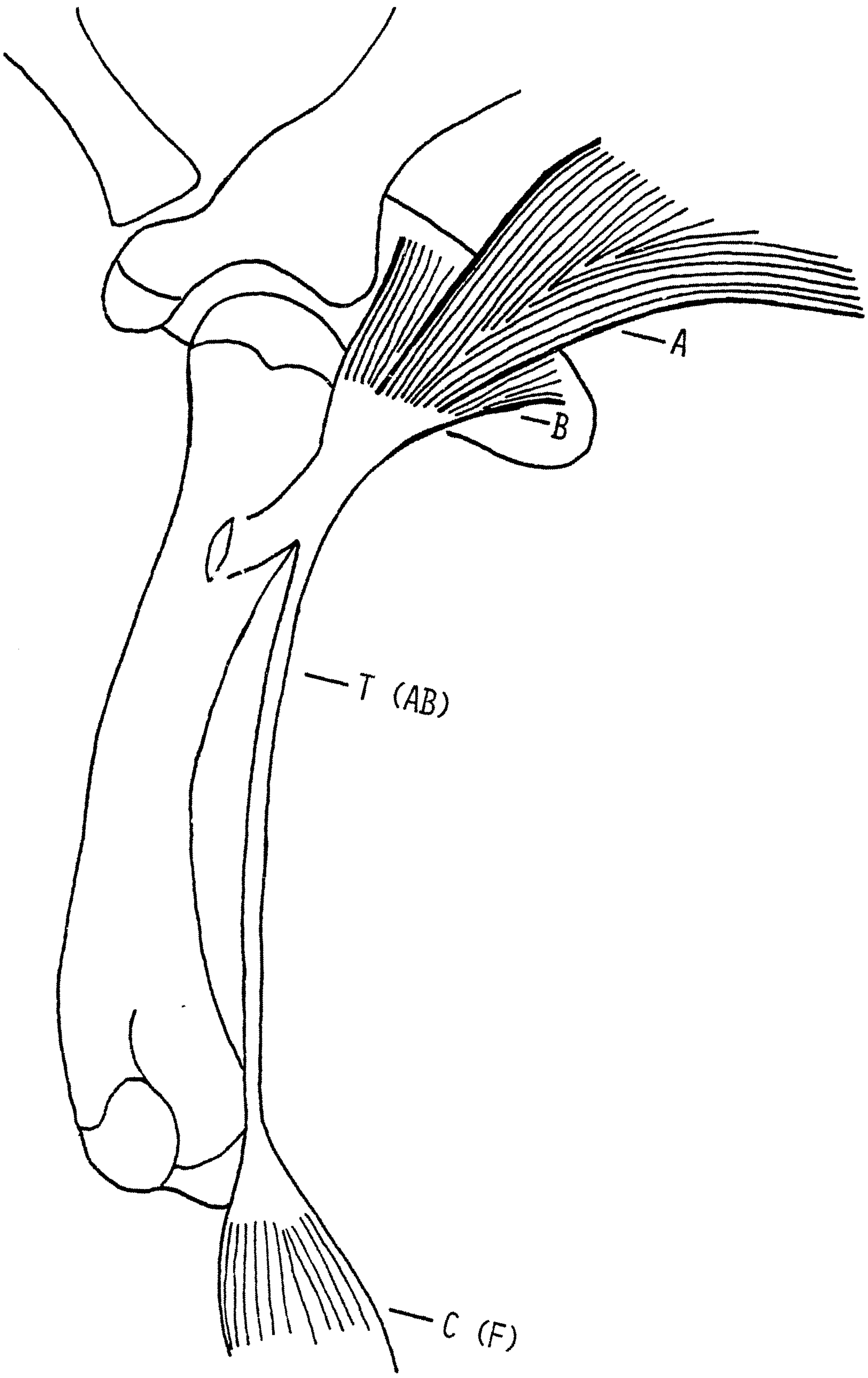
The musculature of the Caudal Region

Coccygeo-femoralis Longus. The main retractor of the hindlimb in the Crocodilia is the M. coccygeo-femoralis longus (M. caudofemoralis).

The M. coccygeo-femoralis longus of the alligator (Figure 1) originates according to Romer (1923a) on the ventral surfaces of the processes of the third to thirteenth caudal transverse vertebrae. My dissections, however, have shown that the origin is also upon the centra of these vertebrae. The insertion in all crocodilians is mainly on the fourth trochanter (Figure 4) Romer (1923a). I have traced tendons to the medial and lateral surfaces of the head of the femur and I agree with Romer that this muscle inserts upon the fascia of the M. gastrocnemius (Figure 1). Romer's reconstruction of the M. coccygeo-femoralis longus in Tyrannosaurus is the same as its placement in alligators.

The avian homologue, the M. piriformis pars caudofemoralis, originates on the ventral portion of the

Fig. I. Ventral view of the pelvic musculature of crocodilians. A - coccygeo-femoralis longus; B - coccygeo-femoralis brevis; T (AB) - tendon of the coccygeo-femoralis longus and brevis; C (F) - fibular head of the gastrocnemius.


A
B
T (AB)
C (F)

pygostyle and/or by a broad aponeurosis that extends between the tail coverts and pelvis (George and Berger, 1966). The insertion is usually on a small ridge located on the posterio-lateral border of the femur at the level of the insertion of the M. gluteus medius et minimus.

Comparative data

The origin of the M. coccygeo-femoralis longus in Tyrannosaurus rex (Figure 2 and 3) closely resembles that seen in the alligator. The origin of this muscle was on the centra of the caudal vertebrae. In Tyrannosaurus the germane caudal vertebrae are longer dorso-ventrally than they are anterio-posteriorly. In addition, the transverse processes are set high on each vertebrae to facilitate the origin of the M. coccygeo-femoralis longus on the centra. The insertion of this muscle was on the fourth trochanter (Romer, 1923a,b) which, in Tyrannosaurus, is located on the posterio-medial portion of the femur, below its head (Figure 2 and 3).

Russell (1972) reconstructs this muscle with a different insertion position. The insertion lies on the distal posterior surface of the femur just above the

Fig. 2. Lateral view of caudal musculature of *Tyrannosaurus*. A - coccygeo-femoralis longus; B - coccygeo-femoralis brevis; C - gastrocnemius; MO - origin of the ambiens; T (AB) - tendon of the coccygeo-femoralis longus and brevis.

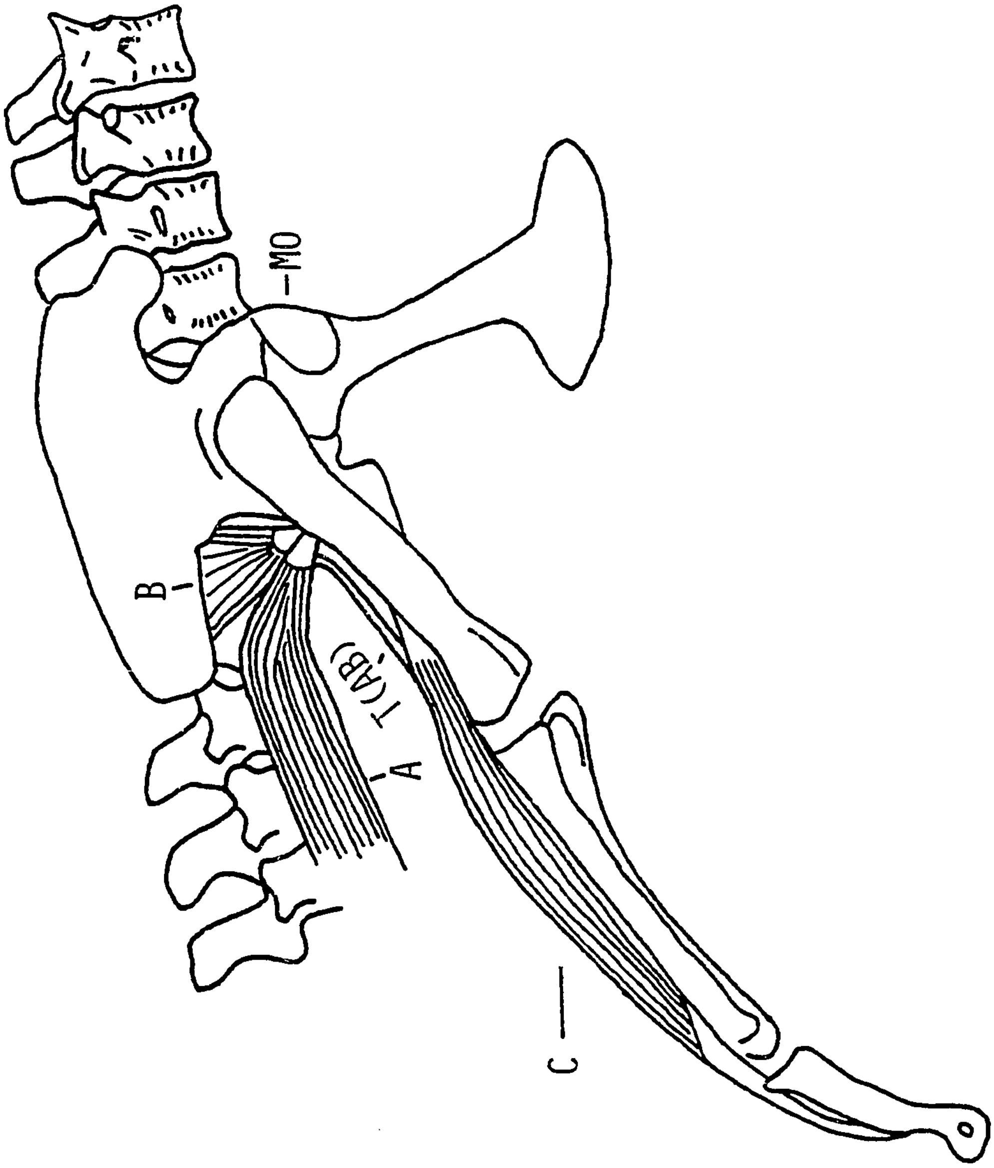
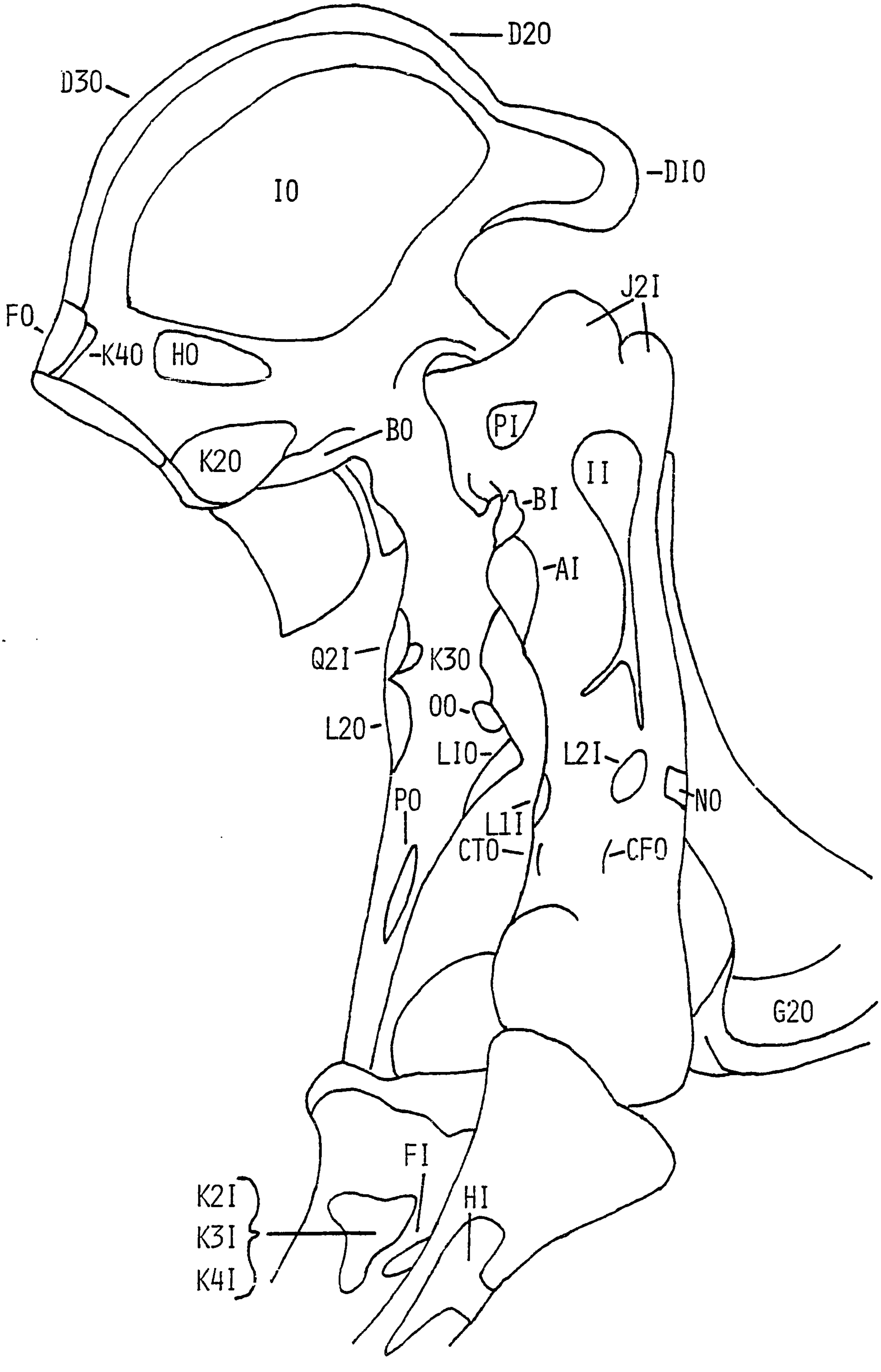

MO
B
T(AB)
A
C

Fig. 3. Muscle scars of the pelvis and hindlimb of Tyrannosaurus. AI - coccygeo-femoralis longus, insertion; BO - coccygeo-femoralis brevis; origin; BI - coccygeo-femoralis brevis, insertion; CTO - gastrocnemius tibial head, part of the origin; CFO - gastrocnemius fibular head, part of the origin; DIO - ilio-tibialis first head, origin; D2O - ilio-tibialis second head, origin; D3O - ilio-tibialis third origin; FO - flexor-tibialis externus, origin; FI - flexor-tibialis externus, insertion; G2O - pubo-ischio-femoralis externus part two origin; HO - ilio-fibularis, origin; HI - ilio-fibularis, insertion; IO - ilio-femoralis, Origin; II - ilio-femoralis, insertion; J2I - pubo-ischio-femoralis internus part two, insertion; K2O - flexor-tibialis internus part two, origin; K2I - flexor-tibialis internus part two, insertion; K3O - flexor-tibialis internus part three, origin; K3I - flexor-tibialis internus part three, insertion; K4O - flexor-tibialis internus part four, origin; K4I - flexor-tibialis internus part four, insertion; LIO - adductor femoris part one, origin; L1I - adductor femoris part two origin; L2I - adductor femoris part two,

insertion; NO - femoro-tibialis internus deep head, origin; OO - pubo-ischio tibialis, origin PO - ischio-trochantericus, origin; PI - ischio-trochantericus, insertion; QI1 - ilio-ischio caudalis, insertion on the ilium; Q2I - ilio-ischio caudalis, insertion on the ischium.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femoral condyles. As evidence he refers to the muscle scars in this position and cites Osborn (1917) in this regard. I have found that Osborn (1917) has incorrectly figured the muscle scars on the femur of Tyrannosaurus and assigns no names to the scars he has drawn. In addition, the muscle scars in this area are on both sides of the posterior surface of the femur. In alligators this is the place for the insertion of the M. adductor femoris (Romer 1923a,b) a muscle Russell has not recognized in his reconstruction. I believe the main reason for Russell's new restoration is his mistaking Gadow and Selenka's (1891) M. caudi-ilio flexorius for the M. coccygeo-femoralis longus. The origin described by Gadow and Selenka (1891) for this muscle is the M. semitendinosus of George and Berger,(1966), Hudson, (1948), Garrod, (1881), Forbes, (1885) and Shufeldt, (1890). Its association with the M. accesorius semitendinosi is a convincing argument for this muscle being the M. semitendinosus. The counterpart for the M. coccygeo-femoralis longus according to Gadow and Selenka, (1891) is the M. caudilio femoralis, not the M. caudi-ilio flexorius which Russell describes as the former muscle. Walker, (1977) does not discuss the attachments of the M. coccygeo-femoralis longus or brevis in theropods.

Coccygeo-femoralis Brevis.

In the Crocodilia, the M. coccygeo-femoralis brevis (the M. caudofemoralis brevis of lizards) originates in two locations (Figures 1 and 4). One slip arises from the ventral rim of the ilium, posterior to the acetabulum. The other slip originates on the last sacral and first caudal vertebrae (Romer, 1923a).

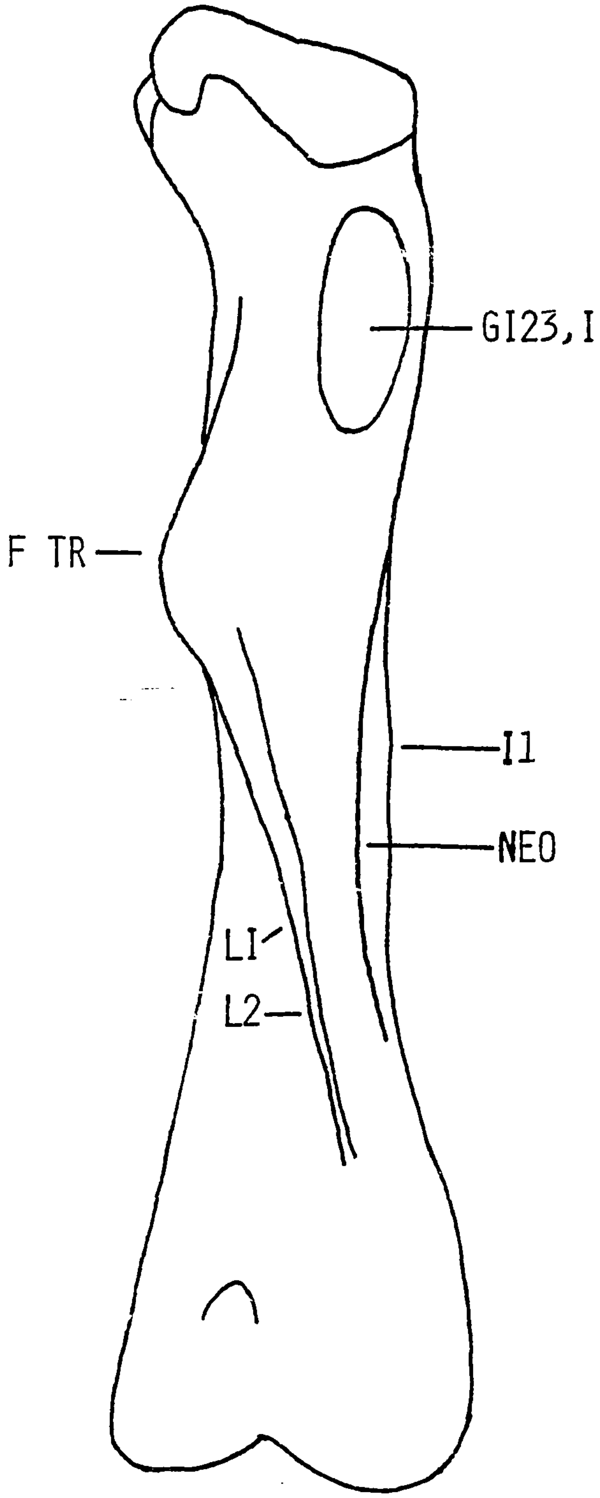
The insertion of the M. coccygeo-femoralis brevis of crocodilians is with the longus on the posterior of the fourth trochanter (Figure 4).

The avian homologue, the M. piriformis pars ilio-femoralis, originates on the ventral rim of the posterior iliac crest. With the fusion of the ischium to the ilium the origin on the last sacral and first caudal vertebrae is lost. This condition has not yet occurred in Archaeopteryx. The insertion is on the posterior lateral surface of the femur lateral to the insertion of the pars caudofemoralis when both parts are present.

Comparative data

The origin of the M. coccygeo-femoralis brevis

Fig. 4. Posterior view of the muscle scars on the femur of crocodilians except Gavialis. F TR - fourth trochanter; GI,2,3,I - insertion point of the pubo-ischio femoralis externus parts one, two and three; Il - insertion ridge of the ilio-femoralis; LI - insertion of the adductor femoris part one; L2 - insertion of the adductor femoris part two; NEO - femoro-tibialis externus, origin.


GI23,I
F TR
I1
NEO
L1
L2

of _Tyrannosaurus_ (Figures 2 and 3) is almost identical with that of all crocodilians. The posterior ventral rim of the ilium is indented for the origin of part of this muscle. In both _Alligator_ and _Tyrannosaurus_ the ilium is well separated from the ischium, exposing the first caudal and last sacral vertebrae. This space facilitates the passage of the M. coccygeo-femoralis longus and brevis to the femur. The insertion of the brevis remained on the fourth trochanter just above the insertion of the longus. It should be noted, that it is unknown whether the longus and brevis sent tendons or slips to the M. gastrocnemius or fibula as they do in the Crocodilia (Romer, 1923a). It does seem probable, however, that this was indeed the case, since femoral retraction would then cause the automatic flexion of the crus. Romer reconstructs the M. coccygeo-femoralis brevis in _Tyrannosaurus_ as it appears in _Alligator_. It should be noted that this muscle is the M. caudi-ilio-femoralis of Gregory and Camp, (1913). Russell, (1972) also adheres to the _alligator_ plan for the M. coccygeo-femoralis brevis.

The musculature of the Ilium

M. Ilio-tibialis.

This muscle consists of three heads in the Crocodilia, all originating along the dorsal rim of the iliac blade (Romer, 1923a) (Figure 5). The first and most anterior head originates above and slightly anterior to the second head on the anterior dorsal portion of the ilium. The second head, which is the largest, continues along the dorsal rim of the ilium, ending approximately in line with the posterior rim of the acetabulum. The origin of the third and last head is discontinuous with the second. It arises on a small portion of the posterior iliac blade along its rim.

The insertion of the first head in the Crocodilia is on the dorsal and distal fascia of the M. femoro-tibialis externus (Figures 6,7,8). The second head forms an aponeurosis with the M. femoro-tibialis at the knee (Romer, 1923a). The third head also contributes to this aponeurosis, but according to Romer, it also sends a tendon to the insertion of the second head of the ambiens.

The M. ilio-tibialis in many birds also has three heads (Gadow and Selenka, 1891), which arise from the dorsal rim of the anterior (which the Crocodilia lack)

Fig. 5. Lateral view of the muscle scars on the pelvis of crocodilians except Gavialis (after Romer, 1923a). BO - coccygeo-femoralis brevis, origin; D1 - ilio-tibialis; part one; D2 - ilio-tibialis part two; D3 - ilio tibialis part three; F - flexor-tibialis externus; G2 - pubo-ischio femoralis externus part two; G3 - pubo-ischio femoralis externus part three; H - ilio-fibularis; I - ilio-femoralis; K2 - flexor-tibialis internus part two; K3 - flexor-tibialis part three; LI - adductor femoris part one; L2 - adductor femoris part two; MI - ambiens part one; O - pubo-ischio tibialis; QI - ilio-ischio caudalis, insertion on the ilium; Q2 - ilio-ischio caudalis, insertion on the ischium.

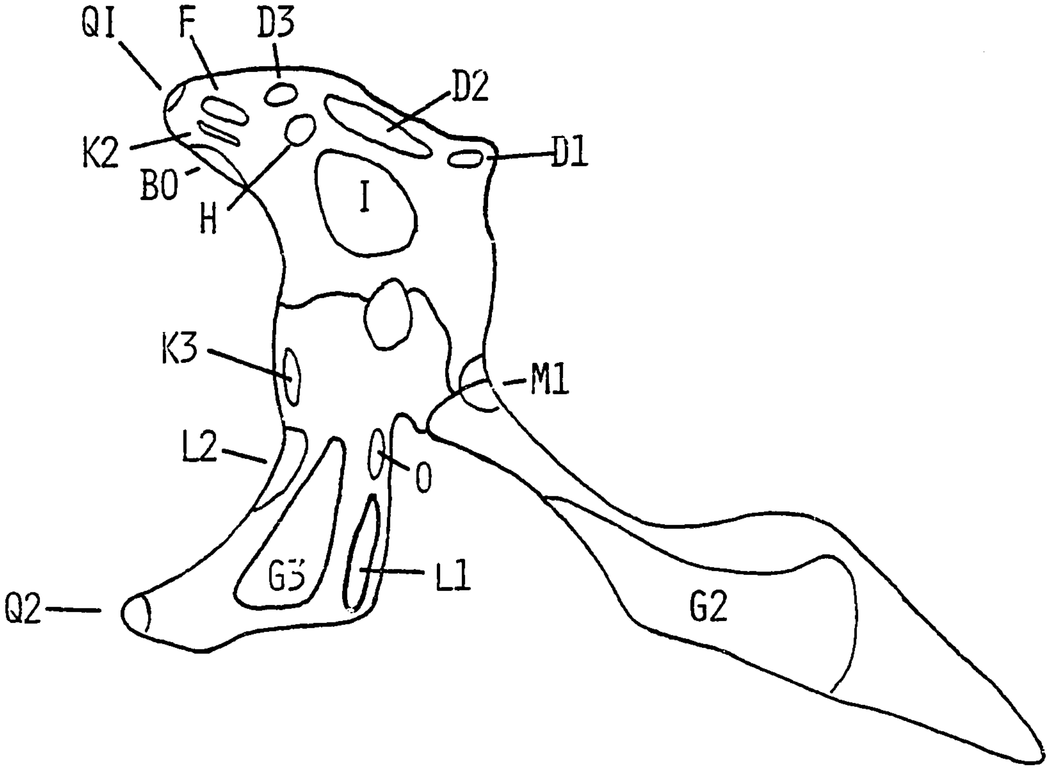

QI
F
D3
D2
K2
D1
BO
H
I
K3
M1
L2
O
G3
L1
Q2
G2

Fig. 6. Crocodylinae condition of the ambiens. D1 - ilio-tibialis part one; M1 - ambiens part one; M2 - ambiens part two; N1 - femoro-tibialis internus, superficial head.

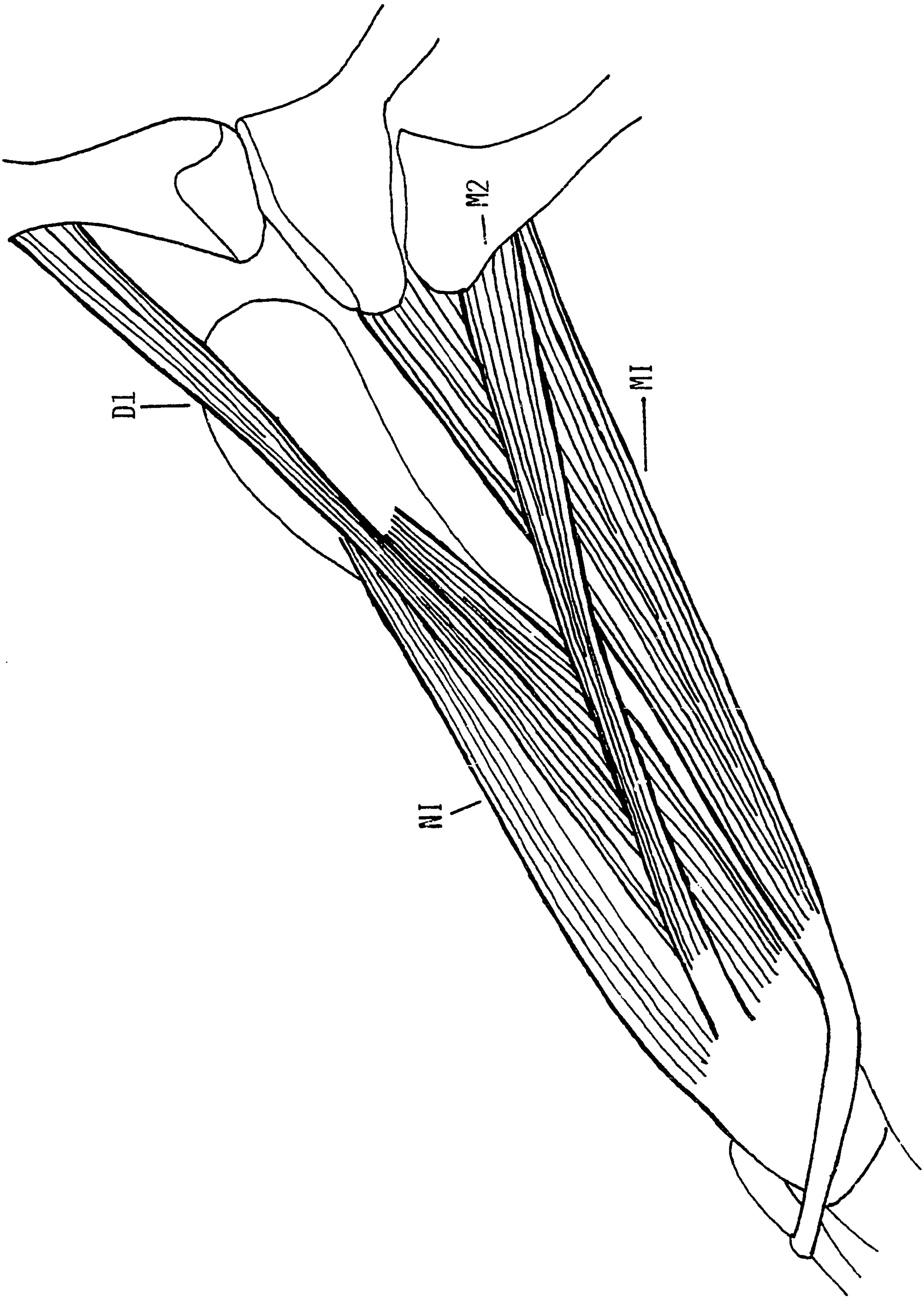

M2
MI
D1
NI

Fig. 7. Alligatorinae condition of the M. ambiens. Symbols as in Fig. 6.

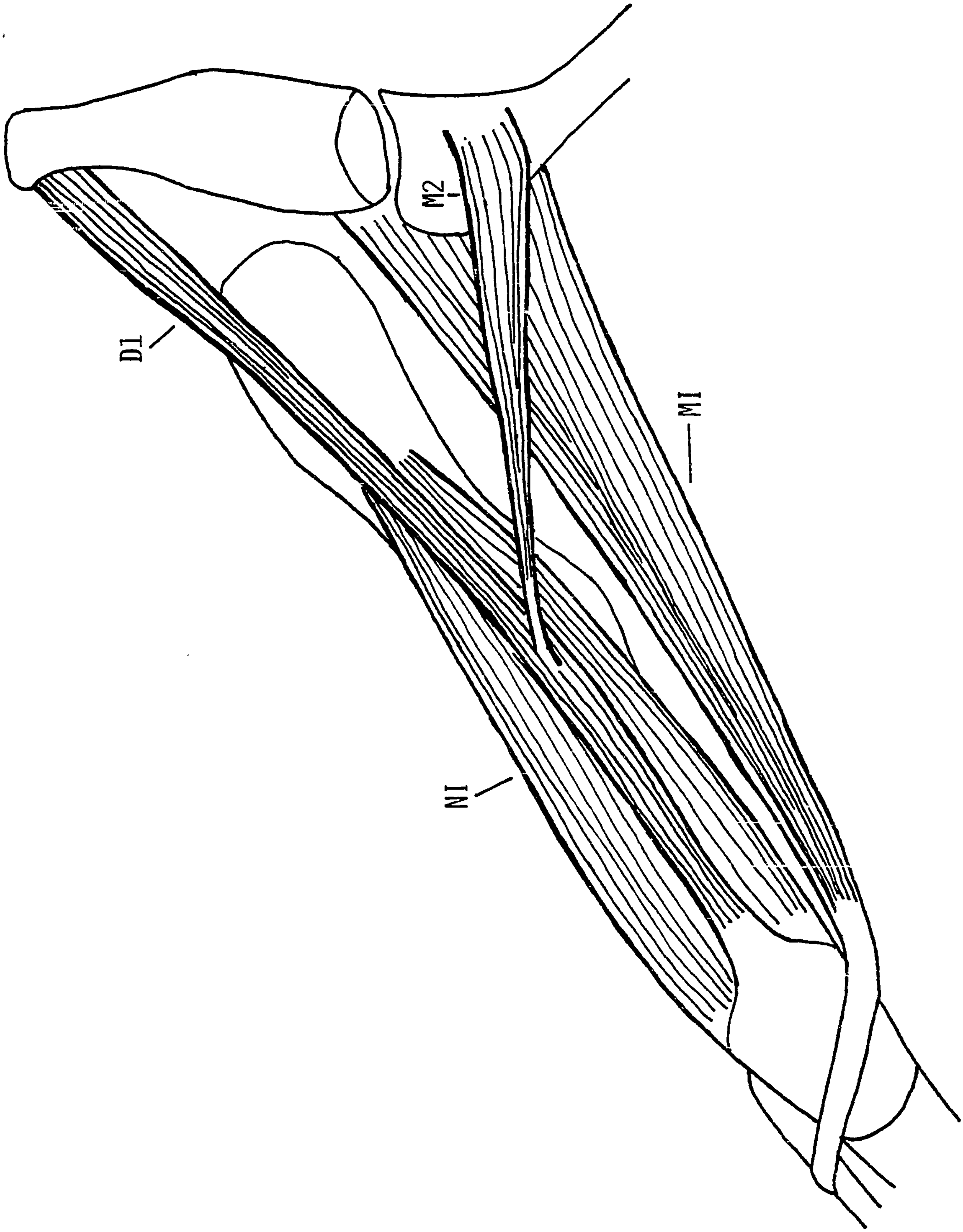
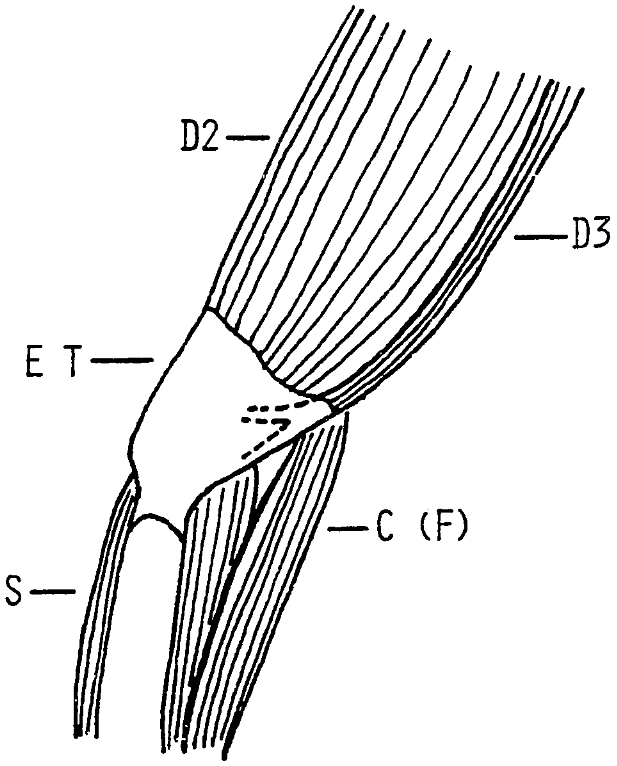

M2
D1
M1
N1

Fig. 8. Lateral view of the muscles about the knee joint in crocodilians (M. peroneous removed). C (F) - gastrocnemius fibular head; D2 - ilio-tibialis part two; D3 - ilio-tibialis part three; ET - extensor tendon; S - extensor digitorum longus.


D2
D3
E T
C (F)
S

and posterior iliac crests. George and Berger, (1966), however, call the three parts the M. extensor iliotibialis lateralis.

It should be noted that the condition of the avian ilio-tibialis is variable. In many birds, however, there are three heads as previously mentioned. Unlike the condition of this muscle in the Crocodilia, the posterior heads are continuous with each other and are not as distinct. The second and third portions make up an aponeurosis in birds and insert with the M. femoro-tibialis externus on the anterior proximal part of the tibia. The first head of the M. ilio-tibialis of the Crocodilia is probably the M. sartorius of the Aves. The true first head of the M. ilio-tibialis could have migrated forward with the anterior expansion of the ilium in the thecodonts and the thecodont Hallopus.

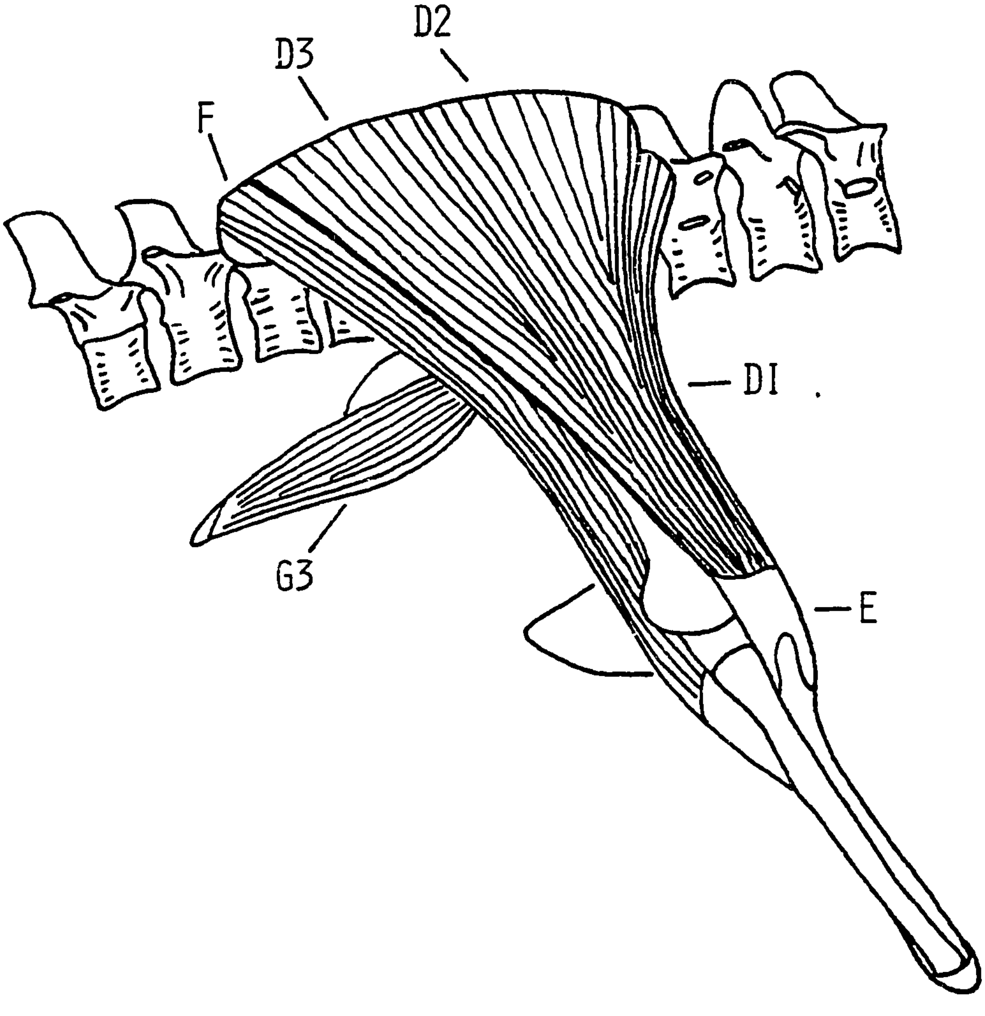
The M. sartorius in birds originates from the anterior iliac process, the dorsal rim of the synsacrum and/or the neural spines of the last few dorsal vertebrae. The M. sartorius may have two parts, a superficial head and a deep head (George and Berger, 1966). The insertion is by tendon on the base of the inner cnemial crest and to the patellar ligament. The aponeurosis of the M. ilio-tibialis along with that of both parts of the femoro-tibialis make up the patellar ligament.

Comparative data

The condition of the M. ilio-tibialis in _Tyrannosaurus_ (Figures 3 and 9) was similar to that seen in both the Aves and crocodilians. Three parts of this muscle were present, originating along the dorsal rim of the ilium. The scars for this muscle on _Tyrannosaurus_ indicate that the third and second heads are continuous in their origin. The origin of the first head, represented in birds by the M. sartorius is on the expanded anterior iliac process. The insertion of the first head is on the proximal, anterior surface of the inner cnemial crest. The second and third heads insert on the lateral face of the inner cnemial crest, probably on the surface of the M. femoro-tibialis internus and the proximal, anterior and lateral part of the head of the fibula (all by aponeurosis). The insertion of this muscle contributes to the extensor tendon between the femur and shank. The Crocodilia as well as _Tyrannosaurus_ lack a patella. (The inner cnemial crest on the tibia of _Tyrannosaurus_ may have acted partially as a patella).

Romer (1923b) reconstructs the three heads in _Tyrannosaurus_ as they are represented in the Alligator. The second head is the largest because of the preacetabular expansion of the ilium in theropods and

Fig. 9. Superficial musculature of the pelvis of *Tyrannosaurus*. DI - ilio-tibialis part one; D2 - ilio-tibialis part two; D3 - ilio-tibialis part three; E - extensor tendon; F - flexor tibialis externus; G3 - pubo-ischio-femoralis externus part three.


D2
D3
F
DI
G3
E

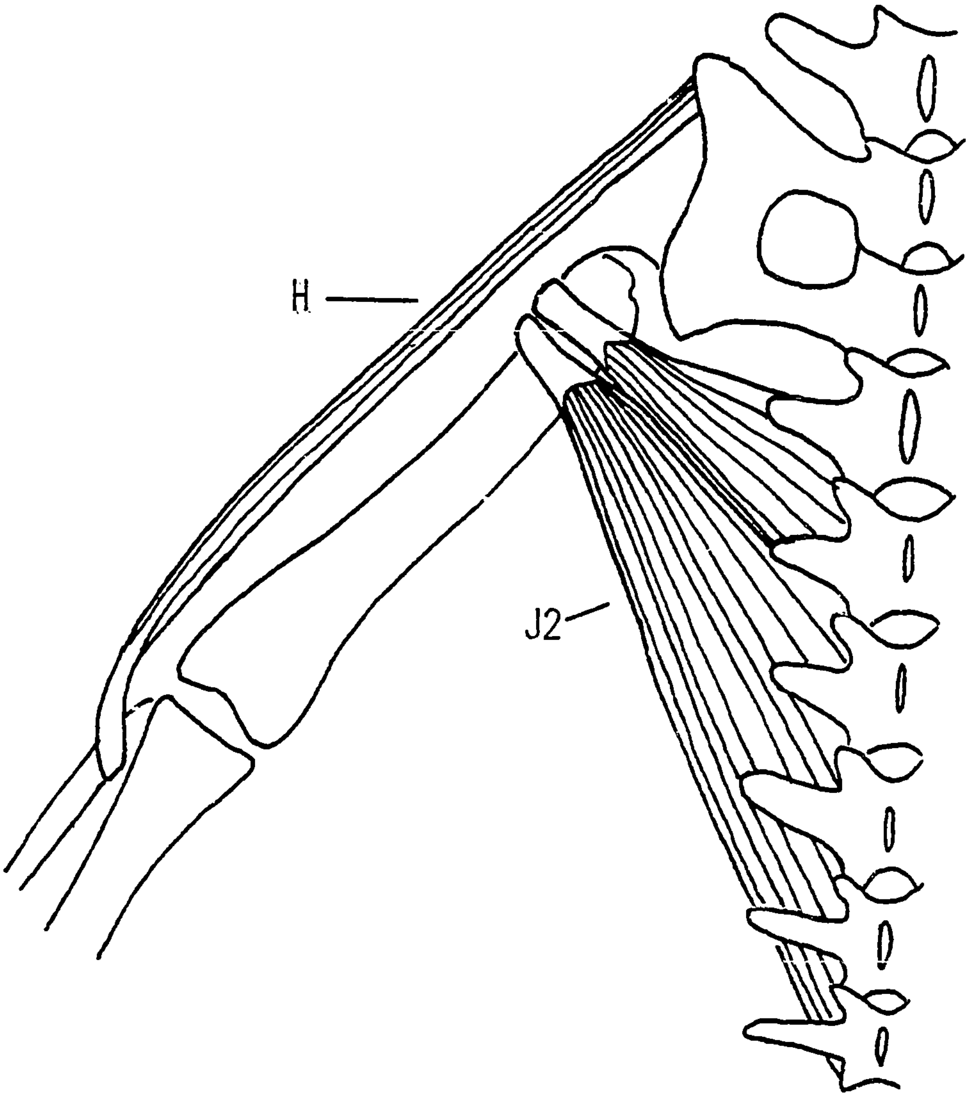
some thecodonts. The insertions also remain as they are in the alligator. It should be noted that crocodilians do not have an inner cnemial crest. However, the crest is present in theropods, and thus it is reasonable to place the insertion of at least the first head on this structure.

Russell's reconstruction of this muscle is similar to that of Romer, (1923a). The main difference, which is relatively insignificant, is that all three heads of the M. ilio-tibialis are fused. While I agree with the second and third head being continuous, the first head is quite separate as indicated by the muscle scars Romer, (1923b). The condition where the third and second head are completely fused while the first head remains separate was described by Gregory and Camp, (1918). Walker only illustrated the first head of the M. ilio-tibialis, the M. sartorius. Scars for the origin are to be found on the anterior iliac process in Tyrannosaurus.

M. Ilio-fibularis.

The M. ilio-fibularis of the Crocodilia arises on the ilium between and slightly ventral to the second and third heads of the ilio-tibialis. The insertion in the Crocodilia is by tendon to the fibula. This

Fig. 10. Dorsal view of certain crocodilian pelvic muscles. H - ilio-fibularis; J2 - pubo-ischio femoralis internus part two.



H
J2

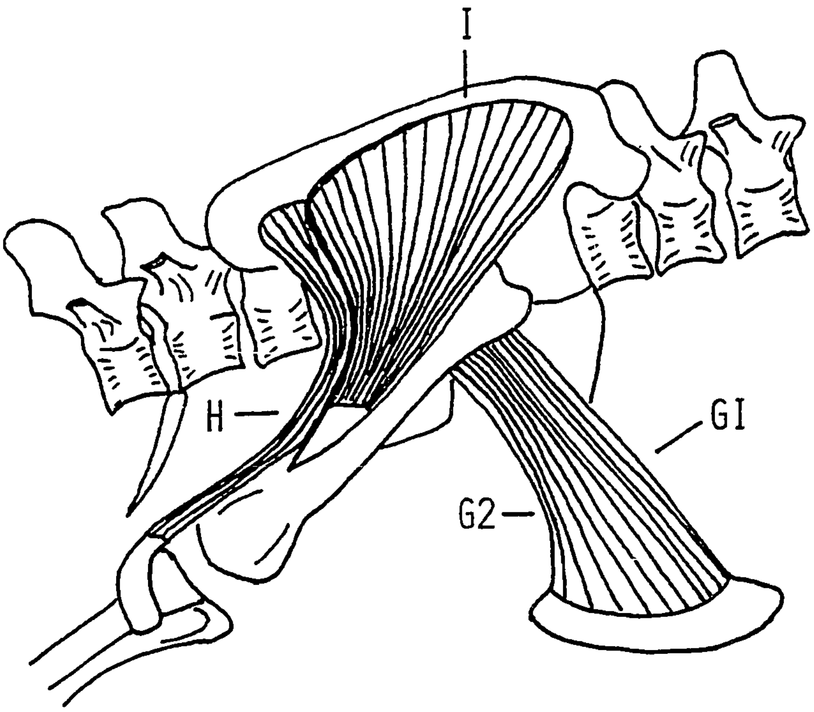
tendon passes from the proximo-lateral part of the fibula to the medial side, passing over its anterior surface. In addition, this muscle inserts into the external head of the M. gastrocnemius.

In most birds the M. ilio-fibularis (M. biceps femoris) originates from the posterior part of the anterior iliac crest (George and Berger, 1966). The insertion of this muscle is more complex. The insertion of the M. ilio-fibularis is on the posterior surface of the proximal portion of the fibula (George and Berger, 1966). In some birds, (for example, the Anatidae) the M. ilio-fibularis also inserts on the fascia of the M. gastrocnemis. The M. ilio-fibularis of most birds passes through a biceps loop, which acts as a pulley for this muscle. The M. ilio-fibularis is much better developed in birds than in the Crocodilia.

Comparative data

The M. ilio-fibularis (Figures 3 and 11) takes its origin on the ilium in much the same position that it occupies in <u>Alligator</u> that is, just ventral to the third head of the M. ilio-tibialis. I believe, however, that this muscle was larger than its crocodilian counterpart. The insertion was probably by tendon beginning on the lateral side of the proximal part of

Fig. 11. The deep pelvic muscles of _Tyrannosaurus_. GI - pubo-ischio-femoralis externus part one (probably fused to pubo-ischio-femoralis externus part two); G2 - pubo-ischio-femoralis externus part two; H - ilio-fibularis; I - ilio-femoralis.


I
H
GI
G2

the fibula and then running over its anterior face to insert on the medial surface, as it does in crocodilians.

Romer, (1923b) reconstructs this muscle in Tyrannosaurus as it is in the alligator. While there is a well marked muscle scar on the lateral surface of the fibula in all theropods and sauropods there is no clear cut scar on the ilium. Gregory and Camp, (1918) suggest an origin for this muscle above and just posterior to the acetabulum in Ornitholestes. Again, there are not clearly defined muscle scars in this region. The origin for the M. ilio-femoralis occupies this area in the alligator. Thus it may well be assumed that since in both alligators and many birds this muscle originates above and posterior to the M. ilio-femoralis, the interpretation of Romer, (1923b) is probably correct. Russell (1972) reconstructs this muscle in coelurosaurs with much the same attachments as given by Romer, except that his origin for the M. ilio-fibularis is on the distal, lateral surface of the ilium where the M. flexor tibialis internus part 2 and M. flexor tibialis externus originate in the alligator. Walker,(1977) cites Russell, (1972) as having found the ilium in theropods divided into two large fossae by a ridge. While Russell believes that these two fossae were filled by the two heads of the M. ilio-femoralis, Walker feels that the posterior of the two was for the origin of the M. ilio-fibularis. This view was introduced by Gregory and Camp, (1918). As I will discuss later I have found no such ridge dividing the ilium in any theropod.

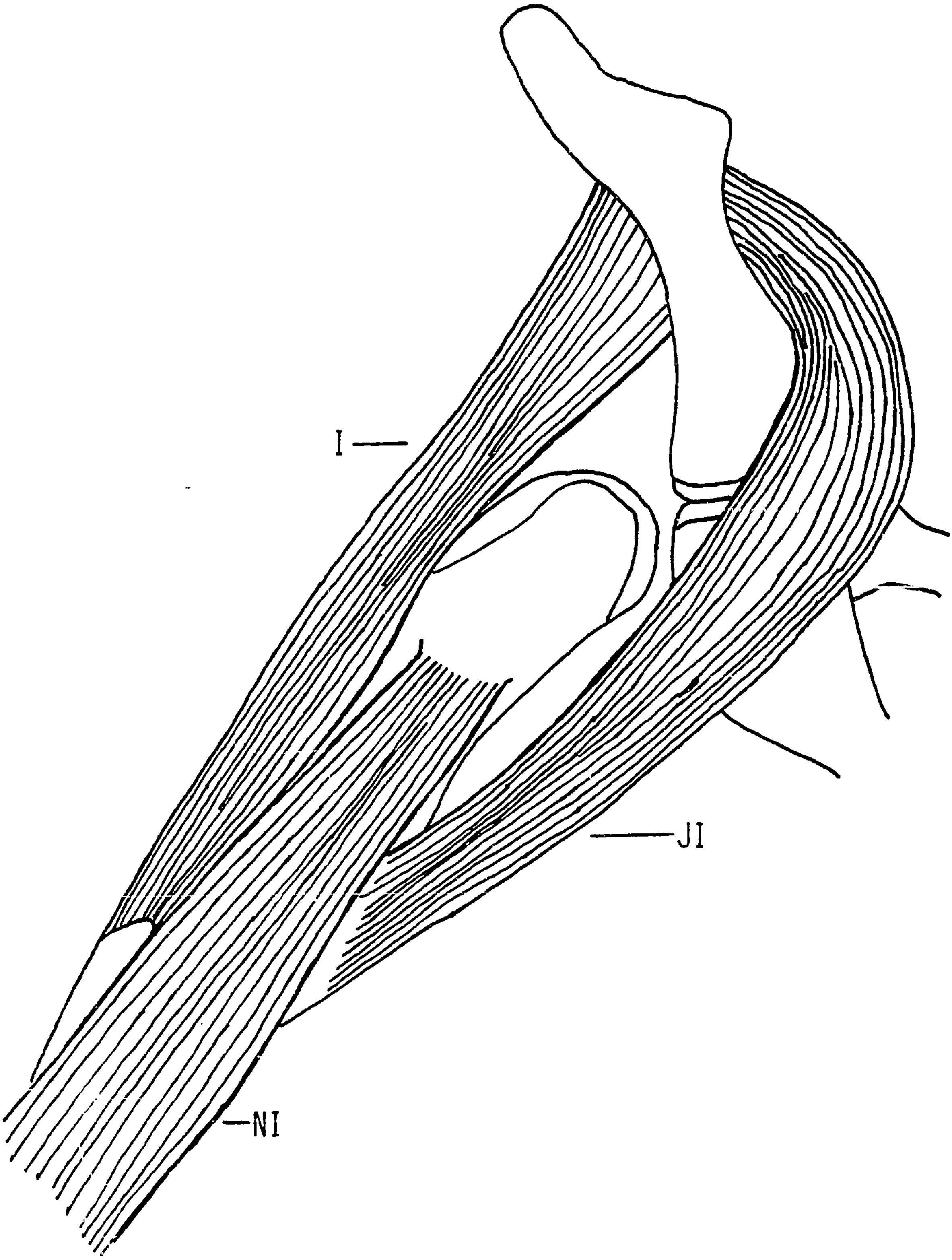
M. Ilio-femoralis.

The origin of the M. ilio-femoralis in crocodilians is on the blade of the ilium below the second head of the M. ilio-tibialis, extending nearly to the acetabulum. (Figures 5 and 12).

The insertion of this muscle is along the lateral surface of the femur. The insertion lies on a ridge, here named the abductor-ridge, between the M. femoro-tibialis internus on its anterior border and the M. femoro-tibialis externus on its posterior border (Figure 13).

The M. ilio-femoralis in many birds has two heads, the M. iliacus and the M. gluteus medius et minimus. According to Romer, the avian homologue of the M. ilio-femoralis is the latter, which is also known as the M. ilio-femoralis externus (Gadow, 1882b). In contrast to archosaurs the M. ilio-femoralis of birds is small, but still arises from the ilium below the M. ilio-tibialis. This muscle inserts on a tuberosity on the lateral side of the femur, directly below the greater trochanter in the birds which retain the M. ilio-femoralis.

Fig. 12. Anterior view of the deep crocodilian pelvic muscles. I - ilio-femoralis; JI - pubo-ischio-femoralis internus, part one; NI - femoro-tibialis internus.


I
JI
NI

Comparative data

In *Tyrannosaurus*, the M. ilio-femoralis (Figure 11) is quite large. Muscle scars indicate that most of the space between the origin of the M. ilio-tibialis and the acetabulum is occupied by this muscle. The insertion is the same as in crocodilians. Below the greater trochanter, on the posterio-lateral side of the femur is a large rugosity for the beginning of the insertion which then tapers in muscle bulk distally along a ridge. A nearly identical scar can be seen on the femur of all crocodilians. The rugosity for the insertion of this muscle is comparable to that seen in the birds which possess the M. ilio-femoralis internus.

Romer, (1923b) reconstructs this muscle in *Tyrannosaurus* as occupying most of the area between the ilio-tibialis and the acetabulum. This insertion point is down the midline of the lateral surface of the femur. Here there are no scars for the M. ilio-femoralis. The only major scars are found directly posterior to the m. ilio-femoralis in Romer's (1923b) restoration from which, according to his reconstruction, originates the M. femoro-tibilis externus. Russell (1972) departs from the usual placement (insertion) of the M. ilio-femoralis from a reptilian to a mammalian position based on the development of the greater trochanters and the vertical posture of the legs. However, the only animals which insert gluteal muscles directly onto the greater trochanters are mammals, whose greater trochanters are not homologous to those of either birds or dinosaurs. They cannot be homologous since their common ancestor would likely be among captorhinomorph reptiles which lacked these trochanters. Thus, it is more prudent to follow the insertion of this muscle as set forth by Romer, (1923a) and modified slightly by myself, considering the origin and insertion of this muscle throughout the Reptilia, in birds and to judge from its obvious muscle scars on the bones of theropods. In addition, Russell (1972), defines two heads of the M. ilio-femoralis based on the presence of a ridge on the lateral surface of the ilium and a fissure dividing the greater trochanter into two parts. In the theropods that I have examined (these include *Tyrannosaurus rex*, AMNH 5027; *Gorgosaurus sternbergi*, AMNH 5664; *Struthiomimus altus*, AMNH 5339, *Deinonychus antirrhopus* YPM 5205 and *Ornitholestes hermanni*,ANMH 619) there is no ridge on the ilium. Furthermore, since the the M. ilio-femoralis does not insert into the greater trochanter, a notch in the greater trochanter dividing it into two parts has no effect on the M. ilio-femoralis. Inspection of the greater trochanter of *Struthiomimus altus* shows that the notch could be for the passage of the tendon from the M. pubo-ischio-femoralis internus part two onto the proximal part of the femur.

Gregory (in Romer, 1923b) reconstructs the origin of this muscle in theropods. His restoration is the same as that of Romer, (1923b).

Walker, (1977) places the insertion of the M. ilio-femoralis of theropods onto the lesser trochanter. He does this because "the trochanter of birds is in the same position as the lesser trochanters of advanced thecodonts and dinosaurs". Walker (1977) has noted the probability that the M. ilio-femoralis is homologous to the three M. ilio-trochanterici and the M. ilio-femoralis externus of birds. He cites Romer, (1962:280) as having changed his mind from homologizing the ilio-trochanterici with the M. pubo-ischio-femoralis internus to the M. ilio-femoralis. As further evidence, Walker notes that there is no capture of the M. ilio-trochanterici by the ilium in the development of the chick. Furthermore, the ilium develops higher than the transverse processes of the presacral vertebrae. Finally Walker, (1977) states that the M. ilio-trochanterici divide the heads of the M. femoro-tibialis of birds in the same fashion as the M. ilio-femoralis does in the alligator.

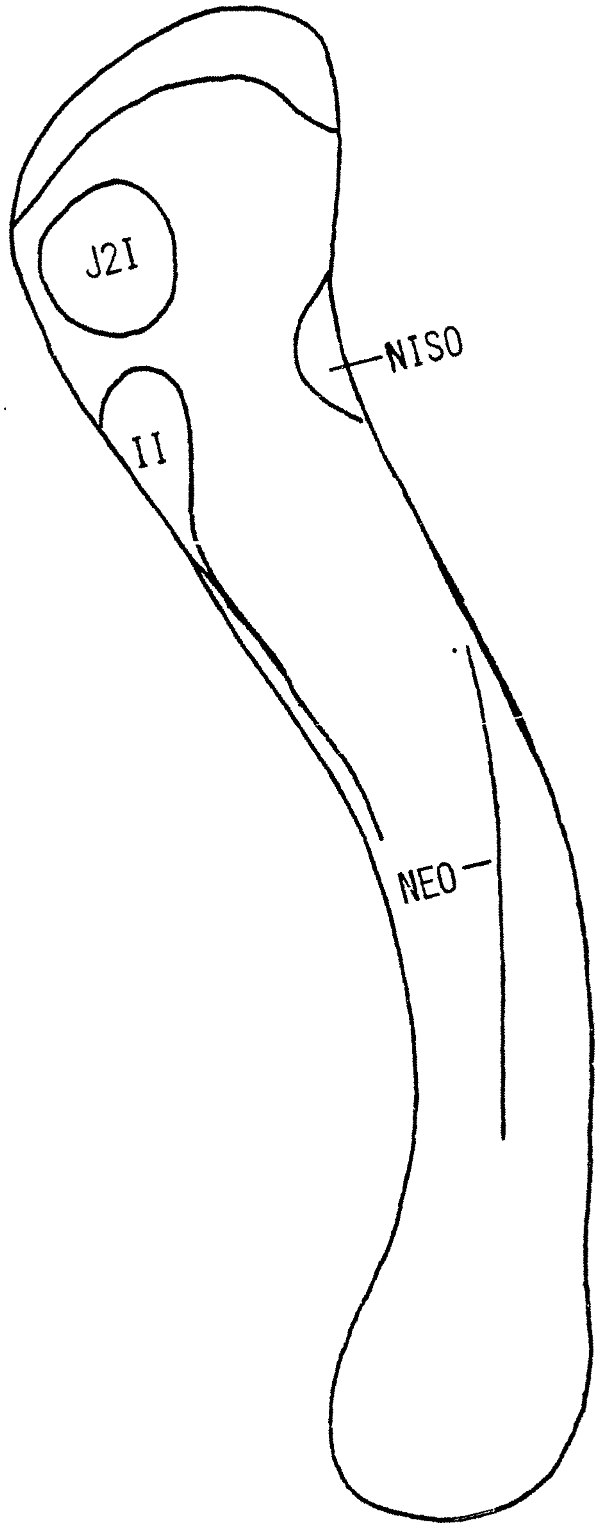
Firstly, I have doubts whether Romer changed his mind as to the homologies of the M. ilio-femoralis and the M. pubo-ischio-femoralis internus. The change was made in a chart with no explanation. Prior to this Romer, (1923a, 1927) had argued in text and chart for homologizing the M. ilio-femoralis with only the M. ilio-femoralis externus of birds.

Walker, (1977) is incorrect in the next two points he makes. First, the ilium of birds, especially during days five through seven is lower in position than Walker states (Romer, 1927). Second, contrary to the study by Walker, (1977) the M. ilio-trochanterici do not divide two heads of the M. femoro-tibialis in birds in the same manner as the M. ilio-femoralis divides the M. femoro-tibialis in alligators. The ilio-trochanterici insert much too high on the femur in birds to accomplish this and insert almost at right angles to the insertion of the M. ilio-femoralis externus of birds (M. gluteus medius et minimus) and the M. ilio-femoralis of Alligator. We do not see the capture of the M. ilio-trochanterici by the ilium since in the development of the chick, the preacetabular part of the ilium has already closed the excavation for the passage of the M. pubo-ischio-femoralis internus part two to the femur and thus we have no hope, at least in the chick of seeing ontogeny recapitulate this phylogenetic event (Lance and Jones, 1979). Furthermore, trying to find examples where ontogeny recapitulates step by step changes in morphology from one state to a derived condition is indeed rare. The ilium of *Archaeopteryx* resembles the developing chick ilium in that the closure of excavation of the ilium has already occurred. If *Archaeopteryx* is a primitive bird then the hope of finding the capture of the M. Iliotrochanterici by the ilium in the development of birds has probably been precluded.

Pubo-ischio-Femoralis Internus.

In crocodilians the pubo-ischio-femoralis is composed of two heads (Figures 10,12,and 13), the second taking its origin from the first six lumbar vertebrae, the first head from the internal surface of the ilium and ventral portions of the sacral ribs (Romer, 1923a). The insertion of the second head of this muscle in the Crocodilia is by two tendons which insert into the posterio-lateral surface of the femur below its head. The first head of the internus inserts into a large depression on the

Fig. 13. Lateral view of the crocodilian femur (except Gavialis) and its muscle scar anatomy. I1 - ilio-femoralis, insertion; J2I - pubo-ischio-femoralis internus part two insertion; NEO - femoro-tibialis externus, origin; NISO - Femoro-tibialis internus superficial head, origin.


J2I
NISO
II
NEO

internal surface of the femur medial to the fourth trochanter. This muscle is represented in birds by the three heads of the M. iliotrochantericus and the M. iliacus. The M. iliotrochantericus anterior arises from the anterior part of the ilium and from the iliac process along the lateral edge of the ilium (George and Berger, 1966). The M. iliotrochantericus medius originates just in back of the origin of the anterior head in front of the acetabulum (George and Berger, 1966). The M. iliotrochantericus posterior is the largest of the three, originating from the anterior iliac fossa. It is interesting to note that Archaeopteryx also displays a large anterior iliac fossa which is unlike any known theropod. The M. iliacus originates from the ventral rim of the anterior portion of the ilium, medial to the origin of the M. iliotrochantericus anterior and medius (George and Berger 1966). The M. iliotrochantericus anterior and medius insert on the latero-proximal surface of the femur below its head. The medius inserts just in front of the anterior. The M. iliotrochantericus posterior inserts on the lateral surface of the greater trochanter. This insertion is the same as for the second head of the M. pubo-ischio-femoralis internus. It seems that the second head of the M. pubo-ischio-femoralis has migrated upward onto the ilium in birds. This analysis although based just on origin and insertion, is reasonable since the insertion of the M. iliacus and the M. iliotrochantericus arterior and medius are directly comparable to the first head of the M. pubo-ischio-femoralis internus and the first and second heads of the M. pubo-ischio-femoralis externus respectively. Thus, the pubic musculature is completely accounted for aside from the muscles which crocodilians share with birds in name and homology.

Comparative data

The pubo-ischio-femoralis internus in *Tyrannosaurus* has lost its origin on the pubis and ischium as compared with non-archosaurian reptiles (Romer, 1923a,b). Instead it is composed of two heads, the second (Figures 14 and 15) taking its origin from the first six vertebrae (Romer, 1923a,b) and the first head (Figures 3,14 and16) from the ventral portion of the ilium anterior to the acetabulum (Romer, 1923a,b).

Here, there is seen a large concavity for the origin of this muscle. In addition, the anterior

Fig. 14. Anterior view of the pelvis and its muscle scars of Tyrannosaurus. G2I - pubo-ischio-femoralis externus part two, insertion; G3O - pubo-ischio-femoralis externus part three, origin; J2I - pubo-ischio-femoralis internus part two, insertion; RO - obliquus abdominis externus, origin.

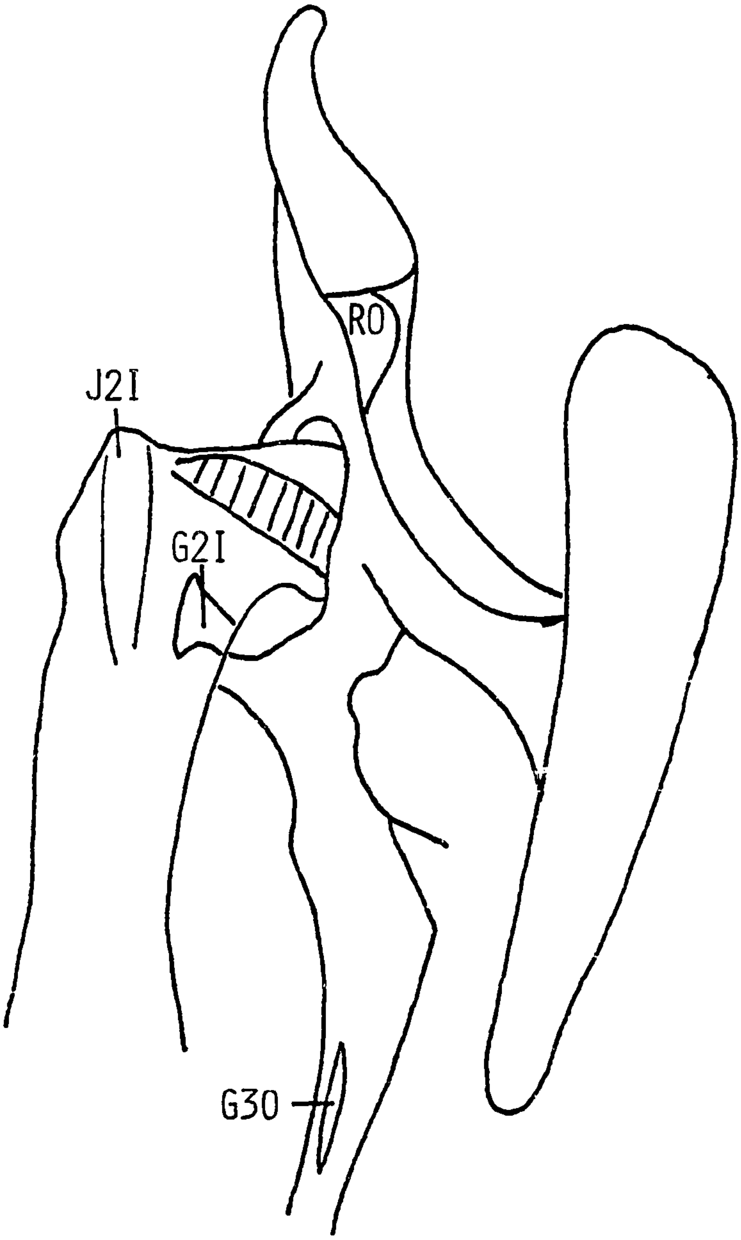

RO
J2I
G2I
G30

Fig. 15. Lateral view of the deep muscles of the pelvis of *Tyrannosaurus*. J2 - pubo-ischio-femoralis internus part two; K2 - flexor-tibialis internus part two; K3 - flexor-tibialis internus part three; L1 - adductor femoris; N - femoro-tibialis deep head; T (M) - tendon of the ambiens part one.

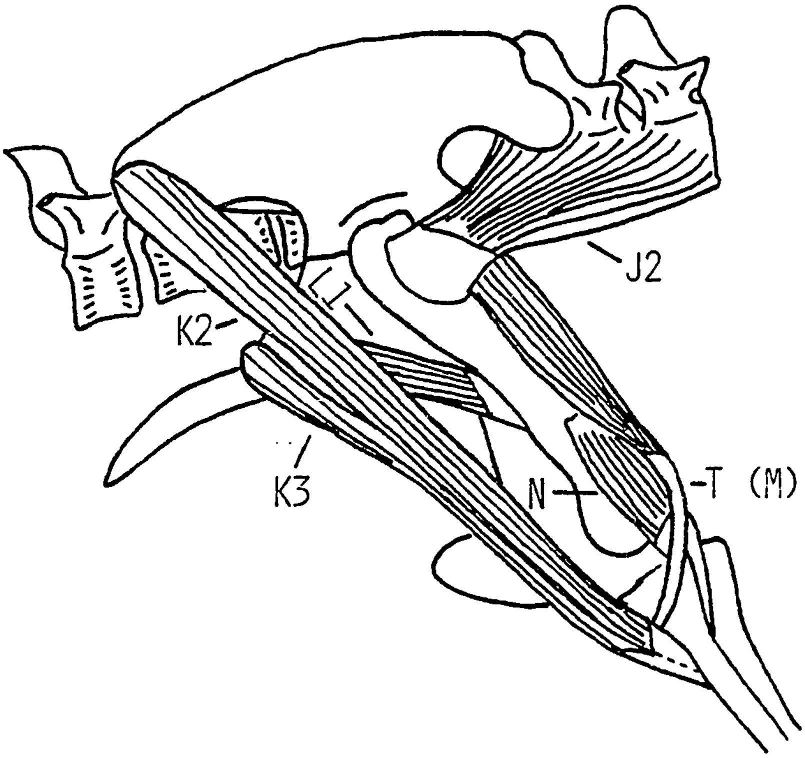
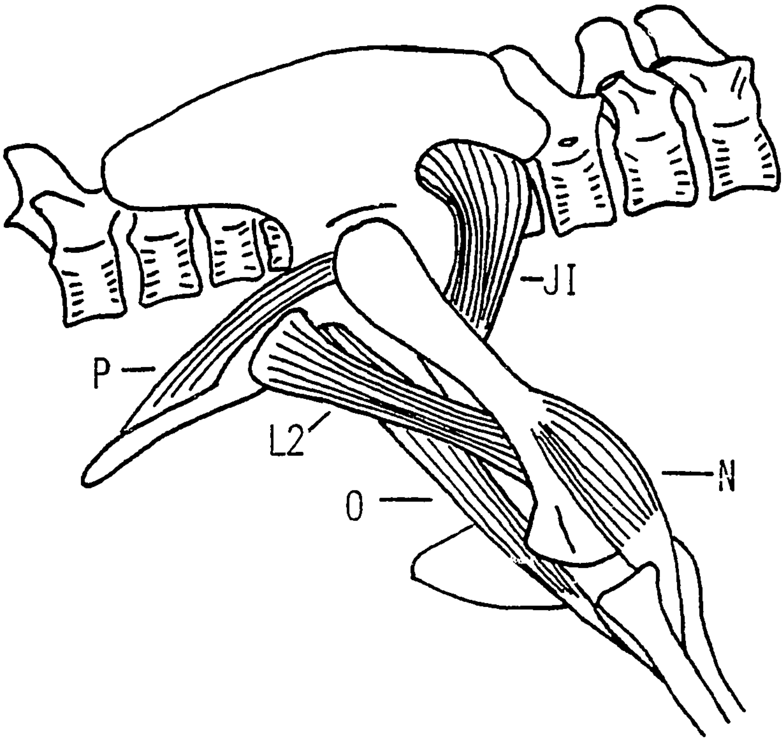

J2
L1
K2
K3
N
T (M)

Fig. 16. Lateral view of the pelvic musculature of *Tyrannosaurus*. JI - pubo-ischio femoralis internus part one; L2 - adductor femoris part two; N - femoro-tibialis deep head; O - pubo-ischio tibialis; P - ischio-trochantericus.


JI
P
L2
N
O

blade of the ilium is severly excavated for the passage of both heads of this muscle to the femur. The second head inserts on the lateral, anterior and medial surfaces of the greater trochanter. The first head inserts in a well marked depression on the medial surface of the fourth trochanter. The condition of both of these muscles is nearly identical with those found in crocodilians.

Romer (1923b) reconstructs the M. pubo-ischio-femoralis internus in Tyrannosaurus as it is in Alligator. Russell's reconstruction bears a close resemblance to the reconstruction by Gregory in Romer (1923b). Both Gregory (1923) and Russell (1972) reconstruct a pubic head for the M. pubo-ischio-femoralis internus. In the living archosaurs there is no pubic head of this muscle (Romer, 1923a,b). The area used for the origin of the pubic head in Russell's (1972) restoration is the origin for the M. obliquus abdominis and second head of the M. ambiens. The pubic head of the pubo-ischio-femoralis internus, as restored by Russell (1972) represents the M. pubo-ischio-femoralis externus part one of Alligator which according to Romer (1923b) is absent in theropods. In my opinion, part one probably is fused to part two. Muscles that originate from the same area and run parallel to one another usually become fused (George and Berger, 1966). The origin of pubic head (Russell, 1972) also interferes with the origin of the obliquus internus. Both Russell (1972) and Gregory and Camp, (1918) reconstruct a M. quadratus lumborum which according to Russell (1972) represents the second head of the M. pubo-ischo-femoralis internus. Thus, Russell follows Gadow's (1882a,b) terminology for the muscle.

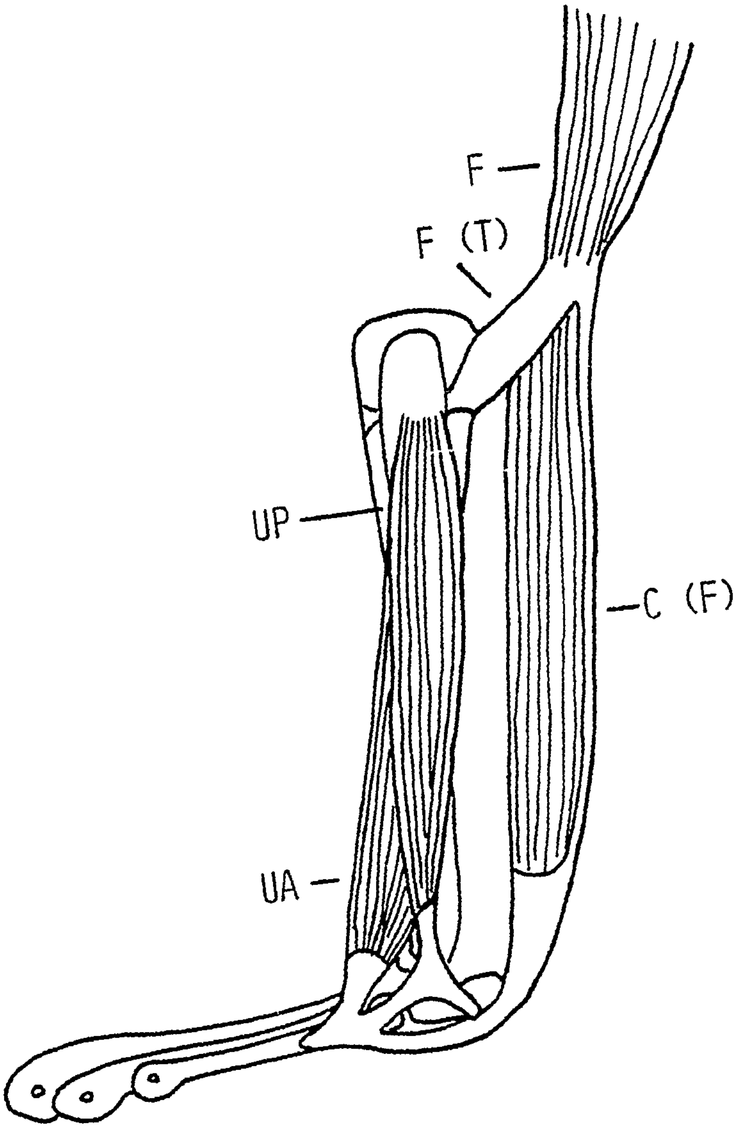
The M. quadratus lumborum, lies in the lumbar region behind the peritoneum. The quadratus lumborum attaches by a broad tendon into the fascia of the transversus absominis and the gastralia. Therefore, the M. "quadratus lumborum" of Gadow, (1882a,b) is actually the M. pubo-ischio femoralis internus part two as determined by Romer, (1923a). The origin of this muscle is not from the ventral rim of anteriormost portion of the ilium, but it is as Romer, (1923b) reconstructed it, from the presacral vertebrae. Russell placed the insertion point for this muscle on the medial surface of the greater trochanters. There are no scars in this area for muscle attachment. It is possible, however, that this muscle may have inserted on the lesser trochanters directly. Russell has also restored an ischiadic head which is the ischiadic head of this muscle in lizards. The problem here is that we are not dealing with lacertilian morphology but archosaurian morphology. Living archosaurs and birds whose musculature is known do not have this muscle. Russell places the ischiadic head of the internus into the muscle scars for the insertion of the M. ilio-ischio caudalis and scars for the origin of M. adductor femoris part two. The insertion of the M. ilio-ischio caudalis by Russell (1972) is actually the muscle scar for the origin of the M. flexor tibialis internus part three, a muscle which Russell does not mention even though it is large in crocodilians. Russell's placement of the M. pubo-ischio-femoralis part one is in agreement with both Romer and my own observations. Walker (1977) homologizes the M. pubo-ischio-femoralis internus with that of the lizard. Thus, all parts of this muscle found in lizards, i.e., the ventralis, medialis and dorsalis are reconstructed on the pelvis of Tyrannosaurus. The ventralis originates on the internal border of the pubis below the M. ambiens while the medialis and dorsalis originate above it. The medialis originates on the proximal portion of the pubis, while the dorsalis originates on the internal surface of the ilium. The dorsalis inserts on the medial surface of the lesser trochanter while medialis and ventralis insert on the medial surface of the femur below its head.

Since the hindlimb morphology of lizards is not similar to that of alligators or birds I reject Walker's restoration of this muscle in Tyrannosaurus. Walker has also apparently left out many muscles such as the M. pubo-ischo-femoralis externus, M. ambiens part two, M. flexo-tibialis externus and internus. I also reject the homology between the processus lateralis pubis of lizards, and a roughened area at the edge of the pubis in Stagonolepis. This roughened area is the site of the epiphyses in young alligators and the attachment of cartilage forming the gastralia abdominal basket. Also, the pubic apron of lizards does not resemble that of archosaurs. In fact, the pubic 'apron' of lizards resembles most reptiles having a pubic symphysis and fairly short and stout pubes. The condition of the specimens of Stagonolepis is such that roughened areas may represent worn or erosinal surfaces due to processes of fossilization. It should be noted that much of the material comprising the specimens of Stagonolepis is made up of impressions in coarse sandstone and is not bone.

M. Flexor Tibialis Externus.

This muscle arises from the dorsal portion of the ilium, behind the origin of the third head of the

Fig. 17. Lateral view of the shank musculature of crocodilians. C (F) - gastrocnemius, fibular head; F - flexor-tibialis externus; F (T) - tendon of the flexor-tibialis externus; UA - peroneus anterior; UP - peroneus posterior.


F
F (T)
UP
C (F)
UA

ilio-tibialis in the Crocodilia (Figure 5). The insertion in the Crocodilia is in three places: 1) inserts primarily, on the posterior proximal part of the tibia (Figure 17) and from this insertion two tendons arise; 2) One tendon is sent between the tibia and fibula, inserting on the anterior face of the tibia; 3) The other tendon is sent the length of the M. gastrocnemius to insert on the hamate process of the fifth metatarsal (Figure 17). The M. flexor tibialis externus of birds (M. semitendinosus of George and Berger, 1966) arises from the posterior part of the ilium and from the transverse process of the first free caudal vertebra (George and Berger, 1966). This muscle is the most posterior of the superficial muscles of the ilium. In many birds, the M. flexor tibialis externus inserts on the posterior, proximal surface of the tibiotarsus and the fascia of the gastrocnemius. The M. accesorius semitendinose when present, usually inserts on the distal and posterior portion of the femur in the popliteal fossa.

Comparative data

The condition of this muscle (Figures 3 and 6) in Tyrannosaurus is again similar to that of crocodilians. The origin is on the dorso-posterior surface of the ilium behind the origin of the third head of the M. ilio-tibialis. This muscle extended the length of the posterior surface of the femur to insert on a groove on the lateral, posterior surface of the proximal portion of the tibia. As in the Crocodilia, the tibia and the fibula of *Tyrannosaurus rex* are separated just below their proximal ends. This space allows the passage of two tendons, one from the M. ilio-fibularis and the other from the M. flexor tibialis externus, which run to the anterior face of the tibia. A strong tendon was also sent to the reduced fifth metatarsal if the crocodilian plan is followed.

Romer reconstructs this muscle in *Tyrannosaurus* from just ventral to the third head of the M. ilio-tibialis to the proximal posterior surface of the tibia. Close examination of the ilium of *Tyrannosaurus* revealed a muscle scar for the origin just posterior to the origin in Romer's restoration (1923b). The origin was still ventral to M. ilio-tibialis. The insertion point is not clearly represented by Romer (1923b).

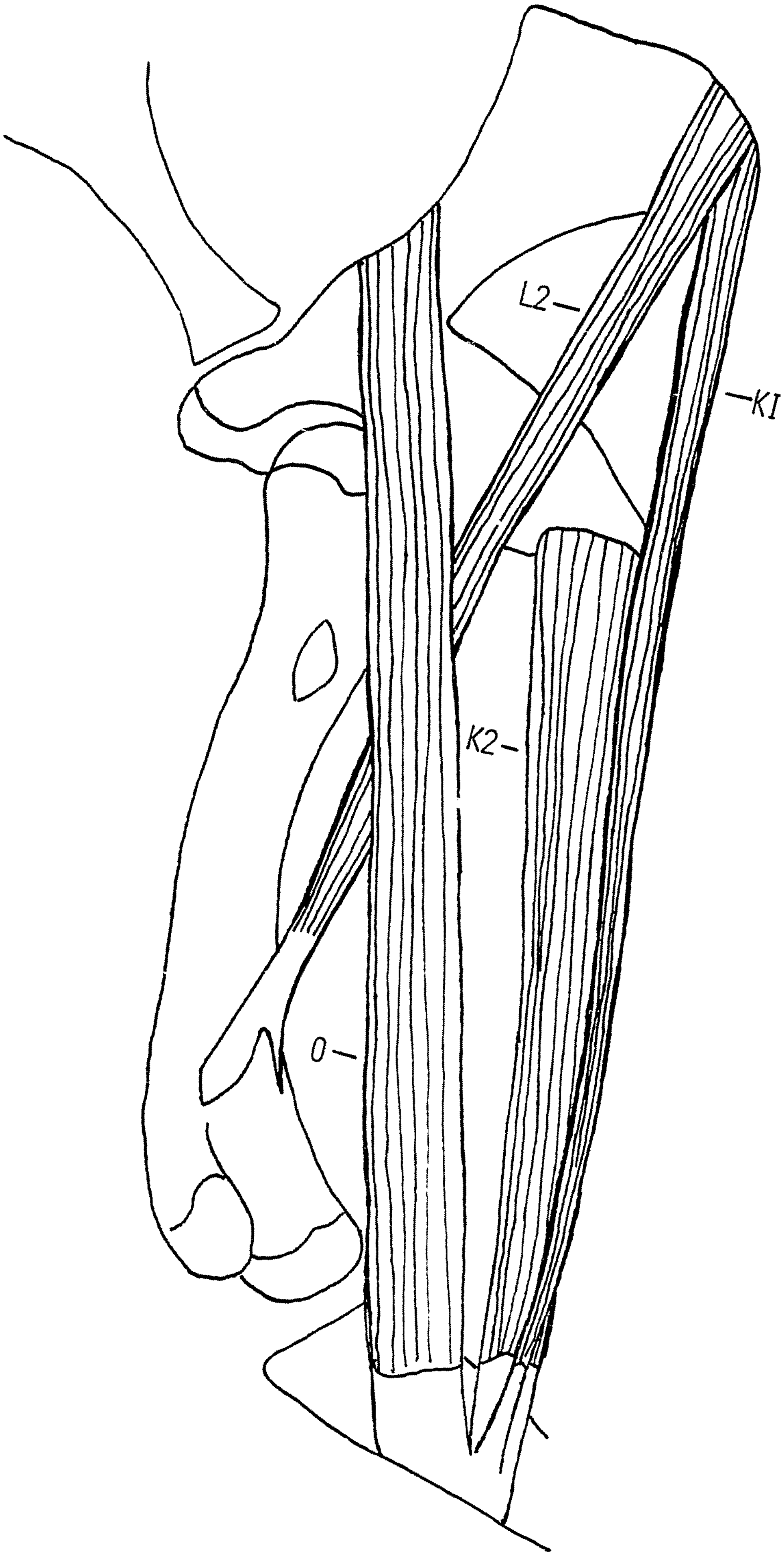
Russell reconstructs both the M. flexor tibialis externus and internus as one muscle the M. flexor tibialis. His interpretation of the insertion lies on the proximal, posterior surface of the tibia. Gregory reconstructs the flexor tibialis externus as it is placed in the alligator.

Flexor Tibialis Internus.

This muscle in the Crocodilia is composed of four heads (Figures 5 and 18). The first head originates on the posterio-internal border of the ischium (Romer, 1923a). The second head of this muscle takes its origin on the ilium, just posterior and slightly ventral to the flexor tibialis externus (Romer,1923a). The third head originates near the posterior rim of the ischium, just below the acetabulum (Romer,1923a). The fourth head arises on the ilio-ischiadic ligament in lizards. The Crocodilia, however, lack this ligament (Romer, 1923a). Thus, the fourth head originates with the M. flexor tibialis externus.

All parts of the M. flexor-tibialis internus of the Crocodilia insert on the proximal part of the tibia. The first and second head insert together on the posterio-medial face of the tibia. The insertion is by aponeurosis which covers the tibia from its postero-medial insertion, continuing around the medial side to the anterior face of the tibia. The third and fourth heads insert together on the posterio-proximal part of the tibia, below its head. The insertion of the fourth part is continuous with that of the M. flexor tibialis externus. The flexor tibialis internus (M. ischio-flexorius of Gadow and Selenka, 1891; and the

Fig. 18. Ventral view of the crocodilian pelvic musculature with fascia removed. KI - flexor-tibialis internus part one; K2 - flexor-tibialis internus part two; L2 - adductor femoris part two; O - pubo-ischio-tibialis.


L2
KI
K2
O

M. semimembranosus of George and Berger, 1966) has in most birds only one head. It usually originates by aponeurosis from the posterio-ventral portion of the ischium, above the ischiopubic fenestra (George and Berger, 1966). This muscle may, in addition to the above, originate on the pubis. In most birds studied this muscle inserts on the anterio-medial surface of the tibiotarsus, below its head (George and Berger 1966). The tendon of the M. flexor tibialis internus is usually connected in some way with the raphe of the M. semitendinosus and M. gastrocnemius.

Comparative data

I believe the condition of the M. flexor tibialis internus (Figures 3,15, and 16) in Tyrannosaurus to be similar to that seen in Crocodilia. Unlike the pelvis of birds, the ischium is well separated from the ilium in both the Crocodilia and Theropoda. In addition, both groups lack an ilio-ischiadic ligament (Romer, 1923a). The first head of this muscle is small in crocodilians and may not be represented in theropods. The origin of the second head is below that of the flexor tibialis externus, along the posterior-ventral rim of the ilium. The origin of the third part is well marked. A depression for the origin is located on the ischium posterior and ventral to the acetabulum. Based on the loss of the ilio-ischiadic ligament, I feel that the fourth head of this muscle inserted with the M. flexor tibialis externus as it does in the alligator. This is speculation since there is no muscle scar evidence for the existence of part four of the flexor tibialis internus. The insertion of part two of this muscle following the crocodilian plan, is on the posterior surface of the tibia. The third part inserts into a depression on the posterior surface of the tibia, medial to the insertion of the flexor tibialis externus. The fourth part, if present, inserts just medial to the flexor tibialis externus.

Romer, (1923b) restores the first head of this muscle midway down the lateral surface of the ischium. I have found no muscle scar in this area. His reconstruction for the second head follows that of the alligator (Figures 4 and 5) in Romer, (1923b). Muscle scars are present but are a few inches below the scar for the M. flexor tibialis externus, not directly under it as Romer has restored it. Romer reconstructs the third head as it is represented in the alligator. The position of this muscle scar is identical between theropods and Alligator. Thus, this is yet another case of synapomorphy between the two groups. Romer also restores a fourth head lying directly under the M. flexor tibialis externus. While the presence of this muscle is not entirely certain (Romer, 1923b), the remarkable one for one correspondance with the previous muscles weighs in its favor. In addition there is a probable scar on the tibia for this muscle.

As already noted, Russell (1972) combines M. flexor tibialis externus and all parts of the flexor tibialis internus into one muscle. The insertion is placed directly on the proximal, posterior surface of the tibia. The rugosities Russell used in the bone are for the attachment of the joint capsule and associated ligaments and cartilages. The placement of the muscle on the very top of the joint capsule would have restricted the very motion the action of the muscle was to produce, namely the flexion of the crus.

Gregory and Camp, (1918) reconstruct the M. flexor tibialis internus as it appears in Alligator. they are conservative in their restoration of only part two and part three of this muscle. Only these parts have been reconstructed because on the pelvis these are the only scars present for this muscle.

The Musculature of the Ischium

Pubo-ischio Tibialis.

The pubo-ischio tibialis in the Crocodilia has lost its origin on the pubis and arises entirely from the anterio-proximal lateral surface of the ischiadic blade (Romer ,1923a). The insertion is on the medial posterio-proximal portion of the tibia. A tendon is sent around the medial side, to the anterior surface of the tibia. (Figures 5 and 18). According to Romer, (1923a) Gadow,1882b) and Gregory and Camp, (1918) birds lack a pubo-ischio tibialis. Gadow, (1882b) also states that alligators also lack this muscle but Romer feels that this muscle is Gadow's part one of the M. flexor-tibialis internus. (see discussion by Romer, 1923a, page 540).

Comparative data

The origin of the pubo-ischio tibialis (Figures 3 and 16) in Tyrannosaurus is well marked having the exact location as that seen in crocodilians. That is, this muscle has lost its origin on the pubis and arises entirely from the anterior-proximal lateral surface of the ischiadic blade (Romer, 1923b). The insertion is on the medial surface of the proximal part of the tibia, just above the insertion of the M. ilio-tibialis internus parts I and II.

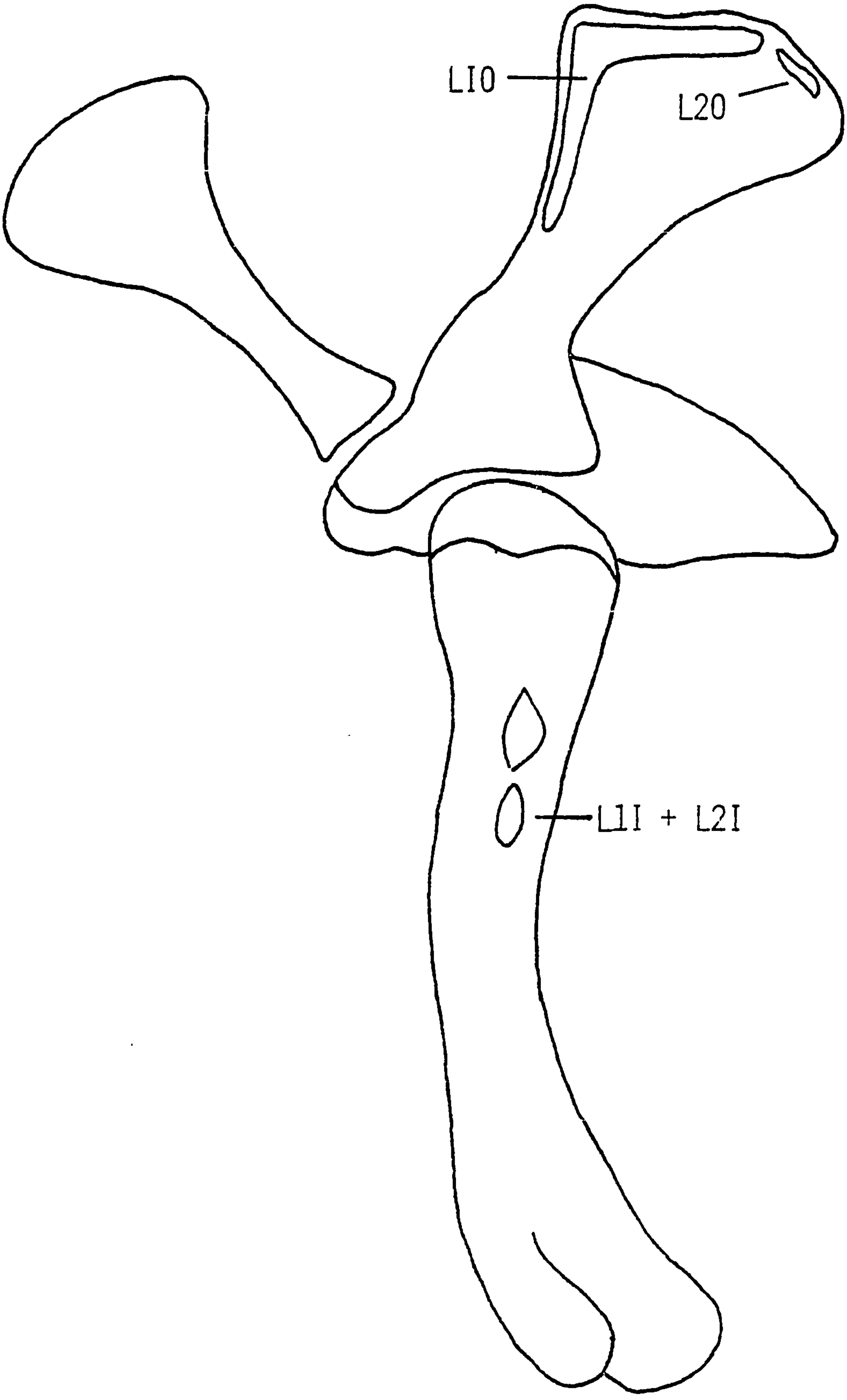
Neither Russell nor Gregory and Camp restore this muscle. It should be noted that Romer is probably correct in restoring this muscle, since I have found scars for this muscle in theropods, alligators and ornithischian dinosaurs.

Adductor Femoris.

The M. adductor femoris in the Crocodilia has two heads (Figures 4,5 and 18) of the first part is located on the distal, lateral surface of the ischium. The origin of the second part lies beneath the third part of the M. pubo-ischio-femoralis externus on the posterio-distal, lateral surface of the ischiadic blade, posterior to the origin of the first head.

The insertion of the first part of the M. adductor femoris in crocodilians except Gavialis is along the adductor ridge on the posterior face of the femur. The insertion of both parts one and two in Gavialis occurs in a deep pit distal to the fourth trochanter (Figure 19). The second part inserts above the first which is the larger of the two. These muscles are separated near their origin by the third part of the M. pubo-ischio-femoralis externus and distally by the passage of the M. pubo-ischio tibialis. Part of this

Fig. 19. Ventral view of the adductor muscle scar anatomy of <u>Gavialis</u>. L1O - adductor femoris part one, origin; L1I - adductor femoris part one, insertion; L2O - adductor femoris part two, origin; L2I - adductor femoris part two, insertion.


L10
L20
L1I + L2I

muscle inserts into the distal, posterio-medial surface of the femur. In birds, this muscle is termed the M. adductor longus et brevis (George and Berger, 1966) and the M. pubo-ischio femoralis (Gadow and Selenka, 1891). In many birds, there are two parts, the pars externa and pars interna. Both parts arise from the ventral margin of the ischium, posterior to the obturator foramen (George and Berger, 1966). The pars externa takes its origin immediately above that of the pars interna. The insertion in birds somewhat resembles the condition in the Crocodilia. The pars externa and interna insert on the posterio-medial portion of the distal third of the femur (George and Berger, 1966). In addition both parts fuse in the region of the popliteal fossa and send tendons into the pars media of the gastrocnemius.

Comparative data

The origin of this muscle in Tyrannosaurus is in two places. The first head originated on the lateral border of the ischium, below and posterior to the origin of the M. pubo-ischio tibialis. The second head originated just medial to and above the scar for the origin of the M. flexor-tibialis internus part three. The presence of two heads (Figures 2, 15, and 16) is indicated by the scars for this muscle on the femur. In _Tyrannosaurus_ there are two scars, one on either side of the femur on its posterior surface. Adductor one inserted into the medially placed scar. Adductor two inserted just below adductor one. However, there is a part of adductor two which inserts into the lateral part of the femur in _Tyrannosaurus_.

Romer has restored this muscle in _Tyrannosaurus_ with the insertion the same as in _Alligator_. The reduction and caudal elongation of the ischium apparently has not changed the attachments of the adductor femoris.

Russell does not restore the adductor muscles in coelurosaurs. Gregory and Camp restore two adductor muscles, the M. adductor longus and M. adductor magnus (M. ischio-femoralis). The M. adductor magnus is placed in the same location as the M. adductor femoris part one. The M. adductor longus is placed directly below the acetabulum on the ventrally directed hook on the ischium.

Ischio-trochantericus.

This muscle is small in the Crocodilia, taking its origin on the internal surface of the ischium (Figure 5). The insertion is by tendon on the lateral surface of the femur in a small area just below its head (Romer, 1923a).

In birds, this muscle is represented by the ischio-femoralis (Romer, 1923a). In contrast to crocodilians, the M. ischio-trochantericus of birds has migrated to the lateral surface of the ischium due to the fusion of the ischium to the ilium, to originate posterior to the obturator foramen and dorsal to the M. adductor longus it brevis. The insertion is in a depression on a ridge, which is posterior to the greater trochanter (George and Berger, 1966).

Comparative data

The M. ischio-trochantericus (Figures 3 and 16) in Tyrannosaurus may have migrated to the lateral side of the ischium. There is a possible muscle scar for the origin of this muscle midway down the ramus of the ischium on the lateral surface. The insertion may have been in the depression on the posterior surface of the head of the femur, internal to the greater trochanter. This muscle is small, even in crocodilians and may not be represented in all theropods.

Romer retains the Alligatorine position for this muscle in Tyrannosaurus. This muscle is probably more laterally placed since the ischia have a more elongate and continuous symphysis. Russell places this muscle in much the same position as Romer, while Gregory and Camp (1918) did not restore the M. ischio-trochantericus.

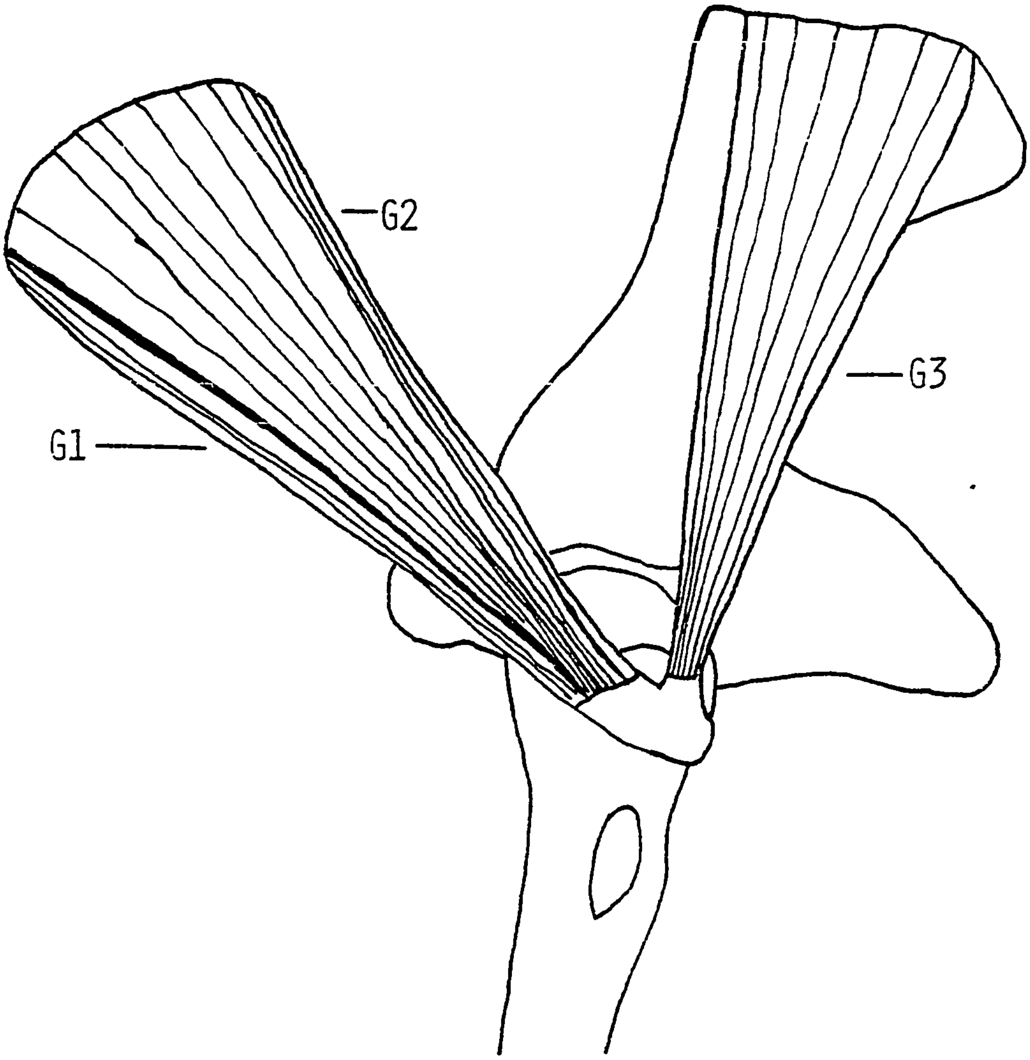
The Musculature of the Pubis

Pubo-ischio-Femoralis Externus.

The M. pubo-ischio-femoralis externus in the Crocodilia has three parts (Figures 4,6, and 20). The first part originates on the internal surface of the pubis and prepubic cartilage (Romer, 1923a). The second part arises from the lateral surface of the pubis and ventral surface of the prepubic cartilage (Romer, 1923a). The third part originates on the lateral surface of the ischium, posterior to the origin of the first part of the M. adductor femoris (Romer, 1923a). The insertion of this muscle is in two places. The tendons of parts one and two combine in the area in front of the femur to insert on posterio-medial surface of the head of the femur. They continue backward to insert on the posterio-lateral surface of the femur, joining the tendon of the third part in this area (Romer, 1923a).

In birds this muscle is represented by the M. obturator externus and internus. The externus arises in many birds from the area around the obturator

Fig. 20. Ventral view of the deep crocodilian pelvic musculature. G1 - pubo-ischio-femoralis externis part one; G2 - pubo-ischio-femoralis externus part two; G3 - pubo-ischio- femoralis externus part three.


G2
G1
G3

foramen (George and Berger, 1966). In some birds, for example in many passerines, the externus may have two heads (George and Berger, 1966). The internus arises on the medial surface of the pubis, the ischiopubic membrane and ischium. The origin extends from the beginning of the ischiopubic fenestra to the end of the ischium and corresponding length of the pubis. The M. obturator externus inserts by tendon on the proximal part of the femur. The internus sends a tendon through the obturator foramen to insert on the posterior part of the femur just under its head (George and Berger, 1966).

Comparative data

This muscle has two parts in Tyrannosaurus (Figures 3,6,11 and 14). The first head has disappeared or fused to the second part, since muscle scars show only scars for part two of this muscle on the pubis. The second part originates on the distal segment of the pubis on the lateral surface. Part two of this muscle inserts directly below and slightly lateral to the head of the femur. The insertion continues from this point medially to enwrap the neck of the femur on its posterior surface. The tendon of part three joins that of the second in this area.

In addition, the third part of this muscle also inserts on the posterior and posterior-medial surface of the greater trochanter. The third head originates entirely on the ventral surface of the ischium. In order to view the scar on the ischium of carnosaurs, an observer must stand beneath the pelvis facing caudally.

According to Romer (1923b), the first head of the M. pubo-ischio-femoralis externus is not present, based on the absence of strong gastralia in front of the pubis for the attachment of the M. rectus abdominis. Because of this Romer felt that the rectus continued on to insert into the pubis, thus, covering the origin of the first head of the M. pubio-ischo-femoralis externus. Russell suggests that in ornithomimids this is not the case, since there is according to Sternberg (1933) a thickening of the gastralia posteriorly. It is my opinion that the first head was not present for two reasons. Firstly, there are no muscle scars on the internal surface of the pubis. Secondly, the two pubes are fused distally a condition not found in crocodilians. Thus, in order for the origin of the first head not to interfere with either the M. rectus abdominis anterior or the oblique muscles this muscle probably migrated laterally or was lost. If the muscle migrated it probably fused with the second head since both would then originate in the same place. Romer restores the third head from the lateral surface of the ischium. The insertion points of this muscle are placed by Romer on the medial surface of the neck of the femur above the insertion for the M. pubo-ischio-femoralis internus part I.

As discussed above, Russell, (1972) reconstructs three heads of this muscle although he refers to the first head as the M. pubo-ischio-femoralis internus, pubic head. The second head originates on the lateral, distal surface of the pubic while the third head originates along the lateral surface of the ischium. All three heads insert into the anterior and posterior surfaces of the fourth trochanter. As Russell has drawn them in his restoration, five muscles insert in this one area in contrast to three in Romer's and my own restorations. The origins of this muscle in Gregory and Camp, (1918) are somewhat different, and in my opinion confused. For the most part they did not distinguish the names of the different parts of this muscle. Thus, the M. pubo-ischio femoralis externus (M. obturator externus) originates from the proximal, lateral surface of the pubis. It also originates on the lateral surface ischium. The M. pubo-ischio-femoralis posterior (M. obturator internus) originates on the internal surface of the ischium in their restoration.

Ambiens.

In crocodilians the M. ambiens has two heads (Figure 5). The first head originates at the junction of the ilium and pubis, anterior to the acetabulum (Romer, 1923a). The second head takes its origin on the internal surface of the pubis near its proximal end (Romer, 1923a).

The insertion of the M. ambiens in the crocodilians is two distinct locations. The first head inserts into the extensor tendon continuing around the knee to the lateral surface of the fibula near its head and runs on the internal surface of the fibular head of the M. gastrocnemius. The tendon passes internal to the calcaneal tuber to insert into the fifth metatarsal (Figures 7 and 8). The second head inserts on the surface of the M. femoro-tibialis internus at a point about two thirds down the length of the femur. In birds, this muscle is still referred to as the M. ambiens and has but one head. The origin of the M. ambiens in birds resembles the condition in the Crocodilia, arising from the pubis under the acetabulum (George and Berger 1966). The insertion of the M. ambiens in birds resembles that of the first head of this muscle in Crocodilia. The M. ambiens here also sends a tendon across the knee to the lateral surface of the fibula (George and Berger

1966). There it fans out to give rise to some of the long flexors of the digits.

Comparative data

In Tyrannosaurus, the origin of the M. ambiens is well marked at the extreme proximal part of the pubis and part of the ilium in front of the acetabulum (Figures 1 and 15). It is not known whether two heads are present (as in crocodilians). I feel that only the first head is present, since the second head is barely represented in alligators and is entirely absent in birds. The M. ambiens in Tyrannosaurus probably inserted into the aponeurosis (extensor tendon) formed by both parts of the M. femoro-tibialis and parts of the M. ilio-tibialis. It is likely that the tendon continued down the crus to the fifth metatarsal, as it does in crocodilians.

Romer, (1923b) restores both heads of the M. ambiens, in Tyrannosaurus placing them exactly as they are in the alligator. There may have been a second head to the M. ambiens based on the large scar on the proximal portion of the pubis. The insertion point cannot be traced as it is the connective tissue of the M. femoro-tibialis (Crocodylinae) or M. ilio-tibialis part three (Alligatorinae)

Russell does not restore the M. ambiens since he finds no muscle scars in ornithominids. However, my own observations of ornithominids are that muscle scars are present in the same place as in all other theropods. The problem here probably lies with the specimens Russell has examined since some specimens are not preserved well enough for muscle scar examination. Gregory and Camp (1918) restore only one head of this muscle whose origin is on the proximal part of the pubis in front the origin of the M. pubo-ischio-femoralis externus.

The Musculature of the Thigh

Femoro-tibialis.

In crocodilians, the M. femoro-tibialis has two parts, the internus and externus (Figures 4,6,7,8,12 and 13). The internus arises from the anterior face of the femur at the level of the insertion of the M. pubo-ischio-femoralis internus part two. The externus originates on the posterior, lateral surface of the shaft of the femur, just posterior to the insertion of the M. ilio-femoralis. The insertion of the M. femoro-tibialis internus is into the common extensor tendon (Romer, 1923a). The external head inserts into the common extensor tendon as well as the tendon of the first head of the ambiens (Romer, 1923a).

The M. femoro-tibialis in birds is represented by the M. femoro-tibialis externus, medius and internus. The externus is composed of two heads, a proximal and a distal head (George and Berger, 1966). The proximal head originates on the lateral and anterior-lateral surface of the femoral shaft, while the distal head originates from the posterio-lateral surface of the femur, farther down the shaft, (George and Berger, 1966). The origin of the M. femoro-tibialis medius is located on the trochanteric ridge and anterior face of the femur (George and Berger, 1966). The M. femoro-tibialis medius inserts on the patella as well as contributing to the patellar ligament. The M. femoro-tibialis internus inserts by tendon on the medial surface of the inner cnemial crest. It should be noted that in many birds two heads of the internus are represented (George and Berger, 1966).

Comparative data

The M. femoro-tibialis in <u>Tyrannosaurus</u> is composed of two heads (Figures 3,15,16). The first head, the internus, is composed of two parts. The origin for the internal part of the internus is well marked on the anterior and lateral surfaces of the shaft of the femur, midway down its length. The internus comprises much of the common extensor tendon which forms an aponeurosis with the M. ilio-tibialis. The medially placed fibers of this muscle probably inserted into the inner cnemial crest. The second more superfical part originates just under the anterior portion of the greater trochanter. Here there is a depression for the origin of this muscle. In addition the femur is rippled along the length of its origin until the muscle scar for the internus is encountered. Thus, this muscle covers much of the lateral and anterior surface of the femur. The insertion was on the proximal portion of the tibia and fibula. The externus lies lateral and above the internus originating along the lateral shaft of the femur. It was bounded posteriorly by the M. ilio-femoralis. The insertion is with the internus.

Shank Musculature of Crocodilians

Tibialis anterior.

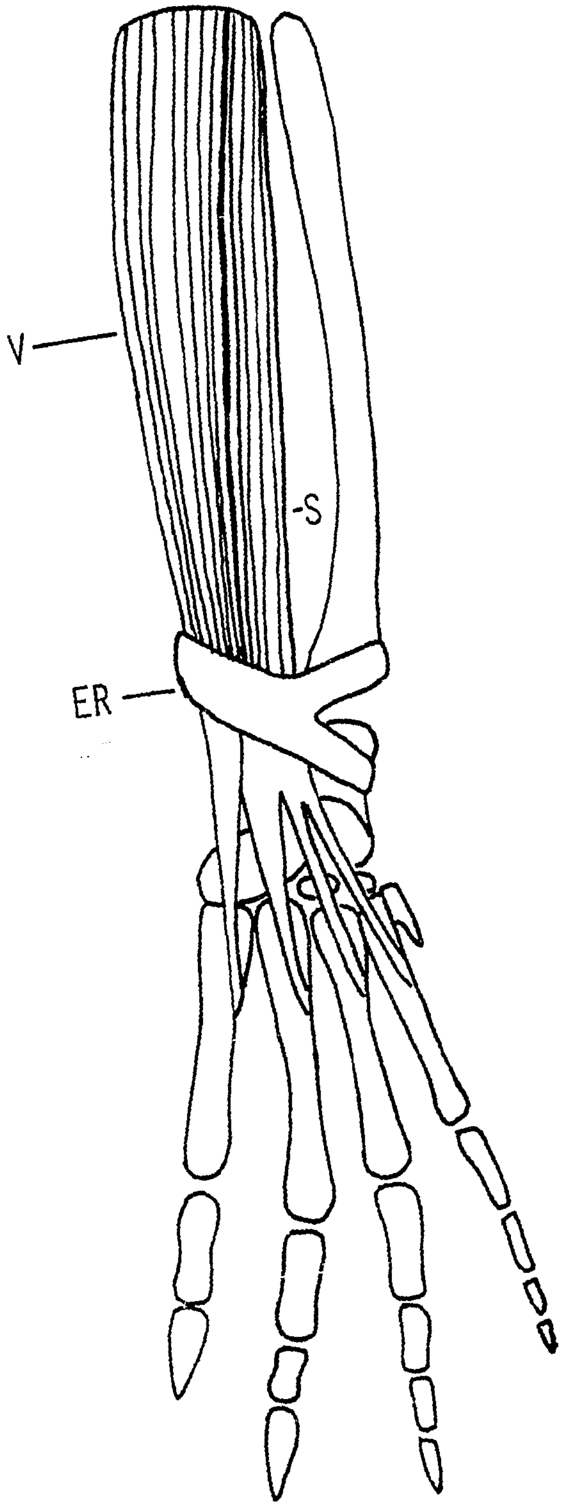
In crocodilians this muscle closely adheres to the M. exterior digiturum longus, (Gadow, 1882b). The muscle originates medially on the tibial tuberosity fibular side of the metatarsal I (Figure 21). Along with the M. extensor digitorus longus, this muscle passes under an extensor retinaculum. The retinaculum runs medially from the distal tibial surface and the medial surface of the astragulus to the lateral surface of the calcaneum and fibula. The rectinacum binds both muscles and prevents the bellying of the extensor muscles during contraction.

Extensor digitorum longus.

The M. extensor digitorum longus originates in both Crocodylinae and Alligatorinae from the tibial tuberosity and shaft of the tibia (Figure 21). This muscle closely adheres to the M. tibialis anterior. The insertion is by tendon to the fibular side of the base of metatarsals II-IV.

M. peroneus. There are two peroneus muscles in both Crocodilinae and Alligatorinae (Figure 17). The first or anterior head of the M. peroneus (Gadow, 1882b) originates along the anterior surface of the shaft of the fibula. The second head or posterior head also originates along the lateral surface of the shaft of the fibula and is more superfically placed. The anterior head inserts into metatarsals IV and V. The insertion of the posterior

Fig. 21. Anterior crocodilian shank musculature. V - tibialis anterior; S - extensor digitorum longus; ER - extensor retinaculum.


V
-S
ER

head is more complex. Not only is there an insertion with the anterior head but a strong tendon is sent posteriorly to loop under the calcaneum. This tendon fuses with that of the M. flexor tibialis externus. Thus a loop under the calcaneum is formed by tendons from both the posterior head of the peroneus and that of the M. flexor tibialis externus.

Gastrocnemius.

In both subfamilies this muscle has two heads, a fibular and tibial head. (Figures 22 and 23). The fibular head is by far the more massive of the two. The fibular head takes its origin mainly from the thick tendon of the M. flexor tibialis externus (Figure 17). Fibers also originate from the fibula, the posterio-lateral border of the extensor tendon and the tendon of the M. ambien. The tendon of the M. coccygeo-femoralis longus also inserts into this head (Figure 3). The origin of the tibial head is on the upper third of the tibial shaft and from the insertion tendon of the M. flexor tibialis internus (Gadow, 1882). The tibial head runs diagonally toward the culcaneal tuber into which it inserts. -A section of this tendon also proceeds to the fifth metatarsal (Gadow, 1882b) and joins with the tendonus loop under the calcaneum

Fig. 22. Posterior view of the crocodilian superficial shank musculature. C (F) - gastrocnemius, fibular head.

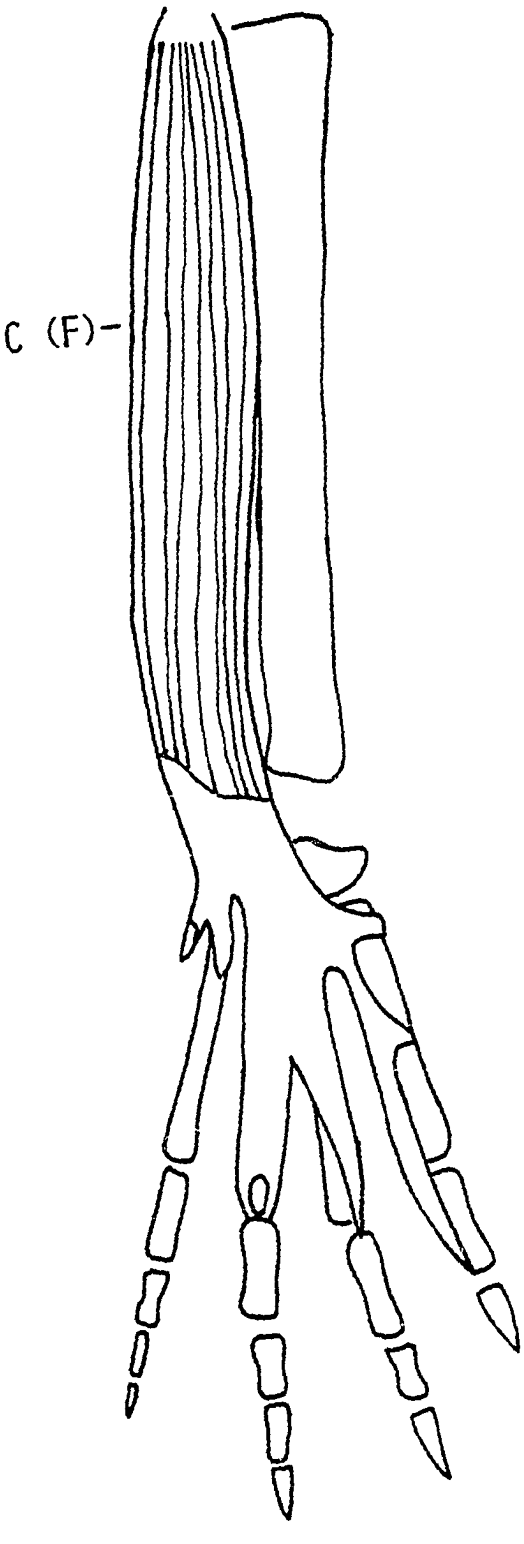
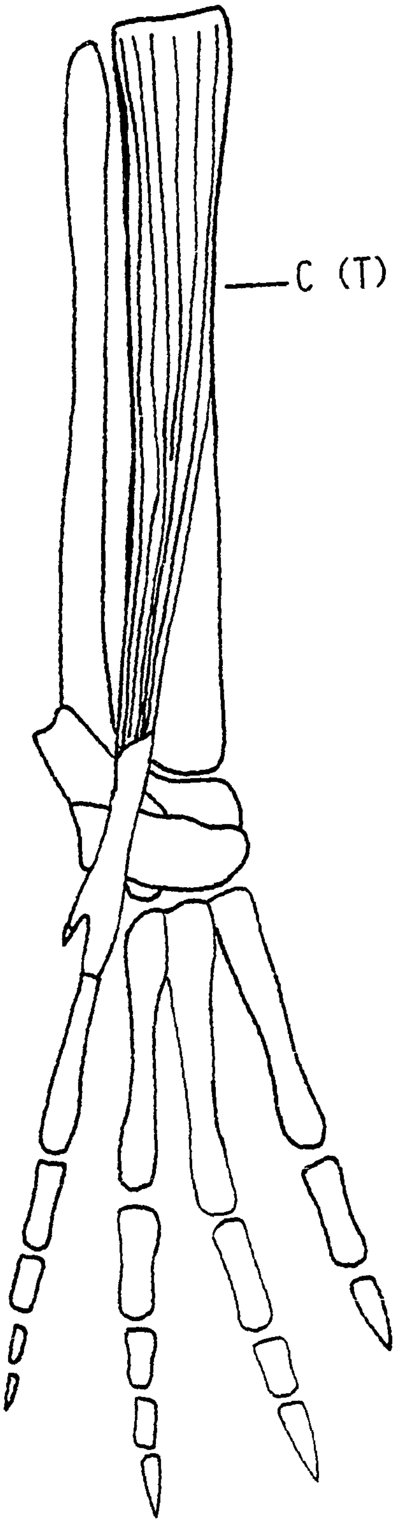

C (F)-

Fig. 23. Posterior view of the crocodilian shank musculature. C (T) - gastrocnemius, tibial head.


C (T)

previously noted. The fibular head is divided into three parts one of which will be placed under a new muscle heading, M. flexor digitorum superficialis. The fibular portion of the M. gastrocnemius has two parts. The first part inserts into the calcaneum and fifth metatarsal. The second part passes internal to the calcaneal tuber to insert into the first and fourth metatarsal. A tendon also extends from the first metatarsal to the lateral surface of the proximal phalanx of the first digit. In addition, tendons continue from the plantar aponeurosis to insert into the distal ventral surfaces of metatarsals II, III, and IV. The manner in which they insert forms a loop through which the tendon of the M. flexor digitorum longus passes. In the Crocodilinae the second part is the larger of the two while the first part is larger in Alligatorinae. It should be noted that both the M. ambiens tendon and the tendon of the M. flexor-tibialis externus run on the internal and external surfaces respectively of the fibular head of the M. gastrocnemius. The M. ambiens tendon is laterally placed. The M. flexor tibialis externus and M. ambiens insert into the fifth metatarsal.

Flexor digitorum Superficialis

Another muscle (Figure 24) which contributes to the loop for the M. flexor digitorum longus originates from the ventral calcaneal surface, (part. 1) and the plantar aponeurosis (Parts 2 and 3). It is composed of three parts.

The first part contributes to the loop on metatarsal IV. The next part medially helps form the medial loop for the III tendon. The third part forms the medial part of the loop on the II metatarsal.

Flexor Digitorum longus.

The M. flexor digitorum longus comprises the second plantar layer. This muscle is composed of two heads (Figure 25). The first head I consider to be the fused external and internal head of lizards. The second head (often termed the M. soleus, Gadow, 1882) originates from the tendon of the M. flexor tibialis externus and runs external to the fibular head of the M. gastrocnemius. Just above the calcaneum the tendon forms and turns medially to insert into the tendon of the M. flexor digitorum longus. The insertion of this fused muscle is to the terminal plalanx of digits one, two and three. As previously noted the tendons run through a loop formed by the M. flexor digitorum superficialis and M. gastrocneminus. It should be noted that the wide tendon of both flexor digitorum

Fig. 24. Second plantar layer beneath the plantar aponeurosis of the fibular head of the gastrocnemius. W - flexor digitorum superficialis.

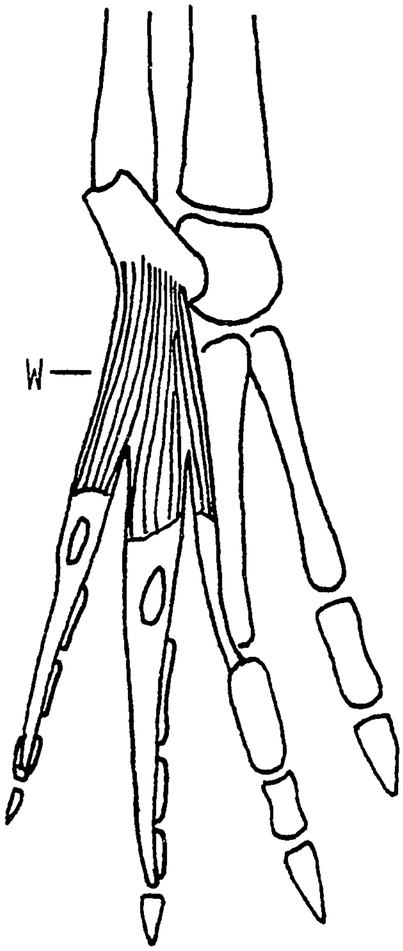
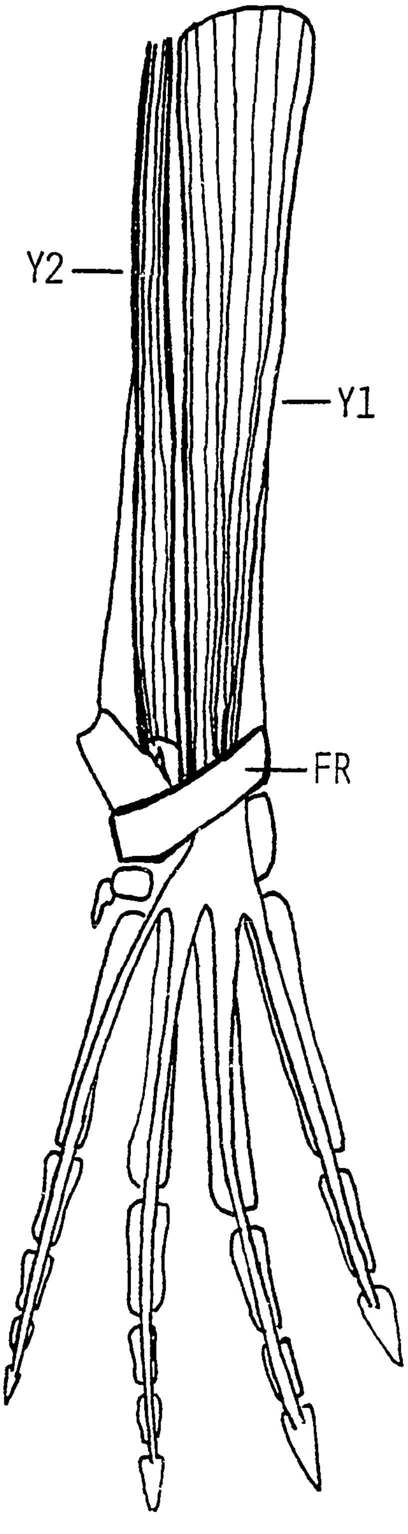

W

Fig. 25. The deep crocodilian posterior shank musculature. FR - flexor retinaculum; Y1 - flexor digitorum longus, part one; Y2 - flexor digitorum longus, part two (soleus).


Y2
Y1
FR

longus muscles overlying the metatarsals are fleshy. Although Gadow, (1882b) interprets this as the M. flexor digitorum brevis, there is, however, yet another layer of muscle dorsal to the longus. This muscle is the brevis. Finally both heads of the M. flexor digitorum longus are covered by a flexor retinaculum as they pass beneath the tarsus. This is true for the Crocodilinae, but I have not found this structure to be present in the Alligatorinae.

Flexor Digitorum brevis

This muscle underlies the M. flexor digitorum longus. It originates from the ventral surface of the metatarsals (Figure 26). The insertion is to the base of the proximal phalanx of each digit. The action of this muscle is to flex the digits.

Tibialis posterior

The M. tibialis posterior originates on the external surface of the tibia (Figure 27). Since there is a torsion in the tibia so that its widest surface faces medially and laterally, the M. tibialis posterior is a large muscle. Some fibers may originate from the internal surface of the fibula (Gadow, 1882b). The

Fig. 26. Deepest plantar flexor region of crocodilians.

Z - flexor digitorum brevis.

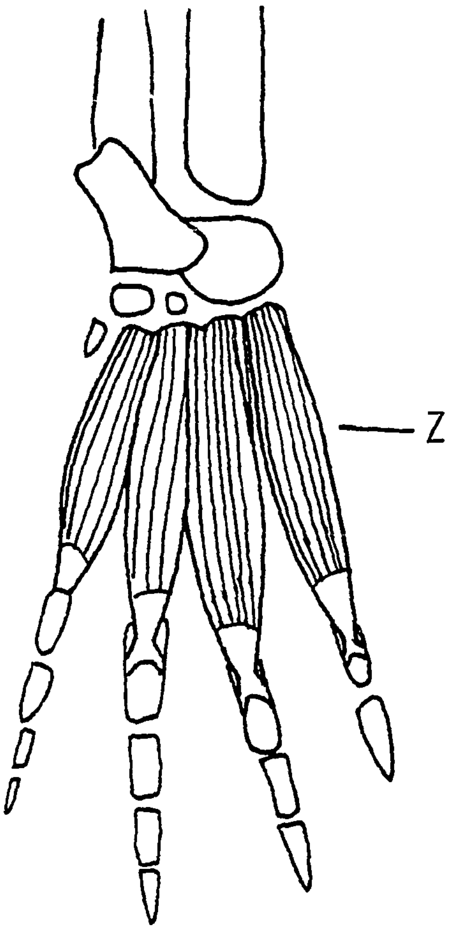
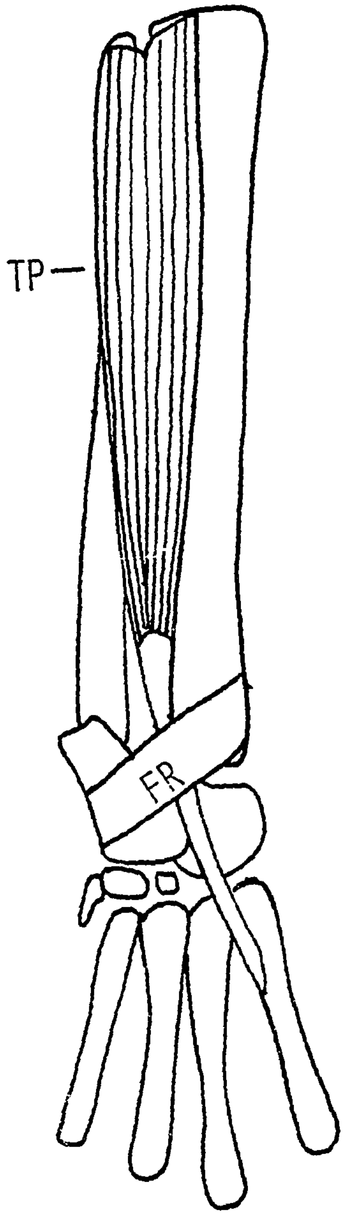

Z

Fig. 27. Deep view of the posterior crocodilian shank musculature. TP - tibialis posterior; FR - flexor retinaculum.


TP
FR

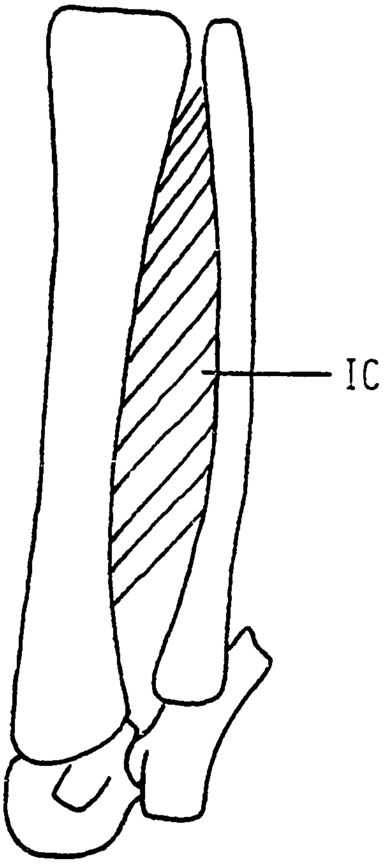
fibers converge to form a short tendon which loops under the posterior malleolus of the tibia to insert on the medial, proximal surface of matatarsal I. The muscle is a strong inverter and flexor of the pes. There is a retinaculum binding this muscle, extending from the distal posterior surface of the tibia to the posterior surface of the fibula.

Another muscle is described by Gadow (1882b) as belonging possibly to the M. tibialis posterior. This muscle originates from the distal third of the posterior fibula surface (Gadow, 1882b) and inserts into the cavity of the dorsal surface of the calcaneal tuber. I doubt that this muscle is part of the M. tibialis posterior as the origin and insertion of these two muscles are quite disjunct and not similar. However, embryological study may provide the final answer. I am naming this muscle the M. fibulo-calcaneum, a flexor of the foot.

Interosseus cruris.

In the shank there is a sheet of muscle whose fibers run diagonally between the tibia to the fibula (Figure 28). This muscle extends the length of the tibia and fibula.

Fig. 28. Deep anterior view of the crocodilian shank musculature. IC - interosseus cruris.


IC

Summary of the Muscle Scar Data

The following is a summary list of hind limb muscles and their muscle scars on theropod bones.

M. Ilio-tibialis. Scars of the origin are present along the rim of ilium. The most anterior scar is for the first head. It cannot be determined where the second head ends and the third begins. The insertion scars can be confused with those of the M. femoro-tibialis internus since both insert onto the cnemial crest. The tendons of the M. ilio-tibialis lie over and are fused to the M. femoro-tibialis externus and internus.

Ambiens. It is unknown whether there are two heads or one. There is a well marked scar for the origin of the first head in all theropods. It is found at the junction of the pubis with the pubic peduncle. The insertion has no scar.

Femoro-tibialis internus. The origin is well marked on the lateral surface and a fossa just below the greater trochanter. Another part of this muscle is found on the anterior surface of the femur two-thirds down the length of the shaft. The insertion as noted cannot be distinguished from the M. ilio-tibialis.

M. Femoro-tibialis externus. Scars for this muscle lie on the posterior lateral surface of the distal third of the femur. Insertion appears to be on the proximal anterior lateral surface of the tibia.

M. Ilio-fibularis. The origin is not marked by any scar. The insertion is well marked on the proximal lateral surface of the fibula in all saurischian dinosaurs.

M. Pubo-ischio-femoralis internus. The origin of part I is not marked but the excavation of the ventral surface of the preacetabular portion of the ilium is found throughout both orders of dinosaurs. The insertion is well marked on the greater and lesser trochanters of the femur. The origin of part II is well marked on the anterior surface of the ilium and sacrum. In sauropods a large vertical opening is present between the ilium and first sacral vertebra for the passage of this muscle. The insertion is well marked on the anterior surface of the fourth trochanter.

M. ilio-femoralis. The origin lies in a large depression on the ilium. The insertion is on a slight ridge running down the posterior lateral surface of the femur.

M. Ischio-trochantericus. No distinct evidence for this muscle.

M. Flexor-tibialis externus. The origin has no certain muscle scar. The insertion is represented by scars on the back of the proximal segment of the tibia.

M. Flexor-tibialis internus. Part I has no scar for its origin. Since this part inserts with part II of this muscle, its presence cannot be determined. Part II has no scars for its origin. The insertion is marked on the posterior surface of the tibia. Part III has a well marked facet on the ischium. Its insertion. is next to that of the M. flexor tibialis externus and therefore it is not possible to distinguish between the two. Part IV has no scar for its origin. The insertion is with that of the M. flexor tibialis externus and cannot be distinguished as separate from the latter.

M. Pubio-ischio tibialis. This muscle has a definite scar on the ischium. The insertion is with that of parts I and II of the M. flexor-tibialis internus and on the proximal medial surface of the tibia. The insertion is well marked-more so in ornithopod ornithischian dinosaurs.

M. Adductor-femoris. Both parts of this muscle have definate scars on the ischium for their origin. Scars are also present on the femur for the insertion of both parts.

M. Pubo-ischio-femoralis externus. Since the pubes bear an extended pubic symphsis (as compared to crocodilians) it is impossible to distinguish scars for the origin of part I and part II of this muscle.

The lateral and anterior pubic rami bear scars for both parts of this muscle. Scars are present on the ischium for the third part of this muscle. There are scars for all parts under and posterior to the femoral head. Distinct scars for the insertion of each of the three parts cannot be determined.

The Shank Musculature

The full reconstruction of the shank muscle is not possible. The reason being that there are too few muscle scars present and in many areas muscles insert together. There are, however, a few exceptions.

M. Gastrocnemius. Although there are no clearly identifiable scars for the origin, the insertion scars for this muscle are prominent. The insertion is on the posterior surface of metatarsals II and IV.

M. Flexor digitorum longus. There are no distinct scars for the origin. The insertion is found on the flexor tubercle of the terminal phalanx.

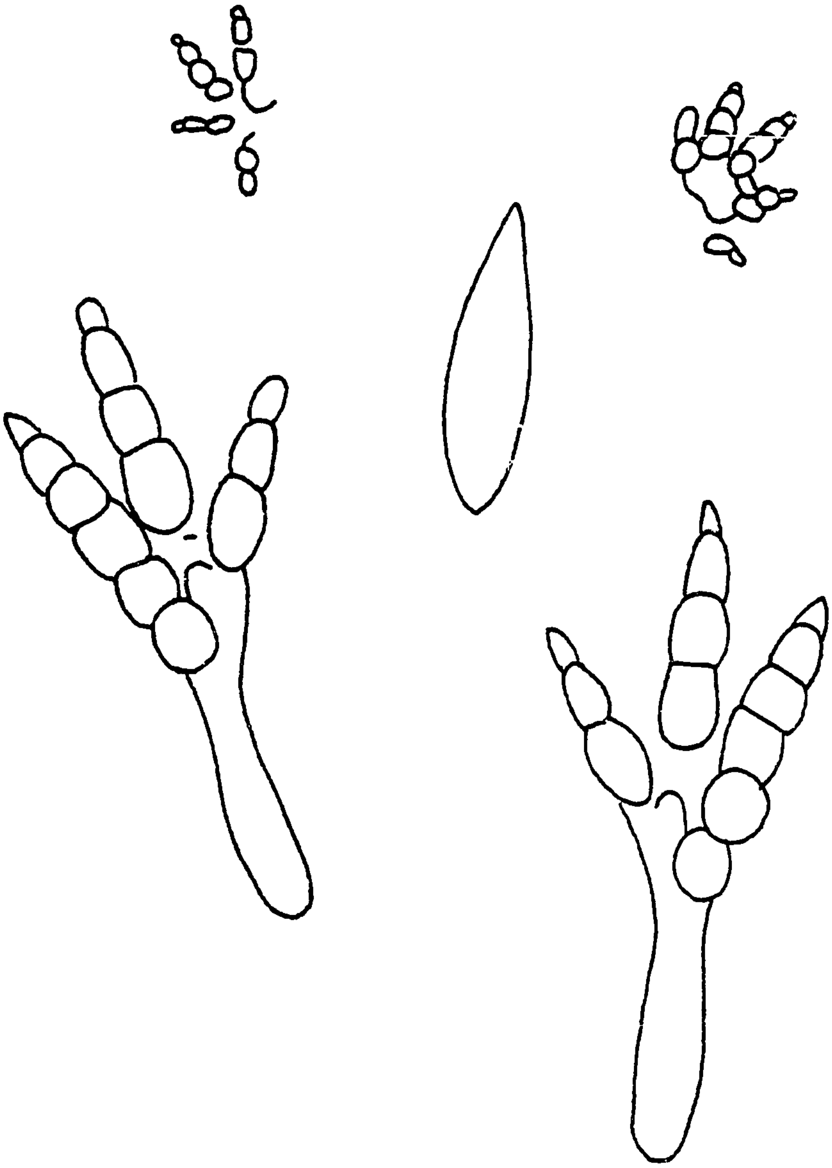
FUNCTIONAL ANALYSIS OF THE BIPEDAL GAIT OF ARCHOSAURS

Theropods, in general, were highly adapted for a cursorial life. Modifications are seen in the skeletal morphology as well as in the musculature which are adaptations to a bipedal life style. In carnosaurs, rugosities are present on the neural arches and processes on the postzygopophyses of the cervical vertebrae. The postorbital and supraoccipital bones of Tyrannosaurus and other theropods bear deep scars. This is an indication that ligaments run between these skull elements and the cervical vertebrae. In addition, large muscles were also present in the cervical region, running along the vertebrae to the skull. These muscles together with the ligaments would keep the head from oscillating during running. The neural arches as well as the centra of the cervical vertebrae in carnosaurs are compressed anterio-posteriorly and thick. Since there are no special modifications in the dorsal vertebrae for the support of the head, the massive and short cervical vertebrae probably performed much of this function. The cervical vertebrae are elongate and not modified in coelurosaurs, presumably because the head of these creatures was considerably lighter.

The cervical region of carnosaurs is short, the vertebrae being anterio-posteriorly compressed. The dorsal vertebrae, are not compressed. Indeed, it would be unusual if the opposite condition was present since all carnosaurs were obligatory bipedal cursors. An elongate neck and large skull would increase the presacral weight, a condition not associated with bipedal progression. This observation excludes birds since their bones are pneumatic, thin walled and their skulls lack teeth.

The pelvis of theropods is peculiar in shape. This structure, however, was apparently a successful adaptation for bipedal locomotion since it changed little for over one hundred million years. In lateral view one is struck by the underdevelopment of the ischium of the saurischian pelvis, especially in Cretaceous carnosaurs. The pubis, in contrast, is considerably expanded. The two pubes are robust and fuse distally, ending in an oval platform. It was hypothesized by Goodrich,(1930) that theropods sat by using the pubis and hindlimbs as a tripod. As evidence for Goodrich's hypothesis I submit a diagram (Figure 29) depicting the footprints of a seated late Triassic dinosaur which may show the impression of the pubes between the hind feet. (Hitchcock, 1848). Hitchcock, (1848) has interpreted this impression as the breast of a dinosaur. The impression could represent a structure in the anterior abdominal region rather than one in the thorax. It should be noted, that dinosaurs do not have bony

Fig. 29. Footprints of a seated Late Triassic dinosaur possible impression of the pubis.



sterna (except some ornithischian dinosaurs which have sternal precursors). The coracoids are the only bones in the thorax except the ribs. These structures are plate-like and are therefore probably incapable of making such a narrow impression.

Referring back to the ischium, one can interpret its small size as evidence for a reduction of ischial musculature. The main retractors of the hindlimb are located on the caudal vertebrae and posterio-internal surface of the ilium. This condition is nothing innovative since most, if not all, living limbed lizards, and all living archosaurs possess it. The degree to which this condition is carried is one difference between the extinct theropods and living archosaurs. The enhancement of the caudal musculature and that of the ilium has removed the need for much of the ischial musculature (and therefore the distal portion of the ischium) performing the same task.

One must use caution, however, when interpreting the size of the pubis. The expansion of this bone may not have been caused by any need for larger or additional muscles for the protraction of the femur, but rather, for the strength needed to support the weight of the body while resting. The main protractors of the thigh of archosaurs are not located on the pubis, in contrast to the study of Coombs (1978), but are located instead on the anterior internal surface of the ilium and centra of the presacral vertebrae (Romer, 1923a,b). For this reason, the femur could have been protracted in front of the pubis.

The ilium in all theropods is expanded in both an anterior and posterior direction. This expansion serves two functions. First, the musculature moving the thigh is expanded and its angle of application is changed and second, the larger ilium facilitates a larger number of sacral attachments to the pelvis. It should be noted that the sacral ribs number five in Tyrannosaurus and are short and stout when compared with ornithopods.

The tail is very long in theropods, a condition which is necessary in bipedal reptiles. Not only was the large tail used as a counterweight and place of origin for muscle, but it probably was used as a defensive weapon as well.

PROTRACTION OF THE THIGH AND EXTENSION OF THE SHANK

The protractors of the thigh consist of the M. pubo-ischio-femoralis internus parts one and two, M. pubo-ischio-femoralis externus parts one and two,

M. ilio-tibialis parts one and two, and the M. ambiens The origin of the M. pubo-ischio-femoralis internus part two is located higher and more anterior then its insertion (Figure 30). Contraction causes the femur to be lifted upward and forward. The insertion is on the medial surface of the fourth trochanter. The placement of the insertion gives this muscle some force in moving the thigh. Placement of the insertion nearer the proximal end of the femur would have increased the length of stride to its optimum (Hildebrand, 1974). This condition is found in the other part of this muscle, the M. pubo-ischio-femoralis internus part two. The insertion is close to the pivot point. A contraction of this muscle moves the hindlimb through a greater distance than the second part, but with less force.

The M. pubo-ischio-femoralis externus parts one and two has two functions. The first is the protraction of the femur as a high gear muscle. The second and most important function was to turn the leg outward as it is brought forward, a maneuver which keeps the thigh from knocking on the pubes. This movement of the thigh is observed in locomotion of the extant bipedal and quadrupedal reptiles (Figure 31). For example, as the right leg is brought forward the immediate presacral portion of the body is bent to

Fig. 30. Probable lines of actions of some pelvic muscles of theropod dinosaurs (dorsal view) A - coccygeo-femoralis longus; B - coccygeo-femoralis brevis; G - pubo-ischio-femoralis externus parts one and two; J2 - pubo-ischio-femoralis internus, part two; M- Ambiens.

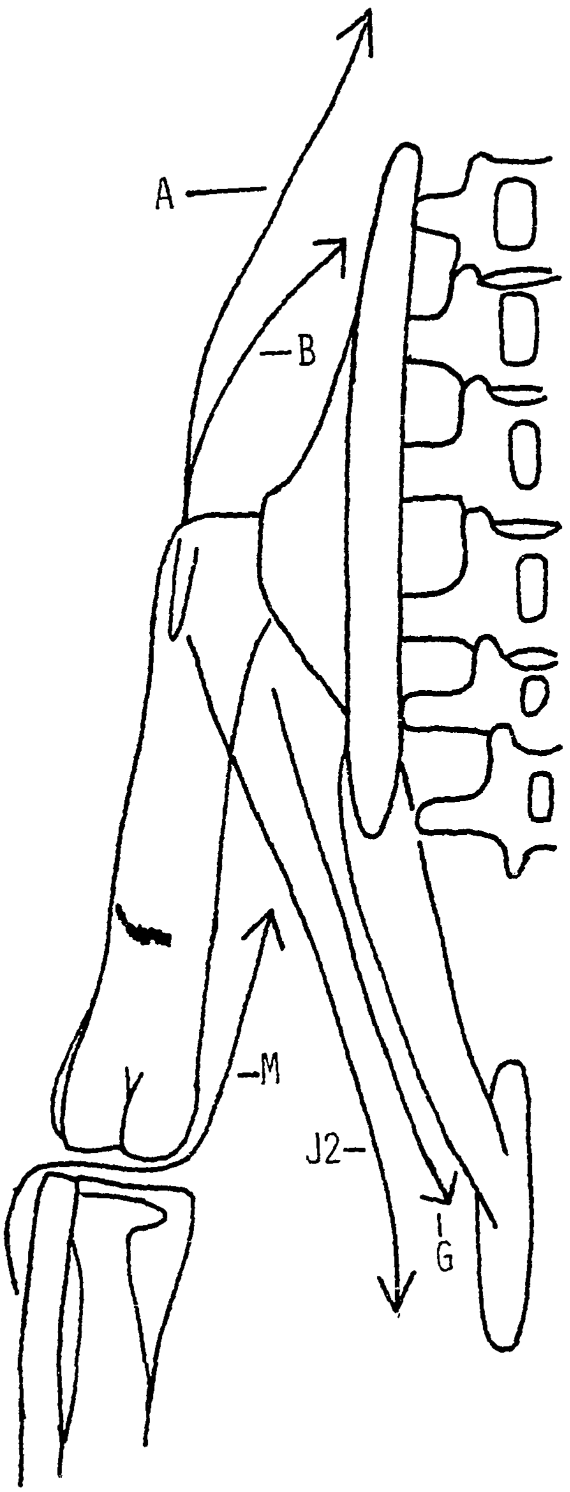
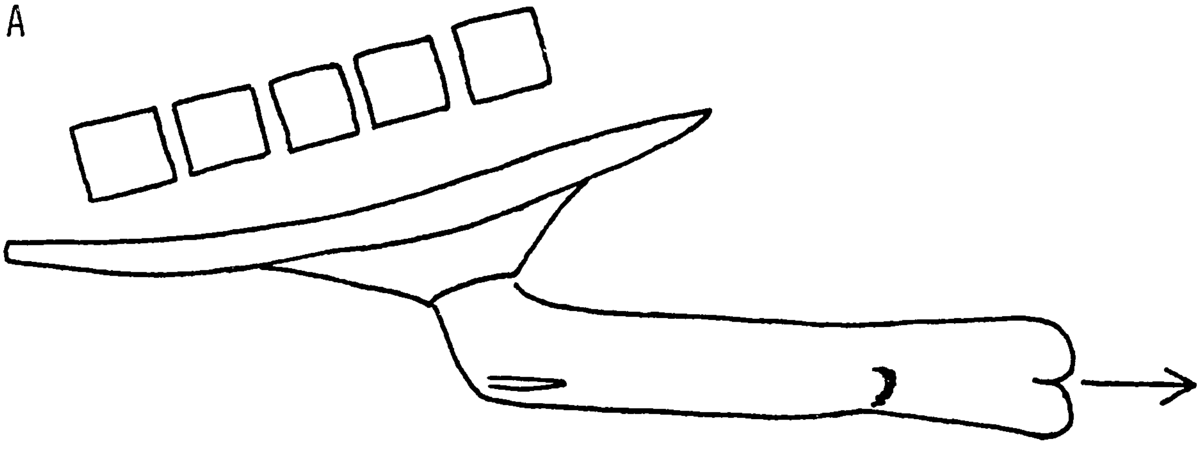
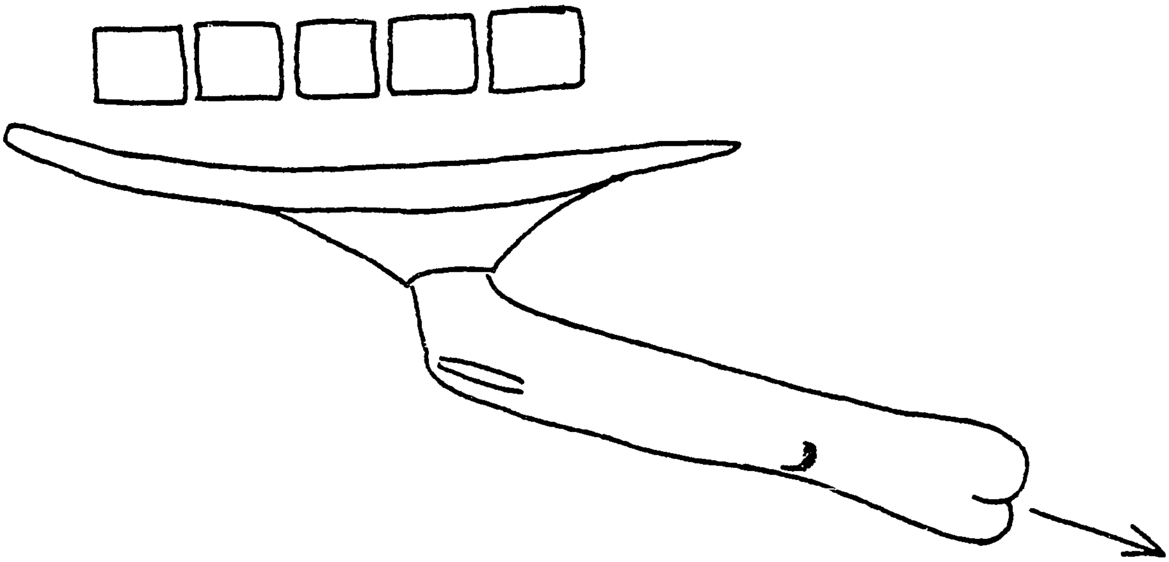

A
B
M
J2
G

Fig. 31. A - position of femur of theropod without pelvic pivot.. B - position of femur of theropod with pelvic pivot.

A



B



the left out of the way of the right leg and the anterior and middle part of the trunk is bent back to the right (after Schaeffer, 1941; Snyder, 1949). Since the musculature is almost identical with that of an alligator, I submit that Tyrannosaurus as well as all carnosaurs may have run in a similar fashion.

Thus far in protraction, one sees a high gear and a medium gear equivalent to fourth gear and third gear respectively in an automobile. The muscles of the low gear which supply the power for protraction and are most important in the initiation of movement, are the three heads of the M. ilio-tibialis and to a smaller extent the M. ambiens. All these muscles insert into the extensor tendon (aponeurosis)between the femur and tibia. Hence, they are low gear with respect to the femur and high gear muscles in extending the shank.The ilio-tibialis is one of the largest muscles of the hindlimb. The M. ambiens, on the other hand, is of moderate size but is quite a special muscle. The M. ambiens not only inserts into the extensor tendon, but it also sends a tendon to the gastrocnemius (Romer, 1923a,b). This tendon extends the length of the shank to insert into the fifth metatarsal. When the M. ambiens is contracted the femur is brought forward and is kept from turning too far medially by the M. pubo-ischio-femoralis externus. As the femur is brought forward, the shank is extended. The angle formed by the femur and tibia using the joint between them as the vertex as the pes is put on the ground would be about ninety degrees. The pes as it touches the substrate is fully dorsi flexed. The M. ambiens at this point will by virtue of the prominent tendon to the fifth metatarsal work with the M. gastrocnemius to extend the pes. The extensors of the shank are the M. ilio-tibialis parts one through three and M. femoro-tibialis internus and externus. The M. ilio-tibialis mentioned previously, is a high gear muscle for the shank. The M. femoro-tibialis internus and externus also fall into this category. It should be noted that movement of the shank occurs while it is off the ground. For this reason low gear muscles are not needed. In addition, the lightening of the distal segments by inserting the massive parts of the musculature closer to the body (which move the distal segment of limb) increases the efficiency of the locomotion, since it is the distal segment of the limbs which has the greatest velocity and must be moved through the longest distance (Hildebrand, 1974). Correlated with this improved efficiency are the modifications of the joints. In theropods, the joints below the acetabulum are all hinge joints which allow movement mostly in a back and forth direction. Muscles which would cause movement in other directions, such as rotators are reduced or never developed (Hildebrand, 1974). The morphology also contributes to the economy of energy by loss of the lateral and reduction of the medial digit. In theropods only digits two, three and four play any meaningful role in the propulsive phase of locomotion. Only these digits have well developed metatarsals, which are crowded together to compensate for the loss of strength due to the reduction of metatarsals one and five (Hildebrand, 1974). It should be noted that the fibula is somewhat reduced distally.

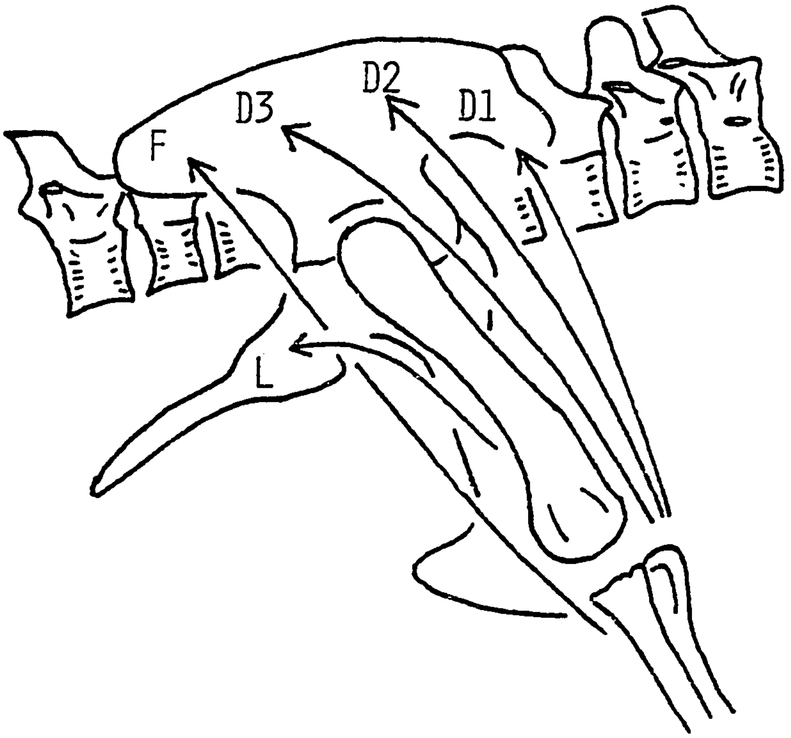
RETRACTION OF THE FEMUR AND FLEXION OF THE SHANK

The retractor muscles and flexors of the hindlimb are many and somewhat more complex than the protractors. One might expect this condition, since it is these muscles which provide the propulsive force for the limb. These muscles are the M. coccygeo-femoralis brevis and longus, M. ilio-fibularis, M. ilio-femoralis, M. flexor-tibialis externus, M. flexor tibialis internus, M. pubo-ischio tibialis, adductor femoris, M. ischio-trochantericus, M. pubo-ischio-femoralis externus part three, M. ambieas (mentioned earlier), M. gastrocnemius and flexors of the digits (Figure 32).

I have previously noted that the limb is brought forward by the protractors of the thigh, extensors of the shank and by virtue of the lateral pivoting of the pelvis in the horizontal plane. To bring the leg back and therefore propel the body upward and forward all of the muscles noted above are used. The muscles which rotate the pelvis, the M. dorsalis trunci, M. rectus abdominis and muscles which move the tail in order to balance the animal while running, the M. dorsalis caudae and M. ilio-ischio caudalis, will be discussed later.

Before the pes contacts the ground the retractors of the thigh, flexors of the shank, and flexors of the pes go to work. The low gear muscles of the pes are the flexors of the digits, the M. flexor digitorum longus and brevis M. flexor digitorium superficialis (which send long tendons to the digits, thus saving weight) and the other short distal flexors. The M. gastrocnemius is the main extensor of the pes which also serves to flex the shank. The two heads of the M. gastrocnemius, the tibial and fibular heads, originate on the posterior portion of the femur just above the condyles. The major origin of the fibular head is the tendon of the M. flexor-tibialis externus. The in lever effective arm of the

Fig. 32. Probable lines of action of pelvic and hindlimb musculature of Tyrannosaurus. D1 - first head of the ilio-tibialis; D2 - second head of the ilio-tibialis;D3 - third head of the ilio-tibialis; F - line of action of the flexor musculatures of the shank; the flexor-tibialis externus and parts two and three of the flexor-tibialis internus; L - adductor femoris.


D2
D3
D1
F
L

M. gastrocnemius is long, which is expected for a muscle which is extending the pes from its fully flexed position (Figure 33).

The flexors of the shank and pes are working with the femoral retractors to straighten the joint between the femur and the tibia and fibula which will push the body upward. Most of the flexors of the shank arise from the ilium and insert close to proximal portion of either the tibia or fibula. These are more examples of reducing the weight of the distal segments and increasing the length of the stride. The flexors of the shank are the high gear M. pubo-ischio tibialis, M. ilio-fibularis and the slightly lower gear M. flexor tibialis externus and internus (Figure 34). The relatively low gear flexor is the tendon of the M. coccygeo-femoralis longus which serves as an automatic flexor of the shank because of its attachment by tendon to the fibula (Romer, 1923a).

The femoral retractors supply most of the force for propulsion of the body. The main force was supplied by the M. coccygeo-femoralis brevis and longus. The longus is an especially massive muscle, more so than the brevis. Both these muscles are relatively low gear in nature. The M. ilio-femoralis is also a retractor of the femur, but by its insertion on the latero-posterior surface of the femur, this

Fig. 33. Probable lines of action of the pelvic musculature of *Tyrannosaurus*. A - coccygeo-femoralis longus; B - coccygeo-femoralis brevis; C - gastrocnemius (both heads); G (1,2) pubo-ischio-femoralis externus, parts one and two; I - ilio-femoralis, possible lines of action; J1 - pubo-ischio-femoralis internus, part one; J2 - pubo-ischio-femoralis internus, part 2; M - ambiens.

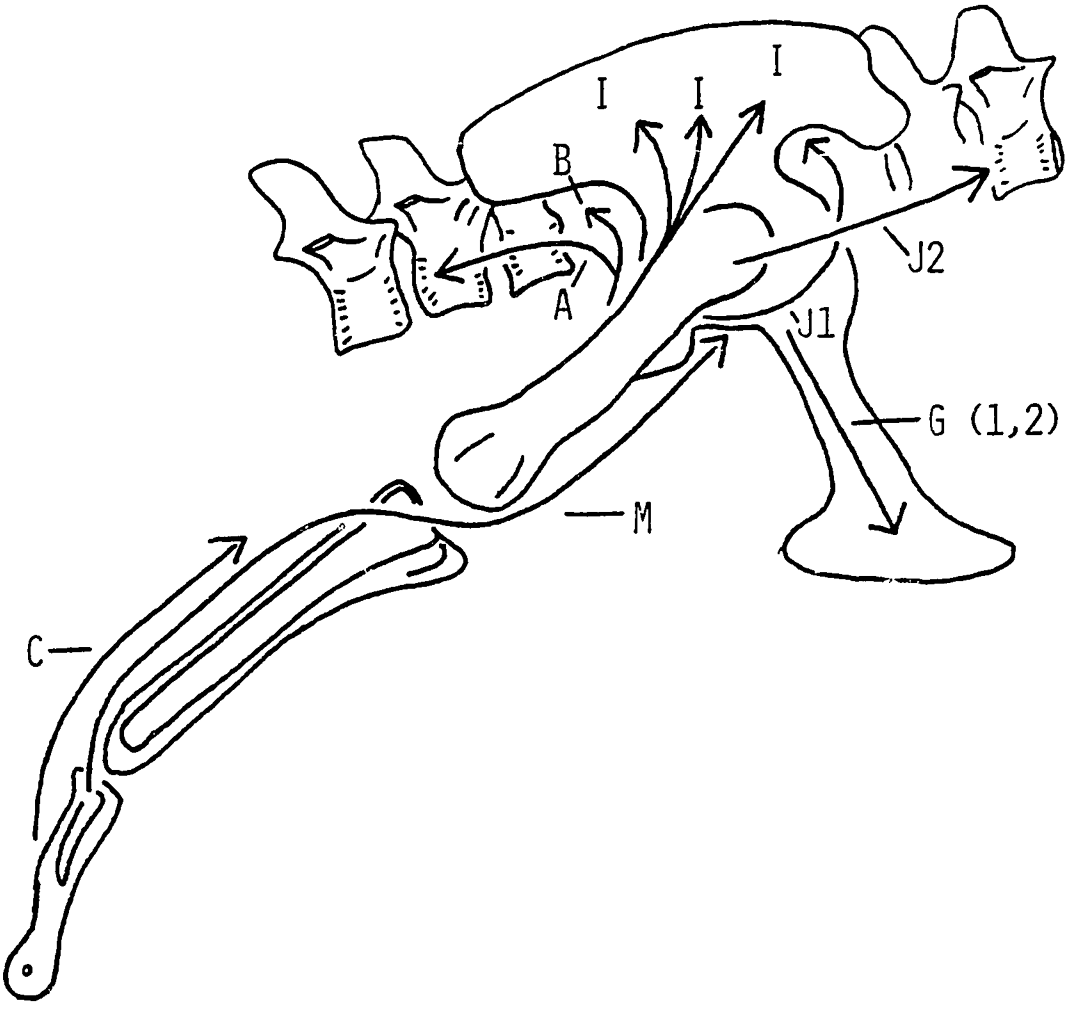
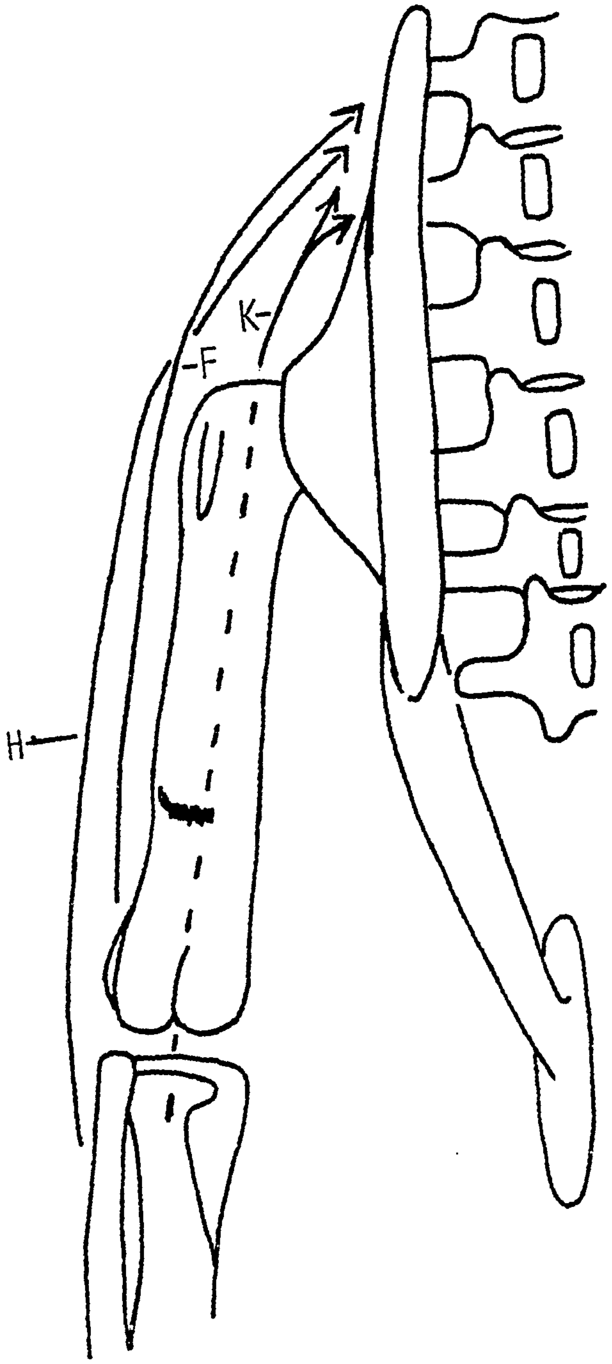

I
I
I
B
A
J2
J1
G (1,2)
M
C

Fig. 34. Probable lines of action of the shank flexors (dorsal view); F - flexor-tibialis externus; H - ilio-fibularis; K - flexor-tibialis parts two and three.


K
F
H

muscle could also serve to abduct the thigh. The M. ilio-femoralis along with the M. adductor femoris and M. coccygeo-femoralis longus and brevis are the low gear muscles of retraction. The M. adductor femoris because of the out turning of the femur (referred to earlier) was still an adductor in a strict sense. In a functional sense, the M. adductor femoris also aids in retraction of the femur. The high gear muscles of retraction are the M. pubo-ischio femoralis externus part three and the M. ischio-trochantericus.

HOW BIPEDAL ARCHOSAURS RAN

Bipedal archosaurs ran much the same way as bipedal lizards do today. The only difference is the more upright posture of the saurischian dinosaurs, because the legs are vertically placed under the body. By having the joints of the leg face the same direction, bipedal archosaurs could have added extra force to their stride in the same manner as bipedal lizards. That is, with the joints facing in the direction of the stride, the torques of the in lever systems of muscles become additive (Hildebrand, 1974, chapter 19). Bipedal locomotion in archosaurs was more efficient than its counterpart in lizards since the joints face the same direction naturally (Osborn, 1917). Lizards must add a maneuver to get the hindlimb in a position to make the torques additive since the femur is normally perpendicular to the body. The maneuver performed is a lateral rotation of the pelvis by the epaxial musculature attached to the pelvis. This allows the pes to contact the ground in an anterior direction. This pivoting of the pelvis could have been less extreme in archosaurs because of the position of joints described above. In having the joints face the same direction the length of stride is also increased. Adding to this is the elongation of the tibia and fibula and metatarsals in theropods. The body of archosaurs was probably held at approximately twenty-three degrees above the horizontal. This angle, however, would vary somewhat during the gait. As the right hindlimb was brought forward the pelvis would be rotated in the horizontal plane to the left by the M. dorsalis trunci and the M. rectus abdominis posterior (from observation of living alligators and dissection of crocodilians). This would serve to increase the length of the stride. While this is occurring the immediate presacral portion of the trunk is bent to the left while the more anterior portion is bent back towards the right. The immediate presacral bend allows the leg to be fully protracted. The second bend is needed to maintain balance. To compensate for the pivoting of the pelvis, the hindlimb is rotated laterally by the M. pubo-ischio-femoralus externus part two. The M. ambiens keeps the leg from being rotated too far. The M. ilio-tibialis and the M. pubo-ischio-femoralis internus are responsible for lifting the femur vertically, bringing it forward and extending the shank. The M. femoro-tibialis internus also aids in the extension of the shank. The shank is never fully extended in protraction. To do so, would change the force from the weight of the body from a compressive to a shearing one when the pes is placed back on the ground (Hildebrand, 1974, chapter 19). The pes, however, is flexed even as it contacts the ground. The digits and the distal portions of the metatarsals are the elements which make contact with the ground. At this point, the propulsive phase of the gait begins. The M. flexor digitorum longus and brevis were used in the flexion of the digits. Here then, is the first joint which is used in propulsion. The second occurs between the proximal and distal segments of the ankle. The power to this joint is supplied by both heads of the M. gastrocnemius which probably inserted by means of a plantar aponeurosis into deep grooves in the second and fourth metatarsals as in modern lizards and archosaurs. The joint between the femur and tibia and fibula is flexed by a number of muscles mentioned previously. The fourth joint occurs between the acetabulum and the head of the femur. As the right hindlimb is retracted and joints one through three are straightened, the pelvis is pivoted back to the right to allow the left leg to be protracted. The tail which had been flexed laterally to the right is now shifted to the left in order to balance the animal. It should be noted that the animal could have moved its tail independently of the legs since living archosaurs move the tail with or without moving the legs (by using the M. ilio-ischio caudalis and the caudal part of the M. dorsalis trunci). The tail is mainly bent just posterior to the ilium and ischium. The M. dorsalis trunci also aids in making this bend. Both muscles are responsible for bending the tail along the rest of its length.

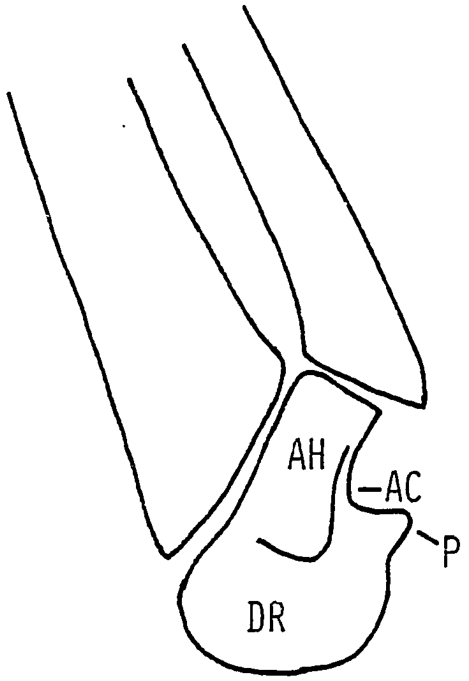
The Intratarsal Joint and the Bipedal Gait.

The intratarsal joint of crocodilians has been described by Heune (1908), Schaeffer (1941, Romer (1966), Walker (1972) and Cruickshank (1979). Schaeffer (1941) has described a double joint between the proximal tarsal elements. The first area of articulation is on the medial and lateral surface of the calcaneum and astragalus respectively. The second point of articulation is on the posterior surface of the astragalus and on the tongue of the calcaneum. In the first articulation there is a wedge-shaped shelf of bone running anterior to posterior on the astragalus. (Figure 35 and 36).It is most prominent toward the anterior surface. Just above this wedge-shaped projection (astragalar peg) is a distinct groove, the articulating groove also running in an anterior to posterior direction. Facing these structures on the surface of the calcaneum is a sulcus for the reception of the astragalar peg (Figure 36a). Posterior to the calcaneum socket is another flange, the calcaneal tongue which fits into the articulating groove of the astragalus. Thus, the first articulation is actually double. The second articulation is a sort of gliding joint between a rounded surface of the astragalus,the astragalar trochlea and slightly concave tongue of the calcaneum. (Figure 36a). This forms the secondary joint.

The astragalus is firmly united by ligaments to the tibia and does not move with pes (Schaeffer, 1941). The calcaneum is movable. The astragalus sends a projection dorso-laterally to meet the fibula. The articulating, rounded condyle of the calcaneum (here named the fibular condyle) also articulates with the fibula. (Figure 35 and36). The main weight of the fibula

Fig. 35. A - Anterior view of the crocodilian astragalus; AH - anterior hollow; AC - articulating channel; DR - distal roller P - peg; T - trochlear surface; B - posterior-medial view of the astragalus. Symbols as in A.

A



B

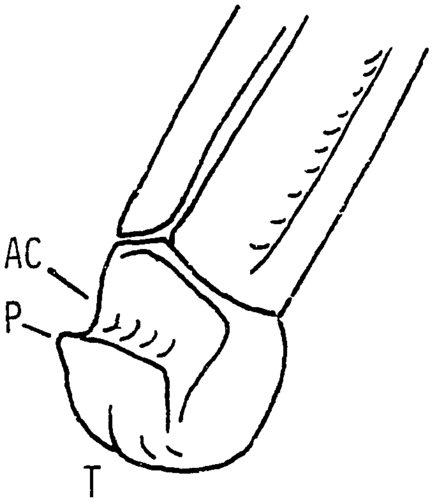
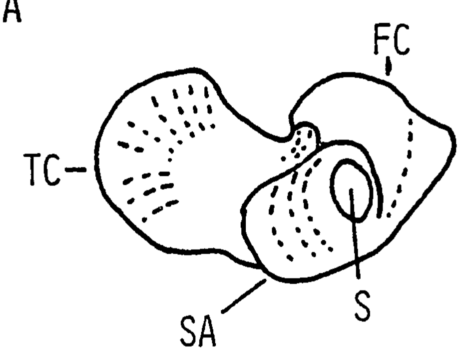
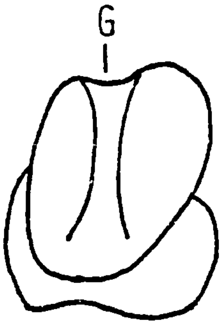


Fig. 36. A medial view of the crocodilian calcaneum. S - socket for peg of the astragalus; SA - secondary articulation of the calcaneum; TC - tuber calcaneum; FC - fibular condyle. B. posterior view of the tuber calcaneum. G - groove for tendons of shank and pelvic musculature.

A



B



appears to be borne by the astragalus (Figure 35a). There is a menisceal cartilage between the fibular condyle of the calcaneum and the fibula (Figure 36a,b).

Movement Within the Ankle.

The calcaneum does not move in a large arc. The fibular condyle cannot move more than thirty degrees before becoming disarticulated from the cartilage, if the fibula remains stationary. In addition, the calcaneal tuber restricts the movement that can occur. During plantar flexion of the pes the calcaneal tuber will move dorsally to lie against the posterior surface of the fibula which is covered by muscle.

In studying the shank musculature it is here noted that the intra-tarsal joint is adapted to a sprawling gait, while crocodilians and probably early thecodonts planted their foot forward in locomotion, the action of the major flexors of the pes would pull the pes in a postero-lateral direction. This postero-lateral pull would cause the pes to slide in about a forty to forty-five degree angle, if it were not for elongate scutes in the crocodilian pes. The reason for this lies in the insertion points of the musculature and the osteology of the tibia. The major flexors of the ankle-that is, both heads of the M. gastrocnemius do not have their main insertion on the calcaneum. The tibial head of the M. gastrocnemius runs diagonally from the tibia to the fibula side of the fifth metatarsal joing the tendons of the peroneus muscles, the tendons of the M. flexor tibialis externus and M. ambiens and fibular head of the M. gastrocnemius. Thus, the main force of these flexor muscles comes to bear on the lateral side of the pes. This would cause strong eversion of the pes, (in crocodilians). Furthermore the short flexors of the pes originate from the calcaneum and fibula also pulling the digits posterio-laterally.

In describing the major elements of the shank musculature I noted that most of the flexor musculature passes over the calcaneal tuber or medial to it. The tendons of the M. flexor tibialis externus, M. ambiens and part of the tibial head of the gastrocnemius pass over a groove in the calcaneal heel (Figure 35b) on their way to the fifth metatarsal. Only a small part of the tibial head of the gastrocnemius, inserts into the calcaneal heel. A small tendon from the M. flexor digitorus longus inserts with a small muscle, the M. fibulo-calcaneum into the calcaneal tuber. This is in sharp contrast to mammals in which the stout achilles tendon inserts into the calcaneal tuber. The tuber of the calcaneum in both taxa, mammals and crocodilians is used as a lever to increase the torque of the joint. In addition, the calcaneal tuber changes the angle of application of the flexor muscles passing over it in crocodilians.

The Calcaneal Tuber and the Origin of Bipedalism in Archosaurs

The primitive condition of the tarsus in some thecodonts as well as crocodilians appears to be the intratarsal joint. The early proterosuchians such as Chasmatosaurus and Erythrosuchus lack the astragulo-calcaneal specializations (Charig and Reig, 1970) found in crocodilians.

The following Triassic crocodilians display both a calcaneal tuber and intratarsal joint: Protosuchus (Colbert and Mook, 1951) and Orthosuchus (Nash, 1968, 1975). Hallopus victor Marsh, has been reclassified by Walker, (1970) from the Coelurosauria to the Crocodilia. Tarsitano and Hecht (1980) have demonstrated, however that Hallopus cannot be designated a crocodilian since the speciman is too poorly preserved to domonstrate any synapomorphies with the Crocodilia. Triassic pseudosuchians also have developed at least a calcaneal tuber and perhaps an intratarsal joint exemplified by Euparkeria, (Ewer, 1965), Lagosuchus and Gracilasuchus (Bonaparte, 1975); Romer, (1972a,b,c). The aetosaurs, Typothorax and Stagonolepis (Walker, 1961) also possess intratarsal joints and calcaneal tubers. Finally Segisauris, a supposed coelurosaur, also has a calcaneal tuber. I will have more to say about the classification of this taxon later.

Thus the intratarsal joint is a well established method of ankle movement within the Archosauria (Cruickshank,1978;1979).The problem with the calcaneal tuber and intratarsal joint as noted above is that it is associated with a quadrupedal gait and it provides an extra evolutionary step in the attainment of a mesotarsal joint and a bipedal gait. We see in the fossil record that early proterosuchians did not have an intratarsal joint but probably a functional mesotarsal joint (Charig and Reig, 1970). They base their interpretation on the fact that there is no special articulation between the astragalus and calcaneum. The astragalus was probably not bound to the tibia and that there was little development of a calcaneal tuber. Therefore it is surprising that a dinosaurian mesotarsal joint (Wells and Long, 1974) did not evolve from such a primitive state directly instead of going through an intratarsal stage as depicted by progressive pseudosuchians. That the latter, longer route has occured is borne out by the fossil record and the structure of the mesotarsal joint of dinosaurs. Firstly, the most progressive of the pseudosuchian thecodonts such as Lagosuchus and

Segisaurus have calcaneal tubers. Secondly, in theropod dinosaurs the astragalus is locked into the tibia (Wells and Long, 1974), a condition found in Triassic crocodilians and aetosaurs.

The steps needed to change a crocodilian intratarsal joint to a dinosaur mesotarsal joint are not many. One of the reasons for this as previously noted is that most of the plantar flexors do not insert into the calcaneal tuber. Reducing the calcaneal tuber and the shifting of the tibial head of the M. gastrocnemius from the fifth metatarsal to metatarsal II and IV would help create a mesotarsal joint. The intratarsal joint, curiously enough, is also preadapted for becoming a mesotarsal joint. The double wedge and groove of the intratarsal joint could serve as a locking device between the astragalus and calcaneum. This would couple the calcaneum with the already immovable astragulus to create an archosaurian mesotarsal joint. A similar adaptation has also occurred in mammals. The locking of the calcaneum to the astragalus results in a joint similar in function to the metatarsal joint of dinosaurs. The calcaneal tuber then acts as a lever to increase the torque of the joint. Thus, having a calcaneal tuber does not mean that an intratarsal joint is present. The additional requirement is that the calcaneum and astragalus be independent of one another.

The Theropod-Pseudosuchian Boundary

Bonaparte, (1972,1975) first realized the importance of the tarsus in determining the phylogeny of pseudosuchian thecodonts. Bonaparte (1975) separated primitive intratarsal lineages from those thecodonts which had a reduced calcaneum (*Lagosuchus*) and tended toward a mesotarsal joint.

Building upon Bonapartes work it is possible to fix the boundary between pseudosuchian thecodonts and theropod dinosaurs. The boundary line centers on modifications for bipedal progression. Those archosaurs which have an intratarsal joint regardless of geologic age should be placed in the Thecodontia. Those that have passed through the intratarsal joint to evolve a mesotarsal joint should be placed in the dinosaur grade.

It is generally believed that all dinosaurs are derived from thecodonts which were bipedal or had bipedal tendencies, (Romer, 1956,1966). It is my opinion that one may correlate bipedalism or quadrupedal locomotion for a fossil with the presence or absence of the intratarsal joint. This can then be used in characterizing the thecodont-theropod boundary.

I believe it is possible to determine which forms were normally bipeds and those forms which were normally quadrupeds. In order to do this it is necessary to determine what constitutes a biped and what constitutes a quadruped.

The primary character complex which can be used for this purpose is the tarsus. As previously noted an intratarsal joint is associated with quadrupedal progression in archosaurs (excluding pterosaurs). In an intratarsal joint the fibular condyle of the calcaneum faces dorsally and the calcaneal tuber faces posterio-laterally. In order to plantar flex the foot the calcaneum must rotate in a counter clockwise direction. The musculature for this turning is not great and as previously described the foot is pulled laterally as well as posteriorly. This condition is not suitable for bipedal progression. The position of the calcaneum insures a plantigrade condition since in crocodilians there are no muscular modifications of the gastrocnemius as found in birds and mammals. That is, in mammals the M. gastrocnemius is large and allows a digitgrade condition. Mammals whose Achilles tendon has been severed cannot attain a digitgrade type gait. In birds the deep head of the M. gastrocnemius is large, forms a stout tendon comparable to an Achilles tendon and is responsible for lifting the metatarsals off the ground.

If one tries to make an intratarsal joint as it is into a mesotarsal joint one is doomed to failure. In bringing a crocodilian, for example, up on its toes the calcaneal tuber is automatically brought up against the posterior surface of the tibia. This prevents any flexion of the foot except for some possible gliding movement between the calcaneum and the distal tarsals. Bringing the intratarsal into this digitgrade position also precludes bipedalism for the following reasons. As the calcaneal tuber is brought dorsally, the fibular condyle of the calcaneum is directed forward and upward. Unless dislocation is to occur, the shank must also move forward as well as the femur. This movement causes a forward shift of the center of gravity of the pelvis. If it were not for the forelimbs the animal would fall to the ground. It is interesting to note that digitgrade bipedal mammals have solved this problem. Although kangaroos and jumping mice have calcaneal tubers, they have modifications which allow the center of gravity to be brought back so that balance can be maintained. They have done this in a way that they are able to use the calcaneal tuber as a lever to multiply the "in force". In these forms the tail is long and fleshy and is used as a counter-balance to the presacral region. The presacral region is shortened as compared to a quadruped and is held at a steep angle above the horizontal to shift the center of gravity backward. Finally the femur is shortened to keep the limb from being positioned too far forward and to reduce its radius of gyration. Furthermore, mammals have increased the surface area of the astragalar condyle and have lowered the position of the calcaneal tuber. Thus, the tuber does not push up against the crus during rotation of the tarsus. These modifications are not found in crocodilians.

The modifications for bipedal progression in theropods are in my opinion as follows:

A) An immovable joint between astragalus and calcaneum resulting in a mesotarsal joint.

B) A tail which is stout and at least one half the length of the body.

C) An offset rounded femoral head forming a cylinder (Hotton, Personal Communication).

D) A large preacetabular portion of the ilium.

E) At least three sacral vertebrae.

F) Digitigrade gait and mesotarsal joint.

G) Cnemial crest on the tibia.

H) Slight scapular build with reduced forelimbs shorter than hindlimbs, or moderately developed pectoral girdle and forelimbs correlated with a reduction in the skull and neck.

The above list of characters needs explanation. The first requirement, that of a mesotarsal joint has already been discussed at length. The second, tail length is necessary to maintain the balance of the animal. Snyder, (1949,1954) has noted that the tail length of bipedal lizards must be at least two-thirds the body length in order for a lizard to maintain a bipedal stance. Although we cannot make such precise statements concerning theropods it appears that all bipedal saurichians had a tail that was at least one-half the length of the body. This takes into account the addition of plaster caudal vertebrae to some theropods. The third requirement, an off set femoral head is necessary to bring the legs under the body for support, provide more movement (roller-concavity), permit better fit of the femoral head into the acetabulum and allow the limb to swing in a fore to aft arc to increase the stride length and torque. A large preacetabular portion of the ilium and the development of the inner cnemial crest belong to the same character complex, that is the development (size) and forward migration of the M. ilio-tibialis. The M. ilio-tibialis not only extends the shank but is also important in lifting the entire limb anterio-dorsally. The inner cnemial crest provides the surface area and in lever for this muscle. It is interesting that Snyder (1949, 1952) also noted that in bipedal lizards the possession of an anterior process of the ilium was necessary for bipedal locomotion. Next, an increase in number of sacral vertebrae is necessary in order to support the weight of the body and to anchor securly the pelvis to the vertebral column. Reason "F", a digitigrade gait is a reflection of the ankle structure and development of the gastrocnemius. A digitigrade gait is an indication of a functional mesotarsal joint. The mesotarsal joint is a more effecient joint since it functions in the same direction as the movement of the animal. The elevation of the metatarsals to form a digitigrade gait is a direct result of the size and formation of the M. gastrocnemius and an Achilles tendon. This condition is seen in mammals and birds and was apparently present in theropod dinosaurs. In fact in a mammal if the M. gastrocnemius is cut the animal cannot maintain a digitigrade condition. A digitigrade condition increases the length of the stride. The last point, the reduction of the forelimbs is important in theropod dinosaurs. The slight build of these limbs reduces the weight in front of the center of gravity. The smaller the forelimbs the larger the skull may become. The large skull of Tyrannosaurus increases the downward torque of the presacral region. To compensate the forelimbs are reduced. The large forelimbs in birds are compensated by the reduction of the skull size, loss of teeth and the highly pneumatic condition of the skull. In addition the forelimbs are closer to the center of gravity than is the head. Thus, the torques produced by increases in weight of the pectoral region are not as great as the torque that would be produced by an increase in the size of the head.

The existence of five specimens of Archaeopteryx, the earliest bird, provides us with an insight into the development of bipedalism in birds, since Archaeopteryx was an obligate biped on land. Thus, we are able to see frozen in time, an intermediate step in the evolution of bipedalism in birds. We know from studies of reptiles (Snyder, 1949) that a counter balance system using the tail is necessary to maintain balance while locomotion in a bipedal posture is underway. In contrast to reptiles, modern birds have a reduced tail which is useless as a counter balance. The tail of Archaeopteryx while not approaching the reduction of modern birds is still much shorter in proportion to its body size as compared to the tails of bipedal lizards and dinosaurs. More importantly the tail of Archaeopteryx is lightly built, being much more slender and shorter (not counting feathers which have little weight) than the tail of Compsognathus, a coelurosaurian contempory of Archaeopteryx, which is slightly larger in size than Archaeopteryx. In fact, in contrast to Archaeopteryx, the bones of Compsognathus are robust and do not compare with the lightly built skeleton of Archaeopteryx. Therefore, since the tail in Archaeopteryx does not appear to have had the length or bulk necessary for the reptilian method of counterbalance, the evolution of a different bipedal mode of locomotion had to have already begun in these Jurassic birds. In Archaeopteryx we see some of the same adaptations to bipedal progression as in kangaroos and jumping mice that is, the femur is shorter in comparison to the tibia. In most birds the tibiotarsus is elongate while the femur is shortened. This is one method of preventing the forward migration of the center of gravity. In addition the bulk of the hindlimb musculature in birds inserts into the femur or the proximal end of the tibiotarsus. Shortening the femur allows most of the muscular weight to be concentrated close to the body reducing the moment of inertia of the limb. As previously noted the femur is moved through a smaller arc than the elongate tibia and thus it is more energy efficient to carry the musculature for the movement of the hindlimb closer to the pivot point. For these reasons, it is the tibiotarsus which elongates to increase stride length and maintain balance not the femur. Archaeopteryx has not reached this level of femoral reduction (the femur being less than two-thirds the length of the tibiotarsus in most birds), but has a tibiotarsus versus femur ratio which is larger than that of any known theropod. Apparently one of the primary characters of birds aside from feathers is the reflexed pubis (Heilmann, 1926), a character whose functional significance lies in the attainment of a bipedal posture. The reflexed pubis with its loss of the pubic apron in birds other than <u>Archaeopteryx</u> was a necessary step in the evolution of bipedalism in birds. The reason being that with the reduction of the tail the animal's presacral region cannot be balanced. To circumvent this problem the reflection of the pubis allows the viscera to shift posteriorly under the legs. This method was apparently used by some ornithischian dinosaurs (Galton, 1969) although not to the degree seen in birds. The problem of these ormithopods was a bit different but necessitated the same sort of adaptation. The viscera of herbivores are much longer than those of carnivores and therefore take up more space and weigh more. The problem of balance may be slightly compounded by these ornithischian dinosaurs by keeping gastroliths in their gizzards and by their numerous teeth. This all adds up to more presacral weight. In order to allow the viscera to shift posteriorly and to evolve longer intestines for more complete digestion, the pubes must be rotated backward.

This also means that the weight of the pubis and its associated musculature is also shifted backward which could be an aid to counterbalancing the presacral region. It should be remembered that these ornithopods had long, bulky (elongate neural and haemal spines presumably for the origin of large caudal musculature) tails which were of use as a counterbalance. Birds do not have this luxury and for that reason had to open not only the pubic symphysis but the ischial symphysis as well. This is a modification (opening the ischial symphysis) that ornithopods do not exhibit. In birds the presacral region is short and highly pneumaticized. In addition the neck and skull of birds are slender and light and there are of course no teeth in the mouth. All of this, no matter how petty it seems, nonetheless serves to reduce the presacral weight-something which must be done if the tail is no longer of use as a counterbalance.

Previous Restorations

The previous restorations giving theropods an avian stance (Bakker 1975 ; Russell, 1972 ; Newman, 1970) and the traditional stance of theropods (Osborn, 1906 and Marsh 1893) are incorrect. In both types of restorations there are errors in the cervical, pelvic and hindlimb regions of theropods.

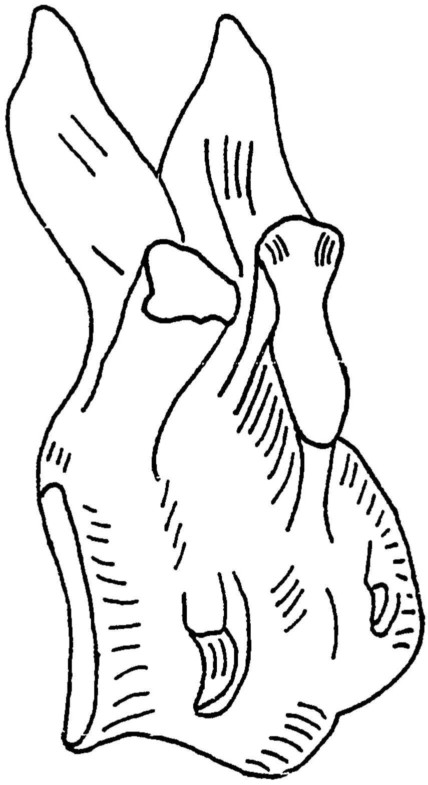
The Hallux

The hallux has been a source of error in the restorations of theropods (Hecht, 1976; Tarsitano and Hecht, 1980). In most restorations (Osborn, 1899, 1905, 1906, 1916; Gilmore, 1920; Ostrom, 1969, 1976b, 1978; and Romer, 1956, 1966) the hallux is reflexed as in birds. The reason for this erroneous view is the placement of metatarsal I into the muscle scar of the tibial head of the M. gastrocnemius (Tarsitano and Hecht, 1980). Furthermore, in theropods whose pes were found in articulation such as, *Coelophysis bauri* AMNH 7223-7224; *Saurornthoides mongolensis* AMNH 6516 and *Velociraptor mongoliensis*, all show a hallux which is not reversed and at most medially directed at an acute angle well below ninety degrees. Another theropod, *Compsognathus longipes* BSP 563, found in articulation also shows a hallux which is essentially parallel to digit two. It should be remembered that in the functionally tridactyl foot of theropods the digits are not parallel to one another. The hallux probably was positioned at an angle from metatarsal II not very different from the angle between digits two, three and four. The phalanges of the hallux of Compsognathus are preserved in natural articulation. Metatarsal I has been shifted out of position by metatarsal IV which has slid underneath metatarsal I during preservation. For this reason, Ostrom. (1978) incorrectly stated that *Compsognathus* had a reflexed hallux. Additional evidence that *Compsognathus* and other theropods did not have a reflexed hallux like that of *Archaeopteryx* or other birds is its position on metatarsal II and its morphology. Metatarsal I is positioned at the mid-length of metatarsal II in theropods whose peces were found in articulation. This is in sharp contrast to the avian condition where metatarsal I is positioned at the distal third of Metatarsal II (Tarsitano and Hecht, 1980). Finally the hallux of all theropods (if one is present) bears a terminal ungual which is drastically reduced when compared to the other terminal unguals in the same animal and to *Archaeopteryx*. The terminal ungual of the hallux of *Archaeopteryx* is as large as those of the other digits. This leads me to believe the hallux of *Archaeopteryx* was functional whereas those of theropods were going through a reduction phase. The reduction phase in theropods was an adaptation for cursorial life style much like that of the evolution of the horse. Since it is the distal segments of a limb which must be moved through the longest arc it is an energy saving process to lose unnecessary weight such as a non-functional hallux. Thus the loss or reduction of the hallux could reduce the movement of inertia of the limb.

The Traditional Stance of Tyrannosaurus by Osborn

Osborn and Brown erected the specimen of Tyrannosaurus rex AMNH 5027, with approximately forty-five degree bends occurring between the third and fourth cervical vertebrae and the first dorsal and tenth cervical vertebrae (it should be noted that some parts, such as the humerus and femur have been cast from AMNH 973). The recent reconstructions by Newman, (1970) are more extreme, with approximately a ninety degree bend occurring between the first dorsal and tenth cervical vertebrae and two forty-five degree bends between the first and second, and the second and third cervical vertebrae. To achieve these bends, the spaces between the centra of the vertebrae noted above have been over exaggerated and have been placed in unnatural positions. The reason for constructing the neck in this manner is the fused condition of the first dorsal and tenth cervical vertebrae in Tyrannosaurus (Figure 37). The anterior face of the tenth cervical centrum is directed at approximately forty-five degrees from the horizontal. In order to allow the head to be held parallel to the

Fig. 37. The fused tenth cervical and first dorsal vertebrae of *Tyrannosaurus rex* AMNH 5027.

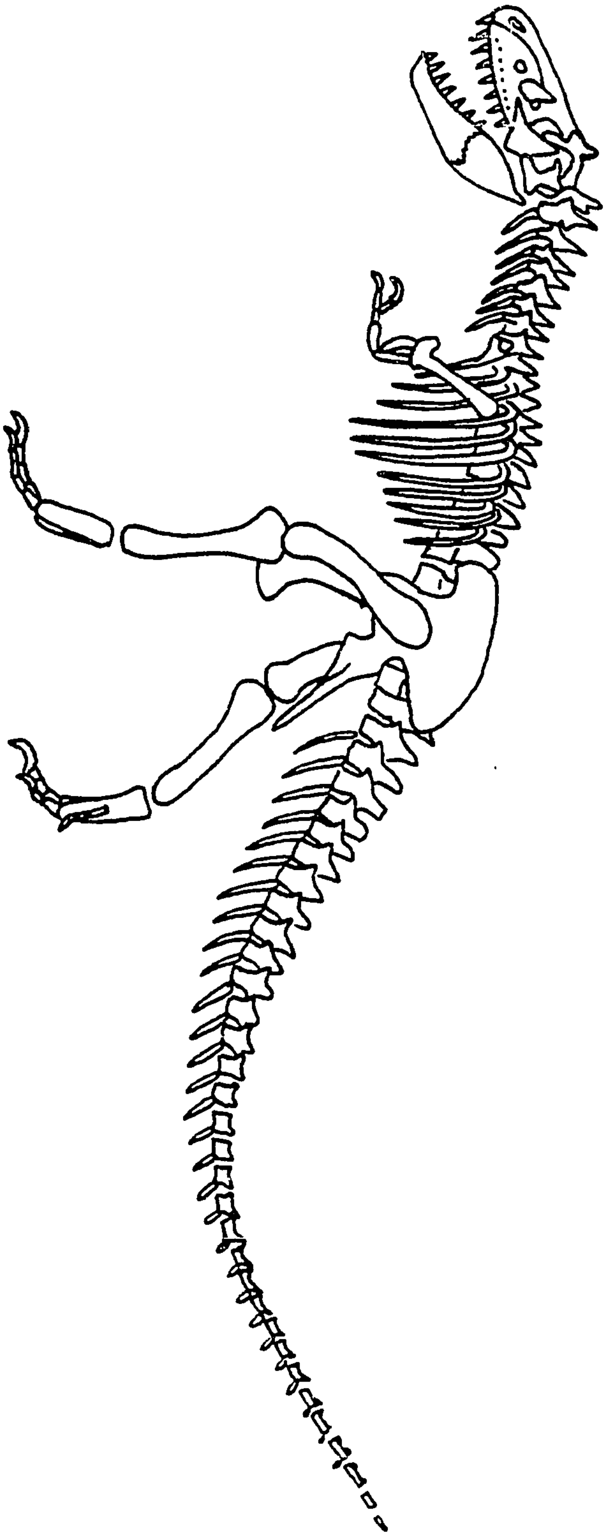


ground another bend is needed. An inspection of the type specimen, AMNH 973 and another specimen, AMNH 5866, revealed an absence of fusion among the cervical vertebrae. (It should be noted, that specimen 5866 is the type specimen for Dynamosaurus imperiosus Osborn. Osborn,(1906) states, however, that Dynamosaurus imperiosus is generically identical with Tyrannosaurus and more than likely the same species). Furthermore, there is also an absence of fusion in the sister genera, Gorgosaurus and Albertosaurus. The specimen, AMNH 5027, is probably aberrant with regard to the fused vertebrae.

In the standard pose of Tyrannosaurus, (that of Marsh and Osborn) the vertebral column is held at approximately a forty-five degree angle above the horizontal plane. In this position the protraction of the femur would cause the thigh to be extended to a position nearly parallel to the ground. In the Osborn restoration of Tyrannosaurus, the vertical component of the muscular effort is far too great in order for the thigh to be brought appreciably forward. Thus, the vertebral orientation would unneccessarily limit the stride length. Retraction of the thigh would not impart very much force to the ground in the stance it now occupies in the American Museum of Natural History. The reason for this is the main retractors of the hindlimb would have to be almost in a full state of contraction in order for Tyrannosaurus to have stood in the posture presented by Osborn. To summarize, the main difficulty of this stance lies in holding the vertebral column at approximately a forty to forty-five degree angle.

In contrast to the study of Coombs, (1978), the major protractors of the thigh originate on the presacral vertebrae, and the anterior and internal surfaces of the ilium. Only the M. pubo-ischio-femoralis externus parts I andII originate on the pubis. The rotation of the vertebral column downward to achieve a horizontal position for the dorsal vertebrae and pelvis would impare the function of the protractor muscles. Since skeletal muscle normally does not contract more than thirty per cent of its resting length, the M. pubo-ischio-femoralis internus would not lift the thigh if the vertebral column was horizontal. Thus, the tilting of the presacral vertebrae and ilium upward at an angle of approximately twenty degrees above the horizontal would enable the muscles to lift the thigh (Figure 38). Because the major femoral protractors of theropods originate on the presacral vertebrae and ilium the femur could be protracted anterior to the pubes. The upward tilting of the presacral vertebrae is seen in the bipedal progression of lizards (Snyder 1949,1954). Ratite birds such as Struthio only appear

Fig. 38. A diagrammatic representation of the new posture of *Tyrannosaurus rex*.



to have a horizontal vertebral column and synsacrum. This is really not the case. The ilium is tilted upward while the presacral vertebrae slope slightly downward giving the appearance of a horizontal column. The presacral region can slope downward since the M. pubo-ischio-femoralis internus in birds has migrated upward on the ilium (Romer, 1923a). The horizontal placement of the vertebral column also causes morphological errors in the neck. As noted in the Osborn restoration the neck is broken in two places. The same is true of the so-called avian posture of theropods. The neck would have had to have been broken in two places in order for the head to be held in an avian position. Part of the reason for this is that the position of the occipital condyle in many birds is different from that of theropods. The occipital condyle of theropods is situated well above the angle of the jaws and is directed more horizontally than the occipital condyle of most birds. The condyle in most birds is near the angle of jaws and is directed posterio-ventrally. It should also be noted that birds probably had a neck which is more flexible than that of any archosaur owing to the heterocoelus condition of the vertebrae. The necks of carnosaurs are bulky and short with amphicoelus vertebrae. Thus, sharp bends necessitated by a horizontal vertebral column are biomechanically improbable.

Conclusion

Although there is a one to one correspondence between the muscles of the hindlimb among crocodilians and birds, the placement, size and number of heads of each muscle are different. These differences are the result of the evolution of flight among birds. The loss of the tail as a counter-balance in birds has brought about changes in the morphology of the entire animal. These changes were the lightening and shortening of the presacral region, the posterior directed pubis, the opening of the pubic and ischial symphysis, the development of a synsacrum, the shortening of the femur, the elongation of the tibiotarsus, the development of a mesotarsal joint and the reduction of the inner and outer digits. The crocodilians have not undergone any significant hindlimb morphological changes since the Jurassic. Except for the exclusion of the pubis from the acetabulum and the reduction of the preacetabular portion of the ilium, the crocodilian pelvis closely resembles the saurischian pelvis. For this reason the musculature of theropods is more similar to crocodilians than it is to birds.

Based on the morphology of the hindlimb, I believe it is possible to determine whether or not a fossil archosaur was bipedal. Major considerations in this regard concerns the sacrum, presacral length and bulk, caudal length and bulk, upright posture and the tarsus. The intratarsal point of crocodilians and thecodonts is associated with a plantigrade, quadrupedal gait. The movable calcaneum with its small surface area of the fibular condyle and the calcaneal tuber, assures a plantigrade gait. Since the primary flexors of the tarsus insert on the fifth metatarsal the line of pull of these muscles is both laterally and posteriorly. This is indicative of a sprawling gait and not an active bipedal cursorial animal. For this reason I base the distinction between a thecodont and dinosaur on whether the animal was (at one time in its evolution, such as Sauropods (Romer, 1966) bipedal. This is primarily based on the presence or absence of an intratarsal joint. The possession of the intratarsal joint depicts primitiveness and is a character state of thecodonts.

Only from morphological studies of related living taxa can the interpretation of fossil vertebrates have some degree of reality. If such studies of the living taxa are ignored than reconstruction of fossil vertebrates can become arbitrary. There are limitations of the functional analysis of fossil vertebrates. For example, it is known from observations in the field

(Cott, 1962) that crocodilian have at least four different types of gait, including bipedal progression. The bipedal progression occurs only during rapid locomotion when enough momentum has been attained. The bipedal posture is not stable nor maneuverable and should not be confused with the true bipedalism of birds and theropod dinosaurs. From a morphological study of modern crocodilians we probably could not have predicted the different gaits including galloping crocodilians. However, our studies of crocodilian functional morphology (Gadow, 1882b; Romer, 1923a;) could not have precluded the possibility of these different gaits. Thus, from the observation of the living vertebrates and through the identification of morphology with function one can attempt to interpret the function of similar and homologous morphologies of fossil vertebrates. In addition, while it may be impossible to define precise limits of form-function complexes one can eliminate functions and reconstructions which either do not have a morphological basis or violate biomechanical principles.

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