

Pelvic and Hindlimb Musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda)

Matthew T. Carrano^{1*} and John R. Hutchinson^{2†}

¹Department of Anatomical Sciences, State University of New York at Stony Brook, Stony Brook, New York 11794-8081

²Department of Integrative Biology, University of California, Berkeley, California 94720-3140

ABSTRACT In this article, we develop a new reconstruction of the pelvic and hindlimb muscles of the large theropod dinosaur *Tyrannosaurus rex*. Our new reconstruction relies primarily on direct examination of both extant and fossil turtles, lepidosaurs, and archosaurs. These observations are placed into a phylogenetic context and data from extant taxa are used to constrain inferences concerning the soft-tissue structures in *T. rex*. Using this extant phylogenetic bracket, we are able to offer well-supported inferences concerning most of the hindlimb musculature in this taxon. We also refrain from making any inferences for certain muscles where the resulting optimizations are ambiguous. This reconstruction differs from several previous attempts and we evaluate these discrepancies. In addition to providing a new and more detailed understanding of the hindlimb morphology of *T. rex*—the largest known terrestrial biped—this reconstruction also helps to clarify the sequence of character-state change along the line to extant birds. *J. Morphol.* 253:207–228, 2002.

© 2002 Wiley-Liss, Inc.

KEY WORDS: Saurischia; avian evolution; functional morphology; extant phylogenetic bracket; soft-tissue; osteology

Crown-group birds and crocodylians are the sole surviving members of the clade Archosauria. This group also includes an extraordinary diversity of extinct taxa, many of which differed substantially from their extant relatives in morphology. Archosaurs thus present a frustrating group with which to employ the extant phylogenetic bracket (EPB; Bryant and Russell, 1993; Witmer, 1995) because extant members of the group often provide conflicting information for interpreting extinct forms. As an example, the extinct clade Pterosauria includes over 100 genera of volant forms, but their flight capabilities were derived independently from those of birds and appear to have involved substantially different anatomical modifications (e.g., Padian, 1991; Unwin, 1999).

This frustration is reciprocal: extant birds and crocodylians are often not even mutually enlightening because of the substantial morphological, physiological, and behavioral differences between these two groups. Studies of extant archosaurs often cast these differences in terms of birds and the origin of

flight, noting that crocodylians are presumably similar to the ancestral archosaurian state (Romer, 1923a,b; Walker, 1977; Tarsitano, 1983; Hutchinson and Gatesy, 2000). Yet the remarkable transformations that led to the origin of birds could have occurred anywhere within nonavian ornithodirans. Furthermore, the fossil record documents the acquisition of numerous specializations within Crocodylia as well, suggesting that extant members of this clade are not merely proxies for the ancestral archosaur, although they indeed retain many plesiomorphies.

However, several recent studies (Gauthier, 1986; Gatesy, 1990, 1995; Padian and Chiappe, 1998; Carrano, 1998a, 2000; Hutchinson and Gatesy, 2000; Hutchinson, 2001a,b) have managed to clarify the sequence of character acquisition along the line to extant birds. These studies concur that many “avian” features were acquired in a stepwise fashion and thus characterize various more inclusive ornithodiran clades. The hindlimb apparatus of extant birds is actually an assemblage of ancestral dinosauromorph, tetanuran theropod, and avian apomorphies. Although a truly “avian” hindlimb was not present until well within the clade Aves, several features previously regarded as “avian” were present in

Contract grant sponsors: the Field Museum of Natural History, the University of California Museum of Paleontology, the UCMP Welles Memorial Fund, the Jurassic Foundation, National Science Foundation; Contract grant number: IBN 9407367 (to S.M. Gatesy); Contract grant sponsors: the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and a Sigma Xi (Berkeley Chapter) Grant-in-Aid of Research.

*Correspondence to: Matthew T. Carrano, Department of Anatomical Sciences, Health Sciences Center T-8, State University of New York at Stony Brook, Stony Brook, NY 11794-8081.
E-mail: mcarrano@mail.som.sunysb.edu

†Current address: Biomechanical Engineering Division, Stanford University, Stanford, CA 94305-4038.

DOI: 10.1002/jmor.10018

nonavian theropods (Gatesy, 1995; Carrano, 1998a, 2000; Hutchinson, 2001a,b).

Consequently, the evolution of the avian hindlimb was not solely linked to the origin of flight. Rather, the general structural similarities between the hindlimb skeletons of most dinosaurs implies that this organization was inherited from a common, bipedal ancestor. Many muscle attachment scars visible on basal dinosauriforms are similar to those present in dinosaurs, including birds (Hutchinson, 2001a,b), but differ from those of crocodylians. This suggests that many of the changes in hindlimb musculature seen in dinosaurs were associated with the transition to bipedalism and were inherited wholesale by birds. Subsequent modifications within dinosaurs are apparent as well (Dilkes, 2000; Carrano, 2000) but have generally received less attention.

Despite these recent works, much resolution on this issue has been lacking, largely due to the difficulties inherent in reconstructing soft tissues in extinct taxa. For example, although it seems clear that subdivision of the deep dorsal thigh muscles was already under way in nonavian theropods (Carrano, 2000; Hutchinson, 2001b), the timing of this event (or events) is difficult to pinpoint. Here again, the differences between the two lineages of extant archosaurs have a confounding effect, as do persistent controversies regarding muscle homologies.

However, a recently discovered specimen of *Tyrannosaurus rex* (FMNH PR 2081, "Sue"), displays a combination of excellent preservation and large size that has rendered its muscle attachment sites exceptionally clear. As a result, it is now possible to determine the arrangement of hindlimb muscles in *Tyrannosaurus* with considerably greater phylogenetic and osteological support. In addition to updating Romer's (1923b,c) now-canonized reconstruction of saurischian musculature, this provides an opportunity to evaluate subsequent, less widely received attempts (Walker, 1977; Tarsitano, 1981, 1983). Finally, our new reconstruction is relevant to understanding the evolutionary sequence of the unusual avian hindlimb.

Museum abbreviations: AMNH, American Museum of Natural History, New York; BHI, Black Hills Institute, Hill City, SD; CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; MOR, Museum of the Rockies, Bozeman, MT; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, AB; UCMP, University of California Museum of Paleontology, Berkeley, CA.

MATERIALS AND METHODS

Caution is warranted when attempting to reconstruct the musculature of any extinct animal (McGowan, 1979, 1982; Bryant and Seymour, 1990), particularly a member of a group (such as nonavian dinosaurs) that may have differed significantly from its extant relatives in locomotor habit (Gatesy, 1990, 1995; Carrano, 1998a; Hutchinson and Gatesy, 2000). Parsimony requires a con-

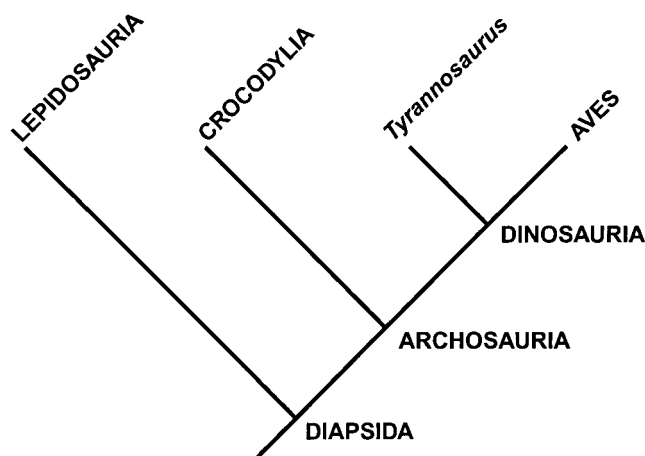


Fig. 1. Phylogenetic framework used in this study, based on Gauthier (1986).

servative reconstruction of the primary pelvic and hindlimb musculature in dinosaurs—i.e., one that requires a minimum number of inferred differences from extant forms (Rowe, 1986). However, the concept of what constitutes a single “difference” is a mutable one, and as a result these hypotheses can be mitigated by information from osteology. The particular sizes and functions of these muscles remain more speculative, because novel combinations of muscles, or changes in muscle position and orientation—let alone their specific motor patterns—cannot be observed in extinct taxa. Nonetheless, careful examination of fossil specimens can reveal consistent topographic indicators of many (but not all) muscle attachment sites and the EPB (Witmer, 1995) provided by birds and crocodylians provides constraints on inferring soft tissue homology from these osteological landmarks (but see Discussion).

Phylogenetically based hypotheses of homology (Patterson, 1982; McKittrick, 1994) form a vital component of hypotheses of musculoskeletal anatomy in extinct taxa (for more comments, see Discussion). Although nearly all previous studies (e.g., Romer, 1923a,b,c) were conducted prior to the dominance of cladistic methodology in evolutionary biology, many nonetheless utilized a general (if vague) phylogenetic framework in determining homologies and presence/absence for muscles. What these studies lack is the specific rigor of the EPB for soft tissue reconstruction (e.g., Bryant and Russell, 1993; Witmer, 1995) and its reliance on homology rather than analogy. Any muscle reconstruction consists of multiple independent hypotheses of homology, and must fail or persevere based on the evidence and methodology used to formulate and test it; examples include Norman (1986), Parrish (1983, 1986), Rowe (1986, 1989), Gatesy (1990), and Dilkes (2000). The major advantage of this method lies in its explicit, a posteriori approach: muscle reconstructions emerge following a broad analysis of taxa within a phylogenetic context and ambiguities can be made clear.

Procedure

Our reconstruction uses an explicit phylogenetic framework (Fig. 1) as a context within which soft tissue and osteological data (Carrano, 1998b; Hutchinson, 2001c) from extant and extinct taxa were interpreted via the EPB (Witmer, 1995, 1997). Extensive direct observations of extant archosaurs (two crocodylians, three paleognaths, and 16 neognaths) and other saurians (seven lizards, two turtles, and *Sphenodon*), as well as numerous extinct archosaurs (several hundred nonavian dinosaurs, 15 birds, 10 crocodylians, and 30 other taxa), provide the anatomical framework. Multiple specimens of *Tyrannosaurus rex* (MOR 009, 555; AMNH 5027; CM 9380 [= AMNH 973]; UCMP 136517; BHI 3033; RTMP 81.12.1) contributed to the osteological dataset, but we

TABLE 1. Homologies of the hindlimb muscles in extant archosaurs

Crocodylia	Aves
Triceps femoris	
M. iliotibialis 1 (IT1)	M. iliotibialis cranialis (IC)
Mm. iliotibialis 2, 3 (IT2, IT3)	M. iliotibialis lateralis (IL)
M. ambiens (AMB)	M. ambiens (AMB)
M. femorotibialis externus (FMTE)	M. femorotibialis lateralis (FMTL)
M. femorotibialis internus (FMTI)	M. femorotibialis intermedius (FMTIM) and M. femorotibialis medialis (FMTM)
M. iliofibularis (ILFB)	M. iliofibularis (ILFB)
Deep dorsal group	
M. iliofemoralis (IF)	M. iliofemoralis externus (IFE) and M. iliotrochantericus caudalis (ITC)
M. iliofemoralis/puboischiofemoralis internus 2	M. iliotrochantericus cranialis (ITCR) and M. iliotrochantericus medius (ITM)
M. puboischiofemoralis 1 (PIF1)	M. iliofemoralis internus (IFI)
Flexor cruris group	
M. pubo-ischio-tibialis (PIT)	[absent]
M. flexor tibialis internus 1 (FTI1)	[absent]
M. flexor tibialis internus 2 (FTI2)	[absent]
M. flexor tibialis internus 3 (FTI3)	M. flexor cruris medialis (FCM)
M. flexor tibialis internus 4 (FTI4)	[absent]
M. flexor tibialis externus (FTE)	M. flexor cruris lateralis pars pelvica (FCLP)
Mm. adductores femores	
M. adductor femoris 1 (ADD1)	M. puboischiofemoralis pars medialis (PIFM)
M. adductor femoris 2 (ADD2)	M. puboischiofemoralis pars lateralis (PIFL)
Mm. puboischiofemorales externi	
M. puboischiofemoralis externus 1 (PIFE1)	M. obturatorius lateralis (OL)
M. puboischiofemoralis externus 2 (PIFE2)	M. obturatorius medialis (OM)
M. puboischiofemoralis externus 3 (PIFE3)	[absent]
M. ischiochantericus (ISTR)	M. ischiofemoralis (ISF)
Mm. caudofemorales	
M. caudofemoralis brevis (CFB)	M. caudofemoralis pars pelvica (CFP)
M. caudofemoralis longus (CFL)	M. caudofemoralis pars caudalis (CFC)
Mm. gastrocnemii	
M. gastrocnemius externus (GE)	Mm. gastrocnemii pars lateralis (GL) et intermedia (GIM)
M. gastrocnemius internus (GI)	M. gastrocnemius pars medialis (GM)
Digital flexor group	
M. flexor hallucis longus (FHL)	M. flexor hallucis longus (FHL)
M. flexor digitorum brevis (FDB)	[absent]
M. flexor digitorum longus (FDL)	M. flexor digitorum longus (FDL)
Digital extensor group	
M. extensor digitorum longus (EDL)	M. extensor digitorum longus (EDL)
M. extensor digitorum brevis (EDB)	[absent]
M. extensor hallucis longus (EHL)	M. extensor hallucis longus (EHL)
Other lower leg muscles	
M. tibialis anterior (TA)	M. tibialis cranialis (TC)
M. popliteus (POP)	M. popliteus (POP)
M. fibularis longus (FL)	M. fibularis longus (FL)
M. fibularis brevis (FB)	M. fibularis brevis (FB)

Although some variability exists within birds and crocodylians regarding muscle size, shape, and even presence, the condition listed represents that inferred for the common ancestor of each group.

rely primarily on one particularly large, well-preserved, and complete specimen (FMNH PR 2081).

We use extant taxa to establish homology arguments for the muscles of the pelvis and hindlimb in archosaurs. The homologies and nomenclature of the deep dorsal and flexor cruris thigh musculature remain controversial (Romer, 1923a, 1942; Rowe, 1986; Carrano, 2000), so we discuss alternative interpretations. These homology arguments are placed in a phylogenetic context through the compilation of a data matrix and the mapping of character states onto a “consensus” phylogenetic framework (Fig. 1) in MacClade 3.08 (Maddison and Maddison, 1992). Additional extinct taxa that refined polarity for osteological character were included; see above and Hutchinson (2001a,b,c). The distribution of osteological character states reveals the most parsimonious (i.e., least speculative) reconstruction of the soft tissues of *Tyrannosaurus rex*. Congruence of character states with preserved osteological features (bone surfaces and structures) allows completion of the final step: reconstructing muscles on a skeleton. We consider origin and insertion sites independently and cite levels of inference (see below; Table 2).

Levels of Inference

Witmer (1995, 1997) provided a useful metric of the level of speculation inherent in a soft tissue reconstruction, which he termed “levels of inference.” If soft tissue data from extant bracket taxa (for archosaurs, Crocodylia and Neornithes) unequivocally support the reconstruction of an unpreserved feature on an extinct taxon (i.e., both outgroups to the fossil taxon have the feature), the reconstruction is a Level I inference. Equivocal support from extant taxa (i.e., one outgroup lacks the feature) is a Level II inference and the unequivocal absence of support from extant taxa (i.e., both outgroups lack the feature) is a Level III inference.

If inferences lack conclusive data from the osteological correlates of soft tissues, they are called Levels I', II', and III' inferences (Witmer, 1995). Such inferences have less support than the matching Levels I, II, and III inferences, but more than one at the next overall level (i.e., Level I' is preferred over Level II). For example, extant Crocodylia and Neornithes have an adductor muscle head (M. adductor femoris 1 or M. puboischiofemoralis

TABLE 2. Muscles inferred as present in *Tyrannosaurus rex*

Muscle	Origin	Insertion
IT1	anteroventral rim of lateral ilium (I)	tibial cnemial crest (I)
IT2	dorsal rim of lateral preacetabular ilium, above IFE + ITC (I)	tibial cnemial crest (I)
IT3	dorsal rim of postacetabular ilium (I)	tibial cnemial crest (I)
AMB	pubic tubercle (I)	tibial cnemial crest (I), plus secondary tendon to digital flexors (I')
FMTE	lateral femoral shaft (I)	tibial cnemial crest (I)
FMTI	anteromedial femoral shaft (I)	tibial cnemial crest (I)
ILFB	lateral postacetabular ilium between FTE and IFE (I')	fibular tubercle (I)
IFE	lateral surface of ilium (I)	femoral trochanteric shelf (II)
ITC	lateral surface of ilium (I), anterior to IFE (II)	femoral lesser trochanter (II)
IFI	iliac preacetabular fossa (II)	anteromedial proximal femur (I)
ITM + ITCR	unresolved homology (but Level II)	femoral accessory trochanter (II)
PIT	[absent]	[absent]
FIT1	? (possibly ischial shaft; II')	? (possibly medial proximal tibia; II')
FIT2	?	?
FIT3	ischial tuberosity (II)	medial proximal tibia (I')
FIT4	?	?
FTE	lateral postacetabular ilium (I)	medial proximal tibia (I') posterior to IFE and ILFB (I')
ADD1	anteroventral edge of obturator process (I')	medial scar on posterior surface of distal femoral shaft (I)
ADD2	scar on posterodorsal ischial shaft, distal to ischial tuberosity (II)	lateral scar on posterior surface of distal femoral shaft (I)
PIFE1	anterior surface of pubic apron (II)	femoral greater trochanter (I)
PIFE2	posterior surface of pubic apron (II)	femoral greater trochanter (I)
PIFE3	lateral surface of obturator process, between ADD1 and ADD2 (II)	femoral greater trochanter (I)
ISTR	medial surface of ischium (II)	lateral surface of proximal femur (I)
CFB	iliac brevis fossa (II)	lateral surface of fourth trochanter (I)
CFL	caudal vertebral centra 1–15 (I)	medial surface of fourth trochanter (I)
GL	posterior femur, distal to ADD2 (I)	plantar surface of metatarsals II–IV (II)
GM	medial proximal tibia, anteromedial to FTE (I)	plantar surface of metatarsals II–IV, with GL (II)
FDL	posterior femur with GL, distal to ADD2 (I)	ventral pedal phalanges (I)
FDB	?	?
FHL	posterior femur with GL and FDL, distal to ADD2 (I)	ventral hallucal phalanges and ungual (I)
EDL	anterior region of femur and/or tibia (II')	dorsal surfaces of pedal phalanges (II)
EDB	?	?
EHL	distal fibula (II)	dorsal surface of hallucal ungual (I)
TA	anterior proximal tibia (I)	anterior proximal metatarsal shafts (I)
POP	distal tibial shaft (II)	distal fibular shaft (II)
FL	anterolateral fibula, tibia (I')	posterolateral ankle (I')
FB	distal and lateral to FL on fibula (I')	anterolateral ankle (I')

Muscles are listed by abbreviation (see Table 1), along with the level of inference (I, I', II) required using the EPB method. ? = unresolved at present.

pars medialis) present on the anteroventral edge of the ischium. No muscle scars are correlated with this muscle head (it is a fleshy attachment), so reconstructing the M. adductor femoris 1 on *Tyrannosaurus* is a Level I' inference. *Not* reconstructing this muscle requires additional speculation and would be a Level III' inference. In contrast, reconstructing M. pubotibialis in *Tyrannosaurus* (or any other extinct archosaur) would be very speculative (Level III') because extant archosaurs lack this muscle and there is no osteological evidence for it in the fossils; omitting M. pubotibialis is thus a Level I' inference.

In this study, we minimally require Level II inferences: in order to reconstruct a soft tissue feature, at least one extant taxon must have the trait *and* the osteological correlate that is homologous with the corresponding osteological correlate in the extinct taxon. Homologous osteological correlates may be character states (taxic homologs), characters (transformational homologs), or topologically equivalent bone surfaces (Hutchinson, 2001a,b). A Level I inference has the strongest support, followed by Level I' and Level II inferences. We do not make

Level II' inferences, but it is equally parsimonious to include or exclude them; their exclusion reflects our own limitations on the levels of speculation involved. In other words, we infer neither presence nor absence for such features, but refrain from making any statements altogether. Level III and III' inferences are too speculative to infer as present.

Caveats

Integration of neontological and paleontological data can reveal much about musculoskeletal evolution. However, numerous vagaries in the primary anatomical data are grounds for a cautious approach to soft-tissue reconstruction in fossils (Witmer, 1995; Dilkes, 2000; Hutchinson, 2001a,b). Relative position, division, and approximate relative sizes of muscles are often inferable from osteological comparisons of fossils with dissections of extant taxa. Muscle attachment direction can be estimated using Sharpey's

fiber orientations (Russell, 1972; Jones and Boyde, 1974; Walker, 1977) or bone rugosity patterns (Benjamin et al., 1986). Nonetheless, it is exceedingly difficult to quantify muscle size precisely from osteological data alone (McGowan, 1979, 1982; Bryant and Seymour, 1990), and other unpreserved features—such as fiber length, pennation (and hence physiological cross-sectional area), force output, histochemistry, and activation pattern—are even more remotely accessible. Because the cross-sectional area of a muscle often differs in size from the area of muscle scarring (Bryant and Seymour, 1990; Hutchinson, 2001a), we assume that a scarred area allows only a general estimate of that muscle's size.

In addition, ligaments and other collagenous structures can produce scarring identical to that of tendons (Haines and Mo-huiddin, 1968), so these soft tissues must be considered potential candidates for correlation with osteological features that are close to joints. Also, bony features often may be generated by interactions with more than one kind of soft tissue, including muscles, nerves, connective tissues, and vasculature. Conversely, multiple bony features such as adjacent muscle scars may be correlated with a single attachment rather than multiple soft tissues.

Finally, the same general caveats that apply to parsimony reconstruction of phylogeny also apply here. Character and character-state identification are inherently nonobjective procedures, but they are preferred because they are *explicit*. Particularly when dealing with potentially continuous transformations, the inference that a particular change requires one “step” can be difficult to justify. Moving a muscle from the medial to the lateral side of the ilium during the course of evolution, for example, can easily be summarized (and reconstructed) as a single change, when in fact it may have occurred in multiple “steps.” Thus, although we rely on parsimony reconstructions, an important final caveat is that in doing so we engender a perception of simplicity rather than of a subtly complex reality.

NEW RECONSTRUCTION OF THE PELVIC AND HINDLIMB MUSCULATURE OF *TYRANNOSAURUS REX*

This new reconstruction covers ground visited by archosaur workers many times before (Romer 1923a,b,c; Russell, 1972; Walker, 1977; Tarsitano, 1981, 1983), particularly regarding the proximal hindlimb musculature. Here we present anatomical observations and homology arguments for individual muscles, building a comprehensive reconstruction from these discrete units. Comparisons with previous works are presented separately (see Discussion), but our conclusions are consistent with these on many points. However, few authors have reconstructed any aspects of the lower leg muscles of *Tyrannosaurus* (or any other dinosaur), so our conclusions in this regard are mostly novel. Our homology scheme (Table 1) is admittedly tentative because of persistent difficulties in resolving lower leg muscle homologies. We also refer the reader to Dilkes (2000), who provides an excellent, detailed reconstruction of the lower leg muscles in the ornithischian *Maiasaura*; here we mainly offer comparisons with *Tyrannosaurus*. We do not reconstruct many details of the small, individual pedal muscles because of their complexity and the lack of prominent muscle scars. Likewise, the homologies of a few lower leg muscles (*M. tibialis posterior* and *M. pronator profundus* of crocodylians [see Cong et al.,

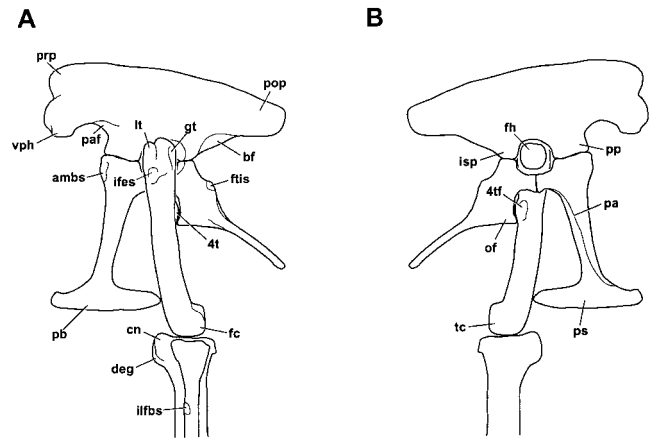


Fig. 2. Pelvic and hindlimb osteology in *Tyrannosaurus rex* (Theropoda), based primarily on FMNH PR 2081. Left side elements are shown in lateral (top) and medial (below) views. amb, M. ambiens scar; bf, brevis fossa; cn, cnemial crest; deg, distal extensor groove; fc, fibular condyle; fh, femoral head; 4t, fourth trochanter; 4tf, medial fossa of fourth trochanter; ftis, M. flexor tibialis internus scar; gt, greater trochanter; ifes, M. iliofemoralis externus scar; ilfbs, M. iliofibularis scar; isp, ischial peduncle; lt, lesser trochanter; of, obturator foramen; pa, pubic apron; paf, preacetabular fossa; pb, pubic boot; pop, iliac postacetabular process; pp, pubic peduncle; prp, preacetabular process; ps, pubic symphysis; tc, tibial condyle; vph, ventral preacetabular hook.

1998], *M. plantaris* of birds) are entirely ambiguous, so we do not discuss them.

Triceps Femoris

Mm. iliobiales 1–3 (IT1–3). *M. iliobialis* is a large, thin, superficial sheet in crocodylians and birds, with three heads that originate along the anterior and dorsal margins of the lateral ilium (Fig. 3). These heads are usually numbered 1–3 from anterior to posterior, but *M. iliobialis* 1 is also termed *M. iliobialis cranialis* (IC; Shroeter and Tosney, 1991) or “sartorius” (Romer, 1923a). *M. iliobialis* 1 is a distinct muscular head in birds and crocodylians, and the pattern of iliac muscle scars visible here suggests that a similar muscle was present in *Tyrannosaurus*. This muscle originated from the anteroventral surface of the iliac blade, attaching along a series of parallel striations near the anteroventral corner. Short, vertical muscle fiber scars are visible along most of the length of the dorsal iliac margin, forming a single anteroposterior line that suggests the attachment of a sheet-like muscle (Fig. 4). Anteriorly, however, the scars diverge to form three roughly parallel lines, stacked dorsoventrally. This may indicate some anterior subdivision of *M. iliobialis*, but the resulting segmental overlap implied by this arrangement is not known in extant archosaurs (see *M. iliofemoralis externus* and *M. iliofibularis*, below). Posteriorly, the line is interrupted at a point approximately above the posterior edge of the acetabulum, marking the location of *M.*

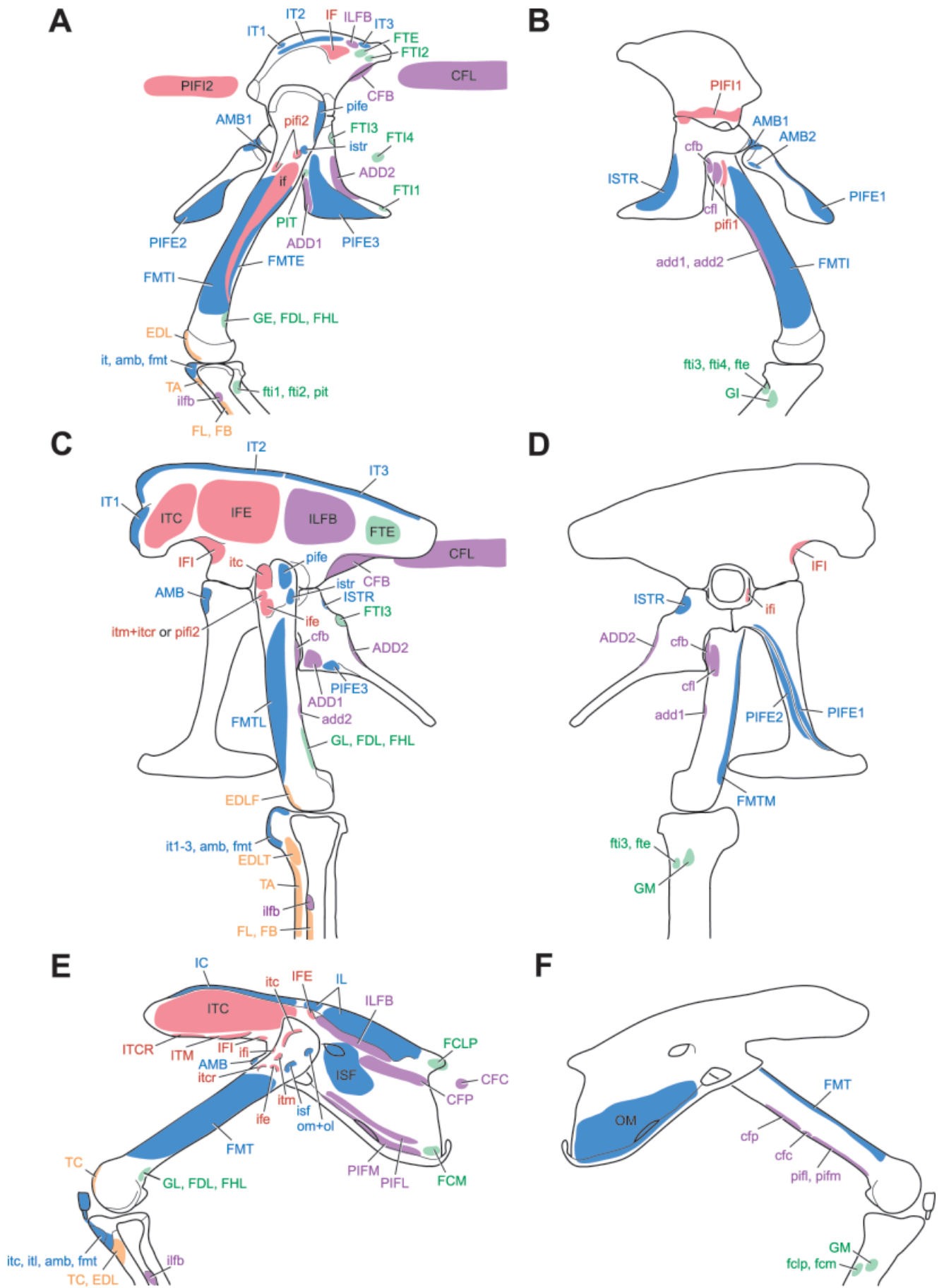


Figure 3

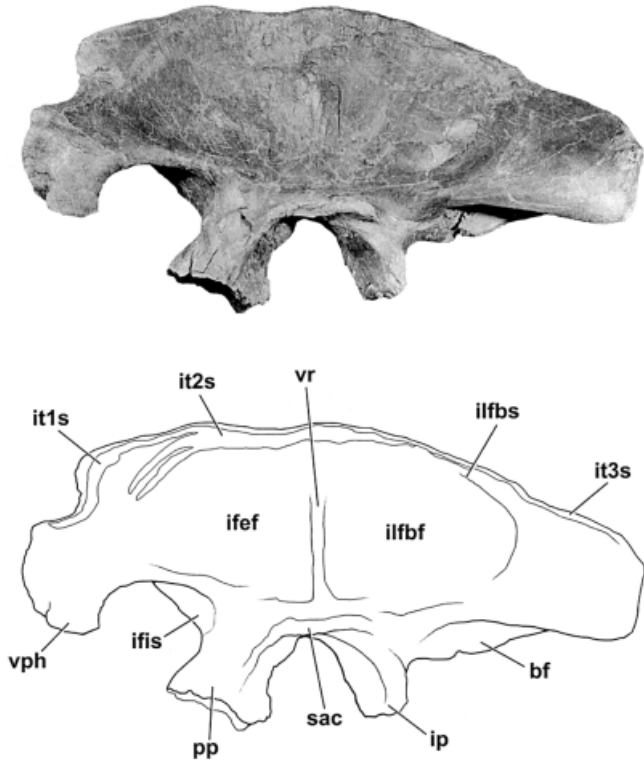


Fig. 4. Osteological correlates present on the ilium of *Tyrannosaurus rex*. Lateral view of right ilium, FMNH PR 2081 (reversed for comparison with Fig. 3). bf, brevis fossa (*M. caudofemoralis brevis* origin); ifef, *M. iliofemoralis externus* origin fossa; ifis, *M. iliofemoralis internus* origin scar; ilfbf, *M. iliofibularis* origin fossa; ilfbs, *M. iliofibularis* origin scar; ip, ischial peduncle; it1s, *M. iliotibialis 1* origin scar; it2s, *M. iliotibialis 2* origin scar; it3s, *M. iliotibialis 3* origin scar; pp, pubic peduncle; sac, supraacetabular crest; vph, ventral preacetabular hook; vr, vertical ridge. Photo courtesy of J. Weinstein and the Field Museum.

iliotibialis 2. A similar line, representing *M. iliotibialis 3*, is present more posteriorly and proceeds to the posterodorsal corner of the ilium. This morphology suggests that *Mm. iliotibiales 2* and *3* of *Tyrannosaurus* were arranged much as they are in extant archosaurs.

Additionally, in extant archosaurs the separate *M. iliotibialis* heads converge with *M. ambiens* and

Mm. femorotibiales to form a common knee extensor tendon that inserts on the cnemial crest of the tibia (see below), via the patella in birds. The same arrangement is inferred for *Mm. iliotibiales 1–3* of *Tyrannosaurus*. However, lacking an ossified patella, the knee extensor tendon of *Tyrannosaurus* probably inserted directly onto the anterolateral surface of the proximal cnemial crest (Fig. 7). In addition, the anterior end of the crest bears a longitudinal groove that is directed towards an anteromedial fibular flange, and some portion of the knee extensor tendon may have passed through this groove and inserted onto the fibula at this point. However, this differs from the condition in extant reptiles and it is possible that some part of a lower leg extensor (*M. extensor digitorum longus*, *M. tibialis anterior*, or *M. fibularis longus*; see below) was attached to this flange.

***M. ambiens* (AMB).** In all extant Reptilia, the single head of *M. ambiens* originates anteroventral to the acetabulum, often from a pubic tubercle (Hutchinson, 2001a). In *Tyrannosaurus*, *M. ambiens* likely originated from a prominent bump on the anterior pubis near the iliac peduncle that represents this same tubercle (Fig. 3; Romer, 1923a; Walker, 1977; Tarsitano, 1981, 1983; Hutchinson, 2001a). As in most tetrapods, it inserted onto the cnemial crest with the remainder of the triceps femoris. In extant archosaurs (and, hence, presumably in *Tyrannosaurus*), *M. ambiens* also sends a secondary tendon through the extensor tendon to the aponeurotic origin of *M. gastrocnemius lateralis* as well as contributing to the tendon of origin of one or more digital flexors. There appears to be no evidence that *M. ambiens* was separated into two heads, as in *Alligator* (see below).

***Mm. femorotibiales* (FMT).** In extant archosaurs, *Mm. femorotibiales* (*internus*/FMTI and *externus*/FMTE in Crocodylia; *medialis*/FMTM, *intermedius*/FMTIM, and *lateralis*/FMTL in Neornithes) originate from most of the available surface of the anterior femoral shaft, between the femoral head and trochanters (proximally) and the condyles (distally). Several intermuscular lines are present on the femoral shaft of *Tyrannosaurus* that delineate the various *Mm. femorotibiales* origins (Fig. 3; Hutchinson, 2001b). The anterior intermuscular line, running from the base of the lesser trochanter down the anterior femoral shaft to the proximal edge of the medial epicondylar crest, likely separated the two *Mm. femorotibiales* components. The posterior intermuscular line, between the base of the greater trochanter and the lateral (fibular) condyle, separated the *M. femorotibialis externus* origin from the *Mm. caudofemoralis brevis* and *adductor femoris 2* insertions. This broad line is continuous distally with a transverse rugose band that leads anteromedially to the proximal tip of the medial epicondylar crest. This crest is a rounded, highly rugose region that likely served as the origin for an additional

Fig. 3. Pelvic and hindlimb musculature in *Alligator* (Crocodylia) (A, left lateral; B, left medial), *Tyrannosaurus rex* (Theropoda) (C, left lateral; D, left medial), and *Gallus* (Aves) (E, left lateral; F, left medial). The extent of the origins for the ILFB and IFE in *T. rex* is ambiguous, as is the exact proximal extent of the TA. The EDLT and EDLF positions are two potential origins for *M. extensor digitorum longus*. Additionally, many other muscle sizes (particularly origins) are not easily bounded in *T. rex*. Note that not all muscles have been included; see text for discussion of equivocal muscle reconstructions. Muscle abbreviations as in Table 1. Colors: green, knee extensor group, PIFE, and ISTR; red, deep dorsal group; blue, tibial flexor group; purple, caudofemorales, adductors, and ILFB; orange, lower limb flexors and extensors.

subdivision of *M. femorotibialis externus*. *M. femorotibialis internus* originated between the anterior intermuscular line (laterally) and the insertion of *M. adductor femoris 1* (medially). This head probably ran over the medial epicondylar crest to meet *M. femorotibialis externus*. From these positions, both *Mm. femorotibiales* heads ran anterolaterally down to the proximal tibia, where they inserted onto the anterolateral cnemial crest as components of the knee extensor tendon.

M. Iliofibularis

The *M. iliofibularis* (ILFB) origin in *Tyrannosaurus* was located on the lateral ilium posterior to the *M. iliofemoralis externus* origin and just ventral to *M. iliotibialis*, as in extant archosaurs (Figs. 2, 3). It is difficult to discern a distinct scar for the *M. iliofibularis* origin, although a faint semicircular line may mark its posterior extent. The central vertical iliac ridge has been suggested as the demarcation between the anterior *M. iliofibularis* and posterior *M. iliofemoralis externus* (Fig. 4; Walker, 1977; Hutchinson, 2001a; but see below). *M. iliofibularis* inserted on a prominent, rounded tubercle on the anterolateral surface of the proximal fibular shaft, again the same as in extant archosaurs (Figs. 2, 3, 7). Thus, *M. iliofibularis* apparently tapered from a large, fleshy origin occupying perhaps one-fourth of the lateral iliac surface to a small, tendinous insertion on the fibula. As in extant archosaurs there was probably a secondary tendinous attachment to the origin of *M. gastrocnemius lateralis* (level I' inference), but there is no osteological evidence for a ligamentous ansa constraining the main tendon (as in birds), so we do not reconstruct it.

Deep Dorsal Group

Assumptions of muscle homologies have particularly significant consequences for reconstructions of the deep dorsal muscles in *Tyrannosaurus*. In crocodylians the embryonic deep dorsal mass develops into three distinct muscles: *M. iliofemoralis* (IF) and two *Mm. puboischiofemorales interni* (PIFI 1 and 2) (Romer, 1927a, 1942; Shroeter and Tosney, 1991). In birds, however, there are five deep dorsal muscles: two *Mm. iliofemorales* (*externus*/IFE, and *internus*/IFI) and three *Mm. iliotrochanterici* (*cranialis*/ITCR, *medialis*/ITM, and *caudalis*/ITC). Some of the homologies between these two groups are uncontroversial: the avian *M. iliofemoralis externus* and *M. iliotrochantericus caudalis* are derivatives of the primitive *M. iliofemoralis*, and the avian *M. iliofemoralis internus* is a derivative of the primitive *M. puboischiofemoralis internus 1* (Gadow, 1880; Romer, 1923a, 1942).

However, the homologies of the final two avian deep dorsal muscles, *Mm. iliotrochanterici cranialis* and *medius*, remain problematic. Although we do

not recount the debate here, the two major hypotheses for the homologies of these muscles may be summarized as: 1) Romer (1923b) and Rowe's (1986) hypothesis that the *Mm. iliotrochantericus cranialis* and *medialis* were derived from the ancestral *M. puboischiofemoralis internus 2*; and 2) Gadow (1880) and Romer's (1923a, 1942) hypothesis that *M. iliotrochantericus cranialis* and *medius* were derived from the ancestral *M. iliofemoralis*. Hypothesis (1) implies that *M. puboischiofemoralis internus 2* was transformed into two distinct muscles and that *M. iliofemoralis* split into *M. iliotrochantericus caudalis* and *M. iliofemoralis externus*, whereas Hypothesis (2) implies that *M. puboischiofemoralis internus 2* was lost on the line to extant birds (which therefore possess no homolog of this muscle) and that *M. iliofemoralis* divided into all four avian muscles. Unfortunately, neither hypothesis makes specific predictions about the condition in a phylogenetically intermediate form such as *Tyrannosaurus*. Therefore, the condition in *Tyrannosaurus* is difficult to resolve and furthermore it does not necessarily shed light on which hypothesis is correct. We consider how each hypothesis of homology affects our reconstruction below.

M. iliofemoralis externus (IFE). In Crocodylia, *M. iliofemoralis* is not divided into the several heads (minimally *M. iliofemoralis externus* and *M. iliotrochantericus caudalis*, and possibly two others; see below) present in Neornithes and it originates from the lateral surface of the ilium above the acetabulum. In Neornithes, *M. iliofemoralis externus* originates on the lateral surface of the ilium, ventral to *M. iliotibialis*, anterior to *M. iliofibularis*, posterior to *M. iliotrochantericus caudalis*, and directly dorsal to the acetabulum and acetabular shelf (Fig. 3). Evidence from muscle insertions on the proximal dinosauriform femur (Hutchinson, 2001b) supports the inference that *M. iliofemoralis* was divided into *M. iliotrochantericus caudalis* and *M. iliofemoralis externus* in *Tyrannosaurus*, even though evidence from the iliac origin is equivocal. In *Tyrannosaurus*, the region of the ilium corresponding to the *M. iliofemoralis externus* origin generally lacks marks for muscular attachments, but it does present a large, concave surface that could have housed a muscle of substantial size. Nonetheless, the specific boundaries of this muscle are unclear. A prominent vertical ridge is present in *Tyrannosaurus* (Figs. 2, 4) and certain other theropods, possibly indicating the posterior boundary of *M. iliofemoralis externus* (Russell, 1972). However, the problematic homology of this ridge throughout Theropoda renders its interpretation as an indicator of the posterior boundary of *M. iliofemoralis externus* premature (Hutchinson, 2001a). *M. iliofemoralis externus* inserted onto a prominent, highly rugose ridge and furrow on the lateral femoral shaft distal to the cleft between the lesser trochanter and the main shaft (Figs. 2, 3, 5), a structure that is homologous with

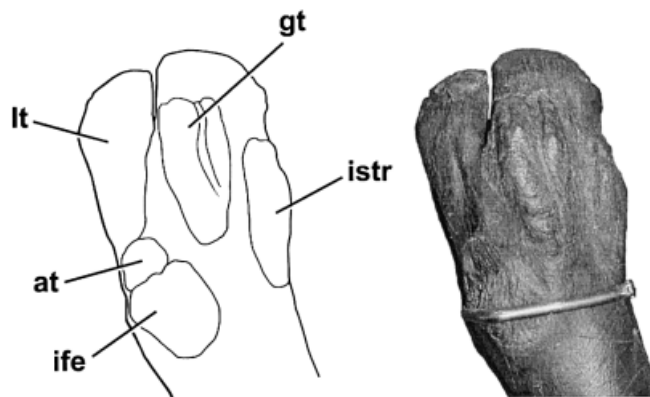


Fig. 5. Osteological correlates present on the proximal femur of *Tyrannosaurus rex*. Lateral view of the right femur, FMNH PR 2081 (reversed for comparison with Fig. 3). at, accessory trochanter; gt, greater trochanter (M. puboischiofemoralis externus insertion); ife, M. iliofemoralis externus insertion scar; istr, M. ischiochantericus insertion scar; lt, lesser trochanter (M. iliotrochantericus cranialis insertion).

the posterior part of the primitive trochanteric shelf (Hutchinson, 2001b).

M. iliotrochantericus caudalis (ITC). M. iliotrochantericus caudalis was derived from the ancestral M. iliofemoralis (Romer, 1923a) and its position topologically reflects this historical relationship. In Neornithes the M. iliotrochantericus caudalis origin is on the lateral surface of the preacetabular ilium, anterior to M. iliofemoralis externus. As with the latter, the specific boundaries for the M. iliotrochantericus caudalis origin in *Tyrannosaurus* are unclear, but they would have been constrained by the placements of M. iliotibialis, M. iliofemoralis externus and M. iliotrochantericus cranialis + medius (Fig. 3). M. iliotrochantericus caudalis inserted onto the lesser trochanter, which is homologous with the anterior portion of the primitive trochanteric shelf (Hutchinson, 2001b). The topology of the lesser trochanter is complex (Fig. 5), with bulbous ridges and striations suggesting the presence of longitudinally oriented Sharpey's fibers (Walker, 1977); these may indicate the approximate line of action of M. iliotrochantericus caudalis.

M. iliofemoralis internus (IFI). Romer (1923a, 1942) and Rowe (1986) agreed that M. puboischiofemoralis internus 1 (PIFI1/"PIFI medialis") of Crocodylia was reduced to M. iliofemoralis internus ("cuppediticus") of Neornithes. In Crocodylia, M. puboischiofemoralis internus 1 originates from the medial surface of the ilium and proximal ischium (Romer, 1923a). In Neornithes, M. iliofemoralis internus originates from a reduced preacetabular or "cuppediticus" fossa (Rowe, 1986; Hutchinson, 2001a) on the lateral ilium at the junction between the anterodorsal portion of the pubic peduncle and the posteroventral edge of the preacetabular process (Fig. 4). The preacetabular fossa is thus the likely site of origin for M. iliofemoralis internus in *Tyrannosaurus*,

indicating that the derived "avian" lateral origin of the muscle was present (Fig. 3). M. iliofemoralis internus apparently inserted on a low bump located distal and anteromedial to the base of the lesser trochanter, in a position similar to its insertion in extant archosaurs.

M. puboischiofemoralis internus 2 (PIFI2/PIFI "dorsalis") and Mm. iliotrochanterici cranialis (ITCR) and medius (ITM). These muscles sit at the core of the controversy surrounding the deep dorsal homologs, and the resulting uncertainty complicates muscle reconstruction in *Tyrannosaurus*. As discussed earlier, it is not known whether M. puboischiofemoralis internus 2 was transformed into Mm. iliotrochanterici cranialis and medius (Hypothesis 1), or was lost entirely during theropod evolution (Hypothesis 2). Because of this we cannot resolve this issue here, but instead present two possible interpretations for the osteological condition observed in *Tyrannosaurus*.

Interpretation 1 (accepting Hypothesis 1) is that M. puboischiofemoralis internus 2 was present in *Tyrannosaurus* but modified from the ancestral condition as part of its transformation into Mm. iliotrochanterici cranialis and medius. In this case, the muscle had not yet achieved its derived origin on the ventrolateral surface of the preacetabular ilium, but occupied an intermediate position. In Crocodylia, M. puboischiofemoralis internus 2 originates from the lateral surfaces of the last six dorsal vertebral centra (Fig. 3). If M. puboischiofemoralis internus 2 was present in *Tyrannosaurus*, it does not seem to have retained this plesiomorphic arrangement. Indeed, the posterior dorsal centra resemble those of the anterior trunk in possessing large lateral pleurocoelous fossae rather than substantial surfaces for muscle attachment. However, the large space medial to the ventral preacetabular hook of the ilium may have been sufficient for both Mm. puboischiofemorales interni 1 and 2 origins, although there are no indications of a division within this space. Alternatively, at least one of these muscles could have shifted laterally onto the ilium, but, again, clear muscle scars are lacking.

The insertion of this muscle would have more closely resembled the condition in Neornithes than that in Crocodylia. In the latter, M. puboischiofemoralis internus 2 inserts on the anterolateral surface of the proximal femur, whereas in the former its presumed derivatives insert on the middle (M. iliotrochantericus medius) and distal (M. iliotrochantericus cranialis) surfaces of the femoral trochanteric crest. In *Tyrannosaurus* there is some segregation of the lesser trochanter into a proximal insertion (for M. iliotrochantericus caudalis; see above) and a distal accessory trochanter (for a second insertion; Hutchinson, 2001b) (Fig. 5). This second insertion point corresponds closely with those for Mm. iliotrochanterici cranialis and medius in Neornithes, and we suggest that it represents the

insertion of a single *M. puboischiofemoralis internus* 2 (= *M. iliotrochantericus cranialis* + *medius*) in *Tyrannosaurus*. This muscle would have passed dorsal and medial to the iliopubic ligament (which spanned the gap between the ventral preacetabular hook and the pubic tubercle; Hutchinson, 2001a) between its origin and insertion.

Interpretation 2 (accepting Hypothesis 2) is that *M. puboischiofemoralis internus* 2 was lost entirely in *Tyrannosaurus* but that an undivided *M. iliotrochantericus cranialis* + *medius* was present. In this scenario, *M. puboischiofemoralis internus* 1 (= *M. iliofemoralis internus*) alone would have occupied the undivided preacetabular fossa medial to the ventral preacetabular hook of the ilium. *M. iliotrochantericus cranialis* + *medius* (= part of *M. iliofemoralis*) originated from the ventrolateral preacetabular ilium, ventral to the *M. iliotrochantericus caudalis* origin and dorsal to the *M. iliofemoralis internus* origin. Although this origin is not clearly indicated by muscle scars, it would have been similar to the *Mm. iliotrochanterici cranialis* and *medius* origins in Neornithes (Fig. 3). From this point, *Mm. iliotrochanterici cranialis* + *medius* would have passed posteroventrally to insert onto the accessory trochanter below the *M. iliotrochantericus caudalis* insertion (see above). The position of the accessory trochanter, at the base of the lesser trochanter (and not on the anterolateral femur), additionally suggests that the muscle inserting here was derived from the primitive *M. iliofemoralis*.

Although these two interpretations differ in the homology assumptions that they adopt, both interpretations agree that a single muscle originating from the ilium inserted on the accessory trochanter, but disagree on the identification and precise origin (medial or lateral) of that muscle.

Flexor Cruris Group

The homologies of these muscles remain poorly resolved, but we proceed with Romer's (1942) scheme because it remains the best articulated. Five muscle heads are present in Crocodylia (and at least four in extant outgroups), whereas two main heads (and one accessory head, with a nebulous history) are present in Neornithes. Thus, this complex muscle group was reduced on the line to extant birds.

M. pubo-ischio-tibialis (PIT). *M. pubo-ischio-tibialis* is present in basal reptiles, reduced in Crocodylia, and absent in birds. Its origin in Crocodylia is on a muscle scar located on the proximal tip of the obturator process of the ischium (Fig. 3). In *Tyrannosaurus* there is no evidence of this muscle scar, so we infer the absence of this muscle.

M. flexor tibialis internus 1 (FTI1). *M. flexor tibialis internus* 1 originated on the posterodorsal ischium at the distal ischial tubercle (Hutchinson, 2001a) and inserted on the posterolateral surface of the proximal tibia. The distal ischial tubercle in

Tyrannosaurus resembles those of *Allosaurus* and many coelurosaurs in being more expansive and diffuse than in primitive theropods such as *Piatnitzkysaurus*. Here it appears as an elongate, roughened oval midway down the ischial shaft. If present, *M. flexor tibialis internus* 1 may have inserted onto a series of oblique ridges and furrows on the posterior proximal tibia, ending distally at a larger, slightly rugose ridge. However, although these origin and insertion scars are present in both theropods and crocodylians, many basal archosaurs lack them, and therefore the phylogenetic conclusions are ambiguous (Hutchinson, 2001a). We thus avoid the Level II' inference of reconstructing *M. flexor tibialis internus* 1 on *Tyrannosaurus*.

M. flexor tibialis internus 2 (FTI2). *M. flexor tibialis internus* 2 originated on the lateral ilium (posterior to *M. iliofemoralis*) in Crocodylia and inserted with *M. flexor tibialis internus* 1 and *M. pubo-ischio-tibialis* on the posterolateral tibia (Fig. 3). Romer (1942, *non* 1923a) considered this muscle to be a second head of the crocodylian *M. pubo-ischio-tibialis*. No scar is present on the lateral ilium of *Tyrannosaurus* and it is not clear whether this muscle was present (a Level II' inference).

M. flexor tibialis internus 3 (FTI3). *M. flexor tibialis internus* 3 ("ischioflexorius," "semimembranosus"; = *M. flexor cruris medialis*/FCM of birds) originates from the lateral surface of the ischial tuberosity in crocodylians. *M. flexor cruris medialis* of birds originates from a similar, albeit more distal, position (Fig. 3). The prominent ischial tuberosity likely marks its origin in theropods (Hutchinson, 2001a) and is indicated by an ovate, rugose scar on a proximal dorsal process of the ischium in *Tyrannosaurus* (Fig. 2). *M. flexor tibialis internus* 3 then inserted onto a rounded, slightly roughened area along the medial surface of the proximal tibia, as in extant archosaurs.

M. flexor tibialis internus 4 (FTI4). In basal tetrapods the *M. flexor tibialis internus* 4 is undivided from other parts of the flexor cruris group, whereas in Crocodylia it originates from ilioischiadic fascia and shares a common tendon with *M. flexor tibialis internus* 3 (hence leaving no muscle scars) (Fig. 3). *M. flexor tibialis internus* 4 is absent in Neornithes. As a result, the presence or absence of this muscle in *Tyrannosaurus* is equivocal (a Level II' inference), and we make no further inferences of it.

M. flexor tibialis externus (FTE). As in extant archosaurs, *M. flexor tibialis externus* ("caudilioflexorius," "semitendinosus"; = *M. flexor cruris lateralis pars pelvica*/FCLP of birds) originated on the lateral surface of the ilium, posterior to the *M. iliofibularis* and *M. iliofemoralis externus* origins (Fig. 3). It apparently occupied some of the lateral postacetabular process, but there are few marks to indicate its specific bounds. However, a faint semi-circular line anterior to the posterior edge of the

ilium in FMNH PR 2081 may mark the posterior extent of this muscle in *Tyrannosaurus* (Fig. 4). The insertion site for *M. flexor tibialis externus* was a tendon shared with *M. flexor tibialis internus 3*, as in extant archosaurs. There is no conclusive evidence bearing on the presence of a pars accessoria head as in birds, so we do not reconstruct one (a Level II' inference).

Mm. Adductores Femores

Two adductor muscles are inferred to have been present in *Tyrannosaurus*, as in crocodylians and birds. In general, these two thin muscle heads originate on the lateral surface of the ischium and insert on the posterior surface of the femur, running roughly parallel to one another between these two bones. Paul (1988) argued on functional grounds that it was unlikely that any muscles originated from the ischial shaft. Based on our dissections of extant taxa and observations of fossil material, we deem it likely that some hindlimb muscles (such as parts of Mm. adductores femores) had fleshy origins from the ischial shaft.

M. adductor femoris 1 (ADD1). This muscle (= *M. puboischiofemoralis pars medialis*/PIFM of birds) probably originated from the anteroventral surface of the ischium, on or near the obturator process in a position similar to that in extant archosaurs. However, the ischium shows little specific evidence of where such attachment might have occurred. Although there are strong ridges along the ventral ischium, these may have been correlated with the attachments for a puboischadic membrane (Hutchinson, 2001a). *M. adductor femoris 1* passed laterally and anteroventrally to insert on the posterior surface of the femoral shaft. The femur bears two distinct, oval attachment sites located on the medial and lateral edges of the posterior shaft surface (Figs. 3, 6), approximately two-thirds of the way towards the distal end. The medial site, more rugose than the lateral, is probably the insertion site for *M. adductor femoris 1*. A thin muscular line runs proximolaterally from this insertion area, probably indicating the attachment of a fascial sheet. These attachments are congruent with the those of extant archosaurs.

M. adductor femoris 2 (ADD2). The origin for *M. adductor femoris 2* (= *M. puboischiofemoralis pars lateralis*/PIFL of birds) was probably from a long scar on the posterior edge of the ischium, distal to *M. flexor tibialis internus 3* and the ischial tuberosity. Crocodylians have an identical origin; in birds the origin is more anteroventral, owing to the reduction of the obturator process and the movement of *M. ischiochantericus* onto the lateral surface of the ischium (see below). Like *M. adductor femoris 1*, *M. adductor femoris 2* ran ventrolaterally to insert on the posterior femur, but inserted on the second (lateral) rugosity. This site is approximately the

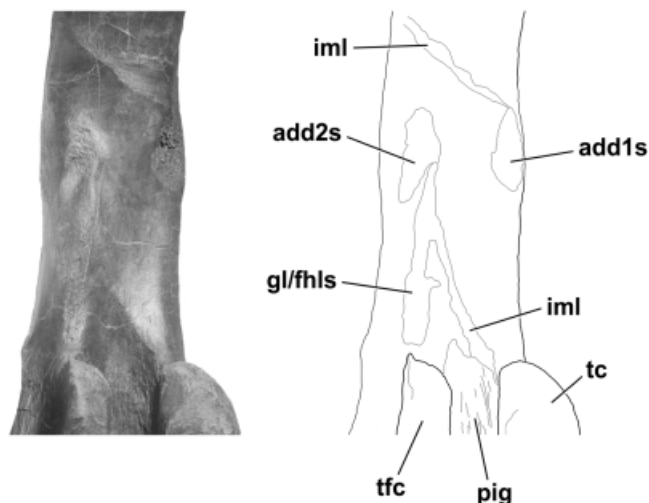


Fig. 6. Osteological correlates present on the posterior femur of *Tyrannosaurus rex*. Posterior view of the left femur, FMNH PR 2081. add1s, *M. adductor femoris 1* insertion scar; add2s, *M. adductor femoris 2* insertion scar; cfbf, *M. caudofemoralis brevis* insertion fossa; 4tr, fourth trochanter; gl/fhls, *M. gastrocnemius pars lateralis*/*M. flexor hallucis longus* origins scar; iml, intermuscular line. Photo courtesy of C. Brochu.

same size as the medial (*M. adductor femoris 1*) site, but is located slightly more distally and is proximally adjacent to a wide longitudinal muscular attachment that runs towards the fibular condyle (Figs. 3, 6). This may represent the origin of *M. gastrocnemius pars lateralis* and other muscles (see below).

Mm. Puboischiofemorales Externi

Basal reptiles have one poorly subdivided head of *M. puboischiofemoralis externus*, whereas crocodylians have three heads and birds have two (*Mm. obturatorii medialis*/OM et *lateralis*/OL). Hutchinson (2001a) and Hutchinson and Gatesy (2000) contended that the three *M. puboischiofemoralis externus* heads of Crocodylia are plesiomorphic for archosaurs, based on the presence of a long pubic apron in these taxa (see Table 2 for *Mm. puboischiofemorales externi* homologies). In extant archosaurs, the various *M. puboischiofemoralis externus* heads share a common insertion onto the lateral surface of the femoral greater trochanter (Hutchinson, 2001b), although in some extant archosaurs it may extend onto the posterolateral or posterior surface as well.

M. puboischiofemoralis externus 1 (PIFE1). The origin for *M. puboischiofemoralis externus 1* in *Tyrannosaurus* was located along the anteromedial surface of the pubic shaft and apron, as in Crocodylia (Fig. 3). Its insertion was onto the lateral surface of the greater trochanter of the femur; this rugose surface bears a series of longitudinal ridges and is distinct from the neighboring *M. iliofemoralis*

externus and *M. ischiotrochantericus* insertions (Fig. 5).

M. puboischiofemoralis externus 2 (PIFE2). The origin for *M. puboischiofemoralis externus* 2 was located along the posteromedial surface of the pubic shaft and apron, as in *Crocodylia* (Fig. 3). In *Tyrannosaurus*, faint longitudinal striations are visible on this surface that may indicate the attachment of this muscle. It shared a common insertion on the lateral greater trochanter with the other *M. puboischiofemoralis externus* components (Fig. 5).

M. puboischiofemoralis externus 3 (PIFE3). *M. puboischiofemoralis externus* 3 took its origin from the obturator process of the ischium, between the *Mm. adductores femores* 1 and 2 origins. Its origin is not clearly distinguishable but is consistent with its placement in crocodylians (Fig. 3). The retention of the obturator process in *Tyrannosaurus* suggests that *M. puboischiofemoralis externus* 3 was still present, rather than lost as in birds (Hutchinson, 2001a). *M. puboischiofemoralis externus* 3 shared a common insertion with the other *M. puboischiofemoralis externus* components onto the lateral surface of the greater trochanter (Fig. 5).

M. Ischiotrochantericus

In crocodylians and outgroups, *M. ischiotrochantericus* (ISTR) originates from the medial surface of the ischium, whereas in Neornithes its homolog (*M. ischiofemoralis/ISF*) has shifted its origin onto the lateral ischium and ilio-ischiadic membrane (Fig. 3). In *Tyrannosaurus*, *M. ischiotrochantericus* originated along the medial surface of the proximal ischium, medial to the *M. flexor tibialis internus* 3 origin. From this point it would have passed laterally over a notch between *M. flexor tibialis internus* 3 and the iliac peduncle, inserting onto the posterolateral surface of the proximal femur (Fig. 5). This insertion is adjacent to that for *M. iliofemoralis externus* and in a position topologically identical to that of extant archosaurs. In *Tyrannosaurus*, this region is highly rugose and bears several striations and bulges, and is separated from the *M. iliofemoralis externus* insertion by a smooth-surfaced gap.

Mm. Caudofemorales

M. caudofemoralis longus (CFL) represents the primary femoral retractor muscle of lepidosaurs and crocodylians (Gatesy, 1990), and its smaller counterpart *M. caudofemoralis brevis* (CFB) is likely important in hip extension as well. In birds, *M. caudofemoralis longus* (= *M. caudofemoralis pars caudalis/CFC*) is a small muscle with a reduced role in locomotion associated with the general avian reduction in femoral retraction (Gatesy, 1990). *M. caudofemoralis brevis* is not normally reduced in extant archosaurs. Both *Mm. caudofemorales* insert on the posterior surface of the femoral shaft, with *M. cau-*

dofemoralis longus usually slightly distal and medial to *M. caudofemoralis brevis* when both are present.

M. caudofemoralis brevis (CFB). In crocodylians and more basal reptiles, *M. caudofemoralis brevis* originates from the medial and (partly) lateral surfaces of the postacetabular ilium as well as the posterior sacral ribs. In birds, *M. caudofemoralis brevis* (= *M. caudofemoralis pars pelvica/CFP*) has lost its medial origin and is confined to the lateral iliac surface (Fig. 3). *M. caudofemoralis brevis* of *Tyrannosaurus* presumably originated mainly within the brevis fossa of the ilium, along its ventral edge posterior to the acetabulum (Figs. 2, 4; Russell, 1972; Hutchinson, 2001a). The fossa is deep but not as wide as in “ceratosaurs” and exhibits many parallel, longitudinal fiber lines within. This origin is thus intermediate between the ancestral (mostly medial) reptilian and derived (fully lateral) “avian” conditions. *M. caudofemoralis brevis* extended anteroventrally from the brevis fossa to insert on the posterolateral shaft of the femur, just lateral and slightly proximal to the raised portion of the fourth trochanter. It extended no further laterally than the posterior intermuscular line and no further distally than a transverse line situated approximately halfway down the shaft. The fourth trochanter itself has a complexly varied topography; at least two distinct attachment regions are evident (Fig. 3). The most elevated portion of the trochanter shows numerous ridges that would have paralleled the *M. caudofemoralis brevis* orientation suggested here.

M. caudofemoralis longus (CFL). As in extant crocodylians and lepidosaurs, *M. caudofemoralis longus* of *Tyrannosaurus* was probably the largest single muscle of the hindlimb. Although this muscle likely originated from the lateral faces of the first 15 caudal vertebrae, its precise size and extent are difficult to estimate. As a general guide, the transverse processes roughly indicate its minimum extent along the caudal series, with those vertebrae past the “transition point” (i.e., lacking transverse processes) lacking *M. caudofemoralis longus* (Gatesy, 1990). *M. caudofemoralis longus* would have passed anteroventrally to insert on the medial portion of the fourth trochanter (Fig. 3). This area is quite rugose and bears numerous small tubercles that presumably represent the attachments of Sharpey’s fibers. In more basal theropods, the raised fourth trochanter is often pendant, including a distally directed process that probably represents the attachment of a secondary tendon of *M. caudofemoralis longus* leading to the posterior knee joint (Dollo, 1888). The lack of such a process in *Tyrannosaurus* suggests that a secondary *M. caudofemoralis longus* tendon was reduced or absent, as is the condition in birds but not other reptiles (a Level II inference; Hutchinson, 2001b).

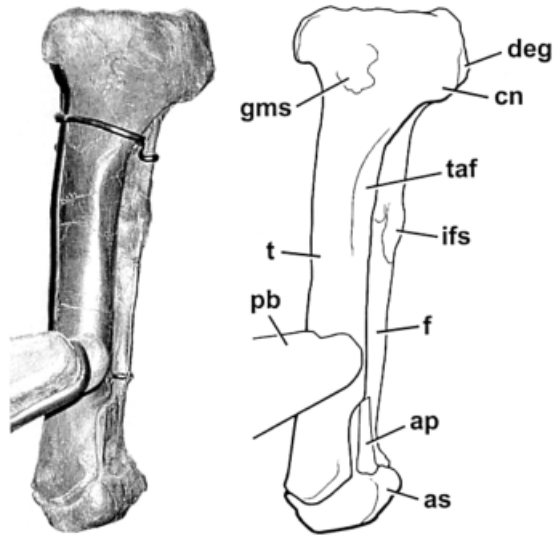


Fig. 7. Osteological correlates present on the tibia and fibula of *Tyrannosaurus rex*. Medial view of the right tibia and fibula, FMNH PR 2081 (reversed for comparison with Fig. 3). ap; ascending process; as, astragalus; cn, cnemial crest; deg, distal extensor groove; f, fibula; gms, *M. gastrocnemius pars medialis* origin scar; ifs, *M. iliofibularis* insertion scar; pb, pubic boot; t, tibia; taf, *M. tibialis anterior* origin facet. Photo courtesy of M. Loewen.

Mm. Gastrocnemii

***M. gastrocnemius pars lateralis* (GL).** As in extant archosaurs, this large muscle originated on the posterior distal femur along a rugose line that passed distally from the *M. adductor femoris* 2 insertion to the fibular condyle (Figs. 3, 6). *M. gastrocnemius pars lateralis* (= *M. gastrocnemius externus*/GE of crocodylians) inserted with *M. gastrocnemius pars medialis* via tendons onto the plantar surface of the pes, particularly an aponeurotic attachment to metatarsals I–V and the bases of their respective digits. Two prominent scars, located midway along the posterior surfaces of the shafts of metatarsals II and IV, mark the insertions of the gastrocnemius (Fig. 8), as in *Maiasaura* (Dilkes, 2000) and many other dinosaurs.

As with all other dinosaurs, *Tyrannosaurus* lacks any evidence of an ossified structure analogous to the calcaneal tuber of mammals. Unlike birds, *Tyrannosaurus* does not have a prominent ossified hypotarsus on the proximal metatarsus for the insertion of *M. gastrocnemius pars lateralis*; thus, it clearly had a muscle insertion intermediate between the ancestral (more distal) and derived (more proximal) condition. As Dilkes (2000) noted, the presence of the avian *M. gastrocnemius pars intermedia* (GIM) head is equivocal because nonbirds lack the muscle (probably a derivative of *M. gastrocnemius pars lateralis*) and it does not leave clear muscle scars in birds. Paul (1988) termed the proximal end of the metatarsus of many theropods a ‘hypotarsus’. We prefer to restrict use of this term to the relatively larger structure on the proximal tarsometatarsus of

many birds. Additionally, the insertion of *Mm. gastrocnemii* seems to have shifted proximally onto the ‘avian’ hypotarsus in basal birds when the more distal muscle scars were lost.

***M. gastrocnemius pars medialis* (GM).** *M. gastrocnemius pars medialis* (= *M. gastrocnemius internus*/GI of crocodylians) originated from the me-

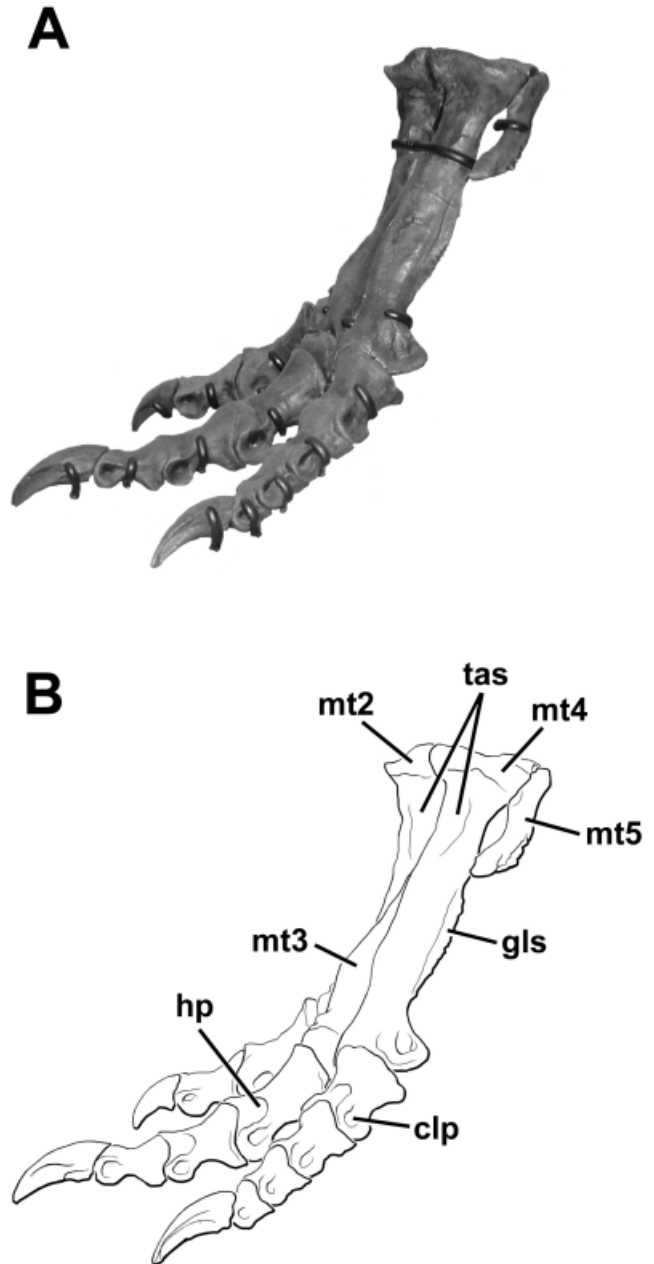


Fig. 8. Osteological correlates present on the ankle, metatarsus, and phalanges of *Tyrannosaurus rex*. Anterodorsolateral view of the left pes, FMNH PR 2081. clp, collateral ligament pit; ft, flexor tubercle; hp, hyperextensor pit (*M. extensor digitorum longus* insertion and ligament attachment); gls, *M. gastrocnemius pars lateralis* insertion scar; mt2, metatarsal II; mt3, metatarsal III; mt4, metatarsal IV; mt5, metatarsal V; tas, *M. tibialis anterior* insertion scars. Photo courtesy of M. Loewen.

dial surface of the proximal tibia, anteromedial to *M. flexor tibialis externus* and *M. flexor tibialis internus* 3 insertions, as in extant archosaurs (Figs. 3, 7). From this point it would have passed down towards the plantar surface of the pes, passing alongside the *M. gastrocnemius pars lateralis* tendon. As Tarsitano (1983) noted, the metatarsal II scar is where metatarsal I is often incorrectly articulated in mounted specimens of nonavian theropods. Instead, a faint, smooth facet located more proximally and laterally on the shaft of metatarsal II probably marks the proper articulation for metatarsal I. The fact that similar scars for the *M. gastrocnemius* insertion are present on the medial metatarsal II in nontheropod dinosaurs further weakens the inference that a retroverted hallux was positioned there. This morphology is intermediate between those of extant crocodylians and birds; in the former, the insertion is more diffuse with attachments to the plantar aponeurosis and metatarsal V; in the latter, it is concentrated on the hypotarsus. As the plantar aponeurosis and metatarsal V were lost in derived theropods (and especially basal birds), the *Mm. gastrocnemii* insertion was presumably focused proximally onto the hypotarsus.

Digital Flexor Group

***M. flexor digitorum longus* (FDL).** This muscle originated from the same general region as *M. gastrocnemius lateralis* and *M. flexor hallucis longus*, again consistent with the anatomy of extant archosaurs (Fig. 3). Although the boundaries of the origin are not clear, one or more additional origin(s) from the proximal tibia and/or fibula are probable given the expansion of the tibial crest, flexor fossa, and posteromedial surface of the fibula, all of which serve as partial origins for digital flexor heads in birds. *M. flexor digitorum longus* passed posterodistally around the ankle joint and separated into distinct flexors for digits II, III, and IV. Each of these tendons passed through the ventral groove in its respective metatarsal to insert serially on each of the pedal phalanges, especially the flexor tubercles of the unguis (Fig. 8).

The presence or absence of *M. flexor digitorum brevis* (FDB) cannot be determined in dinosaurs (a Level II' inference) because birds lack the muscle and muscle scars are unclear in other taxa (Dilkes, 2000). For similar reasons, we cannot determine when the multitude of avian subdivisions of *M. flexor digitorum longus* (*Mm. flexores perforati digitorum* II, III, et IV; *Mm. flexores perforans et perforati digitorum* II et III) evolved, but at least one head of *M. flexor digitorum longus* was present in *Tyrannosaurus*.

***M. flexor hallucis longus* (FHL).** *M. flexor hallucis longus* originated from the same rugose line on the posterodistal femur as *M. gastrocnemius lateralis* (Figs. 3, 6), as in extant archosaurs. It passed

distally to insert on the ventral surfaces of the phalanges and unguis of digit 1.

Digital Extensor Group

***M. extensor digitorum longus* (EDL).** Although Dilkes (2000) noted some confusion over the evolution and homology of this group and *M. tibialis anterior*, we follow the classical nomenclature for these muscles until homologies are better established. The extent and specific origins of *M. extensor digitorum longus*—including whether it attached to the anteromedial fibular flange discussed above (see *M. iliobtibialis*)—remain unclear (Level II' inference). In basal reptiles the origin is from the anterior surface of the lateral femoral condyle, whereas in birds it is from the anteromedial surface of the tibial crest. Therefore its origins can be confidently reconstructed only as the anterior region of the knee joint; Figure 3 shows two possible origins from the femur (EDLF) or tibia (EDLT). *M. extensor digitorum longus* passed down the anterior side of the tibial shaft over *M. tibialis anterior* and then under a retinaculum near the ankle joint (Fig. 3). “Hyperextensor pits” and other rugosities on the dorsal surfaces of the pedal phalanges (Fig. 8) suggest that (like birds) the insertion of the muscle was more distal in *T. rex* than in basal reptiles. Thus, these pits served as muscular (and ligamentous) attachment sites, not solely to provide “room” for the dorsal process of the subsequent phalanx during hyperextension (e.g., Welles, 1984:130).

***M. extensor digitorum brevis* (EDB).** Dilkes (2000) noted that *M. extensor digitorum brevis* originates from the tarsals in nonavian taxa and inserts on the distal phalanges, but is absent in birds (Fig. 3). Thus, reconstructing it in *Tyrannosaurus* is a Level II' inference, which we avoid. An attractive hypothesis for future consideration (intimated by Dilkes, 2000) is that *M. extensor digitorum brevis* became fused to the distal end of *M. extensor digitorum longus* in *Tyrannosaurus* and other dinosaurs, transferring the ancestral insertion of the latter muscle from the proximal metatarsals to the phalanges.

***M. extensor hallucis longus* (EHL).** In crocodylians and lepidosaurs the small *M. extensor hallucis longus* originates from the anterior surface of the distal fibula, whereas in birds it originates from the anteromedial surface of the proximal tibia (correlated with a reduction of the distal fibula) (Fig. 3). In extant taxa (and presumably in *Tyrannosaurus*), the muscle ultimately inserts on the dorsal surface of the hallux unguis. We reconstruct its origin on the distal fibula in *Tyrannosaurus* because the fibula is not strongly reduced and still has a firm connection with the tarsus (Level II inference).

Other Lower Leg Muscles

M. tibialis anterior (TA). Basal reptiles had only one head of this muscle, whereas birds have two (M. tibialis cranialis/TC). Therefore the number of heads in *Tyrannosaurus* is ambiguous (Level II' inference), which is further complicated by the confused homologies of this muscle and M. extensor digitorum longus. However, its origin is less ambiguous (Level I inference), presumably being on the anterior tibia between the anterior and lateral muscular lines (Fig. 3). In *Tyrannosaurus*, this origin is indicated by the presence of slight texturing within these bounds (Fig. 7). If there was a second head it would have originated on the anterior surface of the lateral femoral condyle (Level II' inference), which we do not reconstruct. In birds the M. tibialis cranialis origin is largely restricted to the cnemial crest of the tibia, and because the crest is fairly large in *Tyrannosaurus*, that restriction may have at least partly been present. However, as with M. extensor digitorum longus, the specific boundaries of this muscle remain somewhat unclear. After passing through the extensor retinaculum shared with M. extensor digitorum longus, M. tibialis anterior then inserted onto marked processes on the proximal anterior shafts of metatarsals II (anterolateral edge), III (anterior surface), and IV (anteromedial edge) (Fig. 8), as in *Maiasaura* (Dilkes, 2000) and other dinosaurs. The process on metatarsal II is the most prominent, more closely resembling the condition in Neornithes rather than Crocodylia, although the M. tibialis anterior/cranialis insertion is normally concentrated medially in archosaurs.

M. popliteus (POP). In crocodylians and lepidosaurs, M. popliteus (sometimes called M. interosseus cruris; Tarsitano, 1981) originates from much of the anterior surface between the (broadly separated) tibial (laterally) and fibular (medially) shafts (see Cong et al., 1998) (Fig. 3). In contrast, in birds this muscle is restricted to the medial surface of the proximal fibula and the posterolateral surface of the proximal tibia. Given the close approximation of these bones in *Tyrannosaurus* (and other tetanurans), M. popliteus was likely restricted (relative to the primitive condition) to the region proximal to the fibular crest. Thus, the muscle would have originated from the lateral surface of the proximal tibia, posterior to the fibular crest, and inserted within the expansive medial fossa of the proximal fibula (as noted by Farlow et al., 2000). In *Tyrannosaurus*, this region is marked by a flat, ridged surface that faces posterolaterally. The distal portion of this muscle (often called M. interosseus cruris) was reduced or ligamentous, based on the reduction of the fibular shaft distal to the fibular crest of the tibia, but not entirely lacking as in birds.

Mm. fibulares (= peronei) longus et brevis (FL, FB). In most taxa Mm. fibulares longus et brevis originate from the anterolateral surface of the

fibular shaft and parts of the tibia (see Dilkes, 2000), with M. fibularis brevis slightly lateral and distal to M. fibularis longus (Fig. 3). The origins begin just distal to the M. iliofibularis insertion, and faint striations are present along the anterolateral edge of the fibula in *Tyrannosaurus* in this position. Although the extent of these origins is difficult to determine for *Tyrannosaurus*, they likely occupied similar positions. Considering data from extant taxa, M. fibularis longus would have inserted on the posterolateral surface of the ankle joint, possibly including the rugose area on metatarsal V as well as the calcaneum, whereas M. fibularis brevis inserted on the anterolateral surface of the proximal metatarsus and distal tarsus.

DISCUSSION

Comparisons With Previous Reconstructions

For 75 years, Romer's (1923c) reconstruction of the hindlimb musculature of *Tyrannosaurus rex* has remained the standard against which newer reconstructions have been compared. Few authors have emended, altered, or provided detailed alternatives to Romer's (1923c) hypotheses. Walker's (1977) extensive study on archosaurian pelvic and hindlimb evolution is a notable exception, as it includes pointed criticisms of several of Romer's (1923c) claims. Although Tarsitano (1981, 1983) critiqued both these efforts, in general his results are quite similar to Romer's (1923c). Regardless, all three authors share the tendency to "map" crocodylian muscles onto the saurischian skeleton, shying away from the use of avian data in their reconstructions. This is predicated on the suppositions that the dinosaurian hindlimb retains more similarities to crocodylians than to birds and that the crocodylian hindlimb is an entirely accurate reflection of the common archosaurian ancestral condition. We focus this discussion on the three most elaborate studies of theropod myology—Romer (1923b,c), Walker (1977), and Tarsitano (1981, 1983) (Fig. 9)—reserving comments on other reconstructions for our final discussion.

Romer (1923b,c) (Fig. 9A). It was not possible for us to conservatively reconstruct the thigh musculature of *Tyrannosaurus* to the level of detail shown by Romer (1923b,c). Romer admitted that there was insufficient evidence to reconstruct many aspects of the thigh musculature but did so nevertheless, claiming that (1923c: 612) "the crocodylian arrangement has been followed as being most probable in view of the close similarity in all known points." This view is defensible in some cases (e.g., the locations of the M. ambiens and M. flexor tibialis internus 3 origins), but we consider it viable only if supported by character optimization (in this study, Level II or better inferences). Character optimization must not only consider anatomical data from extant taxa, but osteological data from extinct taxa

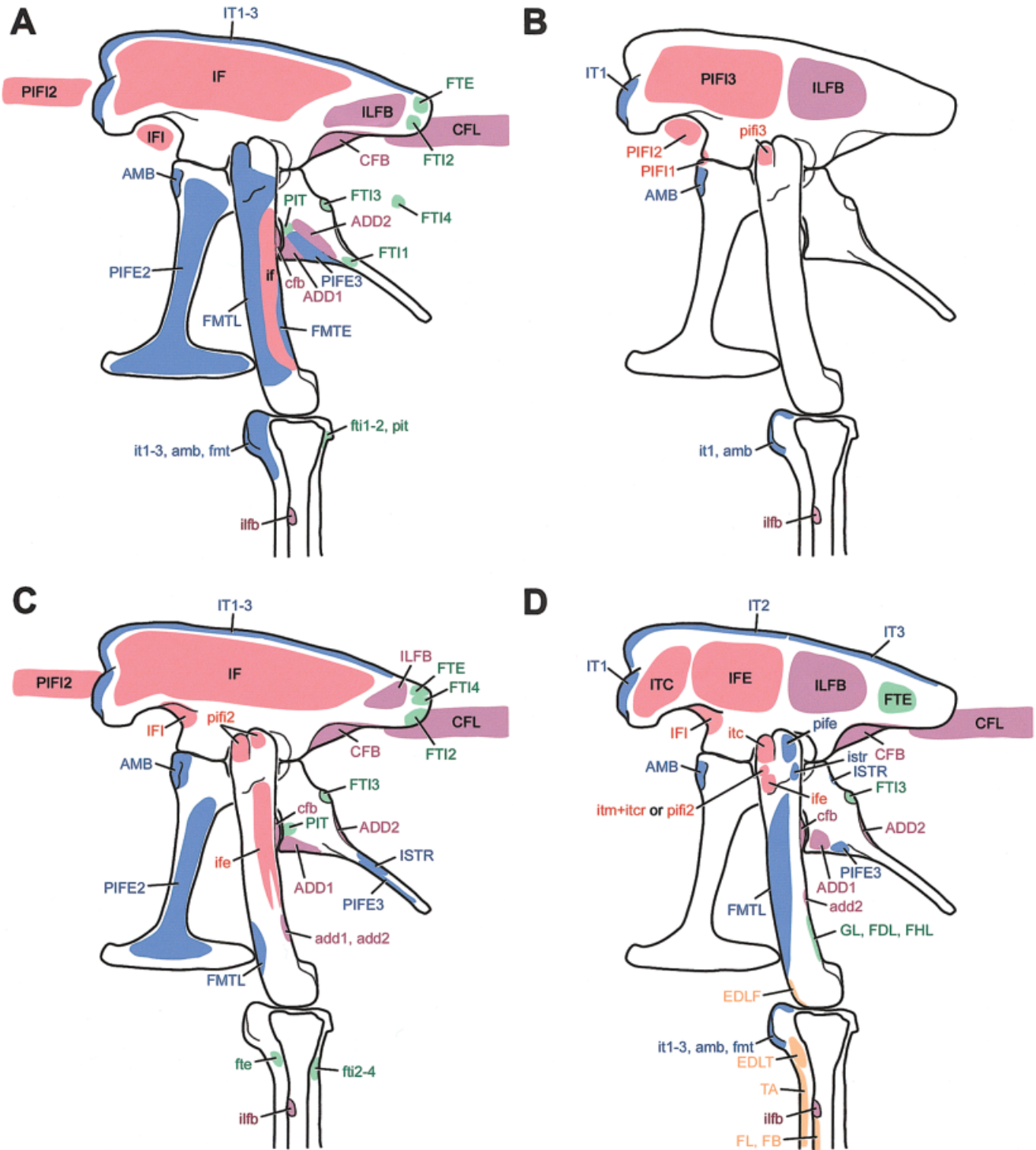


Fig. 9. Current and previous reconstructions of the pelvic and hindlimb muscles in *Tyrannosaurus rex*. All reconstructions are in left lateral view; **A**, **B**, and **C** have been modified from the original illustrations. **A**: Romer, 1923c. **B**: Walker, 1977. **C**: Tarsitano, 1981, 1983. **D**: Present reconstruction. Note that several authors did not choose to reconstruct many of the pelvic and hindlimb muscles; these have been omitted from the reconstructions. Abbreviations as in Table 1; colors as in Figure 3.

as well; such data do not support some of Romer's conclusions.

For example, it is not evident that the flexor cruris muscles of *Tyrannosaurus* were identical to those of

Alligator. Romer (1923c: 610) admitted that *M. flexor tibialis internus 4* cannot be discerned on sau-rischian bones because it originates from soft tissue in *Crocodylia*, but he reconstructed it in *Tyranno-*

saurus anyway, even though this muscle is absent in Neornithes. This presumes that *M. flexor tibialis internus 4* is not an autapomorphy of Crocodylia (a Level II' inference).

In addition, we have not located any muscle scars that might correspond to the *M. pubo-ischio-tibialis* origin in archosaur outgroups. Indeed, it is not apparent even in *Tyrannosaurus*, contrary to Romer's (1923c: 611; also see Tarsitano, 1981, 1983) suggestion. In order to support Romer's contention, it is necessary to demonstrate that *M. pubo-ischio-tibialis* muscle scars are shared first by *Alligator* and *Tyrannosaurus*, and preferably by archosaurian taxa between (or even outside) them. This would constitute evidence of homology for these muscle scars (at least Level II inferences). Because extant birds lack such features, we cannot substantiate the status of these components of the flexor cruris muscle group as archosaurian synapomorphies.

Another clear exception to Romer's assumption is the presence of two heads of *M. ambiens*, which optimizes as a crocodylian autapomorphy (convergent with a few taxa within Squamata and Neornithes). Reconstructing both *M. ambiens 1* and *2* on *Tyrannosaurus* is a Level III' inference; reconstructing a single *M. ambiens* head is a Level I inference; the location of its origin is a Level I inference.

Hutchinson (2001a) contended that the presence of *M. puboischiofemoralis externus 1* is a common archosaurian feature. Romer (1923c: 611) dismissed this possibility because noncrocodylian archosaurs seemed to him to lack a robust posterior gastralium for the insertion of *M. rectus abdominus*, and thus were not specialized enough to possess *M. puboischiofemoralis 3*. However, the differences among the posterior gastralia of archosaurs are not so striking that the insertion of *M. rectus abdominus* on the gastralia and anterolateral surface of the distal pubes ("pubic boot") can be ruled out. In fact, the preserved attachment of the gastralia to this region in many archosaurs allows the inference that *M. rectus abdominus* did attach there, far distal to *M. ambiens* (Russell, 1972; Perle, 1985). This leaves sufficient space for *M. puboischiofemoralis externus 1* to pass between the attachments of *M. ambiens* and *M. rectus abdominus*. Furthermore, the expansive anterior and posterior surfaces of the pubic apron in all archosaurs (lost in ornithischian dinosaurs and ornithurine birds) offer sufficient space for the origins of *M. puboischiofemoralis externus 1* (anteriorly) and *2* (posteriorly).

Romer's placement of the origins of *M. adductores femores 1* and *2* is also subject to reconsideration. Romer (1923c: 611) stated that the origin of *M. adductor femoris 1* was indicated by scarring, whereas the location of *M. adductor femoris 2* had to be inferred from the positions of other muscles. Our analysis supports the opposite hypothesis. A scar is present on the posterodorsal surface of the ischium, distal to the ischial tuberosity (the *M. flexor tibialis*

internus 3 origin) and bounded anteriorly by a proximodistal ridge along the lateral ischium. The scar is an archosaurian synapomorphy (Hutchinson, 2001a) and is present in *Tyrannosaurus*. It is the origin of *M. adductor femoris 2* in *Alligator*; thus, reconstructing that muscle in *Tyrannosaurus* is a Level II inference. We have not seen a well-defined scar for the *M. adductor femoris 1* origin in any archosaur, but reconstructing this origin on the obturator process of the ischium is a Level I' inference. One or two muscle scars for the insertions of *M. adductores femores 1* and *2* are on the posterior surface of the distal femoral shaft in most archosaurs, including tyrannosaurids, so the *M. adductores femores 1* and *2* insertions are Level I inferences.

A formal phylogenetic context reveals other problems with Romer's reconstruction. First, Romer (1923c: figs. 6, 7) reconstructed the insertions of *M. puboischiofemoralis internus 2* and *M. ischiotrochantericus* within the hip joint (on the dorsal surface of the proximal femur), unlike in extant archosaurs. Placing the insertions lateral to the hip joint, i.e., on the lateral surface of the proximal femur, is a Level I inference (Hutchinson, 2001b). Thus the simplest inference (Level II) is that the *M. ischiotrochantericus* insertion shifted proximal to the trochanteric shelf and the *M. puboischiofemoralis internus 2* insertion was on the accessory trochanter.

Second, Romer showed no muscles inserting on the lesser trochanter. Walker (1977) and others (Gregory and Camp, 1918; Russell, 1972 partim; Raath, 1977; Barsbold and Perle, 1979 partim; Perle, 1985) argued cogently that the *M. iliofemoralis* muscle group inserted proximally on the lesser trochanter, not distally on the femoral shaft as Romer (1923c) illustrated (again, Romer assumed complete similarity with Crocodylia). Reconstructing a more proximal *M. iliofemoralis* insertion is also more congruent with neontological and paleontological data. Neornithine birds have at least two *M. iliofemoralis* components: one proximal (*M. iliotrochantericus caudalis*) that inserts in a position corresponding to the lesser trochanter, and one distal (*M. iliofemoralis externus*) that inserts in a position corresponding to the trochanteric shelf (Hutchinson, 2001b). Fossil data from ornithodirans (including basal birds) reveal that at least one muscle attached to the lesser trochanter and moved proximally with it, whereas another muscle reduced with the trochanteric shelf (Hutchinson, 2001b). Thus, the simplest inference (Level II) is that *M. iliotrochantericus caudalis* shifted proximally with the lesser trochanter, whereas *M. iliofemoralis externus* remained in its plesiomorphic position on the trochanteric shelf.

Third, Romer (1923c) placed only the origin of *M. femorotibialis externus* on the lateral surface of the greater trochanter. Hutchinson (2001b) demonstrated that the greater trochanter of archosaurs

(including *Crocodylia* and *Neornithes*) is the insertion of *M. puboischiofemoralis externus*. Romer (1923c: figs. 6–8) showed these muscles inserting on the medial surface of the femur, proximal to the fourth trochanter. No muscle scars are present in that position, whereas scars are preserved on the lateral surface of the greater trochanter, in the same topological position as the *M. puboischiofemoralis externus* insertion in extant archosaurs (a Level I inference). In extant archosaurs, *M. femorotibialis externus* does not originate from the lateral surface of the greater trochanter (*sensu stricto*), nor does a bursa occupy that surface (Hutchinson, 2001b). Confusion about the identity and significance of the greater trochanter has persisted because a phylogenetic context has not been carefully applied. Fossils reveal that the proximal femur rotated 45° medially (Carrano, 2000) in tetanuran theropods, bringing the greater trochanter laterally (Hutchinson, 2001b). Birds inherited this state, and basal birds (except *Archaeopteryx*) combined the lesser and greater trochanters into a trochanteric crest.

Walker (1977) (Fig. 9B). Walker's complex treatise on archosaurian hindlimb anatomy deserves careful consideration (Fig. 5F), particularly because it includes several interesting conclusions about the anatomy of *M. puboischiofemoralis internus* and *M. iliofemoralis*. Walker (1977: 321–326, 342–343) made a complex argument about the arrangement of the heads of *M. puboischiofemoralis internus*, disputing Romer's (1923a,b,c) hypothesis that its origins had shifted dorsally in all archosaurs. Walker's alternative hypothesis hinges on his assertion that the pubic tubercle ("processus lateralis pubis") in basal saurians is homologous with the rugose anterolateral edge of the distal pubes in archosaurs. He contended that, because *M. puboischiofemoralis internus* 1 ("pars ventralis") passes above this point in squamates, this muscle head must also have been present ancestrally in archosaurs, including theropods (a Level III inference). Walker proposed that the "pars ventralis" was lost in crocodylians, ornithischians, and birds in conjunction with modifications of their pubes. Available evidence does not support this hypothesis (Hutchinson, 2001a), but rather supports the hypothesis that *M. puboischiofemoralis internus* 1 originated from the anterior surface of the pubes in *Tyrannosaurus* and other archosaurs (a Level II inference).

Walker (1977: 327–330) also made a strong case against reconstructing the insertion of deep dorsal thigh muscles on the dorsal (proximal) surface of the greater trochanter, because it is certainly an articular surface within the hip joint. He reconstructed the insertion of *M. puboischiofemoralis internus* 2 ("pars dorsalis") in a depression on the lateral surface of the proximal femur. This depression is the insertion of a hip joint ligament, not a muscle, in extant nonavian Sauria. It was strongly reduced in dinosaurs (including birds) as the proximal femur

rotated medially (see above). Walker also presented functional arguments for his reconstruction of *M. puboischiofemoralis internus* 1 ("pars ventralis"), but these are not sustained by independent evidence.

Walker made additional points about the anatomy of *M. iliofemoralis*. His (1977: 334, 344) criticism of the large size of Romer's (1923a,b) reconstructed *M. iliofemoralis* relative to *M. iliofibularis* is difficult to test either way (see Romer, 1923a,b, and Resolved and Unresolved Controversies, below). Finally, Walker (1977: 330–335) advocated reconstructing the insertion of *M. iliofemoralis* on the lateral surface of the lesser trochanter. As stated previously, we support this as a Level II inference.

Tarsitano (1981, 1983) (Fig. 9C). Tarsitano (1981: 68–71) made a convincing argument on phylogenetic and anatomical grounds that *M. puboischiofemoralis internus* 1 ("pars ventralis") did not originate from the anterior surface of the pubic apron in archosaurs. His placement of this origin at least partly within the preacetabular iliac fossa (Rowe, 1986; Hutchinson, 2001a) is supported as a Level II inference. However, the crocodylian insertion of *M. puboischiofemoralis internus* 1 is not into the depression medial to the fourth trochanter (*M. caudofemoralis longus* actually inserts there) and *Mm. femorotibiales* probably were not restricted to a small distal head (see Hutchinson, 2001b). Furthermore, *M. puboischiofemoralis externus* presumably inserted on the greater trochanter, not near the fourth trochanter. Our analysis does support Tarsitano's (1981) case that the division of the crocodylian *M. ambiens* into two heads is autapomorphic.

We cannot, however, replicate some of the detailed anatomical information that Tarsitano cited, including attachment scars for several muscles, particularly a *M. iliofemoralis* insertion on the anterolateral surface of the femoral shaft, or the exact origins and sizes of *M. flexor tibialis externus* and *M. ischiotrochantericus*. These putative scars are not present on the five theropod specimens examined by Tarsitano or any other noncrocodylian fossils that we have studied. Like Romer (1923b,c), Tarsitano defaulted to reconstructing crocodylian anatomy on *Tyrannosaurus* when direct evidence was lacking. He cited data on avian myology but curiously found little similarity between *Tyrannosaurus* and birds.

Like most other authors, Tarsitano dismissed the possibility of the origin of *M. puboischiofemoralis externus* 1 from the anterior surface of the pubic apron, contending that: 1) muscle scars are absent in that region, 2) crocodylian pubes are unusual, and 3) a *M. puboischiofemoralis externus* 1 origin from the pubes would interfere with the attachments of *M. rectus abdominus* and *M. obliquus abdominus*. However, 1) muscle scars are not present at the origin of the crocodylian muscle either, 2) the differences between crocodylian and tyrannosaurid pubes do not require radical differences in muscle origins,

and 3) the abdominal muscle attachments need not preclude a *M. puboischiofemoralis externus 1* pubic origin. *M. rectus abdominus* probably inserted on the pubic boot, in a position topologically equivalent to that in extant archosaurs (Hutchinson, 2001a). *M. obliquus abdominus* could have attached distally on the lateral pubis and proximally at the pubic tubercle, leaving open a proximal exit for *M. puboischiofemoralis externus 1* (as in Crocodylia; Romer, 1923a). Furthermore, the similarities among basal archosauriform pubic aprons (see Romer, 1923a,c; Hutchinson, 2001a) are consistent with similar origins of *Mm. puboischiofemorales externi 1* and *2* in archosaurs ancestrally.

**Resolved and Unresolved Controversies:
Ambiguity of Evidence**

Controversies on saurischian thigh musculature are often more implicit than explicit: few authors cite alternative hypotheses for their reconstructions, or present them in a manner that permits testing of alternatives. These considerations are important because osteological and soft-tissue evidence do not provide unambiguous resolution of all (or even most) aspects of archosaurian hindlimb evolution. When, as here, phylogeny provides the framework upon which inferences of soft-tissue morphology are made, it too must be presented as a component of the argument. Ultimately, only when arguments are rendered explicit can they be directly addressed. Our reconstruction attempts to resolve several persistent controversies, but also deliberately avoids drawing conclusions where the available evidence remains too ambiguous.

We address six specific controversies (Table 2): 1) What muscle(s) attached to the lesser trochanter? 2) What soft tissue(s) attached to the greater trochanter? 3) Was *M. puboischiofemoralis externus 1* or *M. puboischiofemoralis internus 1* (vide Romer, 1923a,b,c; = “pars ventralis” of Walker, 1977) present on the anterior surface of the pubes? 4) How many major parts did *M. puboischiofemoralis internus* have, two or three? 5) What are the relative sizes and extents of *M. iliofemoralis* and *M. iliofibularis*? and 6) Which of the *Mm. iliotrochanterici* are present, and what primitive muscles were they derived from? The proposed reconstruction of *Tyrannosaurus* resolves the first four of these controversies (also see Hutchinson and Gatesy, 2000; Hutchinson, 2001a,b) as follows.

1) We concur with Walker (1977) that the lesser trochanter was the insertion of at least part of *M. iliofemoralis* (specifically, *M. iliotrochantericus caudalis*). The homology of the lesser trochanter with the trochanteric crest of birds (and part of the trochanteric shelf of primitive theropods), and the attachment of *M. iliotrochantericus caudalis* to this structure, supports this argument. This is contra Tarsitano (1981, 1983), Rowe (1989), Dilkes (2000),

and others, who place *M. puboischiofemoralis internus 2* in this location.

2) This analysis reveals that the lateral surface of the greater trochanter was the insertion of *Mm. puboischiofemorales externi 1* and *2*, as in extant archosaurs. Again, this agrees neither with Russell (1972) and Dilkes (2000), who place *M. iliofemoralis externus* in this position, nor Walker (1977) and Tarsitano (1981, 1983), who place *M. puboischiofemoralis internus* there.

3) *M. puboischiofemoralis externus 1* presumably originated from the anterior surface of the pubic apron in archosaurs ancestrally (retained by Crocodylia). No previous authors have advocated this view, whereas some (especially Russell, 1972, and Walker, 1977) have reconstructed an *M. puboischiofemoralis internus* “ventralis” origin from this region.

4) Finally, in *Tyrannosaurus* and other theropods, *M. puboischiofemoralis internus* had two major parts (as in all archosaurs; Rowe, 1986) (see Table 2 and Figs. 2–4). *M. puboischiofemoralis internus 1* presumably originated from the preacetabular (“cuppedicus”) fossa of the ilium (Level II inference); the location of the *M. puboischiofemoralis internus 2* origin is more uncertain (Level II’ inference). Other authors, such as Russell (1972) and Walker (1977), came to different conclusions because they did not use explicit phylogenetic methodology.

Controversy (5), regarding the relative sizes and extents of *M. iliofemoralis* and *M. iliofibularis*, remains unresolved because known fossil theropods retain little muscle scarring on the lateral iliac surface. In particular, although the anterior edge of *M. iliofemoralis externus* and the posterior edge of *M. iliofibularis* are potentially delineated, the demarcation between the two is not. One possibility for resolving this issue would be if the median vertical ridge on the lateral iliac surface of birds and more basal theropods (e.g., tyrannosaurs) was shown to be homologous (Hutchinson, 2001a). In that case, the origin of *M. iliofibularis* would have been just caudal to the ridge (as in Neornithes), and the origins of the deep dorsal thigh muscles (including *M. iliofemoralis*) would have been anterior. Thus, *M. iliofemoralis* would not have been as expansive as Romer (1923b,c) and others thought. Nonetheless, the relative sizes of these and other dorsal thigh muscles currently remain vague. The lateral surface of the ilium is subdivided into preacetabular and postacetabular concavities in Eumaniraptora (Hutchinson, 2001a), so presumably *M. iliofemoralis externus* and *M. iliotrochantericus caudalis* were already in their derived anterior “neornithine” positions and the *M. iliofemoralis* group was subequal in size to *M. iliofibularis*.

Controversy (6) also remains unresolved, but we have been able to clarify certain aspects of this issue. Although we cannot determine the precise homologies of *Mm. iliotrochanterici medius* and *cranialis*,

evidence from *Tyrannosaurus* suggests that only a single, common *M. ilioprochantericus medius* + *cranialis* was present. It apparently inserted onto the accessory trochanter, but its origin (either on the ventrolateral preacetabular ilium or medial to the ventral preacetabular hook) remains unclear. Nevertheless, whether derived from the primitive *M. iliofemoralis* or *M. puboischiofemoralis internus* 2, this muscle reflects a derived condition relative to that of more primitive archosaurs. The implications of its appearance cannot be fully addressed, however, without determining the primitive muscle from which it was derived.

Functional and Evolutionary Implications

Tyrannosaurus rex is frequently hailed as the largest known terrestrial biped and, indeed, comparably large theropods from different lineages (e.g., carcharodontosaurids, spinosaurids, and allosaurids) never significantly exceeded the maximum size attained by *T. rex*. Its bipedalism was inherited from the primitive dinosaurian condition, but received considerable modification in several subsequent in-group clades. These modifications often appear in parallel, suggesting similar mechanical effects with regard to locomotion (Carrano, 2000; Farlow et al., 2000; Hutchinson and Gatesy, 2000).

Tyrannosaurus exemplifies several of these modifications. The ilium is considerably expanded anteriorly and posteriorly over the condition seen in such primitive theropods as *Herrerasaurus*, *Staurikosaurus*, and *Eoraptor*. As reconstructed here, these portions of the ilium represent the origins of several muscles that could flex, extend, or mediolaterally rotate the hip and knee joints (*Mm. iliopropiales* 1–3, *M. ambiens*, *M. iliofemoralis externus*, *M. ilioprochantericus caudalis*, *M. ilioprochantericus medius* + *cranialis*/*M. puboischiofemoralis internus*, *M. caudofemoralis brevis*, *M. iliofibularis*, and *M. flexor tibialis externus*) (Fig. 3). These muscles would have enjoyed a significant anteroposterior extension of their sizes and their lines of action relative to primitive theropods (Novas, 1992, 1996; Carrano, 2000). The increased capacity of these muscles to flex and extend the knee joint may document an increase in the role of lower limb flexion during locomotion, a trend that continues into higher levels of coelurosaur phylogeny (Gatesy, 1995; Carrano, 1998a,b). Expansion of these muscles would also increase their moment arms for hip extension, reflecting a greater capability to generate muscle moments about the hip in order to control hip flexion or retract the femur during locomotion.

It may be significant that the presence of a distinct, raised lesser trochanter commonly occurs in lineages along with anterior expansion of the ilium (Carrano, 2000; Hutchinson, 2001a,b). This supports the inference that elaboration of the primitive *M. iliofemoralis* into *M. iliofemoralis externus*, *M.*

ilioprochantericus caudalis, and perhaps *M. ilioprochantericus medius* + *cranialis* was implicated in both these changes, perhaps related to changes in muscular mechanisms used to support the body during stance (Hutchinson and Gatesy, 2000). Similarly, the adductor complex in *Tyrannosaurus* is modified over the primitive dinosaurian and theropod conditions. Much of the flexor cruris complex was reduced to emphasize posterior muscles, whereas *Mm. adductores femores* 1 + 2 had shifted posteriorly relative to the hip joint, reducing the capacity of the hindlimb muscles to adduct the hip while increasing their capacity as hip extensors (Hutchinson and Gatesy, 2000).

We have also noted some cases in which the lower leg musculature of *Tyrannosaurus* appears to be more derived than the inferred ancestral condition for archosaurs, and thus closer to the avian condition. It is important to note that *Tyrannosaurus* resembles many other theropods and dinosaurs in this regard (Carrano, 2000; Hutchinson, 2001a,b). As a result, although our reconstruction details one specific taxon, it should not necessarily be inferred that *Tyrannosaurus* was the only, or even the first, taxon to evolve these features. The derived conditions present in *Tyrannosaurus* include increases in the sizes and moment arms of several muscles that act about the ankle and pedal joints. For example, the large tibial cnemial crest of *Tyrannosaurus* is correlated with expansions of knee extensors (e.g., *M. iliopropialis*, *M. ambiens*) and several lower leg muscles (e.g., *M. extensor digitorum longus*, *M. tibialis anterior*) and there is evidence for shifts in the insertions of the *M. gastrocnemius pars lateralis*, *M. gastrocnemius pars medialis*, and *M. tibialis anterior* to more derived positions (Fig. 2). The reduction of the plantar aponeurosis and the expansion of the flexor tubercles and extensor attachments on the pes are also likely correlated with the evolution of digitigrady, bipedalism, erect posture, and perhaps changes in lower limb kinematics as well. Reduction of the fibula reflects the increased consolidation of the lower limb (Farlow et al., 2000) as well as changes in lower leg muscle origins, such as the proximal restriction of *M. popliteus*. These changes probably signal a restriction of nonparasagittal motion of joints within the lower limb, such as movement of the fibula relative to the tibia or complex intratarsal motion.

Furthermore, the dominance of knee flexion/extension over hip flexion/extension in avian locomotion (Gatesy, 1990, 1995; Carrano, 1998a,b; Carrano and Biewener, 1999) can potentially be tied to enlargement of the knee flexor muscles. This appears to be associated with posterior iliac expansion and therefore was apparently under way well before the evolution of *Tyrannosaurus*. However, the presence of significant femoral protractors and retractors in this taxon suggests that knee flexion/extension was well developed, but not at the expense of hip flexion/

extension; enlargement of the knee extensors seems to have evolved concomitant with an increase in hip flexion capacity. Subsequent reduction in hip flexion/extension apparently occurred in coelurosaurs even more derived than *Tyrannosaurus* (Gatesy, 1990, 1995; Carrano, 1998a,b).

This reconstruction clarifies much of the muscular anatomy at one point along the evolutionary transition between basal archosaurs and birds. By documenting a unique combination of characters in *Tyrannosaurus*, we have been able to specify the condition for a taxon between the two components of the EPB. In doing so, this helps to partition the major changes that occurred during the evolution of birds into distinct regions of the phylogeny. Additional reconstructions (Hutchinson, 2001a,b,c) will further clarify the stepwise succession of changes within Theropoda (and Coelurosauria).

CONCLUSIONS

In this analysis, we used detailed anatomical examinations of both extant and fossil reptiles to develop a detailed understanding of the osteological correlates of most pelvic and hindlimb muscles in these taxa. When placed into the context of a phylogenetic framework, we were able to employ the EPB method to reconstruct this musculature in the theropod dinosaur *Tyrannosaurus* with previously unattainable accuracy. This method also allowed us to explicitly refrain from reconstructing muscles whose homologies or correlates were ambiguous. The resulting reconstruction differed from previous attempts (e.g., Romer 1923; Walker, 1977; Tarsitano 1981, 1983) not only in its detail but in the specific placement of a number of important muscles.

Our reconstruction of *Tyrannosaurus* reveals that this taxon exemplifies numerous dinosaur modifications of the primitive archosaurian pelvic and hindlimb musculature. These appear to be related to the evolution of parasagittal limb posture in dinosauromorphs (Novas, 1992, 1996; Carrano, 2000; Hutchinson and Gatesy, 2000). Bipedalism in *Tyrannosaurus* was not yet fully “avian,” however, and this taxon displays a combination of characters and character states befitting its phylogenetic position between crocodylians and neornithine birds. Similar studies on other nonavian (and basal avian) ornithodiran archosaurs will greatly clarify the detailed anatomical transformations that occurred on the line to modern birds.

ACKNOWLEDGMENTS

We thank R. Blob, C. Brochu, D. Dilkes, S. Gatesy, K. Middleton, K. Padian, M. Parrish, and L. Witmer for helpful discussions of archosaurian soft tissue anatomy, two anonymous reviewers for their comments on the manuscript, and C. Abraczkas and L. Betti-Nash for assistance with the figures. Sev-

eral of the photographs in this article were used with the kind permission of C. Brochu, M. Loewen (Figs. 7, 8), and J. Weinstein and the Field Museum (Figs. 4, 6). This work is part of MTC’s involvement as a Postdoctoral Researcher in the Field Museum’s “Sue” program. He thanks O. Rieppel and J. Flynn for the encouragement to study FMNH PR 2081, and P. Fraley, L. Lee, P. Zawisha, L. Ewing, P. Hul, T. Shimisu, D. Lopp, C. Ward, L. Barber, and W. Simpson for their generous help with and access to the specimen. The translations of Dollo (1888) and Novas (1992) are available from the Polyglot Paleontologist website (<http://www.uhmc.sunysb.edu/anatomicalsci/paleo>). This work also constitutes part of JRH’s doctoral dissertation research in the Department of Integrative Biology at the University of California. He thanks R. Full, T. Keaveny, R. Kram, and K. Padian for their guidance as members of his dissertation committee. This is University of California Museum of Paleontology contribution number 1744.

LITERATURE CITED

- Barsbold R, Perle A. 1979. Modifications of the saurischian pelvis and parallel evolution in predatory dinosaurs [in Russian]. *Trudy Sovm Sov Mongr Pal Exped* 8:39–44.
- Benjamin M, Evans EJ, Copp L. 1986. The histology of tendon attachments to bone in man. *J Anat* 149:89–100.
- Bryant HN, Russell AP. 1993. The occurrence of clavicles within the Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. *J Vertebr Paleontol* 13:171–184.
- Bryant HN, Seymour KL. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *J Morphol* 206:109–117.
- Carrano MT. 1998a. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. *Paleobiology* 24:450–469.
- Carrano MT. 1998b. The evolution of dinosaur locomotion: functional morphology, biomechanics, and modern analogs. Ph.D. Dissertation, Chicago: University of Chicago.
- Carrano MT. 2000. Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* 26:489–512.
- Carrano MT, Biewener AA. 1999. Experimental alteration of limb posture in the chicken (*Gallus gallus*) and its bearing on the use of birds as analogs for dinosaur locomotion. *J Morphol* 240:237–249.
- Cong L, Hou L-H, Wu XC. 1998. The gross anatomy of *Alligator sinensis* Fauvel [in Chinese with English summary]. Beijing: CIP, China (ISBN 7-03-005979-4).
- Dilkes DW. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Trans R Soc Edinb, Earth Sci* 90:87–125.
- Dollo L. 1888. Sur la signification du “trochanter pendant” des dinosauriens. *Bull Sci France Belgique* 19:215–224.
- Farlow JO, Gatesy SM, Holtz TR Jr, Hutchinson JR, Robinson JM. 2000. Theropod locomotion. *Am Zool* 40:640–663.
- Gadow H. 1880. Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren Gliedmasse der Ratiten. Jena: Fischer.
- Gatesy SM. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* 16:170–186.
- Gatesy SM. 1995. Functional evolution of the hindlimb and tail from basal theropods to birds. In: Thomason JJ, editor. *Functional morphology in vertebrate paleontology*. Cambridge, UK: Cambridge University Press. p 219–234.

- Gauthier J. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The origin of birds and the evolution of flight. San Francisco: Memoirs of the California Academy of Sciences 8. p 1–47.
- Gregory WK, Camp CL. 1918. Studies in comparative myology and osteology. No. III. Bull Am Mus Nat Hist 38:447–563.
- Haines RW, Mohuiddin A. 1968. Metaplastic bone. J Anat 103: 527–538.
- Hutchinson JR. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:123–168.
- Hutchinson JR. 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:169–197.
- Hutchinson JR. 2001c. The evolution of hindlimb anatomy and function in theropod dinosaurs. Ph.D. dissertation, Berkeley: University of California.
- Hutchinson JR, Gatesy SM. 2000. Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology 26:734–751.
- Jones SJ, Boyde A. 1974. The organization and gross mineralization patterns of the collagen fibres in Sharpey fibre bone. Cell Tissue Res 148:83–96.
- Maddison WP, Maddison DR. 1992. MacClade: analysis of phylogeny and character evolution, v. 3. Sunderland, MA: Sinauer Associates.
- McGowan C. 1979. Hindlimb musculature of the brown kiwi, *Apteryx australis mantelli*. J Morphol 160:33–73.
- McGowan C. 1982. The wing musculature of the brown kiwi, *Apteryx australis mantelli*, and its bearing on ratite affinities. J Zool Lond 197:173–219.
- McKittrick MC. 1994. On homology and the ontological relationship of parts. Sys Biol 43:1–10.
- Norman DB. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). Bull Inst R Sci Nat Belgique 56: 281–372.
- Novas FE. 1992. La evolución de los dinosaurios carnívoros. In: Sanz JL, Buscalioni AD, editors. Los Dinosaurios y Su Entorno Biotico: Actas del Segundo Curso de Paleontología in Cuenca. Cuenca, Argentina: Instituto “Juan Valdez.” p 126–163.
- Novas FE. 1996. Dinosaur monophyly. J Vertebr Paleontol 16: 723–741.
- Padian K. 1991. Pterosaurs: were they functional birds or functional bats? In: Rayner JMV, Wootton RJ, editors. Biomechanics in evolution. Cambridge, UK: Cambridge University Press. p 145–160.
- Padian K, Chiappe LM. 1998. The origin and early evolution of birds. Biol Rev 73:1–42.
- Parrish JM. 1983. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia (Reptilia: Archosauria). Ph.D. dissertation, Chicago: University of Chicago.
- Parrish JM. 1986. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. Hunteria 1:1–35.
- Patterson C. 1982. Morphological characters and homology. In: Joysey KA, Friday AE, editors. Problems of phylogenetic reconstruction. New York: Academic Press. p 21–74.
- Perle A. 1985. Comparative myology of the pelvic-femoral region in the bipedal dinosaurs. Paleontol J 1985:105–109.
- Raath MA. 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology. Ph.D. dissertation, Salisbury: Rhodes University.
- Romer AS. 1923a. Crocodylian pelvic muscles and their avian and reptilian homologues. Bull Am Mus Nat Hist 48:533–552.
- Romer AS. 1923b. The ilium in dinosaurs and birds. Bull Am Mus Nat Hist 48:141–145.
- Romer AS. 1923c. The pelvic musculature of saurischian dinosaurs. Bull Am Mus Nat Hist 48:605–617.
- Romer AS. 1927a. The development of the thigh musculature of the chick. J Morphol Physiol 43:347–385.
- Romer AS. 1927b. The pelvic musculature of ornithischian dinosaurs. Acta Zool 8:225–275.
- Romer AS. 1942. The development of tetrapod limb musculature — the thigh of *Lacerta*. J Morphol 71:251–298.
- Rowe T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. J Morphol 189:327–346.
- Rowe T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. J Vertebr Paleontol 9:125–136.
- Russell DA. 1972. Ostrich dinosaurs from the late Cretaceous of western Canada. Can J Earth Sci 9:375–402.
- Shroeter S, Tosney KW. 1991. Spatial and temporal patterns of muscle cleavage in the chick thigh and their value as criteria for homology. Am J Anat 191:325–350.
- Tarsitano S. 1981. Pelvic and hindlimb musculature of archosaurian reptiles. Ph.D. Dissertation, New York: City University of New York.
- Tarsitano S. 1983. Stance and gait in theropod dinosaurs. Acta Pal Pol 28:251–264.
- Unwin DM. 1999. Pterosaurs: back to the traditional model? Trends Ecol Evol 14:263–268.
- Walker AD. 1977. Evolution of the pelvis in birds and dinosaurs. In: Andrews SM, Miles RS, Walker AD, editors. Problems in vertebrate evolution. Linnean Society Symposium Series 4. p 319–358.
- Welles SP. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda): osteology and comparisons. Palaeont AbtA 185:85–180.
- Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge, UK: Cambridge University Press. p 19–33.
- Witmer LM. 1997. The evolution of the antorbital cavity in archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. J Vertebr Paleontol Mem 3:1–73.