Review

The evolution of hindlimb tendons and muscles on the line to crown-group birds[☆]

John R. Hutchinson*

Biomechanical Engineering Division, Stanford University, Durand 209, BME, Stanford, CA 94305-4038, USA

Abstract

The anatomy and functions of muscle–tendon complexes and their bony attachments in birds and their outgroups show how the major pelvic limb muscle groups evolved. Fossils reveal that most changes evolved after the divergence of archosaurs in the Triassic, particularly in the dinosaurian precursors to birds. Three-dimensional limb control became concentrated at the hip joint; more distal joints and muscles were restricted to flexion or extension early in dinosaur evolution. Hip extensors expanded even though the primary femoral retractor M. caudofemoralis longus was reduced. Hip flexors and two-joint 'hamstring' muscles were simplified to a few large heads. Knee extensors increased their sizes and moment arms early in bipedal dinosaurs, but the patella and cranial cnemial crest evolved later in birds. Lower limb muscles expanded as ossifications such as the hypotarsus increased their moment arms. The ossification of lower limb tendons, particularly in extensors, is a recent novelty of birds. Muscles and tendons that develop large forces, stresses, and moments to stabilize or move the limbs became increasingly prominent on the line to birds. Locomotion evolved in a stepwise pattern that only recently produced the derived limb control mechanisms of crown-group birds, such as the strongly flexed hip and knee joints.
© 2002 Elsevier Science Inc. All rights reserved.

Keywords: Bird; Dinosaur; Evolution; Fossil; Locomotion; Muscle; Sesamoid; Tendon

1. Introduction

The pectoral limb of crown-group birds (Neornithes) is obviously specialized for aerial locomotion, but the role of the pelvic limb in terrestrial locomotion also has changed dramatically from the ancestral reptilian condition. As in the wing, in the leg these changes of function are reflected by numerous morphological changes that evolved on the line to Neornithes (Gatesy, in press). Tendons and their associated bones and muscles constitute most of these specializations (Raikow, 1985), many of which involve osteological changes that alter muscle moment arms (Alexander and Dimery, 1985).

For example, unlike in most other reptiles, the massive neornithine knee extensors have a well-ossified patella and two cnemial crests that maintain large moment arms about the knee for the common 'triceps' extensor tendon. Likewise, the ankle extensors of Neornithes are proportionately larger than in other reptiles, and the hypotarsus helps the 'Achilles tendon' preserve a large moment arm about the ankle. Additionally, the tendons of the digital flexor (and other lower limb) muscles frequently have ossified portions, and the muscles themselves are divided into more

heads. In contrast, some other groups such as hip adductors and abductors are reduced or greatly modified (Hutchinson and Gatesy, 2001).

Evolutionary morphologists and biomechanists are interested in questions such as, when did these and other specializations present in the hindlimbs of extant birds evolve? Are they mostly unique to crown clade birds, or do they characterize a more inclusive clade(s)? If some specializations were present in ancestral theropods, how similarly to extant birds did these animals move? Unfortunately, because of the abundance and complexity of neornithine specializations, and the extinction of most potentially informative outgroups to birds, such questions have been difficult to answer. Yet the recognition that birds are descendants of theropod dinosaurs has helped uncover new insights into such questions (Prum, 2002).

Tendons help evolutionary biologists and biomechanists to bridge the gap between paleontological and neontological data because they have concentrated attachment sites on bones that are rich in Sharpey's fibres, which themselves are ossified collagen fibers (Hoyte and Enlow, 1966; Haines and Mohuiddin, 1968; Jones and Boyde, 1974; Reid, 1984; Benjamin et al., 1986; Hurov, 1986), in addition to fibrocartilage. These obvious 'muscle scars' (actually formed by tendons, not muscle fibers), tubercles, sesamoids, and trochanters are often fossilized. Furthermore, fibrocartilages may form not only within tendon attachment sites on bone, where scars are preserved, but also within 'wrap-around tendons' passing over smooth bone surfaces where tendons experience compression (Alexander and Dimery, 1985; Benjamin and Ralphs, 1998). Thus smooth bone surfaces (such as canals or sulci for tendons) are also often indicative of the course of muscle–tendon complexes. The evolution of tendons and their associated muscles across a wide phylogenetic spectrum can consequently be tracked (Bryant and Russell, 1992; Witmer, 1995, 1997). If reliable form-function relationships exist for a given muscle-tendon complex, anatomical changes can be used to reconstruct locomotor evolution. In contrast, the attachments of muscles and thin aponeuroses are more diffuse and subtle (Bryant and Seymour, 1990), and thus harder to distinguish in fossils, although recent discoveries of soft tissue fossils are promising (Kellner, 1996; Sasso and Signore, 1998; Martill et al., 2000).

Application of explicit, outgroup-based phylogenetic methodology and study of more extant and fossil specimens has recently brought exciting new clarity to the study of avian locomotor evolution (Gatesy, 1990, 1995; Gatesy et al., 1999; Gatesy, in press, Gatesy and Dial, 1996; Carrano, 1998, 2000; Farlow et al., 2000; Hutchinson, 2001a,b; Hutchinson and Gatesy, 2001; Carrano and Hutchinson, 2002). Herein, I review and synthesize available information on the evolution of hindlimb muscle–tendon complexes from basal reptiles to Neornithes. I then discuss how these anatomical changes relate to the origins of the novel locomotor mechanics of extant birds. This constitutes the first intensive study of the evolution of all major muscle–tendon complexes of bird pelvic limbs, integrating neontological and paleontological information in a phylogenetic context with a character-taxon data matrix to see how bird legs evolved.

2. Materials and methods

As in my previous studies (Hutchinson, 2001a,b), I gathered data on soft tissue attachments and their osteological correlates to divide characters into character states (Appendix A), constructing a character-taxon data matrix (Appendix B) in MacClade 4.03 (Maddison and Maddison, 2001). I then mapped these states onto a phylogenetic framework (Fig. 1). This procedure allowed me to reconstruct the evolution of muscle–tendon complexes (Appendix C), following the procedure of Witmer (1995) and others. To simplify the analysis, some paraphyletic taxa were scored for ancestral states (basal diapsids, archosauromorphs, crocodylomorphs, and tetanurans in Fig. 1 and Appendices A, B and C).

I examined extant and fossil skeletal material from a broad range of archosauromorph taxa in order to collect osteological data, cited by specimen number in the text as necessary. I dissected the hindlimb musculature of specimens of extant Reptilia, including (numbers of specimens are in brackets): Chelonia (*Cheldyra* sp. [2], *Terrapene* sp. [2]), *Sphenodon punctatum* [1], Squamata (*Amphibolurus* [1], *Anolis* sp. [3], *Heloderma suspectum* [1], *Iguana iguana* [5], *Phrynosoma* sp. [2], *Tupinambis* sp. [1], and *Varanus* spp. [6]), and Crocodylia (*Alligator mississipiensis* [10]), Paleognathae (*Casuarius casuarius* [2], *Eudromia elegans* [1], *Struthio camelus* [5]), and Neognathae
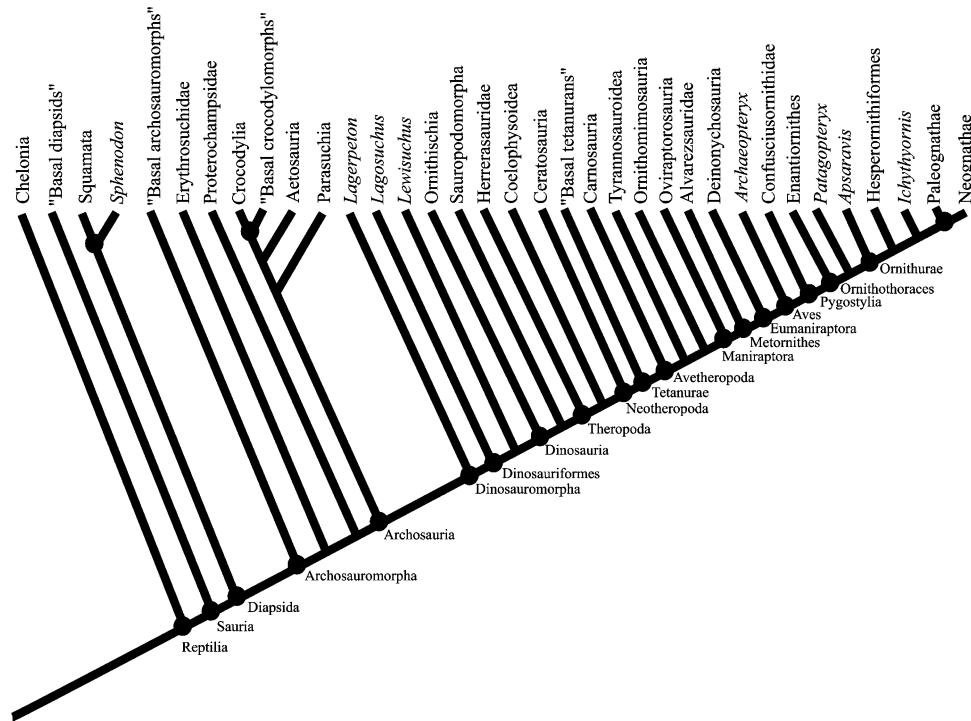
Fig. 1. Phylogenetic framework used to map anatomical characters in this study. Based on a 'consensus' of Gauthier et al. (1988), Sereno (1991), Novas (1996), Chiappe (1996), Chiappe (2001), Norell et al. (2001), and Norell and Clarke (2001), and references therein; see Hutchinson (2001a) for explanation of this consensus framework. The phylogenetic positions of Chelonia, Herrerasauridae, and Alvarezsauridae remain contentious, but other proposed positions do not greatly change my results. The relationships of all other taxa included are relatively stable in recent cladistic analyses. Clades not labeled include Lepidosauria (*Sphenodon* + Squamata), Crocodylomorpha ('basal crocodylomorphs' + Crocodylia), and Neornithes (Paleognathae + Neognathae).

(*Anas platyrhynchos* [3], *Cariama cristata* [1], *Chen* sp. [1], *Columba livia* [6], *Cygnus olor* [1], *Fulica* sp. [1], *Gallus gallus* [100+], *Lophura ignita* [1], *Gavia* sp. [1], *Meleagris gallipavo* [12], *Numida numida* [5], *Oceanodroma* sp. [1], *Pavo pavo* [1], *Phalacrocorax* sp. [1], and *Phasianus* spp. [8]). I obtained specimens from the California Academy of Sciences (San Francisco, CA), East Bay Vivarium (Berkeley, CA), Ruth Ellsey (Rockefeller Wildlife Refuge, LA), licensed breeders, biological supply companies, and other legitimate sources.

These anatomical data supplemented my review of the literature on reptilian myology. I used general references on non-avian reptilian myology (Gadow, 1882; Perrin, 1892; Gregory and Camp, 1918; Romer, 1922; Haines, 1935; Ribbing, 1938; Kriegler, 1961) as well as references for specific taxa. Literature used for Chelonia included Zug (1971) and Walker (1973), and for *Sphenodon* includes Osawa (1898), Byerly (1925), and Russell (1988). I consulted squamate myology refer-

ences including Mivart (1867), Mivart (1870), Sanders (1870a), Sanders (1870b), Sanders (1874), De Vis (1884), Rabl (1916), Davis (1934), Snyder (1954, 1962), Romer (1942), Harris (1963), Russell (1988), Surahya (1989), Landsmeer (1990), and Zaaf et al. (1999). Crocodilian myological literature included Haughton (1865a), Haughton (1868), Hair (1868), Reese (1915), Romer (1923a,b), Tarsitano (1981), Gatesy (1990, 1997), and Cong et al. (1998).

Neornithine myology is reviewed in Gadow and Selenka (1891), Beddard (1898), Hudson (1937), Howell (1938), George and Berger (1966), Raikow (1985), McKitrick (1991), and Vanden Berge and Zweers (1993). The myology of paleognaths was covered by Haughton (1865b), Haughton (1867a), Haughton (1867b), Garrod and Darwin (1872), Firbas and Zweymüller (1971), Hudson et al. (1972), McGowan (1979), Vanden Berge (1982), Mellett (1994), and Patak and Baldwin (1998). Neognath myology was detailed, for example, by Miller (1937), Fisher (1946), Hudson

Table 1
Muscle homologies for Reptilia

Muscles	Chelonia	*Sphenodon*	Squamata	Crocodylia	Neornithes
Dorsal thigh					
(1) Triceps femoris					
(a) M. iliotibialis	IT	IT	IT	IT	IT
(b) M. ambiens	AMB	AMB	AMB	AMB1+2	AMB
(2) M. iliofibularis	ILFB	ILFB	ILFB	ILFB	ILFB
(3) Deep dorsals					
(a) M. iliofemoralis	IF	IF	IF	IF	IFE
	*	*	*	*	ITC
(b) M. puboischiofemoralis internus	PIFI1+2	PIFI1+2	PIFI1	PIFI1	IFI
	*	*	PIFI2	*	*
	PIFI3	PIFI3	PIFI3	PIFI2	ITCR
	*	*	*	*	ITM
(c) M. femorotibialis	FMT	FMT	FMT	FMTE	FMTL
	*	*	*	FMTI	FMTIM
	*	*	*	*	FMTM
Ventral thigh					
(4) Flexor cruris					
(a) M. pubo-ischio-tibialis	PIT	PIT	PIT1	–	–
	*	*	PIT2	PIT	–
	*	*	PIT3	FTI2	–
(b) M. flexor tibialis internus	FTI1	FTI1	FTI1	FTI1	–
	FTI2	FTI2	FTI2	FTI3	FCM
	*	*	*	FTI4	–
(c) M. flexor tibialis externus	FTE	FTE	FTE	FTE	FCLP
	–	–	–	–	FCLA
(5) M. pubotibialis	PUT	PUT	PUT	–	–
(6) M. adductor femoris	ADD	ADD	ADD	ADD1	PIFM
	*	*	*	ADD2	PIFL
(7) M. puboischiofemoralis externus	PIFE	PIFE	PIFE	PIFE1	OL
	*	*	*	PIFE2	OM
	*	*	*	PIFE3	–
(8) M. ischiotrochantericus	ISTR	ISTR	ISTR	ISTR	ISF
(9) Mm. caudofemorales	CFB	CFB	CFB	CFB	CFP
	CFL	CFL	CFL	CFL	CFC
Lower leg					
(10) Mm. gastrocnemii	GM	GM	GM	GM	GM
	*	*	*	*	GIM
	GL	GL (2)	GL (2)	GL	GL
(11) Digital flexors	FDL	FDL	FDL	FDL	FDL and 5+ others
	FHL	FHL	FHL	FHL	FHL
	FDB	FDB	FDB	FDB	FDB
(12) Digital extensors	EDL	EDL	EDL	EDL	EDL
	EHL	EHL	EHL	EHL	EHL
	EDB	EDB	EDB	EDB	–
	TA	TA	TA	TA	TC (2)
(13) Other lower leg muscles					
(a) M. pronator profundus	PP	PP	PP	PP	–
(b) M. popliteus	POP	POP	POP	POP	POP
(c) M. interosseus cruris	IC	IC	IC	IC	–
(d) M. fibularis longus	FL	FL	FL	FL	FL
(e) M. fibularis brevis	FB	FB	FB	FB	FB

These follow Romer (1922), Romer (1923b), Romer (1927), Romer (1942), Rowe (1986), Hutchinson (2001a), and Carrano and Hutchinson (2002), with abbreviations used in this study. See text and Appendix A for details. '*' indicates that the muscle is not divided; '–' indicates that the muscle is absent; '(2)' indicates that two parts are present.
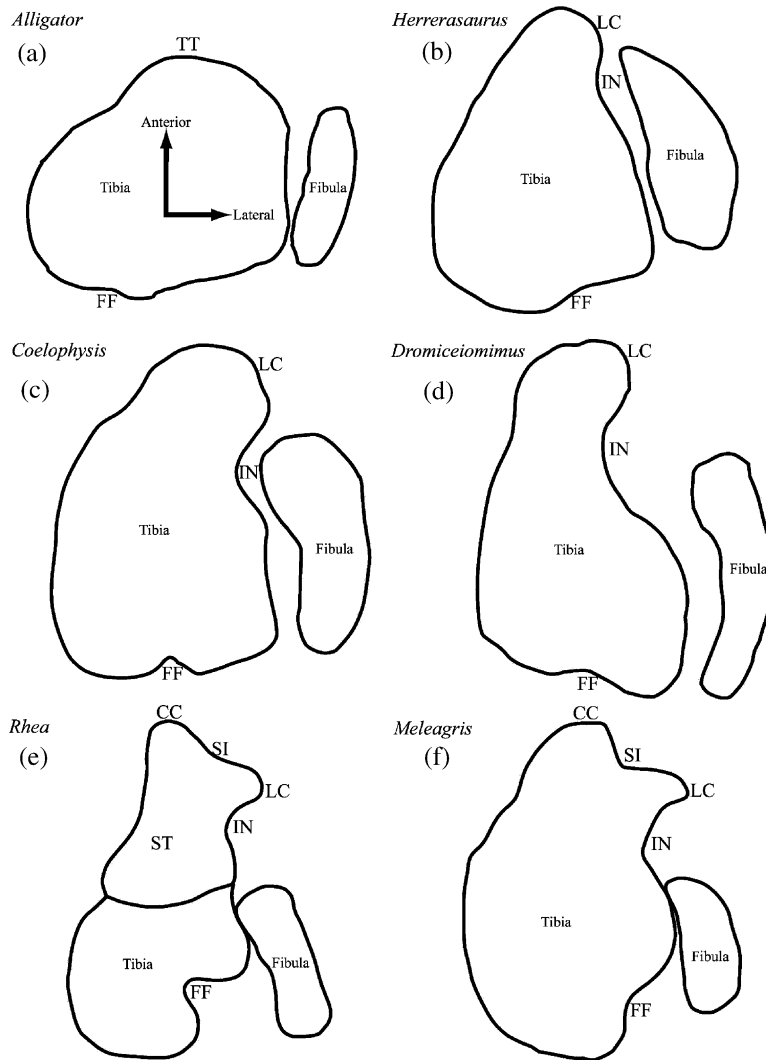
Fig. 2. Morphology of the knee joint region. Right tibia and fibula in proximal view. (a) Alligator (Crocodylia; UCMP 71672); (b) *Herrerasaurus* (Herrerasauridae; PVSJ 373; reversed left side); (c) *Coelophysis* (Coelophysoidea; UCMP 129618; reversed left side); (d) *Dromiceiomimus* (Ornithomimosauria; ROM 852, reversed left side); (e) Juvenile *Rhea* (Paleognathae; UMCP 129668); (f) Adult *Meleagris* (Neognathae; personal collection). *Abbreviations*: CC, cranial cnemial crest; FF, fossa flexoria; IN, incisura tibialis; LC, (lateral) cnemial crest; SI, sulcus intercnemialis; ST, proximal tibial sesamoid incompletely fused as a 'tibial epiphysis.' Not to scale.

et al. (1959), Harvey et al. (1968), Raikow (1970), Cracraft (1971), Gatesy (1999a), and Verstappen et al. (1998). I used McKitrick's (1991) data matrix for neornithine muscles and my own observations to map characters onto a phylogeny based on Cracraft and Clarke (2001) to code ancestral states for Paleognathae and Neognathae.

I adopted Romer's (1922), Romer's (1923b), Romer's (1942) muscle homologies, with Rowe's (1986) revision of deep dorsal thigh muscle homologies (Table 1). Nomenclature used is for simplicity, not a revision of official nomenclature. Additional discussion and details are in Hutchinson (2001a), Hutchinson (2001b), Hutchinson and Gatesy (2001), and Carrano and Hutchinson (2002). Anatomical nomenclature for Aves generally follows Baumel et al. (1993), but English names for some structures are used because many non-ornithologists will be more familiar with these terms. Non-avian reptilian anatomical nomenclature follows Romer (1922), Romer (1923b) and similar traditional nomenclature. Directional references (cranial, medial, etc.) refer to a hindlimb

oriented in a fully adducted, digitigrade, and extended (vertical) position with the condyles facing caudally.

3. Results

Appendix C outlines the series of character state changes that evolved in Reptilia on the line to Neornithes. I focus on the key transitions that my analysis and previous studies have elucidated, with an emphasis on tendons and associated structures, especially those of considerable biomechanical importance. This focus requires me to make sweeping generalizations about the details of reptilian anatomy, but my point is to cover general patterns rather than minute details and variation, which are important but beyond the scope of this study.

For each muscle group considered, I outline the sequence of changes in the number of muscle heads, the origin(s), and the insertion(s). I move from more to less-inclusive clades on the line to Neornithes: from basal Reptilia to archosaurs, dinosaurs, theropods, tetanuran theropods, basal birds (Aves/Avialae), and Ornithurae (Fig. 1). I divide the results into a section on the thigh muscles, whose evolution previous authors covered in some detail (e.g. Gregory and Camp, 1918; Romer, 1922, 1923a,b,c; Charig, 1972; Walker, 1977; Rowe, 1986; Novas, 1996), and then a section on the lower leg muscles, which few authors have considered (Tarsitano, 1981; Dilkes, 2000; Carrano and Hutchinson, 2002). Some smaller, less well-understood muscle groups such as the intrinsic muscles of the pedes and other highly variable distal muscles are not covered in this analysis.

4. Thigh muscles

4.1. 'Triceps' group

The three major divisions of this complex have separate origins, but most fibers and aponeuroses converge through and around the intercondylar sulcus (and patellar sulcus in Neornithes) of the femur and then insert as one or more common tendons onto a tibial tuberosity on the cranial surface of the proximal tibia. In lepidosaurs this tuberosity is a separate intratendinous ossification that is distinct from the secondary ossification centres of the epiphyses (Haines, 1940, 1942, 1969), but so far there is no evidence of this in basal archosauromorphs. In basal dinosaurs the tuberosity expanded into a cnemial crest (Novas, 1996), which became especially large in theropod dinosaurs on the line to birds (Fig. 2). In birds, this crest constitutes the lateral cnemial crest (Chiappe, 1996).

A second crest, the cranial cnemial crest, is a neomorph of Ornithurae and related taxa (Chiappe, 1996, 2001; Hutchinson, 2001b). It appears to be a 'traction epiphysis,' often referred to as the 'tibial epiphysis' (Fig. 2; sesamoid fused to a long bone; Parsons, 1904; Barnett and Lewis, 1958) that forms from a separate ossification centre early in neornithine development (Parsons, 1905; Hogg, 1980). Presumably an unossified sesamoid-like or intratendinous precursor of the cranial cnemial crest was present ancestrally in reptiles as a distal part of the triceps extensor tendon.

A fibrocartilaginous or fibrous 'patelloid' is associated with the knee extensor tendon in some extant turtles and crocodilians, whereas an ossified patella evolved convergently in mammals, lepidosaurs, and birds (Parsons, 1908; Pearson and Davin, 1921; Haines, 1940, 1942, 1969; Carter et al., 1998). Patella-like sesamoids have been found in some basal reptiles (e.g. Rieppel, 1989), yet their absence in all known non-avian archosaurs demonstrates that a bony patella is ancestrally absent for Archosauria. Fossils show that Ornithurae is the most inclusive archosaurian clade that has an ossified patellar sesamoid. The patella even fuses onto the cranial cnemial crest in some birds (Heilman, 1926; Barnett and Lewis, 1958), creating a double traction epiphysis for the insertion of the triceps tendon. Its ancestral state for Neornithes is most parsimoniously interpreted as a free sesamoid.

Pearson and Davin (1921) suggested that the patella was ancestrally part of the cnemial crest but became an independent sesamoid later. Available fossil and ontogenetic data do not support this idea (Barnett and Lewis, 1958; Hogg, 1980; Chiappe, 1996, 2001)—the patella and cranial cnemial crest evolved concurrently as separate ossifications in Ornithurae.

4.1.1. M. iliotibialis (IT)

The single weakly subdivided head of basal reptiles was split into three separate heads in archosaurs. These heads originate from the dorso-lateral iliac surface in all taxa, superficial to other thigh muscles. Fossils show how the expansion of
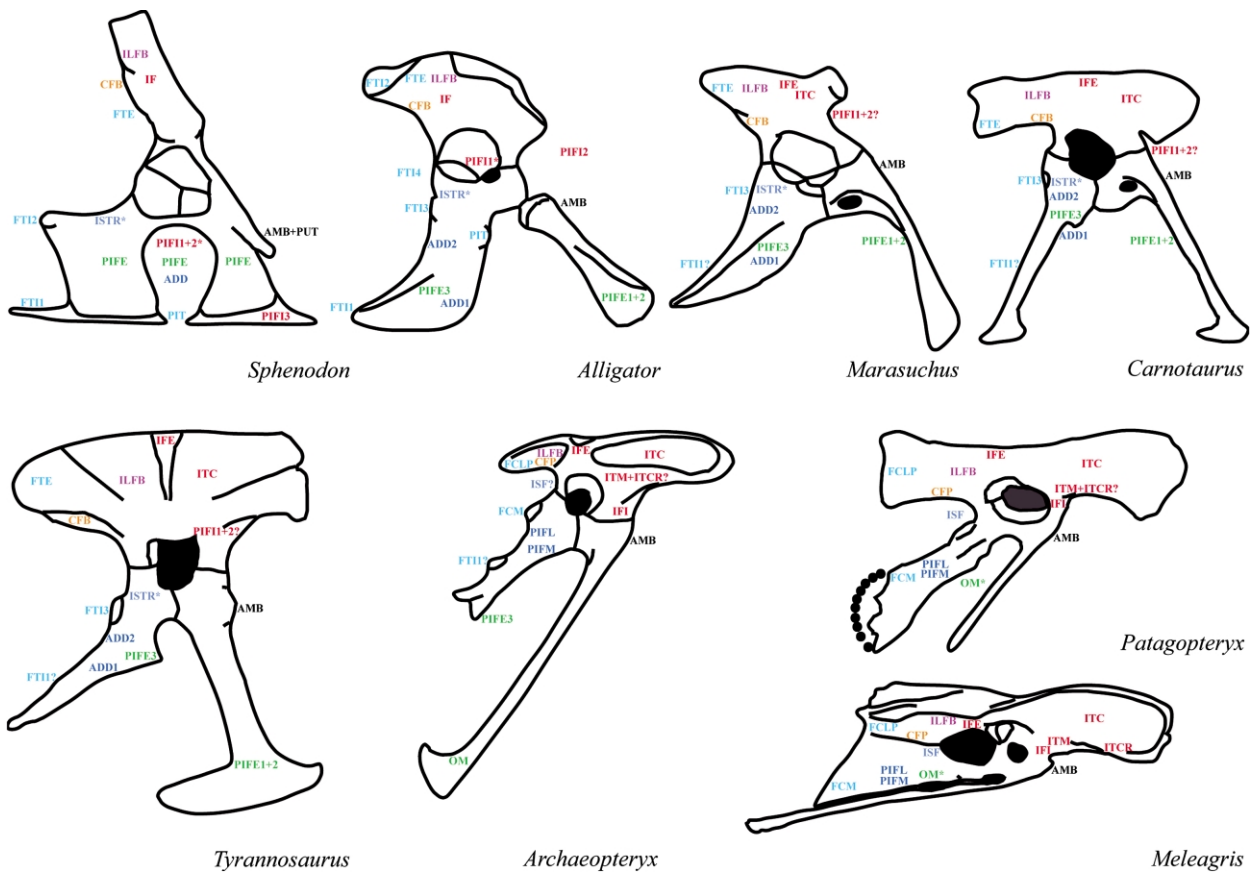
Fig. 3. Evolution of pelvic muscle origins on the line to crown-group birds. Modified from Hutchinson (2001a), showing the relative positions of some thigh muscle origins and their approximate changes during reptilian evolution (from right to left, top to bottom is toward Neornithes). Note that some origins (marked with asterisks) are medial and some muscles (IT, CFL/CFC, OL) are not shown; see text for details and Table 1 for muscle abbreviations. Not to scale.

the ilium (Fig. 3) relates to the expansion of these and other dorsal thigh muscles on the line to birds (Romer, 1923a; Walker, 1977; Carrano, 2000; Hutchinson, 2001a).

4.1.2. M. femorotibialis (FMT)

The small single (or slightly subdivided) head of basal reptiles was enlarged and split in archosaurs, presumably having two heads (lateral and medial) as in crocodilians. The surface of the femoral shaft is richly textured with Sharpey's fibers that indicate the expansive origin (Reid, 1984). Intermuscular lines on the femoral shaft suggest that a third head is a recent novelty of birds, but how recent remains ambiguous (Dilkes, 2000; Hutchinson, 2001b). Muscle scarring on the craniomedial surface of the distal femur in theropod dinosaurs indicates the presence of a distal subdivision of the lateral head of M. femorotibialis

that is ancestrally present in Neornithes (Mc-Kitrick, 1991).

4.1.3. M. ambiens (AMB)

Reptilia ancestrally had this muscle as a single head (two heads convergently in a few squamates, crocodilians, and birds) originating from the craniolateral surface of the proximal pubes on a pubic tubercle near the acetabulum (Hutchinson, 2001a). In Neornithes this configuration has changed little except in some birds which have a more iliac origin (e.g. Mellett, 1994), in some cases related to a reduced contribution of the pubis to the acetabular rim and pubic tubercle. In archosaurs, M. ambiens not only contributes to the extensor tendon, but also has a secondary tendon that perforates the extensor tendon, or even perforates the patella as an apomorphic condition in some birds (Heilman, 1926; McKitrick, 1991). The sec-
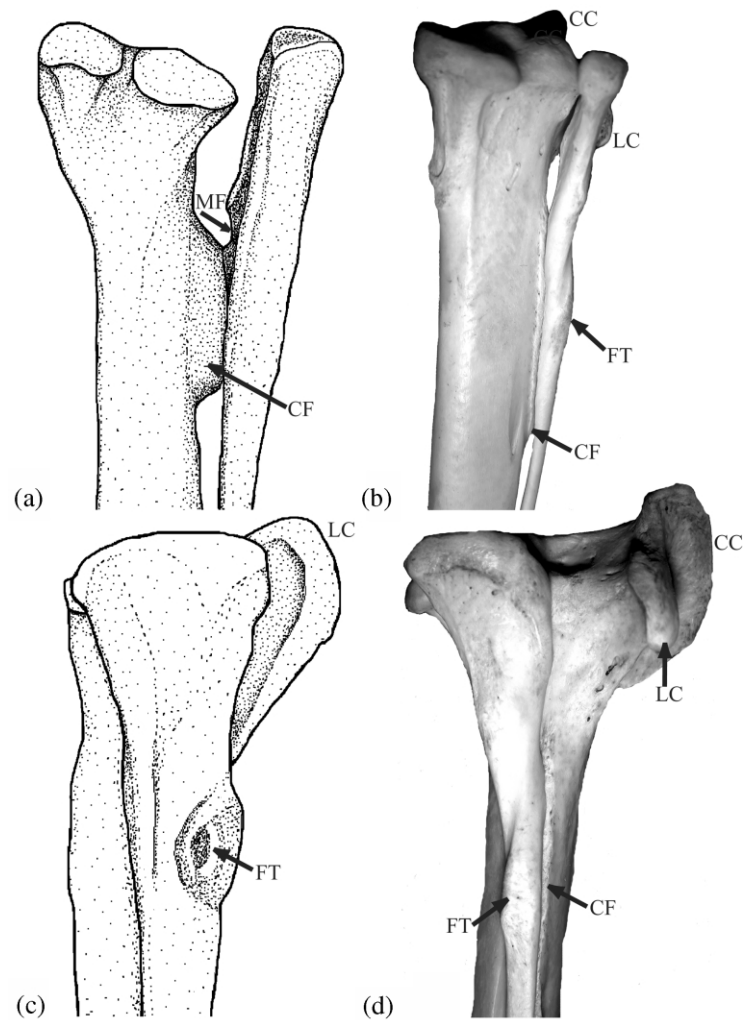
Fig. 4. Morphology of the proximal tibia and fibula. Right proximal tibia and fibula in caudal (a, b) and lateral (c, d) views. (a, c) *Tyrannosaurus* (Tyrannosauroidea; AMNH 5027; reversed left side); (b, d) Adult *Meleagris* (Neognathae; personal collection). Abbreviations: CF, crista fibularis; FT, tuberositas M. iliofibularis; LC, (lateral) cnemial crest; MF, medial fibular fossa. Not to scale.

ondary tendon then inserts laterally onto the aponeurosis of origin of one or more digital flexors and sometimes the lateral head of M. gastrocnemius (Haughton, 1865a,b; Gadow, 1882; Gadow and Selenka, 1891; Romer, 1923a).

4.2. M. iliofibularis (ILFB)

This muscle originated caudodorsal to the acetabulum (between M. iliofemoralis and M. flexor tibialis externus) on the lateral iliac surface and inserted on the craniolateral surface of the proximal fibular shaft in basal Reptilia. Its origin did not change markedly on the line to crown-group birds, although it expanded with the iliac surface

in dinosaurs (Fig. 3). In extant archosaurs the tendon has a secondary tendon of attachment to the lateral head of M. gastrocnemius, which may be the ancestral condition for Archosauria although it is variable in birds (Beddard, 1898; Romer, 1923b; McKitrick, 1991). In theropod dinosaurs, the insertion for the tendon became well marked by a tubercle that shifted caudally on the line to birds, possibly as the origin of M. fibularis longus (see below) moved proximally.

The tendon of M. iliofibularis influences the morphology of the proximal tibiotarsus in birds and other theropods (Fig. 4). Müller and Streicher (1989; also see Müller, 1986; 1989; Streicher and

Müller, 1992; Fuss, 1996) showed that a cartilaginous sesamoid-like 'c-element' is ephemerally present early in bird development as a connection between the M. iliofibularis tendon of insertion and the tibia. This c-element develops in a syndesmosis joining the medial surface of the fibula to an ossified fibular crest on the lateral surface of the tibia, functionally connecting the M. iliofibularis tendon from the lateral fibula through the fibula itself to the lateral tibia.

Consequently, the fibula and tibia are bound more tightly together in birds and extinct theropods, limiting fibular motion to slight pronation and supination (mediolateral rotation about the tibia; Fuss, 1996). Additionally, the syndesmosis prevents luxation of the fibula during the contraction of muscles attached to the fibula, or when joint contact forces are applied at the fibular–femoral articulation. This is important because the distal fibula is not braced by a connection with the tarsal joint (Müller and Streicher, 1989; Streicher and Müller, 1992). The presence of the M. iliofibularis tubercle, fibrous scarring on the medial fibula, and the fibular crest on the tibia in theropod dinosaurs (Fig. 4) shows that this functional complex was assembled early on the line to Neornithes (Müller and Streicher, 1989; Farlow et al., 2000).

Another specialization of birds relating to the tendon of M. iliofibularis is a ligamentous ansa that forms a pulley on the caudal side of the knee joint to constrain the line of action of the M. iliofibularis tendon. In extant and fossil Ornithurae, there are several tubercles on the caudolateral edge of the lateral femoral condyle that indicate the attachments of this ansa. Hence the ansa for the M. iliofibularis tendon may have been present in Ornithurae (Hutchinson, 2001b). However, this osteological correlation is somewhat tentative because some lower limb muscles (e.g. M. gastrocnemius lateralis) also originate nearby on the femur and could produce similar tubercles.

4.3. Deep dorsal group

Although the homologies of these muscles remain perplexing (Romer, 1923a,b; Walker, 1977; Rowe, 1986; Carrano and Hutchinson, 2002), general aspects of the evolution of these muscles are clear.

4.3.1. M. iliofemoralis (IF)
Reptilia had one head of this muscle originating from the lateral surface of the ilium, dorsal to the

acetabulum and cranial to M. iliofibularis (Fig. 3). It inserted on the caudolateral side of the femoral shaft, initially on an internal trochanter and then in basal archosaurs shifting laterally onto the femoral shaft (Hutchinson, 2001b). On the line to Neornithes, this muscle became fragmented into at least two heads (M. iliotrochantericus caudalis and M. iliofemoralis externus; ITC + IFE). This change is revealed in the fossil record by the divergence of two insertions (Fig. 5): one (for the tendon of M. iliotrochantericus caudalis) on the lesser trochanter of the femur, and another on the trochanteric shelf of the femur (for the tendon of M. iliofemoralis externus). These insertions moved laterally as the proximal femur was twisted medially to form an offset femoral head (Carrano, 2000; Hutchinson, 2001b).

If the insertions of these muscles are any guide to their relative sizes, in basal dinosaurs the two muscles were subequal in size. In theropod dinosaurs, the M. iliotrochantericus caudalis portion became larger as the preacetabular ilium and lesser trochanter expanded (Carrano, 2000), whereas the M. iliofemoralis externus portion reduced to a small origin from a process above the acetabulum in basal birds (Fig. 3; Hutchinson, 2001a,b). Finally, in basal birds the lesser trochanter fused to the greater trochanter to form a trochanteric crest (Fig. 5; Chiappe, 2001), and the trochanteric shelf became only a slight muscle scar in Ornithurae (Hutchinson, 2001b).

The insertion of M. iliofemoralis is more fleshy in non-avian Reptilia, and more tendinous in Neornithes, so the evolution of the lesser trochanter probably signals transformation into a more tendinous insertion (Fig. 5). This inference is corroborated by rugose striations that are rich in Sharpey's fibers (see below) and became increasingly prominent on the lesser trochanter as it expanded in theropods. Additional fibrocartilage was presumably present where the tendon wraps around the sharp edge of the lesser trochanter. In contrast, the trochanteric shelf was initially rugose but was reduced to a pit or tubercle in tetanuran theropods, especially Ornithurae.

4.3.2. M. puboischiofemoralis internus 1 (PIFI1)
The single head in basal reptiles originated craniomedially from the pelvis. The origin shifted dorsolaterally on the line to birds (Fig. 3) as the ventral pelvis was reduced (Hutchinson, 2001a), occupying a ventrolateral preacetabular ('cuppe-
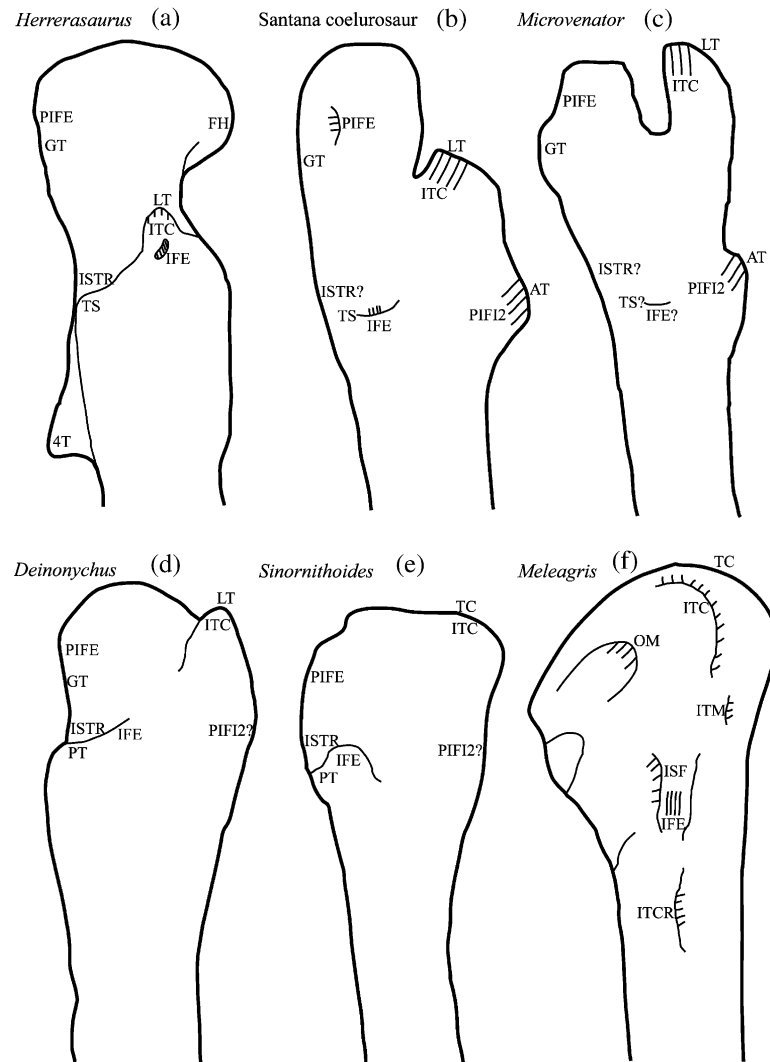
Fig. 5. Evolution of femoral trochanters on the line to crown-group birds. Right proximal femur in lateral view with approximate orientation of surface fibers indicated (striations). (a) *Herrerasaurus* (Herrerasauridae; PVSJ 373); (b) Santana coelurosaur (Martill et al., 2000; reversed left side); (c) *Microvenator* (Oviraptorosauria; AMNH 3041); (d) *Deinonychus* (Deinonychosauria; MCZ 4371; reversed left side); (e) *Sinornithoides* (Deinonychosauria/Troodontidae; IVPP V9612); (f) *Meleagris* (Neognathae; personal collection). *Abbreviations*: 4T, fourth trochanter; AT, accessory trochanter; GT, greater trochanter; LT, lesser (anterior) trochanter; PT, posterior trochanter; TC, trochanteric crest; TS, trochanteric shelf. See Table 1 and text for muscle abbreviations (IFE, ISTR/ISF, ITC, PIFE/OM, PIFI2/ITM+ITCR). Not to scale.

dicus') iliac fossa in tetanuran theropods, then moved further laterally in basal birds as the fossa was reduced onto the lateral surface of the ilium (Norell et al., 2001), becoming M. iliofemoralis internus (IFI) of Neornithes. Muscle scars on a variety of fossil and recent femora show that the tendon of insertion changed little, remaining on the medial (or slightly craniomedial) surface of the proximal femur (Dilkes, 2000; Hutchinson, 2001b).

4.3.3. M. puboischiofemoralis internus 2 (*PIFI2*)

Depending on the homology assumed, this muscle was either lost on the line to birds or split into two heads (Mm. iliotrochanterici cranialis et medius [ITCR+ITM] in Neornithes; Carrano and Hutchinson, 2002). In either case, it originated craniomedially from the ventral pelvis as a single head in basal reptiles, shifted its origin dorsally in basal archosaurs as the ventral pelvis was reduced (Romer, 1923b; Hutchinson, 2001a), and had a

lateral iliac origin in Ornithurae if not earlier (Fig. 3; Carrano and Hutchinson, 2002). The insertion of the tendon is commonly identifiable as muscle scarring on the craniolateral surface of the proximal femur. It developed into a large accessory trochanter in some tetanuran theropods (Fig. 5; Norell et al., 2001), but was reduced to smaller muscle scars in basal birds (Hutchinson, 2001b).

Rowe (1989), Novas (1996), and Dilkes (2000) reconstructed the insertion of the M. puboischiofemoralis internus 2 tendon, not M. iliofemoralis, on the lesser trochanter. This inference does not concur with available fossil and neontological data. First, the Sharpey's fibers on the lesser trochanter in fossil archosaurs are oriented mostly proximodistally (Fig. 5; Walker, 1977). Presumably these striations indicate the normal orientations of collagen fibers within the tendon of insertion and any surrounding fibrocartilage. The origin of M. puboischiofemoralis internus 2 is cranial to that of M. iliofemoralis in extant Reptilia (Fig. 3). Thus in order to connect the M. puboischiofemoralis internus 2 origin and insertion in a non-avian theropod, the femur would need to be oriented in a bizarre retracted position. The femur would be oriented in a more reasonable protracted position if part of M. iliofemoralis inserted on the lesser trochanter, because the origin of M. iliofemoralis is comparatively caudal; ancestrally above the acetabulum rather than far cranial to it.

Second, a lesser trochanter-like structure (or muscle scarring) in basal archosaurs such as phytosaurs and aetosaurs (Hutchinson, 2001b) is located where M. iliofemoralis inserts in crocodilians, distal to the insertion of M. puboischiofemoralis internus 2. These osteological correlates shifted proximally and cranially on the line to birds, matching the path of the shift of the M. iliofemoralis insertion. In contrast, the insertion of M. puboischiofemoralis internus 2 only shifted slightly cranially, demonstrated by the accessory trochanter and other muscle scars (Hutchinson, 2001b).

Third, the lesser trochanter expanded and shifted proximally in theropods, ultimately (in basal birds) reaching the proximal position where a part of M. iliofemoralis (M. iliotrochantericus caudalis) inserts in Neornithes. Reconstructing the insertion of the M. puboischiofemoralis internus 2 tendon on the lesser trochanter would require either a swapping of tendon insertions on the line to birds (not evidenced by fossils), an unusual orientation of the femur (contradicted by fossil articular sur-

faces; e.g. Charig, 1972; Farlow et al., 2000), or a different interpretation of deep dorsal muscle homologies (for discussion see Carrano and Hutchinson, 2002).

4.4. Flexor cruris group

Because the homologies of these muscles (the long flexors *sensu* Romer, 1923b) are even more poorly resolved than the deep dorsal group (Romer, 1923b, 1942; Ribbing, 1938; Russell, 1988; Hutchinson, 2001a), my description will be brief. One slightly subdivided superficial head (M. puboischiotibialis; PIT) and three deeper muscle heads (Mm. flexores tibiales interni 1, 2, et externus; FTI1+2 and FTE) were present ancestrally in reptiles (Russell, 1988). These heads mainly originated from an arch of ligaments, aponeuroses, and proximal tendons that extended caudoventrally from the pubic tubercle onto the ischial tuberosity and then onto the caudoventral corner of the ilium (Romer, 1922).

As these ligaments were reduced in basal archosauromorphs (Hutchinson, 2001a), the flexor cruris group likewise was reduced, becoming fragmented into five smaller heads in crocodilians. Ultimately, birds lost all but two heads of the flexor cruris (Mm. flexores crures lateralis et medialis; FCLP+FCM of Neornithes), corresponding to two deeper muscles: M. flexor tibialis internus 2 (FTI3 of Crocodylia) and M. flexor tibialis externus. These heads originated from the caudolateral border of the ischium and ilium respectively. Birds also evolved an accessory head (M. flexor cruris lateralis pars accessoria; FCLA) of unresolved homology; Romer (1923b), Romer (1942) considered the accessory head to possibly be a novel slip of M. gastrocnemius lateralis.

Unfortunately, the fossil record reveals few details about the evolution of this muscle–tendon complex (Fig. 3; Dilkes, 2000, Hutchinson, 2001a). Two processes on the dorsal edge of the ischia might represent the origins of two ancestral parts of M. flexor tibialis internus, one of which was lost eventually (Hutchinson, 2001a). The origin of M. flexor tibialis externus is mainly from the lateral side of the ilium in archosaurs, relating to the reduction of the ilio-ischiadic ligament.

The ancestral insertions of the flexor cruris tendons were in an oblique mediolateral line across the caudal side of the proximal tibia, with connections to the heads of Mm. gastrocnemii and parts

of the origins of some digital flexor muscles. Ancestrally in Neornithes, the tendons form a common insertion (McKitrick, 1991) that is only medial, with the accessory head inserting on the popliteal region of the femur after originating from a raphe on the main lateral head. Data from fossil muscle scars are equivocal, so is not clear when the tendons of insertion became more concentrated medially, but apparently this condition evolved by the loss of the lateral tendon of insertion of Mm. flexores tibiales internus 3+4 et externus. Nonetheless, the homologues of M. puboischiotibialis, M. pubotibialis, and M. flexor tibialis internus 1+ 4 were eliminated on the line to birds.

4.5. M. pubotibialis (PUT)

This muscle—assigned by Romer (1923b) to the flexor cruris, but Romer (1942) considered it more similar to the adductors—originated in basal reptiles from near the pubic tubercle and pubo-ischiadic ligament (Fig. 3), inserting on the caudolateral surface of the proximal tibia. However, as Romer (1923b), Dilkes (2000), and others have noted, M. pubotibialis was lost in archosaurs, probably relating to reduction of the pubic tubercle and associated ligaments (Hutchinson, 2001a).

4.6. M. adductor femoris (ADD)

The adductor group was a single head originating from the pelvic ligaments and ventral pelvic symphyses in basal Reptilia. Muscle scars signal that the two heads present in extant archosaurs (Mm. adductores femoris 1 et 2 of Crocodylia; Mm. puboischiofemorales medialis et lateralis [PIFM+PIFL] of Neornithes) had evolved in their common ancestor with reduction of the pelvic ligaments (Romer, 1923b; Hutchinson, 2001a). These two heads originated from the lateral surface of the ischium (Fig. 3) and were moved more laterally by the elimination of the ischial symphysis in basal birds (Hutchinson and Gatesy, 2001). Their ancestral insertions on the caudal surface of the distal femur shaft did not change markedly (Dilkes, 2000; Hutchinson, 2001b).

4.7. M. puboischiofemoralis externus (PIFE)

This appears to be another muscle that was weakly subdivided in ancestral Reptilia but subsequently split into multiple heads in archosaurs (Fig. 3). Changes of the surface area on the ventral pelvis for the origin of this muscle show how it was divided into three heads (Mm. puboischiofemorales externi 1–3) in basal archosaurs, originating from much of the lateral and craniomedial surfaces of the pubes and ischia. The origin was moved caudally by the retroversion of the pubes in maniraptorans, especially basal birds (Fig. 3). An 'obturator tuberosity' on the ischium in some maniraptorans and basal birds marks the attachment of a ligament that forms the ventral boundary for the passage of the tendon of the medial head through the obturator foramen (Hutchinson, 2001a). This muscle group was reduced to two heads (Mm. obturatorii lateralis et medialis; OL+ OM) when the third head was lost with the obturator process of the ischium in basal birds (Fig. 3; Hutchinson, 2001a). The lateral head was reduced on the pubis, whereas the medial head shifted its origin caudally onto a pubo-ischiadic membrane with the elimination of the pubic symphysis in basal birds, especially Ornithurae (Hutchinson and Gatesy, 2001).

The common tendon of insertion for M. puboischiofemoralis externus shifted its position on the line to birds (Fig. 5). The posterior ridge of the proximal femur was the insertion in ancestral Reptilia (Romer, 1956), but this ridge was reduced into what is termed the greater trochanter in basal archosaurs. The greater trochanter rotated laterally as the femoral head gained a more medial orientation in tetanuran theropods (Hutchinson and Gatesy, 2001). In some birds, the proximal femur has a shelf distal to the insertion of the tendon of M. obturatorius medialis that prevents the tendon from slipping distally (Hutchinson, 2001b).

4.8. M. ischiotrochantericus

This muscle originated from the medial surface of the ischium in ancestral Reptilia, but it shifted onto the lateral surface of the ischium and ilio-ischiadic membrane (becoming M. ischiofemoralis [ISF] of Neornithes) as the ischial symphyses disappeared in basal birds (Fig. 3; Hutchinson, 2001a). Its insertion remained fairly conservative on the line to birds, positioned on the caudolateral side of the proximal femur. Similar to the previous muscle group, a shelf-like prominence (trochanteric shelf, or posterior trochanter) or groove guides the line of action of the tendon in some theropod taxa, including birds (Fig. 5; Hutchinson, 2001b).
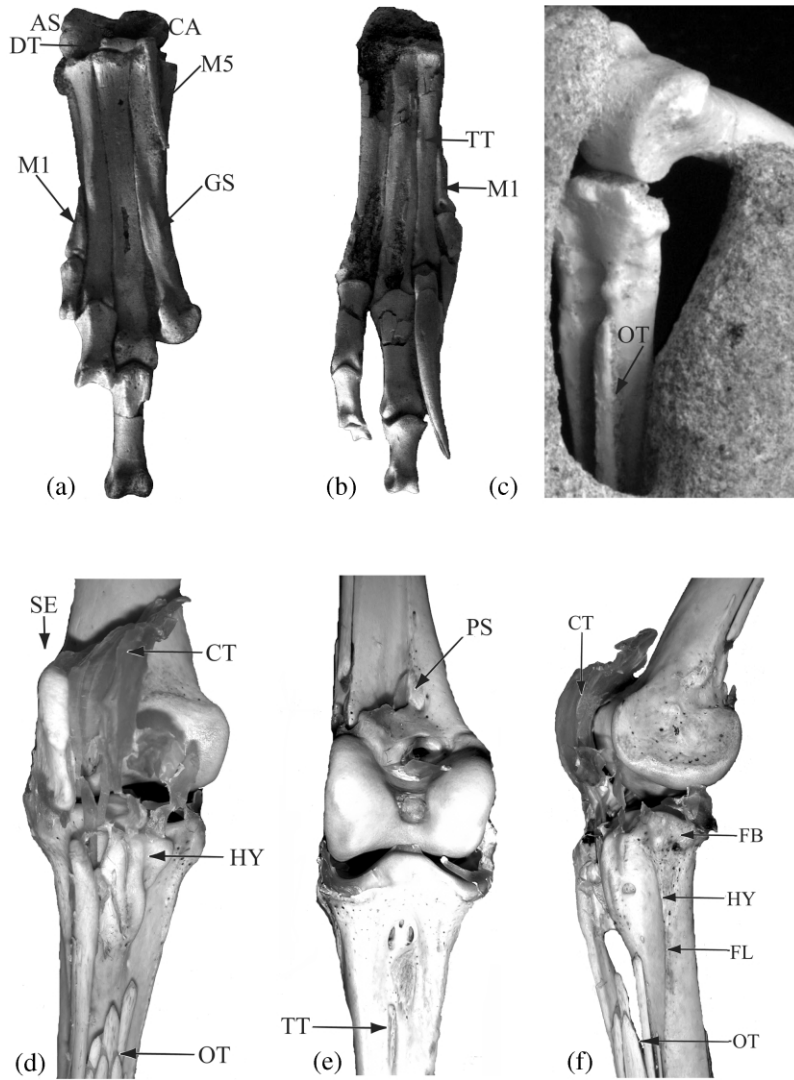
Fig. 6. Morphology of the ankle joint region and pes. (a, b) *Velociraptor* (Deinonychosauria/Dromaeosauridae, modified from Norell and Makovicky, 1997) right (a) or reversed left (b) pes in caudal (a) and cranial (b) views; (c) *Apsaravis* (IGM 100/1017; right distal tibiotarsus and proximal tarsometatarsus in oblique caudolateral view); (d–f) *Meleagris* (Neognathae; personal collection) right distal tibiotarsus and proximal tarsometatarsus in caudal (d), cranial (e), and lateral (f) views. *Abbreviations*: AS, astragalus; CA, calcaneum; CT, tibial cartilage; DT, distal tarsal (AS, CA, and DT are fused to the tibiotarsus in the birds pictured); FB, Tuberculum m. fibularis brevis; FL, Sulcus m. fibularis longus; GS, M. gastrocnemius insertion scar; HY, hypotarsus; M1, metatarsal I; M5, metatarsal V; OT, ossified tendons; PS, Pons supratendineus (supratendinal bridge); SE, ankle sesamoid; TT, Tuberositas m. tibialis cranialis. Not to scale.

4.9. Mm. caudofemorales

As Gatesy (1990), Gatesy (1995) and others have shown, the main head of this muscle group, M. caudofemoralis longus (CFL), was a relatively large muscle in basal Reptilia, originating from much of the ventrolateral surfaces of the caudal vertebrae. It remained large in basal theropods but was reduced in a stepwise sequence on the line to birds, becoming restricted to the pygostyle in basal birds and referred to as M. caudofemoralis pars caudalis (CFC).

Likewise, the insertion of M. caudofemoralis longus was a large tendon attaching to the caudal surface of the femur in ancestral Reptilia, with a secondary tendon leading from the distal end of the muscle to the caudal side of the knee joint, contributing to the origin of M. gastrocnemius
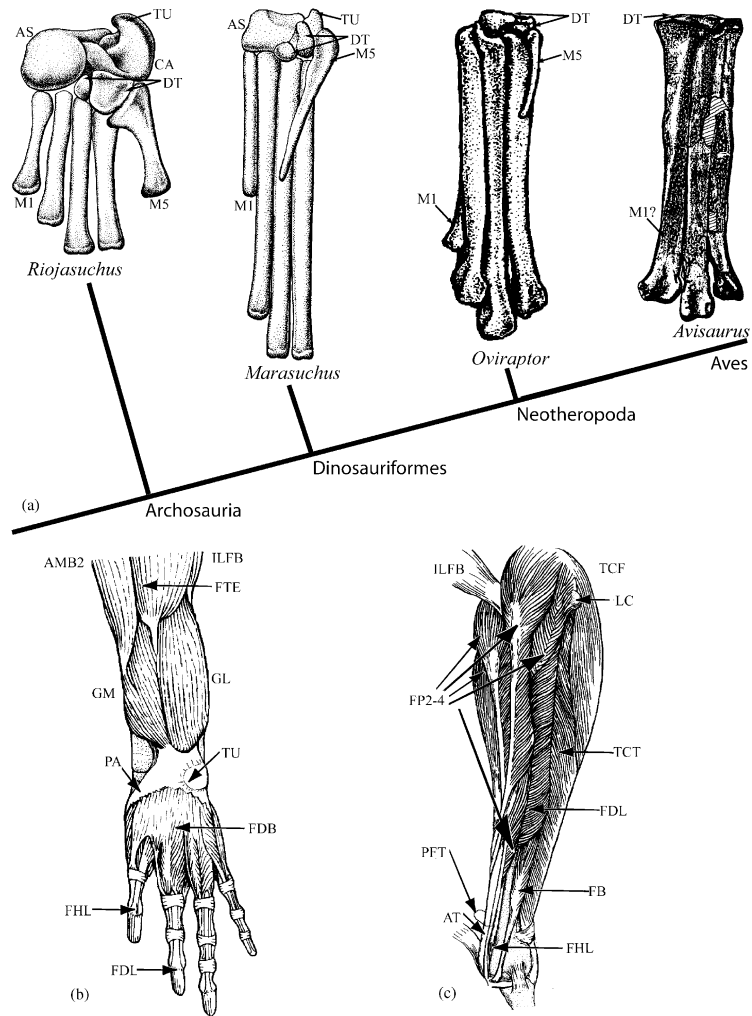
Fig. 7. Evolution of the tarsus (a) and associated lower limb tendons and muscles (b, c). (a) Metatarsals and tarsals (or tarsometatarsus) in caudal view: *Riojasuchus* (basal archosaur, modified from Sereno, 1991); *Marasuchus* (basal dinosauriform, modified from Sereno, 1991); *Oviraptor* (Oviraptorosauria, modified from Barsbold et al., 1990); and *Avisaurus* (Enantiornithes, modified from Brett-Surman and Paul, 1985); (b) Right lower limb of *Alligator* (Crocodylia; modified from Cong et al., 1998) in caudal view with superficial muscles shown; (c) Right lower limb of *Meleagris* (Neognathae; modified from Harvey et al., 1968) in lateral view with deeper muscles shown (Mm. gastrocnemii, etc. removed). *Abbreviations* as in Fig. 6 plus: AT, 'Achilles tendon' of Mm. gastrocnemii (cut); LC, lateral cnemial crest; PA, plantar aponeurosis; PFT, tendons of perforated digital flexors; TU, calcaneal tuber. Muscle abbreviations in Table 1 and the text; TCT and TCF are the tibial and femoral heads of M. tibialis cranialis; FP2–4 are the perforated digital flexor muscles. Not to scale.

lateralis. In basal archosaurs the attachment is even more robust, developing a fourth trochanter (Fig. 5; Dollo, 1883, 1888) that is marked with dense Sharpey's fibers (Reid, 1984). The trochanter and both tendons of insertion were reduced on the line to birds with the rest of the muscle–tendon complex. Hutchinson (2001b) and Carrano and Hutchinson (2002) suggested that the secondary tendon was lost when the fourth trochanter became less pendant (Dollo, 1883, 1888) in basal theropods.

Gatesy (1990), Gatesy (1995) elegantly showed how the main tendon then underwent stepwise reduction with the fourth trochanter in tetanuran theropods. The fourth trochanter was reduced to a small pit or scar in basal birds.

The second head of this muscle group, M. caudofemoralis brevis (CFB), has received less attention. Hutchinson (2001a; intimated by Romer, 1923b and others) proposed the homology of this muscle with M. caudofemoralis pars pelvica (CFP)

in Neornithes. M. caudofemoralis brevis did not change much on the line to Neornithes (Fig. 3). My analysis shows that it is not a neornithine autapomorphy as other authors have presumed (e.g. Vanden Berge, 1982; Vanden Berge and Zweers, 1993; Novas, 1996; Dilkes, 2000). Its origin was more medial from the postacetabular iliac region and caudosacral vertebrae in basal Reptilia, but became fully lateral on the line to birds. This shift is signalled by the evolution of a medial ridge on the ilium in basal archosaurs, becoming a 'brevis fossa' in basal dinosaurs. The fossa reduced onto the lateral surface of the ilium in basal birds and their closest non-avian relatives (Hutchinson, 2001a), but the muscle remained fairly large as M. caudofemoralis longus was reduced. The tendon of insertion remained on the caudal surface of the femoral shaft, lateral to the tendon of M. caudofemoralis longus, on the lateral side of the fourth trochanter (when present).

5. Lower leg muscles

Some of these inferences were detailed further by Dilkes (2000) and Carrano and Hutchinson (2002). Müller (1986), Müller (1989) hypothesized that some of these muscle groups atavistically returned to a putative ancestral state when the relative size of the fibula was experimentally increased in chicks; I will compare the results of my phylogenetic analysis to his developmental analysis when appropriate. Fig. 6 and Fig. 7 show most relevant anatomical features mentioned here.

5.1. Mm. gastrocnemii

Two heads, one lateral and one medial (GL, GM), were present in basal Reptilia, usually separated by the tendon of insertion of M. flexor tibialis externus (Fig. 7B), although lepidosaurs evolved a third head as a subdivision of the lateral head. At some point on the line to Neornithes a third head (M. gastrocnemius pars intermedia; GIM) evolved, probably as a subdivision of the medial head. Yet muscle scars do not clarify when this happened, because a large portion of the intermediate head originates from nearby soft tissues.

Ancestrally in Reptilia, the lateral head of M. gastrocnemius originated from an area proximal to the lateral femoral condyle on the caudal surface of the femur, with a contribution from the second-

ary tendon of M. caudofemoralis longus. The medial head originated from the medial side of the proximal tibia, with connections to the medial tendons of insertion of the deeper flexor cruris muscles. McMurrich (1905) contended that a femoral origin was ancestral for Reptilia, but my analysis shows that the femoral origin of the medial head is apomorphic for lepidosaurs. These origins changed little on the line to birds, although M. iliofibularis and M. ambiens (see above) had secondary tendinous attachments to the proximal aponeuroses of the these heads in ancestral archosaurs (Fig. 7B), and the medial head expanded with the cnemial crest in basal dinosaurs, becoming larger than the lateral head.

The tendons of the gastrocnemius muscle group follow a similar route along the caudal surface of the knee joint and crus in extant Reptilia until they approach their insertions near the ankle joint; then many differences among taxa are evident (Figs. 6 and 7). In ancestral Reptilia no distinct 'Achilles tendon' was present. The tendons not only inserted onto the tarsals and metatarsals (especially metatarsal V), but also extended distally to form a thick plantar aponeurosis covering the bottom of digits 2–4. In basal archosaurs this insertion was concentrated proximally onto the calcaneal tuber and fifth metatarsal as the plantar aponeurosis was reduced slightly.

Within dinosaurs the plantar aponeurosis was reduced with the calcaneal tuber, fifth metatarsal, and distal tarsals (Fig. 7A). However, the insertions of Mm. gastrocnemii remained robust. More discrete tendinous attachments were formed, indicated by scars on the caudal surfaces of the metatarsal shafts (Fig. 6A; Dilkes, 2000). In basal birds the insertions were focused onto the mid-caudal surface of the proximal tarsometatarsus when the fifth metatarsal was lost. Finally, in Ornithurae the tendons passed over a tibial cartilage (Section 5.2) and were united as an 'Achilles tendon' inserting onto a hypotarsus (Fig. 6D and F Fig. 7C; Chiappe, 1996, 2001; Cracraft and Clarke, 2001). The plantar aponeurosis remains, however, in extant birds as a vestigial fibrous connection to the caudal surface of the tarsometatarsus and the origins of the short flexors of the toes.

5.2. Digital flexor group

On the line to crown-group birds, this muscle group evolved the most subdivisions of any hin-

dlimb muscles, although some rudimentary subdivision was ancestrally present (Kriegler, 1961). In extant Reptilia, only two major heads are present: M. flexor digitorum longus (FDL) and M. flexor hallucis longus (FHL), with other short distal heads such as M. flexor digitorum brevis (FDB) variably present (Fig. 7B; Carrano and Hutchinson, 2002). However, in birds not only are the former two heads present as the deepest parts of this muscle group, but at least five other more superficial heads are homologues of this muscle group: Mm. flexores perforati digiti II, III, et IV and Mm. flexores perforantes et perforati digiti II et III (Fig. 7C; Gadow and Selenka, 1891; George and Berger, 1966). Wortham (1948) showed that M. plantaris in chick embryos is intimately associated with other digital flexors that develop from a deep tibial mass, rather than with the more superficial Mm. gastrocnemii, so M. plantaris is likely another part of the digital flexors in birds. Regardless, on the line to crown-group birds this group was divided from two into seven or more heads. Unfortunately, muscle scarring gives few hints as to how or when this subdivision proceeded.

In basal Reptilia, the main heads of the digital flexors originated close to the lateral head of M. gastrocnemius on the caudal surface of the distal femoral shaft, with additional attachments to the proximal tibia and fibula. M. flexor digitorum brevis originated mainly from the plantar aponeurosis of the pes and adacent metatarsal bone surfaces (Fig. 7B), and thus its origin was partly from the tendons of insertion of Mm. gastrocnemii as well as the digital flexors. As mentioned above, M. ambiens and parts of the flexor cruris evolved secondary tendons that contribute to aponeurotic origins of the digital flexors in archosaurs (Fig. 7B). The five or more extra heads that evolved on the line to birds expanded some of their origins from the distal femur onto the proximal tibia and fibula. In basal dinosaurs, the fossa flexoria (Fig. 2) on the caudal margin of the proximal tibia deepened and probably served as an origin for part of this muscle group. Additionally, basal theropod dinosaurs evolved a peculiar sulcus or fossa on the medial surface of the proximal fibula (Fig. 4) that presumably corresponds to the fibular origin of at least one of these muscle heads (Rowe, 1989), perhaps along with the insertion of M. popliteus (Farlow et al., 2000; Carrano and Hutchinson, 2002; see below). M. flexor digitorum brevis shifted its origin from the plantar aponeurosis to the caudal surface of the metatarsus as the plantar aponeurosis was reduced on the line to birds.

Müller (1986), Müller (1989) suggested that an accessory femoral origin of part of M. flexor perforatus in 55% of experimentally operated chick limbs was an atavistic condition, representing the reappearance of an ancestral origin of this muscle from the femur. The evolutionary pattern is more complex: ancestral Reptilia had a partial femoral origin of M. flexor digitorum longus, which split into many digital flexor heads on the line to Neornithes. However, other parts of the origin came from the tibia and fibula in basal reptiles anyway, so the origin for this muscle group did not change dramatically. Thus there is not strong phylogenetic support for the hypothesis that the experimental chicks had atavistic muscles.

The tendons of the digital flexors (except M. flexor digitorum brevis) all cross the ankle joint, passing through a series of ligaments en route to their insertions on the ventral (plantar) surfaces of the distal ends of the digits (Fig. 7B and C). In ancestral Reptilia the tendons also contributed to the complex plantar aponeurosis (see above and Russell, 1993), but this connection was eliminated in theropod dinosaurs as the insertions became concentrated onto the flexor tubercles of the distal phalanges. As the digits were reduced from five to three main digits in theropods, the tendons were likewise restricted to digits 2–4. Nonetheless, the arrangement of these tendons before they reach the phalanges in extant birds is highly variable (George and Berger, 1966).

In basal birds the insertion of the medial M. flexor hallucis longus tendon changed as the first metatarsal shifted its articulation onto the caudal rather than the medial surface of the tarsometatarsus (Middleton, 2001). Furthermore, in basal birds (especially Ornithurae) the existence of a well-developed trochlea on the caudal surface of the distal tibiotarsus (Chiappe, 2001; Norell and Clarke, 2001) signals the presence of a tibial cartilage (Fig. 6D and F), which is a (sometimes ossified) sesamoid-like structure developing underneath the tendon of M. gastrocnemii and perforated by the digital flexor tendons.

Another striking feature of the digital flexor tendons is that they are frequently ossified in Neornithes (Fig. 6; Ranvier, 1875), albeit seldom fossilized. Vanden Berge and Storer (1995, p. 73) queried whether intratendinous ossification in birds

is ''phylogenetically 'old'.'' Mapping known occurrences of the ossified distal tendon of M. flexor digitorum longus onto a phylogeny (Cracraft and Clarke, 2001) suggests a plausible scenario. Ossification of the tendon of M. flexor digitorum longus is reconstructed as ancestral for Neornithes, secondarily lost in some groups such as Ratitae. The ornithurine bird *Apsaravis* (Norell and Clarke, 2001) has a fossilized tendon near the caudal surface of the tarsometatarsus (Fig. 6C), in the expected position for an ossified tendon of M. flexor digitorum longus. Thus fossils show that this ossification is likely ancestral for Ornithurae, not just the crown-group, and it would not be surprising if more ossified tendons have been overlooked or unpreserved in fossils. Furthermore, the presence of ossified tendons and other soft tissues in a variety of dinosaurs suggests that there was some latent molecular capacity for tendon mineralization in most or all dinosaurs that was only expressed in some taxa under special biomechanical conditions. Ossification of the tendon of M. flexor hallucis longus may be ancestral for a subclade of extant birds, but like all other ossified pelvic limb tendons it does not presently optimize as ancestral for Neornithes.

5.3. Digital extensor group

This muscle group has been a source of some confusion in the literature, discussed by Dilkes (2000) and Carrano and Hutchinson (2002). The least speculative inference based on the homologies accepted in the previous studies is that ancestrally Reptilia had three main muscle heads: M. extensor digitorum longus, M. tibialis anterior, and M. extensor hallucis longus, and a fourth, more variable distal head, M. extensor digitorum brevis, as well as intrinsic pedal heads of unresolved homology and evolution.

Unlike the digital flexors, the distal tendons of this group did not ancestrally contribute to a thick superficial aponeurosis in ancestral Reptilia, lacked tendons extending to the toes, and are less frequently ossified in Neornithes (Vanden Berge and Storer, 1995). However, like the digital flexors, the tendons passed longitudinally along the crus (but on the cranial side) through a series of constraining ligaments and varied with the number, form, and position of the digits.

5.3.1. M. extensor digitorum longus (EDL)

This head originated cranially from the base of the lateral femoral condyle, lateral to the sulcus for the triceps extensor tendon and distal to the origin of the lateral head of M. femorotibialis. The origin shifted its attachment onto the craniomedial surface of the tibia, becoming distal to the origin of M. tibialis anterior as the cnemial crest expanded in dinosaurs. Intermuscular lines define its longitudinal boundaries in many fossils (Carrano and Hutchinson, 2002). In Ornithurae, an intercnemial sulcus between the lateral and cranial cnemial crests (Fig. 2) was the proximal-most origin of this muscle–tendon complex.

Ancestrally, the tendon passed through retinacula on the cranial side of the distal tibia and proximal metatarsus, and then divided into multiple tendons that inserted on the cranial surfaces of the proximal metatarsals (especially II and III), often fusing with M. tibialis anterior. These insertions shifted distally onto the phalanges and unguals in basal dinosaurs, as demonstrated by large extensor pits and rugosities on the dorsal surfaces of the unguals of basal dinosaurs. With this distal shift their ancestral connection with M. tibialis anterior was reduced. Carrano and Hutchinson (2002) suggested that these changes were accomplished by fusion of M. extensor digitorum brevis to the distal end of M. extensor digitorum longus (see below). In Neornithes, the tibial retinaculum became ossified as a supratendinal bridge (Pons supratendineus; Fig. 6E) over an extensor canal, containing the tendon before it splits into multiple tendons near the ankle. The groove covered by the bridge evolved earlier, in Ornithurae (Chiappe, 1996, 2001; Cracraft and Clarke, 2001; Norell and Clarke, 2001).

5.3.2. M. tibialis anterior (TA)

Reptilia ancestrally had a single head of this muscle, whereas extant birds have two heads (the femoral and tibial heads of M. tibialis cranialis; TC). A scarred fossa in the same location as the M. tibialis cranialis femoral origin in Neornithes suggests that the second (femoral) head evolved in Ornithurae and more basal birds (Chiappe, 2001).

The origin of M. tibialis anterior was from the craniomedial surface of the proximal tibia in ancestral Reptilia, distal to the insertion of the triceps extensor tendon and deep, distal, and medial to M. extensor digitorum longus. It expanded with the

cnemial crest in basal dinosaurs, becoming restricted proximally on the tibia. Once the femoral head of M. tibialis cranialis evolved, its origin was from the cranial surface of the lateral femoral condyle. The femoral head then passed through the incisura tibialis enclosed by the lateral cnemial crest (Fig. 2) down the cranial face of the crus to join the tendon of the tibial head (Fig. 7C). The origins of both heads became superficial, proximal, and lateral—not deep, distal, and medial—to M. extensor digitorum longus (not shown in Fig. 7C but deep to the muscles pictured).

The tendon maintained its insertion on the line to birds, passing through a retinaculum at the distal end of the crus to insert on the craniolateral surfaces of the proximal metatarsals, especially metatarsal I in basal reptiles. The insertion region is marked by several tubercles (Fig. 6B and E) in many dinosaurs and other archosaurs (Brett-Surman and Paul, 1985; Norell and Makovicky, 1997; Dilkes, 2000; Carrano and Hutchinson, 2002). On the line to birds, the tendon maintained its insertion on the medial border of the metatarsus (as tubercles and other scars demonstrate), but the insertion shifted off metatarsal I as the hallux reduced and moved distally in theropod dinosaurs, especially when the hallux became retroverted in basal birds (Middleton, 2001). The increased size of the tubercle (Tuberositas m. tibialis cranialis) on the cranial surface of metatarsal II (and III) in basal birds (Chiappe, 2001) may relate to this concentration of the insertion of M. tibialis cranialis onto metatarsal II as the hallux became retroverted. In extant birds, the two heads fuse at their distal bellies, proximal to the ankle, to form a common tendon of insertion rather than inserting separately. This common tendon passes deep to the Retinaculum extensorium tibiotarsi ('ligamentum transversum') but superficial to the supratendinal bridge.

Alternatively it is worth considering that avian homologies with basal reptiles have been misinterpreted. The muscle named 'M. extensor digitorum longus' in birds could actually be the single homologue of M. tibialis anterior, whereas the two heads of 'M. tibialis cranialis' in birds may be homologues of M. extensor digitorum longus. In this slightly more parsimonious scenario, the heads of M. extensor digitorum longus remained superficial, proximal, and lateral to M. tibialis anterior (the tibial head shifting from the ancestral origin on the femur onto the tip of the cnemial crest), and had a common insertion on the cranial surface of the medial border of the proximal metatarsus, passing over the supratendinal bridge. M. tibialis anterior maintained its deeper, distal, and medial position relative to M. extensor digitorum longus, but it fused distally with M. extensor digitorum brevis to become the only true digital extensor, inserting on the distal toes. I maintain the classical anatomical nomenclature and homologies here, but this alternative hypothesis deserves more ontogenetic, anatomical, and phylogenetic examination.

5.3.3. M. extensor hallucis longus (EHL)

This small, short muscle originated from the craniolateral surface of the distal fibular shaft and inserted on the cranial surface of the hallucal phalanges on basal reptiles. In basal birds its origin shifted onto the craniomedial surface of the proximal tarsometatarsus, and its insertion moved caudally with hallucal retroversion.

5.3.4. M. extensor digitorum brevis (EDB)

This muscle was plesiomorphically present in Reptilia, originating from the proximal metatarsals and tarsals and inserting on the dorsal surfaces of the distal pedal phalanges. In Neornithes it is absent, and coincidentally the tendons of M. extensor digitorum longus insert more distally on the toes rather than the metatarsals (see above). These features led Carrano and Hutchinson (2002; also Dilkes, 2000) to propose that this muscle fused with the distal end of M. extensor digitorum longus in dinosaurs, accomplishing both the 'loss' of this muscle and the distal 'shift' of the M. extensor digitorum longus insertions.

5.4. Other lower leg muscles

5.4.1. M. pronator profundus (PP)

Also known as M. tibialis posticus or posterior (Gadow, 1882; McMurrich, 1905; Romer, 1922; Kriegler, 1961; Tarsitano, 1981), this muscle–tendon complex ancestrally originated as a single fleshy head, associated (and often confused) with M. interosseus cruris, originating from the caudomedial side of the distal fibula, lateral tibia, and proximal tarsals. Its main tendon wrapped around the caudal side of the ankle joint and inserted caudolaterally on metatarsal I, with other tendons variably connecting to the proximal parts of nearby metatarsals II–III and a protuberance on the caudal side of distal tarsal 4, as well as the plantar aponeurosis.

Extant birds lack an identifiable homologue of this muscle, so it was lost on the line to Neornithes, but the timing of this loss remains uncertain. I propose that M. pronator profundus was lost in basal theropod dinosaurs as the distal fibular shaft was reduced, appressed to the tibia (Fig. 4), and then eliminated in basal birds. Its insertion on the hallux reduced concurrently.

5.4.2. M. popliteus and M. interosseus cruris (POP, IC)

There is some disagreement about the homology and nomenclature of this muscle group, but I follow many authors (e.g. Osawa, 1898; Romer, 1922; Snyder, 1954; Landsmeer, 1990) in recognizing these two closely associated muscles as different parts of a tibiofibular muscle group. M. popliteus is typically smaller, is restricted to the proximal end of the crus, and its muscle fibers run at different angles than the larger, more distal M. interosseus cruris (McMurrich, 1905; Walker, 1973; Russell, 1993).

In ancestral Reptilia these two divisions had fleshy attachments spanning much of the space between the fibular and tibial shafts deep to M. pronator profundus. M. interosseus cruris was reduced on the line to birds, whereas M. popliteus was retained (Carrano and Hutchinson, 2002). The formation of a fibular crest on the tibia (Section 4.2, and Farlow et al., 2000) restricted most of the M. popliteus origin to a region proximal to the crest in basal theropods. M. interosseus cruris reduced distal to the crest. As the fibula was reduced in basal dinosaurs, the insertion of M. popliteus became more proximally concentrated, perhaps partly in a large fossa in the medial surface of the proximal fibula (Fig. 4; Section 5.2). In basal theropods, M. interosseus cruris was reduced to a slim muscle or membrane as the distal fibula became appressed to the tibia, then was completely lost in basal birds. Therefore M. popliteus remains as the vestige of this muscle group in extant birds, connecting the caudal side of the proximal-most tibia, near the fossa flexoria (Fig. 2), to the caudomedial proximal fibula.

Müller (1986), Müller (1989) showed that in some cases chicks with experimentally enlarged fibulae atavistically regained a distal muscle resembling M. interosseus cruris. However, in some other cases the proximal M. popliteus was lost, which does not reflect an ancestral condition. Reptilia ancestrally had a proximal division cor-

responding to M. popliteus, retained in Neornithes, so again there is an inconsistent evolutionary signal from experimental atavisms (see M. flexor digitorum longus above).

5.4.3. Mm. fibulares longus et brevis (FL, FB)

These two heads (= 'Mm. peronei anterior et posterior') are common legacies for Reptilia (Dilkes, 2000). The long head originated from the lateral surface of the fibula, especially the region distal to the insertion of M. iliofibularis, and the short head originated just distal and craniolateral to that area. M. fibularis longus shifted its origin onto the proximal tibia and cnemial crests, becoming proximal to the M. iliofibularis tubercle of insertion in basal birds. The origin of M. fibularis brevis moved from the lateral side of the distal fibular to the tibial shaft in basal birds once the distal fibula was lost. Chick embryos with experimentally enlarged fibulae demonstrate that the more distal fibular origin of M. fibularis brevis is atavistically reacquired (Müller, 1986, 1989).

In ancestral Reptilia, the tendon from M. fibularis longus passed along the lateral border of the crus to the caudolateral side of the ankle, inserting on the lateral surfaces of the proximal tarsals and metatarsals (especially the calcaneal tuber and metatarsal V; Fig. 7A) as well as part of the plantar aponeurosis to digit 5. The tendon from M. fibularis brevis ancestrally inserted caudal to the long head near the proximal end of metatarsal V. Similar to Mm. gastrocnemii, these insertions became concentrated proximally onto the lateral side of the tarsometatarsus on the line to birds with the reduction of the plantar aponeurosis, digit 5, and the calcaneal tuber in theropod dinosaurs. This change was conspicuous in basal birds and Ornithurae, which lost metatarsal V and evolved the tibial cartilage that M. fibularis longus inserts on (Fig. 6). In most extant birds, a distal continuation of the tendon of M. fibularis longus passes along a groove (Fig. 6B; Sulcus m. fibularis longus) on the caudolateral side of the proximal tarsometatarsus before it joins M. flexor perforatus digiti III. To my knowledge this sulcus is unknown in birds outside the crown clade. The tendon of M. fibularis brevis maintained its insertion caudal to M. fibularis longus and its sulcus, terminating at a tubercle (Fig. 6B; Tuberculum m. fibularis brevis) on the caudolateral side of the proximal tarsometatarsus.

6. Discussion

This analysis has elucidated several general patterns of the evolution of pelvic limb muscle–tendon complexes on the line to crown-group birds. Many of these changes involve modification of the moment arms (An et al., 1984) and physiological cross-sectional areas (Gans and de Vree, 1987) of muscle–tendon complexes. For example:

(1) Thigh muscles located ventral to the hip joint, and some located dorsally, de-emphasized the ancestral adduction/abduction-based hip control mechanism (Romer, 1923a,b,c; Charig, 1972) in favor of a mechanism employing long-axis rotation of the femur (Hutchinson and Gatesy, 2001). Some muscles such as parts of the flexor cruris group were lost, whereas shifts of the origins and insertions of other 'abductor' (e.g. M. iliofemoralis or M. iliotrochantericus caudalis and M. iliofemoralis externus of Neornithes) and 'adductor' muscles (e.g. M. puboischiofemoralis externus or Mm. obturatorii of Neornithes) changed their moment arms and hence their functions. Romer (1923a), Romer (1923b), Romer (1923c), Charig (1972), Walker (1977), and many others have discussed the relationship of these changes to the evolution of a more erect posture and parasagittal gait in basal dinosaurs, but salient changes also evolved within dinosaurs on the line to birds (Hutchinson and Gatesy, 2001).

The hip joint evolved differently from distal limb joints. Although the importance of adduction and abduction was reduced on the line to birds, the ball-and-socket articulation of the femoral head and acetabulum maintained three degrees of freedom at the hip. Long-axis rotation and adduction/abduction were limited relative to the ancestral condition, yet the morphology of the bones and soft tissues of the hip joint preserved three-dimensional limb control on the line to birds (Hutchinson and Gatesy, 2001). This flexible control mechanism is an integral component of the terrestrial locomotion of extant birds, and fossils help uncover the complex series of stepwise changes that assembled and modified it.

(2) Hip extensor muscles generally expanded, although the primary hip extensor of basal reptiles (M. caudofemoralis longus) was reduced nonetheless (Gatesy, 1990, 1995). The postacetabular head of M. iliotibialis, M. iliofibularis, M. ischiofemoralis, and M. caudofemoralis pars caudalis all increased in relative size with the expansion of postacetabular surface area for muscle origins (Hutchinson, 2001a). Additionally, the moment arms of Mm. adductores femores were modified from hip adduction into extension (Hutchinson and Gatesy, 2001), and part of the flexor cruris group (M. flexor cruris lateralis) gained an accessory hip extensor head. On biomechanical grounds, this is not surprising. The center of mass of the trunk moved cranially on the line to birds (Gatesy, 1990, 1995), incurring a larger hip flexor moment. Therefore hip extensors remained important for supporting the body (Roberts, 2001; Hutchinson and Garcia, 2002) despite the reduction of femoral excursion.

(3) In contrast, hip flexors expanded only slightly, and some were even reduced (e.g. cranial divisions of the flexor cruris group) or lost their hip flexor moment arms (e.g. M. puboischiofemoralis internus or M. iliotrochantericus medius; M. puboischiofemoralis externus or Mm. obturatorii). Hip flexors were ancestrally useful for overcoming limb inertia to protract the limb, but on the line to Neornithes this utility was diminished along with femoral retraction. Crown-group birds have simplified the number of hip flexors from six to two main muscle–tendon complexes: M. iliotibialis cranialis and M. iliotrochantericus cranialis.

(4) The 'triceps' knee extensor musculature was enormously expanded on the line to Neornithes, including expansions of the surfaces for tendon insertion, such as the ossified patella and enlarged cnemial crests, which likewise magnified the knee extensor moment arms of these muscles. Knee extensors were critical in early bipedal dinosaurs for countering large knee flexor moments during locomotion (Roberts, 2001; Hutchinson and Garcia, 2002), and larger moment arms of knee extensor muscles (Alexander and Dimery, 1985) could have prevented muscle stresses from becoming too high. Knee extensors remained important for birds as femoral retraction was reduced in favor of knee flexion and extension (Gatesy, 1990, 1995; Carrano, 1998), despite the reduction of the number of 'hamstring' muscles that cocontract to produce knee flexor moments opposed by the extensors (Roberts, 2001).

(5) 'Hamstring' muscles originating from the pelvis and inserting around the caudal side of the knee joint were simplified from many heads to a few large heads. Some parts of the flexor cruris group were completely lost (e.g. M. puboischioti-

bialis, M. pubotibialis, and 2–3 heads of M. flexor tibialis internus). In contrast, M. iliofibularis and the remnants of the flexor cruris group (Mm. flexor crures lateralis et medialis of Neornithes) became proportionately large, able to simultaneously exert large hip extensor and knee flexor moments that are particularly important early in the stance phase (Roberts, 2001). These changes match an increase of the contribution of knee flexion and extension to stride length on the line to birds (Gatesy, 1990, 1995; Carrano, 1998, 2000; Hutchinson and Gatesy, 2001; Carrano and Hutchinson, 2002). However, current understanding of how such muscles that span multiple joints actually function during locomotion in archosaurs is limited (Roberts, 2001), so it is difficult to correlate anatomical and biomechanical evolutionary changes. Likewise, the importance of secondary tendons, so prevalent in the 'hamstrings' of archosaurs, that merge into the aponeuroses of distal limb muscles and might transmit forces even to the ankles or toes needs further investigation.

Some hypotheses, however, can be ruled out or supported by this analysis. For example, Watson (1869) suggested that perching in birds was enabled by the transfer of the origins of some digital flexors, M. flexor hallucis longus, and M. tibialis cranialis ('anticus') onto the femur 'to procure consentaneous [*sic*] flexion of all the joints from the knee to the toes.' My analysis shows that these muscles ancestrally had at least partial origins from the femur in more basal, non-perching reptiles, so a tight correlation of perching behavior and femoral origins of these muscles is rejected. However, Watson (1869) also inferred that the ansa M. iliofibularis ('biceps loop') had an important role in perching, and my analysis corroborates that this structure is unique to extant birds (and perhaps some close outgroups), so this hypothesis is not falsified by available data. Likewise, Watson's (1869) contention that M. ambiens has no strong correlation with perching is supported by the plesiomorphic presence of this muscle in Reptilia, and its frequent absence in birds (Beddard, 1898; McKitrick, 1991).

(6) Fusion or ossification of many ancestrally separate or unossified structures was a striking trend on the line to birds. Many elements such as the pelvis and sacrum, tibiotarsus, and tarsometatarsus were fused. Additionally, many sesamoid bones and other moment arm-enhancing structures evolved in basal birds, especially Ornithurae. The ungual flexor tubercles, cnemial crests, tibial cartilage, hypotarsus, ansa M. iliofibularis, patella, supratendinal bridge, and ossified tendons each altered limb function by limiting joint or tendon excursion, or increasing the moment arms of tendons (Alexander and Dimery, 1985). In particular, the capacity of muscles to extend joints (or prevent hyperflexion) was enhanced by these innovations, a critical specialization for the rapid terrestrial locomotion of extant birds and their flightless theropod ancestors.

Heterotopic elements such as sesamoids and ossified tendons vary considerably in living animals (Urist, 1980; Sarin, 2000), because their expression is modulated in response to their mechanical environment (Carter et al., 1998; Sarin et al., 1999; Olson, 2000; Sarin, 2000). The prevalence of heterotopic elements in Ornithurae (Bledsoe et al., 1993; Vanden Berge and Storer, 1995; Norell and Clarke, 2001), including early in development (Hudson et al., 1965; Hogg, 1980) is consistent with the inference that these elements evolved in response to altered mechanical loading, such as increased hip and knee flexion and ankle extension, or at least relative increases of forces and moments experienced by the muscles that cross these joints. Sarin (2000) and Sarin et al. (1999) used biomechanical theory to show how sesamoid evolution matches the evolution of loading patterns in other animals.

Curiously, ossified tendons are absent proximal to the knee joint (except M. iliofibularis in owls; Vanden Berge and Storer, 1995). It is tempting to think that this pattern relates to different biomechanical roles of the hip and knee joints (producing power for accelerations) compared to the ankle and toe joints (acting like stiff springs), but Roberts (2001) has shown that the ankle joints of birds can still have high power output. Regardless, the observation that mineralization increases tendon tensile strength, stiffness, and elastic energy storage capacity in birds (Landis et al., 1995; Silver et al., 2001) lends credence to the hypothesis that ossified lower limb tendons in birds enhance their spring-like functions. This anatomical and biomechanical correlation may relate to the evolution of ossified tendons, but caution is warranted because alternative explanations and data have been proffered (Bennett and Stafford, 1988; Olmos et al., 1993), such as preventing tendon fatigue caused by repetitive stresses during intense activities (Buchanan and Marsh, 2001).

Overall, available anatomical and biomechanical evidence concurs that 'modern neornithine' locomotor function was first present in Ornithurae, although many stepwise specializations evolved earlier in archosaurs (Gatesy, 1990, 1995; Gatesy, in press, Sereno, 1991; Gatesy, 1999a,b; Chiappe, 1996; Carrano, 1998, 2000; Farlow et al., 2000; Hutchinson and Gatesy, 2001; Carrano and Hutchinson, 2002).

(7) It is well known that the articular surfaces of limb joints distal to the hip changed to restrict joint rotation to flexion and extension in dinosaurs (e.g. Charig, 1972; Sereno, 1991; Novas, 1996). For example, osteological features almost completely eliminated the ancestral 'crural mechanism' involving pronation/supination of the fibula (Rewcastle, 1983; Landsmeer, 1990; Müller and Streicher, 1989; Müller and Streicher, 1992; Fuss, 1996), and the ankle joint was restricted to a hinge very early in archosaur evolution (Charig, 1972; Sereno, 1991; Novas, 1996). It is less well known that changes of the muscles and tendons crossing these joints enhanced this restriction of joint function. My analysis shows when the capacity of many muscles to plantar-flex (and to a lesser degree, dorsi-flex) the ankle and toes was enhanced by mechanisms such as division of the digital flexors into multiple large heads, or reduction of the plantar aponeurosis and expansion of Mm. gastrocnemii (Carrano and Hutchinson, 2002). Many of these changes first appeared in basal dinosaurs with the origin of bipedalism, erect posture, and digitigrade stance, but others evolved sequentially on the line to Neornithes.

Walker (1972) surmised that the bird ankle joint, in which he included the tibial cartilage, as part of a 'tendon-sling tarsus,' was derived from a crocodilian 'calcaneal heel,' maintaining similar relationships to the tendons of Mm. gastrocnemii and M. fibularis (=peroneus) longus. The origin of birds from crocodilians has since been rejected on other grounds (e.g. Gauthier et al., 1988; Prum, 2002), and there is no convincing developmental or phylogenetic evidence that the tibial cartilage is a vestige of the calcaneal tuber. Yet my analysis supports Walker's hypothesis that a mechanism of ankle joint control based on a calcaneal tuber that provided leverage for Mm. gastrocnemii and other ankle extensors was plesiomorphic for archosaurs. Birds (and dinosaurs in general) subsequently lost this mechanism with the calcaneal tuber, which is curious because this change should have reduced

the relative length of the ankle extensor moment arm. Consequently, dinosaurs lacking a calcaneal tuber probably experienced relatively higher muscle and tendon forces, perhaps facilitating spring-like behavior of muscle–tendon complexes. However, if dinosaurs had proportionately larger muscles as in birds, peak muscle stresses might have remained low (Roberts, 2001). Regardless, the evolution of a large hypotarsus and tibial cartilage in Ornithurae is significant because it would have secondarily increased the ankle extensor moment arm relative to the ancestral dinosaurian condition.

(8) Overall, the number of musculoskeletal changes on the line to crown-group birds was considerable. Rowe (1986) suggested that few myological transformations accompanied the evolution of 'avian' bipedalism despite dramatic skeletal transformations. My analysis shows quite the opposite, although conservatism in some muscles is surprising. A sequence of approximately 151 changes of myological character states evolved on the line to Neornithes (Appendix C). Roughly three traits changed from basal reptiles to Sauria, with lepidosaurs evolving about six unique traits in their lineage, whereas 28 transformations evolved on the line to Archosauria, with crocodylomorphs evolving at least five apomorphies (these numbers are probably slight underestimates, given my emphasis on neornithine apomorphies). In contrast, 18 more modifications had evolved by the origin of Dinosauria. Theropod dinosaurs evolved 39 novel features in a stepwise pattern from basal theropods up to the origin of Aves. Birds themselves evolved some 41 more apomorphies before the origin of Neornithes, and Neornithes may have as many as 22 of its own unique musculotendinous traits (although many of these are ambiguous in fossils). Thus, roughly 120 character state transformations evolved on the line to Neornithes after its divergence from its sister clade, the line to Crocodylia. The evolution of the pelvic limb was a long stepwise sequence of assembly and modification of muscular, tendinous, and osteological traits.

This synthesis of the stepwise series of musculoskeletal changes in the pelvic limb on the line to crown-group birds reveals several areas for productive future research that can reveal more about the history of birds (Prum, 2002). Certainly the hypotheses of muscle homology and character state transformation assumed or proposed here

deserve more examination with additional developmental, histological, anatomical, and paleontological data. Musculoskeletal reconstruction can illuminate the functional significance of systematic characters and unusual anatomical specializations in birds and other sauropsids (Bryant and Russell, 1992; Witmer, 1995), especially when coordinated with biomechanical information (Hutchinson and Gatesy, 2001). Testing hypotheses of the link between form and function in muscle–tendon complexes requires more reliable quantifications of their moment arms (An et al., 1984; Alexander and Dimery, 1985) and physiological cross-sectional areas (Gans and de Vree, 1987). Recent biomechanical research (Delp et al., 1994; Delp et al. 1999; Full and Ahn, 1995) offers promising tools for reconstructing these and other details of musculoskeletal function that would raise the bar for biomechanical research in paleobiology and reveal more about the evolution of archosaur locomotion.

Because tendon attachments to bone are often evident and readily circumscribed in fossils, synthesis of research on tendon (and sesamoid) microstructure, development, and biomechanics (e.g. Benjamin and Ralphs, 1998; Carter et al., 1998; Sarin, 2000; Silver et al., 2001) will uncover clues about locomotor mechanics in extinct animals, reciprocally illuminating how the extant tissues evolved. Furthermore, an emerging understanding of locomotor kinematics, kinetics, and neuromuscular control in extant archosaurs (Gatesy, 1991, 1997, 1999a,b; Reilly and Elias, 1998; Reilly, 2000; Roberts, 2001) needs more integration into an evolutionary perspective in order to unravel how behavioral mechanisms such as erect posture, bipedalism, rapid running (Hutchinson and Garcia, 2002), 'Groucho running' (McMahon et al., 1987), and perching evolved. For together, fossils, phylogeny, anatomy, and biomechanics are more potent tools for testing hypotheses in evolutionary biomechanics than any of them is alone. All of these lines of evidence are crucial for discovering more about the biology of birds and other bizarre archosaurs.

Acknowledgments

Appendix A: Character list

The following characters were scored into the data matrix in Appendix B. Abbreviations for muscle names used here are also listed in Table 1 and some of the figures. Notes in brackets [] correspond to osteological correlates that were observed or assumed, if not otherwise stated in the character description. Ordered characters are noted.

1. M. iliotibialis (IT): number of heads
   0: One or two; weakly subdivided
   1: Three [three separate regions of muscle scarring]
2. IT: origin
   0: Dorsolateral ilium, superficial to other iliac muscles [rugose dorsal rim of ilium]
3. IT: insertion (common 'triceps' extensor tendon); Ordered
   0: Tibial tuberosity
   1: Cnemial crest
   2: Cranial and lateral cnemial crests
4. Patella as ossified sesamoid in extensor tendon
   0: Absent
   1: Present [patellar sulcus present on femur as proximal extension of intercondylar sulcus]
5. M. femorotibialis (FMT): number of heads; Ordered
   0: One; weak subdivision
   1: Two [anterior and posterior intermuscular lines]
   2: Three [medial intermuscular line]
6. FMT: origin
   0: Proximal half of femoral shaft
   1: Bulk of femoral shaft [strong intermuscular lines]

7. FMT: distal subdivision of lateral head
   0: Absent
   1: Present [craniomedial muscle scar on distal femoral shaft]
8. FMT: insertion
   0: With IT, AMB extensor tendon
9. M. ambiens (AMB): number of heads
   0: One
   1: Two
10. AMB: origin(s)
    0: Pubic tubercle; proximally adjacent to PUT (if present)
    1: Cranial preacetabular cartilage and medial proximal pubis
11. AMB: insertion
    0: with IT, FMT extensor tendon
    1: additional secondary tendon perforating extensor tendon, to origins of digital flexors (and GL)
12. M. iliofibularis (ILFB): origin
    0: Dorsal postacetabular ilium, between IF and FTE [scarred region]
13. ILFB: insertion; Ordered
    0: Craniolateral proximal fibula [rugosity]
    1: Craniolateral proximal fibula [tubercle]
    2: Lateral proximal fibula [tubercle]
    3: Caudal proximal fibula [tubercle]
14. ILFB: secondary tendon
    0: Absent
    1: Present, to GL aponeurosis
15. IFLB: insertion induces fibular crest on tibia
    0: Absent
    1: Present
16. ILFB: Ansa
    0: Absent
    1: Present [tubercles on lateral femoral condyle near GL origin]
17. M. iliofemoralis (IF): number of heads
    0: One: IF
    1: Two: M. iliofemoralis externus (IFE) and M. iliotrochantericus caudalis(ITC) of Neornithes [separate insertions evident]
18. IF: origin
    0: Small, above acetabulum
    1: Large, expanded preacetabularly with ilium
    2: Divided into IFE and ITC portions
19. IF (or IFE): insertion

0: Caudolateral [internal trochanter]
1: Craniolateral [trochanter major]
2: Caudolateral femoral shaft between FMT origins [flat shelf; proximal knob]
3: IFE on prominent trochanteric shelf or lateral ridge; ITC separate
4: IFE on reduced scar-like trochanteric shelf; ITC separate
20. IF (or ITC+IFE): insertion type
    0: Fleshy [flat surface or internal trochanter]
    1: Tendinous [bladelike trochanters or fibrous scars]
21. IFE: origin
    0: Absent; not divided from ITC
    1: Above acetabulum on lateral surface of ilium
    2: Reduced to dorsolateral tubercle [processus supratrochantericus]
22. ITC: origin; Ordered
    0: Absent; not divided from IFE
    1: Cranial to IFE on lateral iliac surface
    2: Expanded into preacetabular concavity
23. ITC: insertion; Ordered
    0: Absent; not divided from IFE
    1: Small distal knob-like lesser trochanter
    2: Large blade-like lesser trochanter
    3: Robust lesser trochanter; proximally positioned and closely appressed to greater trochanter
    4: Scar on cranial rim of proximal trochanteric crest [greater and lesser trochanters fused]
24. M. puboischiofemoralis internus 1+2: number of heads
    0: One: PIFI1+2 (PIFI1 of Crocodylia or M. iliofemoralis internus, IFI of Neornithes)
    1: Two: PIFI1 and PIFI2; weakly subdivided (Squamata)
25. PIFI1+2: origin
    0: Craniomedial pubo-ischiadic plate and epipubic cartilage
    1: Medial ilium and proximal ischium [puboischiadic plate reduced]
    2: Ventrolateral ilium [preacetabular 'cuppedicus' fossa]
    3: Lateral ilium [preacetabular fossa reduced]
    4: Lateral pubic peduncle of ilium [preacetabular fossa 'lost']
26. PIFII+2: insertion
    0: Craniomedial femoral shaft [scar]
    1: Craniomedial proximal femur; with PIFI3 [trochanter minor]
    2: Medial proximal femoral shaft [scar]

27. 27. PIFI3: number of heads

    0: One: PIFI3 or PIFI2 (Crocodylia) [one insertion scar]

    1: Two: Mm. iliotrochanterici cranialis (ITCR) et medius (ITM) of Neornithes [two insertion scars]

28. PIFI3 (PIFI2 of Crocodylia or ITCR+ITM of Neornithes): origin

    0: Craniomedial pubes and part of medial ilium [pubo-ischiadic plate]

    1: Lumbar vertebrae [pubo-ischiadic plate reduced]

    2: Ilium [no lumbar vertebrae; preacetabular 'cuppedicus' fossa]

    3: Lateral preacetabular ilium [preacetabular fossa lost]

29. PIFI3 (PIFI2 or ITCR+ITM): insertion

    0: Craniolateral proximal femur [scars]

    1: Accessory trochanter

    2: Cranial and lateral trochanteric crest [two scars]

30. Trochanter minor, with PIFI1+2

31. M. puboischiotibialis (PIT): number of heads; most superficial of flexor cruris

    0: One: PIT1−3; weakly subdivided

    1: Two: PIT1+2 and PIT3 (PIT and FTI2 of Crocodylia)

    2: None; absent

32. PIT1+2: origin

    0: Cranioventral pubo-ischiadic ligament and pubic tubercle; near PUT

    1: Cranial proximal ischium (PIT of Crocodylia) [reduced ligament; scar; PUT lost]

    2: None; absent

33. PIT3: origin

    0: Caudal end of pubo-ischiadic ligament and pelvic symphyses

    1: Caudolateral ilium (FTI2 of Crocodylia); caudoventral to FTE, dorsal to CFB [ligament reduced]

    2: None; absent or not separate from PIT1+2 (same origin)

34. PIT1−3: insertion

    0: Medial proximal tibia; with or proximal to FTI1

    1: None; absent

35. M. flexor tibialis internus (FTI): number of heads

    0: Two: FTI1 and FTI2

    1: Three: FTI1 and FTI2a/b (FTI2a/b=superficial/deep=FTI4/3 of Crocodylia)

    2: One: M. flexor cruris medialis (FCM of Neornithes; equivalent to FTI2b or FTI3 of Crocodylia); FTI1 and FTI4 absent

36. FTI1: origin; caudodorsal to FTI2 and ISTR, near M. ischiocaudalis origin

    0: Ilio-ischiadic ligament or fascia on caudolateral side of distal ischium

    1: Last sacral and proximal caudal vertebrae, fascia

    2: None; absent

37. FTI1: insertion

    0: Caudomedial proximal tibia; with or distal to PIT

    1: Unites distally with FTI2, to GM origin at caudomedial proximal tibia

    2: None; absent

38. FTI2: origin

    0: Cranial end of ilio-ischiadic ligament/fascia, near or on ischial tuberosity and distal ischium

    1: Scar on ischial tuberosity, and ilio-ischiadic fascia (FTI3+4 of Crocodylia)

    2: Proximal dorsal process of ischium, and ilio-ischiadic fascia [ischial tuberosity expanded as process]

    3: Caudolateral distal ischium, and ilio-ischiadic membrane (FCM of Neornithes) [proximal dorsal process lost]

39. FTI2: insertion of tendon of superficial part (FTI2a or FTI4)

    0: Splits distally into two tendons, inserting on medial and lateral proximal tibia around GM origin

    1: Unites distally with FTE and deeper part (FTI2b; FTI3 of Crocodylia)

    2: None; muscle absent or not separate

40. FTI: insertion of deep part (FTI2b or FTI3 or FCM)

    0: Caudal proximal tibia; distal to PUT

    1: Not distinct from superficial part (FTI2a); unites distally with FTI1

    2: Unites distally with FTE (=FCLP) tendon (and FTI4, if present)

41. FTI2 (FTI3+4 of Crocodylia): secondary tendon to GL

    0: Absent

    1: Present

42. M. flexor tibialis externus (M. flexor cruris lateralis pars pelvica; FCLP of Neornithes): origin; most caudodorsal of flexor cruris

0: Ilio-ischiadic ligament/fascia around caudoventral ilium and caudodorsal ischium

1: Caudolateral surface of ilium [muscle scar]

43. FTE: insertion; shared tendon inserts between heads of Mm. gastrocnemii

0: Tendon splits distally; medial tendon to caudomedial proximal tibia near GM; lateral tendon to caudolateral proximal tibia near GL and digital flexors, contributing to plantar aponeurosis

1: Medial proximal tibia (FCLP of Neornithes); with FCM, between GM + GIM

44. FCL pars accessoria head (FCLA)

0: Absent

1: Present, originating from FCLP raphe and inserting in popliteal fossa of femur

45. M. pubotibialis (PUT)

0: Present

1: Absent

46. PUT: origin; most cranial of flexor cruris and distally adjacent to AMB

0: Pubes, proximal to or onto pubic tubercle and pubo-ischiadic ligament

1: None; absent

47. PUT: insertion

0: Caudolateral proximal tibia; between GM and GL; proximal to other flexor cruris parts

1: None; absent

48. M. adductor femoris (ADD): number of heads

0: One

1: Two: ADD1 and ADD2 of Crocodylia, or Mm. puboischiofemorales medialis (PIFM) et lateralis (PIFL) of Neornithes [two insertion scars]

49. ADD: origin

0: Pubo-ischiadic ligament, cranial and deep to flexor cruris

1: Cranial and caudal edges of ischium, separated by PIFE3 [scars; PIFE3 present]

2: Craniolateral edge of ischium, pubo-ischiadic membrane, and caudolateral pubis [PIFE3 absent]

50. ADD: insertion

0: Caudal distal femoral shaft, one scar on adductor ridge

1: Caudal distal femoral shaft, medial and lateral scars

2: Adductor ridge or crista supracondylaris medialis connecting to medial condyle

51. M. puboischiofemoralis externus (PIFE): number of heads

0: One: PIFE1 − 3; weakly subdivided [nearly continuous pubo-ischiadic plate]

1: Three: PIFE1 − 3 [expanded and separated pubic and ischial aprons; obturator process]

2: Two: Mm. obturatorii lateralis (OL) et medialis (OM) of Neornithes, equivalent to PIFE1 and PIFE2; PIFE3 lost [obturator process lost]

52. PIFE1: origin

0: Thyroid fenestra and pubo-ischiadic plate

1: Craniomedial surface of pubic apron and epipubic cartilage

2: Proximal lateral pubis; OL of Neornithes [pubic apron lost]

53. PIFE2: origin

0: Caudal to PIFE1; not separated

1: Caudal surface of pubic apron

2: Medial pubo-ischiadic membrane; OM of Neornithes [pubic apron lost]

54. PIFE3: origin

0: Caudal to PIFE1 + 2; not separated

1: Lateral ischium, remnant of pubo-ischiadic plate [or obturator process]

2: Absent [obturator process lost]

55. PIFE1 + 2: pubic retroversion; Ordered

0: Pubic shaft oriented cranially

1: Pubic shaft near vertical

2: Pubic shaft oriented caudally

3: Ilia, pubes, and ischial lie nearly parallel

56. PIFE: insertion

0: Caudolateral internal trochanter, posterior ridge, and intertrochanteric fossa

1: Tip of trochanter minor and intertrochanteric fossa

2: Caudolateral proximal femur [greater trochanter]

3: Lateral proximal femur [greater trochanter rotated laterally]

4: Groove and pit on caudolateral side of trochanteric crest [greater and lesser trochanters fused]

57. PIFE2 (OM of Neornithes): obturator tuberosity on ischium for tendon

0: Absent

1: Present

58. M. ischiotrochantericus (M. ischiofemoralis; ISF of Neornithes): origin

0: Medial surface of caudal ischium [ischial symphysis]

1: Lateral surface of caudal ischium and ilio-ischiadic membrane [ischial symphysis lost]

59. ISTR: insertion
    0: Caudolateral proximal femur [scar]
    1: Groove proximal to trochanteric shelf
    2: Lateral proximal femur near trochanteric shelf [reduced trochanteric shelf]
    3: Proximal to large posterior trochanter
    4: Caudolateral trochanteric crest [scar; reduced posterior trochanter]

60. M. caudofemoralis brevis (M. caudofemoralis pars pelvica; CFP of Neornithes): origin
    0: Proximal caudal vertebrae and fascia
    1: Proximal caudals, last sacrals, and medioventral ilium [small shelf]
    2: Caudoventral ilium [brevis fossa]
    3: Ventrolateral ilium [brevis fossa reduced onto lateral ilium]
    4: Caudolateral ilium [brevis fossa lost]

61. CFB: insertion
    0: Weakly differentiated from CFL; near internal trochanter
    1: Proximal and lateral to CFL, if separate [fourth trochanter or scar present]
    2: Caudolateral proximal femur [trochanter major]

62. M. caudofemoralis longus (M. caudofemoralis pars caudalis; CFC of Neornithes): origin; Ordered
    0: Ventral centra and transverse processes of caudal vertebrae [no transition zone in caudals]
    1: Restricted to proximal half of tail ['transition zone']
    2: Restricted to proximalmost caudals [tail shortened to 15–30 vertebrae]
    3: Cranioventral pygostyle
    4: None; absent

63. CFL: insertion
    0: Caudal femoral shaft and internal trochanter
    1: Prominent fourth trochanter and medial pit
    2: Small fourth trochanter
    3: Fourth trochanter reduced to a scar
    4: None; absent

64. CFL: secondary tendon to lateral knee region (and GL)
    0: Absent [loss of pendant trochanter or CFL absent]
    1: From distal CFL belly2: From crest-like fourth trochanter
    3: From tip of pendant fourth trochanter

65. Mm. gastrocnemii: number of heads
    0: Two: Mm. gastrocnemii lateralis (GL) et medialis (GM; 'femorotibial gastrocnemius' of Lepidosauria; Russell, 1993)
    1: Three: GM divided into GM and M. gastrocnemius pars intermedia (GIM; Neornithes) or GL divideded into superficial and deep heads of 'femoral gastrocnemius' (Lepidosauria; Russell, 1993)

66. GL: origin
    0: Caudolateral distal femur near lateral condyle [tubercle or scar]

67. GL: insertion
    0: Plantar aponeurosis to metatarsal V and tarsals, then to digits 2–4
    1: Plantar aponeurosis to metatarsal V, process on distal tarsal 4, and calcaneal tuber, then to digits 2–4 [calcaneal tuber present]
    2: Reduced plantar aponeurosis to caudal surfaces of metatarsals II–V [scars; calcaneal tuber and distal tarsal 4 process lost]
    3: Forms lateral part of 'Achilles tendon' onto small flat hypotarsus, then vestigial plantar aponeurosis to caudal surface of tarsometatarsus
    4: Forms lateral part of 'Achilles tendon' onto large grooved hypotarsus, then vestigial plantar aponeurosis to caudal surface of tarsometatarsus

68. GM: origin; medial to TA
    0: Medial proximal tibia
    1: Medial side of (lateral) cnemial crest

69. GM: insertion
    0: Plantar aponeurosis to metatarsal V, calcaneum, then to digit 5
    1: Plantar aponeurosis to metatarsal V, calcaneal tuber, then to digit 5 [calcaneal tuber present]
    2: Plantar aponeurosis to metatarsal V and calcaneal tuber [digit 5 phalanges lost]
    3: Plantar aponeurosis to metatarsal V [calcaneal tuber lost]
    4: Forms medial part of 'Achilles tendon' onto small flat hypotarsus, then vestigial plantar aponeurosis to caudal surface of tarsometatarsus [metatarsal V lost]
    5: Forms medial part of 'Achilles tendon' onto large grooved hypotarsus, then vestigial plantar aponeurosis to caudal surface of tarsometatarsus

70. GIM: origin
    0: Absent; not divided
    1: Caudal side of distal femur, near medial femoral condyle; at distal end of PIFM, PIFL, and FCLA insertions

71. GIM: insertion
    0: Absent; not divided
    1: Joins GM, then forms caudal part of 'Achilles tendon' onto hypotarsus and caudal tarsometatarsus

72. GM and GL: relative size
    0: GL larger than GM [no large cnemial crest]
    1: GM larger than GL (including GIM, if present) [expanded cnemial crest]

73. Digital flexors: number of major heads
    0: Two: M. flexor hallucis longus (FHL) and weakly subdivided M. flexor digitorum longus (FDL); plus third, weakly subdivided, M. flexor digitorum brevis (FDB)
    1: Seven or more (see text)

74. Digital flexors: general origins
    0: Caudolateral distal femur, near lateral condyle and GL, and adjacent proximal tibia and fibula; FDB has plantar aponeurosis origin (reduced with plantar aponeurosis insertion of other digital flexors)
    1: Expanded onto cnemial crest of tibia, fossa flexoria, and proximal fibula
    2: Expanded onto medial fibular fossa or sulcus
    3: Expanded onto much of caudal side of knee region

75. Digital flexors: insertions
    0: Plantar aponeurosis to digits 1–5
    1: Distal phalanges, digits 1–5 [plantar aponeurosis reduced]
    2: Distal phalanges, digits 1–4 [digit 5 phalanges lost]
    3: Flexor tubercles of pedal unguals, digits 1–4

76. Tibial cartilage around digital flexor tendons; Ordered
    0: Absent
    1: Present, small; caudal extension of trochlear surface
    2: Present, large; medially and laterally bordered by sharp crests

77. FDL: tendon of insertion
    0: Not ossified
    1: Ossified

78. FHL: insertion
    0: Caudal side of digit 1; digit remains proximal
    1: Caudal side of digit 1; hallux shifted distally, losing contact with tarsus
    2: Cranial side of digit 1; hallux retroverted onto caudal side of tarsometatarsus and positioned distally

79. M. extensor digitorum longus (EDL): origin
    0: Cranial surface of distal lateral femoral condyle; superficial to TA origin
    1: Cranial proximal tibia; distal, medial and deep to TA origin

80. EDL: insertion
    0: Cranial surfaces of proximal metatarsals II–IV
    1: Dorsal surfaces of phalanges, digits 2–4 [thru extensor sulci to scars and pits]

81. EDL: extensor canal on cranial side of distal tibiotarsus; Ordered
    0: Absent
    1: Present; shallow groove
    2: Present; deep groove enclosed cranially by an ossified supratendinal bridge

82. M. tibialis anterior (TA): number of heads
    0: One
    1: Two (femoral and tibial heads of M. tibialis cranialis of Neornithes; TC) [fossa on craniolateral distal femur for femoral origin]

83. TA: origin
    0: Craniomedial proximal tibia; distal to tibial tuberosity and deep to EDL origin
    1: Femoral fossa and cranial surfaces of cremial crests; proximal and superficial to EDL origin [fossa on femur and two cnemial crests present]

84. TA: insertion
    0: Craniolateral proximal metatarsals I–IV; especially metatarsal I
    1: Tubercles on cranial proximal metatarsals II–IV [metatarsal I shifted distally]
    2: Tuberositas m. tibialis cranialis, on cranial proximal metatarsal II

85. M. extensor hallucis longus (EHL): origin
    0: Craniolateral distal-most fibula
    1: Craniomedial proximal tarsometatarsus [distal fibular shaft lost]

86. EHL: insertion
    0: Cranial surfaces of digit 1 phalanges [hallux not retroverted]
    1: Caudal surfaces of digit 1 phalanges [hallux retroverted]

87. M. extensor digitorum brevis (EDB)
    0: Present
    1: Absent; presumably fused to distal EDL

88. EDB: origin
    0: Cranial surfaces of proximal tarsals
    1: Absent

89. EDB: insertion
    0: Dorsal surfaces of distal phalanges
    1: Absent
90. M. pronator profundus (PP)
    0: Present
    1: Absent [distal fibular shaft lost or appressed to tibia]
91. PP: origin
    0: Caudomedial fibular shaft; associated with IC
    1: Absent
92. PP: insertion
    0: Caudolateral side of proximal metatarsal I (and II–III) and tarsals (especially process of distal tarsal 4)
    1: Absent
93. M. popliteus (POP): origin
    0: Caudolateral proximal tibial shaft
    1: Distal end of flexor fossa; caudolateral proximal tibia [tubercle]
94. POP: insertion
    0: Caudomedial proximal fibula
    1: Medial proximal fibula [fossa, if present]
95. M. interosseus cruris (IC); Ordered
    0: Present, weakly subdivided from POP
    1: Reduced with fibular shaft
    2: Absent [distal fibula lost or appressed to tibia]
96. IC: origin; distal to POP; Ordered
    0: Caudolateral distal tibial shaft
    1: Lateral distal tibial shaft; restricted distal to fibular crest
    2: Absent
97. IC: insertion; Ordered
    0: Medial fibular shaft, distal to head
    1: Medial distal fibular shaft; distal to ILFB

tubercle [fibular crest on tibia]
    2: Absent
98. M. fibularis longus (FL): origin
    0: Lateral fibular shaft; distal to IFLB; between FB and FDL
    1: Lateral side of lateral femoral condyle
    2: Lateral proximal fibular shaft and nearby cnemial crests [distal fibular shaft lost]; proximal to ILFB
99. FL: insertion
    0: Lateral side of metatarsal V; distal to FB; and slight tendon to dorsal surfaces of digit V phalanges
    1: Lateral side of metatarsal V; distal to FB; and calcaneal tuber and slight tendon to dorsal surfaces of digit 5 phalanges [calcaneal tuber present]
    2: Lateral side of metatarsal V, calcaneal tuber, and flexor tendon [digit 5 phalanges lost]
    3: Lateral side of metatarsal V and flexor tendon [calcaneal tuber lost]
    4: Tibial cartilage and through Sulcus m. fibularis longi on tarsometatarsus to tendon of M. flexor perforatus digitorum III [metatarsal V lost]
100. M. fibularis brevis (FB): origin
    0: Craniolateral distal fibula (and tibia); craniolateral and distal to FL
    1: Craniolateral distal tibial shaft [distal fibular shaft lost]
101. FB: insertion
    0: Caudolateral side of metatarsal V (and IV); proximal to FL
    1: Caudolateral proximal metatarsal IV [metatarsal V lost; Tuberculum m. fibularis brevis present]

Appendix B: Data matrix

Data matrix: characters 1–50

Taxon	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890
Chelonia	00000	00000	00000	00010	00000	10030	02001	10210	00000	00000
'Basal diapsids'	?0000	00??0	??0?0	00000	000?0	0????	?????	?????	?????	?0?00
Squamata	00010	00000	00000	00000	00010	00001	00010	00001	00000	00000
Sphenodon	00010	00000	00000	00000	00000	00000	00010	00001	00000	00000
'Basal archosauromorphs'	?0000	00??0	??0?0	00000	000?0	?????	?????	?????	?????	????0 (1)
Erythrosuchidae	?0000	00??0	??0?0	00000	000?0	?????	?????	?????	?????	????0 (1)
Proterochampsidae	?0001	10??0	??0?0	00020	000?0	?????	?????	?1???	?????	?1111
Parasuchia	?0001	10??0	??0?0	00020	000??	0??0?	?????	?1???	?????	?1111
Aetosauria	10001	10??0	??1?0	00020	000??	0??0?	?????	?1???	?????	?1111
'Basal crocodylomorphs'	10001	10??0	??0?0	00120	000?1	0?10?	?????	?1???	?????	?1111
Crocodylia	10001	10011	10010	00020	00001	00101	11110	01121	10011	11111
Lagerpeton	?0001 (1)	10??0	??1?0	0012?	100??	???0?	?????	?1???	?????	????1
Marasuchus	?0101	10??0	??0?0	01231	111??	???0?	?????	?????	?????	????1
Lewisuchus	?0101	10??0	??0?0	01231	111??	?????	?????	?1???	?????	?1111
Ornithischia	10101	10??0	?00?0	01231	111??	2??0?	?????	?????	?????	?1111
Sauropodomorpha	10101	10??0	??0?0	01231	111??	2??0?	?????	?1???	?????	?1111
Herrerasauridae	?0101	11??0	??0?0	01231	111??	???0?	?????	?1???	?????	?1111
Coelophysoidea	10101	11??0	??1?1	01231	111??	???0?	?????	?1???	?????	?1111
Ceratosauria	10101	11??0	??1?1	01231	112??	???0?	?????	?1???	?????	?1111
'Basal tetanurans'	10101	11??0	?01?1	01241	112?2	??21?	?????	?1???	?????	?1111
Carnosauria	10101	11??0	??1?1	01241	112?2	??21?	?????	?1???	?????	?1111
Tyrannosauroidea	10101	11??0	?01?1	01241	112?2	2?21?	?????	?1???	1????	?1111
Ornithomimosauria	10101	11??0	?01?1	01241	112?2	??21?	?????	?1???	?????	?1111
Oviraptorosauria	?0101	1???0	??1?1	01241	113?3	??21?	?????	?1???	?????	?1111
Alvarezsauridae	?0101	1???0	??2?1	01241	113?4	??31?	?????	?????	?????	??1?1
Deinonychosauria	10101	1???0	??2?1	01231	223?3	??21?	?????	?2???	?????	?1111
Archaeopteryx	?010?	1???0	??2?1	01231	223?3	??2??	?????	?2???	?????	??1?1
Confuciusornithidae	?010?	1???0	??2?1	01231	224?3	??2??	?????	?2???	?????	??2?2
Enantiornithes	10101 (2)	1???0	??2?1	11231	224?3	2122?	?????	?2???	?????	?1222
Patagopteryx	?0101 (2)	1???0	??2?1	11241	224?4	2132?	?????	?2???	?????	?1222
Apsaravis	??12	????0	?????	?1?41	??4?4	??3??	?????	?????	?????	?????
Hesperornithiformes	10211 (2)	1???0	??3?1	11241	224?4	2132?	?????	?3???	?????	?1222
Ichthyornis	?021?	1???0	??3?1	?1241	?24?4	??3??	?????	?3???	?????	??2?2
Paleognathae	10212	11000	?0311	11241	22404	21322	22122	23220	11111	11222
Neognathae	10212	11000	10301 (1)	11241	22404	21322	22122	23220	11111	11222

(Continued)

Data matrix: characters 1–50

Taxon	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890

Data matrix: characters 51–100

Taxon	55555 12345	55556 67890	66666 12345	66667 67890	77777 12345	77778 67890	88888 12345	88889 67890	99999 12345	1 99990 67890
Chelonia	00001	00002	44000	00000	00000	00000	00000	00000	00000	00000
'Basal diapsids'	00000	00?00	00???	0????	0?000	00??0	??0??	?????	?????	?????
Squamata	00000	00000	00110	00000	00000	00000	00000	00000	00000	01000
Sphenodon	00000	00000	00110	00000	00000	00000	00000	00000	00000	00000
'Basal archosauromorphs'	???00	00?00	00??? [2]	1?1??	0?010	00??0	??0??	?????	?????	??1??
Erythrosuchidae	???00	00??0	00???	1?1??	0?010	00??0	??0??	?????	?????	??1??
Proterochampsida	11102	00?11	012??	1?2??	0?020	00??0	??0??	?????	?????	??1??
Parasuchia	11102	00011	012??	1?1??	0?010	00??0	??0??	?????	?????	??2??
Aetosauria	11102	00011	012??	1?1??	0?010	00??0	??0??	?????	?????	??1??
'Basal crocodylomorphs'	11102	00011	012??	1?2??	0?020	00??0	??0??	?????	?????	??2??
Crocodylia	11102	00011	01200	10200	00020	00000	00000	00000	00000	00200
Lagerpeton	11102	00?11	?12?? [3]	1?2??	??020	00??0	??0??	?????	???1?	??2??
Marasuchus	11102	00111	112?? [23]	111??1	?1100	0?10?	?0???	?????	??1??	?1???
Lewisuchus	11102	00111	?12?? [3]	11???1	?1?0??	??0??	?????	?????	?1???	1????
Ornithischia	11102 [22 2]	??121 [2]	013?0	111??	1?110	00?10	??0??	?????	???1?	??1??
Sauropodomorpha	11102	00121 [2]	013??	111??	1?110	00?10	??0??	?????	???1?	??1??
Herrerasauridae	11122	00121	113??	111??	1?110	00?10	??0??	?????	???1?	??1??
Coelophysoidea	11102	00121	010??	112??	1?230	01?10	??1??	?????	??11?	??3??
Ceratosauria	11102	00221	010??	213??	1?230	01?10	??1??	???11	1?122	2?3??
'Basal tetanurans'	11102	00221	110??	213??	1?230	01?10	??1??	???11	1?122	2?3??
Carnosauria	11103	00221	110??	213??	1?230	01?10	??1??	???11	1?122	2?3??
Tyrannosauroidea	11103	00221	110?0	213??	1?230	01?10	??1??	???11	1?122	2?3??
Ornithomimosauria	11103	00221	110?0	213??	1?230	01?10	??1??	???11	1?122	2?3??
Oviraptorosauria	11113	00221	120?0	213??	1?230	01?10	??1??	???11	1?122	2?3??
Alvarezsauridae	11113	??221	220?0	213??	1??30	01?10	??1??	???11	1??22	2?3??
Deinonychosauria	11123	10331	220?0	213??	1?230	01?10	??1??	???11	1?122	2?3??
Archaeopteryx	11123	?1331	230??	213??	1??30	01?10 [2]	??1??	???11	1??22	2?3??
Confuciusornithidae	11224	?1341	330??	213??	1??31	01?10 [2]	??11?	???11	1??2?	2?31?
Enantiornithes	11224	?1341	330?0	214??	1??31	01?10 [2]	??21?	???11	1??22	22411
Patagopteryx	22234	11431 [4]	330??	314??	1??32	?1?10 [2]	??21?	???11	1??22	22411
Apsaravis	22234	11441	330?0	3?4??	???32	11?10 [2]	??21?	???11	1??22	22411
Hesperornithiformes	22234	?1441	330?0	314??	1??32	?2?11	?1211	???11	1??22	22411
Ichthyornis	22234	11441	330??	4?5??	1??32	?2??1	?1?11	???11	1??22	22411
Paleognathae	22234	11441	33010	41511	11332	12112	11211	11111	11122	22411
Neognathae	22234	11441	33010	41511	11332	12112	11211	11111	11122	22411

Appendix C: Character mapping

I mapped characters 1–100 for all 35 taxa onto the phylogenetic framework in Fig. 1, using MacClade 4.03 (Maddison and Maddison, 2001) with default options (no ACCTRAN or DELTRAN assumptions) to trace character evolution from Reptilia to Neornithes (see Hutchinson, 2001a for more details). Tree length is 201 steps; consistency index 0.87; retention index 0.96. Format for each node is character number with state in parentheses; * marks changes that are equivocal at one or more nodes below.

Reptilia: All characters 1–100 ancestrally were state 0 except 19(0*), 26(0*), 29(0*), 30(?), 32(2), 34–36(?), 38(2), 39(?), 40(?), 55(0*), 60–62(0*), 63(?), 64(0*). Considering that many of these exceptions result from the derived morphology of Chelonia, states marked 0* were presumed to be ancestrally 0 for Reptilia.

Sauria: 34(1)*, 35(0)*, 36(0)*

Lepidosauria: 4(1), 32(1), 38(0), 39(0)*, 40(1)*, 64(1)

Archosauromorpha: 66(1), 68(1), 74(1), 98(1)

Proterochampsidae + Archosauria: 5(1), 6(1), 19(2), 37(1), 47–53(1)*, 55(2), 59(1)*, 60(1), 62(1), 63(2)*

Archosauria: 1(1)*, 11(1)*, 14(1)*, 39(2)*, 41(1)*, 44–46(1)*

Crocodylomorpha: 25(1)*, 28(1)*, 68(2), 74(2), 98(2)*

Dinosauromorpha: 21(1), 94(1), 98(1)*

Dinosauriformes: 3(1)*, 17(1), 18(2)*, 19(3), 22(1), 23(1), 58(1)*, 67(1)*, 71(1)*, 73(1)*, 79(1)*

Dinosauria: 20(1)*, 26(2)*, 59(2), 63(3)*

Theropoda: 7(1)

Coelophysoidea + Neotheropoda: 13(1), 15(1), 63(0), 73(2), 74(3), 77(1), 83(1), 93(1)*, 98(3)

Neotheropoda: 23(2), 58(2), 66(2), 68(3)*, 89–91(1)*, 94(2), 95(2)*, 96(2)*

Tetanurae: 19(4), 25(2)*, 28(2), 29(1), 61(1)

Avetheropoda: 55(3)

Maniraptora: 23(3), 25(3), 54(1), 62(2)

Metornithes: 13(2), 61(2)

Eumaniraptora: 19(3), 22(2), 37(2)*, 54(2), 56(1)*, 58(3), 59(3)

Aves: 57(1), 62(3)

Pygostylia: 23(4), 48(2), 50(2), 53(2), 55(4), 59(4), 61(3), 75(1), 84(1)*, 99(1)*

Ornithothoraces: 16(1), 27(1)*, 29(2)*, 49(2)*, 68(4), 83(2), 97(2)*, 98(4), 100(1)*

Patagopteryx + *Apsaravis* + Ornithurae: 19(4), 25(4), 28(3), 51(2), 53(2), 54(3), 58(4), 66(3), 75(2)

Apsaravis + Ornithurae: 4(1), 76(1)*

Ornithurae: 3(2)*, 13(3)*, 37(3)*, 77(2)*, 80(1), 82(1)*, 85(1)*

Ichthyornis + Neornithes: 66(4), 68(5)

Neornithes: 5(2)*, 30(2)*, 31(2)*, 33(1)*, 34–36(2)*, 40(0)*, 42(1)*, 43(1)*, 64(1), 69(1)*, 70(1)*, 72(1)*, 73(1)*, 78(1)*, 80(2), 81(1)*, 86–88(1)*, 92(1)*

References

Alexander, R.McN., Dimery, N.J., 1985. The significance of sesamoids and retro-articular processes for the mechanics of joints. J. Zool. 205, 357–371.

An, K.N., Takahashi, K., Harrigan, T.P., Chao, E.Y., 1984. Determination of muscle orientations and moment arms. J. Biomech. Eng. 106, 280–283.

Barnett, C.H., Lewis, O.J., 1958. The evolution of some traction epiphyses in birds and mammals. J. Anat. 92, 593–601.

Barsbold, R., Maryanska, T., Osmólska, H., 1990. Oviraptorosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, CA, pp. 249–258.

Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. (Eds.), 1993. Handbook of Avian Anatomy: Nomina Anatomica Avium. second ed.. Publ Nutall Ornithol Club, Cambridge, MA, pp. 23.

Beddard, F.E., 1898. The Structure and Classification of Birds. Longmans, Green & Co, London.

Benjamin, M., Ralphs, J.R., 1998. Fibrocartilage in tendons and ligaments—an adaptation to compressive load. J. Anat. 193, 481–494.

Benjamin, M., Evans, E.J., Copp, L., 1986. The histology of tendon attachments to bone in man. J. Anat. 149, 89–100.

Bennett, M.B., Stafford, J.A., 1988. Tensile properties of calcified and uncalcified avian tendons. J. Zool. 214, 343–351.

Bledsoe, A.H., Raikow, R.J., Glasgow, A.G., 1993. Evolution and functional significance of tendon ossification in wood-creepers (Aves: Passeriformes: Dendrocolaptinae). J. Morph. 215, 289–300.

Brett-Surman, M.K., Paul, G.S., 1985. A new family of bird-like dinosaurs linking Laurasia and Gondwanaland. J. Vert. Paleont. 5, 133–138.

Bryant, H.N., Russell, A.P., 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philos. Trans. R. Soc. Lond., Ser. B 337, 405–418.

Bryant, H.N., Seymour, K.L., 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. J. Morph. 206, 109–117.

Buchanan, C.I., Marsh, R.L., 2001. Effects of long-term exercise on the biomechanical properties of the Achilles tendon of guinea fowl. J. Appl. Physiol. 90, 164–171.

Byerly, T.C., 1925. The myology of *Sphenodon punctatum*. Univ. Iowa Stud. Nat. Hist. 11, 3–51.

Carrano, M.T., 1998. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. Paleobiology 24, 450–469.

Carrano, M.T., 2000. Convergence and the evolution of dinosaur locomotion. Paleobiology 26, 489–512.

Carrano, M.T., Hutchinson, J.R., 2002. The pelvic and hind limb musculature of *Tyrannosaurus* rex (Dinosauria: Theropoda). J. Morph. 253, 207–228.

Carter, D.R., Mikic, B., Padian, K., 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. Zool. J. Linn. Soc. 123, 163–178.

Charig, A.J., 1972. The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. In: Joysey, K.A., Kemp, T.S. (Eds.), Studies in Vertebrate Evolution. Oliver & Boyd, Edinburgh, pp. 121–151.

Charig, A.J., 1996. Late Cretaceous birds of southern South America: anatomy and systematics of *Patagopteryx* and Enantiornithes. In: Arratia, G. (Ed.), Contributions of Southern South America to Vertebrate Paleontology. Münchner Geowissensch. Abh. A, pp. 203–244.

Chiappe, L.M., 2001. Phylogenetic relationships among basal birds. In: Gauthier, J.A., Gall, L.F. (Eds.), New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom. Peabody Mus. Nat. Hist., Yale University, New Haven, 125–139.

Cong, L., Hou, L.-H., Wu, X.-C., 1998. The Gross Anatomy of *Alligator sinensis* Fauvel: Integument, Osteology, and Myology. Science Press, Beijing In Chinese with English summary.

Cracraft, J., 1971. The functional morphology of the hind limb of the domestic pigeon. Bull. Amer. Mus. Nat. Hist. 144, 171–268.

Cracraft, J., Clarke, J., 2001. The basal clades of modern birds. In: Gauthier, J.A., Gall, L.F. (Eds.), New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom. Peabody Mus. Nat. Hist., Yale University, New Haven, 143–156.

Davis, D.D., 1934. The Collared Lizard: A Laboratory Guide. Macmillan, New York.

Delp, S.L., Ringwelski, D.A., Carroll, N.C., 1994. Transfer of the rectus femoris: effects of transfer site on moment arms about the knee and hip. J. Biomech. 27, 1201–1211.

Delp, S.L., Hess, W.E., Hungerford, D.S., Jones, L.C., 1999. Variation of rotation moment arms with hip flexion. J. Biomech. 32, 493–501.

De Vis, C.W., 1884. Myology of *Chlamydosaurus kingii*. Proc. Linn. Soc. New South Wales 1884 300–320.

Dilkes, D.D., 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Trans. R. Soc. Edinburgh: Earth Sci. 90, 87–125.

Dollo, L., 1883. Note sur la présence chex les oiseaux du 'troisième trochanter' des dinosauriens et sur la fonction de celui-ci. Bull. Mus. R. Hist. Nat. Belg. 2, 13–18.

Dollo, L., 1888. Sur la significance du 'trochanter pendant' des dinosauriens. Bull. Sci. France Belg. 8, 215–224.

Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R., Robinson, J.M., 2000. Theropod locomotion. Am. Zool. 40, 640–663.

Firbas, W., Zweymüller, K., 1971. Über das Hüftgelenk der Ratiten. Morph. Jahrb. 116, 91–103.

Fisher, H.I., 1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. Am. Midl. Nat. 35, 545–727.

Full, R.J., Ahn, A.N., 1995. Static forces and moments generated in the insect leg: comparison of a three-dimensional musculo-skeletal computer model with experimental measurements. J. Exp. Biol. 198, 1285–1298.

Fuss, F.K., 1996. Tibiofibular junction of the South African ostrich (*Struthio camelus australis*). J. Morph. 227, 213–226.

Gadow, H., 1882. Beiträge zur Myologie der hinteren Extremität der Reptilien. Morphol. Jahrb. 7, 329–466.

Gadow, H., Selenka, E., 1891. Vögel. I. Anatomischer Teil. In: Bronn, H.G. (Ed.), Bronn's Klassen und Ordnungen des Thier-Reichs, vol. 6. CF Winter, Leipzig, pp. 1–1008 Abstract 4.

Gans, C., de Vree, F., 1987. Functional bases of fiber length and angulation in muscle. J. Morph. 192, 63–85.

Garrod, A.H., Darwin, F., 1872. Notes on an ostrich lately living in the Society's collection. Proc. Zool. Soc. Lond. 1872 356–363.

Gatesy, S.M., 1990. Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology 16, 170–186.

Gatesy, S.M., 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. J. Zool. 224, 577–588.

Gatesy, S.M., 1995. Functional evolution of the hind limb and tail from basal theropods to birds. In: Thomason, J.J. (Ed.), Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge, pp. 219–234.

Gatesy, S.M., 1997. An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. J. Morph. 234, 197–212.

Gatesy, S.M., 1999a. Guineafowl hind limb function. I: cineradiographic analysis and speed effects. J. Morph. 240, 115–125.

Gatesy, S.M., 1999b. Guineafowl hind limb function. II: electromyographic analysis and motor pattern evolution. J. Morph. 240, 127–142.

Gatesy, S.M. Locomotor evolution on the line to modern birds. In: Witmer, L.M., Chiappe, L.M. (Eds.), Mesozoic Birds: Above the Heads of the Dinosaurs. Academic Press, New York, in press.

Gatesy, S.M., Dial, K.P., 1996. Locomotor modules and the evolution of avian flight. Evolution 50, 331–340.

Gatesy, S.M., Middleton, K.M., Jenkins, F.A., Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399, 141–144.

Gauthier, J.A., Kluge, A.G., Rowe, T., 1988. Amniote phylogeny and the importance of fossils. Cladistics 4, 105–209.

George, J.C., Berger, A.J., 1966. Avian Myology. Academic Press, London.

Gregory, W.K., Camp, C.L., 1918. Studies in comparative myology and osteology. No. III. Bull. Am. Mus. Nat. Hist. 38, 447–563.

Haines, R.W., Mohuiddin, A., 1968. Metaplastic bone. J. Anat. 103, 527–538.

Haines, R.W., 1935. A consideration of the constancy of muscular nerve supply. J. Anat. 70, 33–55.

Haines, R.W., 1940. Note on the independence of sesamoid and epiphyseal centers of ossification. J. Anat. 75, 101–105.

Haines, R.W., 1942. The evolution of epiphyses and of endochondral bone. Biol. Rev. 17, 267–292.

Haines, R.W., 1969. Epiphyses and sesamoids. In: Gans, C., Bellairs, A.d'A., Parsons, T.S. (Eds.), The Biology of the Reptilia, vol. 1. Morphology A. Academic Press, New York, pp. 81–115.

Hair, P., 1868. On the arrangement of the muscular fibres of the alligator. J. Anat. Physiol. 2, 26–41.

Harris, V.A., 1963. The Anatomy of the Rainbow Lizard *Agama agama* (L.). Hutchinson Tropical Monographs, London.

Harvey, E.B., Kaiser, H.E., Rosenberg, L.E., 1968. An atlas of the domestic turkey (*Meleagris gallopavo*), myology and osteology. US Atomic Energy Commission, Div. Biol. Med., US Govt. Print. Office, Washington, DC.

Haughton, S., 1865a. On the muscular anatomy of the leg of the crocodile. Ann. Mag. Nat. Hist. 3, 326–331.

Haughton, S., 1865b. On the muscular mechanism of the leg of the ostrich. Ann. Mag. Nat. Hist. 3, 262–272.

Haughton, S., 1867a. Notes on animal mechanics. No. X. muscular anatomy of the emu (*Dromaeus Novae Hollandiae*). Proc. Irish R. Acad. Sci. 9, 487–497.

Haughton, S., 1867b. Notes on animal mechanics. No. XI. Muscular anatomy of the rhea (*Struthio Rhea*). Proc. Irish R. Acad. Sci. 9, 497–504.

Haughton, S., 1868. On the muscular anatomy of the leg of the alligator. Ann. Mag. Nat. Hist. 4, 282–292.

Heilman, G.A., 1926. The Origin of Birds. Witherby, London.

Hogg, D.A., 1980. A re-investigation of the centres of ossification in the avian skeleton at and after hatching. J. Anat. 130, 725–743.

Howell, A.B., 1938. Muscles of the avian hip and thigh. Auk 55, 71–81.

Hoyte, D.A.N., Enlow, D.H., 1966. Wolff's law and the problem of muscle attachment on resorptive surfaces of bone. Am. J. Phys. Anthr. 24, 205–214.

Hudson, G.E., 1937. Studies on the muscles of the pelvic appendage in birds. Am. Midl. Nat. 18, 1–108.

Hudson, G.E., Lanzillotti, P.J., Edwards, G.D., 1959. Muscles of the pelvic limb in galliform birds. Am. Midl. Nat. 61, 1–67.

Hudson, G.E., Schreiweis, D.O., Wang, S.Y.C., Lancaster, D.A., 1972. A numerical study of the wing and leg muscles of tinamous (Tinamidae). Northwest Sci. 46, 207–255.

Hudson, G.E., Wang, S.Y.C., Provost, E.E., 1965. Ontogeny of the supernumary sesamoids in the leg muscles of the ring-necked pheasant. Auk 82, 427–437.

Hurov, J.O., 1986. Soft-tissue bone interface: how do attachments of muscles, tendons, and ligaments change during growth? A light microscopic study. J. Morph. 189, 313–325.

Hutchinson, J.R., 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool. J. Linn. Soc. 131, 123–168.

Hutchinson, J.R., 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zool. J. Linn. Soc. 131, 169–197.

Hutchinson, J.R., Gatesy, S.M., 2001. Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology 26, 734–751.

Hutchinson, J.R., Garcia, M., 2002. *Tyrannosaurus* was not a fast runner. Nature 415, 1018–1021.

Jones, S.J., Boyde, A., 1974. The organization and gross mineralization patterns of the collagen fibres in Sharpey fibre bone. Cell Tiss. Res. 148, 83–96.

Kellner, A.W.A., 1996. Fossilized theropod soft tissue. Nature 379, 32.

Kriegler, W., 1967. Zur Myologie des Beckens und der Hinterextremität der Reptilien. Morph. Jahrb. 101, 541–625.

Landis, W.J., Librizzi, J.J., Dunn, M.G., Silver, F.H., 1995. A study of the relationship between mineral content and mechanical properties of turkey gastrocnemius tendon. J. Bone Miner. Res. 10, 859–867.

Landsmeer, J.M.F., 1990. Functional morphology of the hindlimb in some lacertilia. Eur. J. Morph. 28, 3–34.

Maddison, D.R., Maddison, W.P., 2001. MacClade: Analysis of Phylogeny and Character Evolution. Sinauer Associates, Inc, Sunderland, MA vers. 4.03.

Martill, D., Frey, E., Sues, H.-D., Cruickshank, A.R.I., 2000. Skeletal remains of a small theropod dinosaur with associated soft structures from the Lower Cretaceous Santana Formation of NE Brazil. Can. J. Earth Sci. 37, 1–10.

McGowan, C., 1979. The hind limb musculature of the Brown Kiwi, *Apteryx australis mantelli*. J. Morph. 160, 33–74.

McKitrick, M.C., 1991. Phylogenetic analysis of avian hindlimb musculature. Misc. Publ. Mus. Zool. Univ. Mich. 179, 1–85.

McMahon, T.A., Valiant, G., Frederick, E.C., 1987. Groucho running. J. Appl. Physiol. 62, 2326–2337.

McMurrich, J.P., 1905. The phylogeny of the crural flexors. Am. J. Anat. 4, 33–76.

Mellett, F.D., 1994. A note on the musculature of the proximal part of the pelvic limb of the ostrich (*Struthio camelus*). J. S. Afr. Vet. Assoc. 65, 5–9.

Middleton, K.M., 2001. The morphological basis of hallucal orientation in extant birds. J. Morphol. 250, 51–60.

Miller, A.H., 1937. Structural modifications in the Hawaiian goose (*Nesochen sandvicensis*): A study in adaptive evolution. Univ. Calif. Publ. Zool. 42, 1–80.

Mivart, G., 1867. Notes on the myology of *Iguana tuberculata*. Proc. Zool. Soc. Lond. 1867 766–797.

Mivart, G., 1870. On the myology of *Chamaeleon parsonii*. Proc. Zool. Soc. Lond. 1870 850–890.

Müller, G., 1986. Effects of skeletal change on muscle pattern formation. Bibliot. Anat. 29, 91–108.

Müller, G., 1989. Ancestral patterns in bird limb development: a new look at Hampé's experiment. J. Evol. Biol. 2, 31–47.

Müller, G.B., Streicher, J., 1989. Ontogeny of the syndesmosis tibiofibularis and the evolution of the bird hindlimb: a caenogenetic feature triggers phenotypic novelty. Anat. Embr. 179, 327–339.

Norell, M.A., Clark, J.M., Makovicky, P.J., 2001. Phylogenetic relationships among coelurosaurian theropods. In: Gauthier, J.A., Gall, L.F. (Eds.), New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom. Peabody Mus. Nat. Hist., Yale University, New Haven, 49–67.

Norell, M.A., Makovicky, P.J., 1997. Important features of the dromaeosaur skeleton: information from a new specimen. Am. Mus. Novit. 3215, 1–28.

Norell, M.A., Clarke, J., 2001. Fossil that fills a critical gap in avian evolution. Nature 409, 181–184.

Novas, F.E., 1996. Dinosaur monophyly. J. Vert. Paleont. 16, 723–741.

Olmos, M., Planell, J.A., Casinos, A., 1993. Tensile fracture loads of leg tendons in birds. Ann. Sci. Nat. Zool. 14, 23–33.

Olson, W.M., 2000. Phylogeny, ontogeny, and function: extraskeletal bones in the tendons and joints of *Hymenochirus boettgeri* (Amphibia: Anura: Pipidae). Zoology 103, 15–24.

Osawa, G., 1898. Beiträge zur Anatomie der *Hatteria punctata*. Arch. Mikrosk. Anat. 51, 481–690.

Parsons, F.G., 1904. Observations on traction epiphyses. J. Anat. Physiol. 38, 248–258.

Parsons, F.G., 1905. On pressure epiphyses. J. Anat. Physiol. 39, 402–412.

Parsons, F.G., 1908. Further remarks on traction epiphyses. J. Anat. Physiol. 42, 388–396.

Patak, A.E., Baldwin, J., 1998. Pelvic limb musculature in the emu *Dromaius novaehollandiae* (Aves: Struthioniformes: Dromaiidae): adaptations to high-speed running. J. Morph. 238, 23–37.

Pearson, K., Davin, A.G., 1921. On the sesamoids of the knee-joint. Biometrika 13, 350–400.

Perrin, A., 1892. Contributions a l'étude de la myologie comparee: membre postérieur chez un certain nombre de batraciens et de sauriens. Bull. Scient. France Belg. 24, 372–552.

Prum, R.O., 2002. Why ornithologists should care about the theropod origin of birds. Auk 119, 1–17.

Rabl, C., 1916. Über die Muskeln und Nerven der Extremitäten von *Iguana tuberculata* Gray. Anat. Hefte. 53, 681–789.

Raikow, R.J., 1970. Evolution of diving adaptations in the stifftail ducks. Univ. Calif. Publ. Zool. 94, 1–52.

Raikow, R.J., 1985. Locomotor system. In: King, A.S., McLelland, J. (Eds.), Form and Function in Birds, vol. 3. Academic Press, New York, pp. 57–147.

Ranvier, L., 1875. Traite Technique d'Histologie. Savy, Paris, pp. 362–364.

Reese, A.M., 1915. The Alligator and its Allies. GP Putnam's Sons, New York.

Reid, R.E.H., 1984. The histology of dinosaurian bone, and its possible bearing on dinosaur physiology. In: Ferguson, M.J.W. (Ed.), The Structure, Development, and Evolution of Reptiles. Academic Press, London, pp. 629–633.

Reilly, S.M., 2000. Locomotion in the quail (*Coturnix japonica*): the kinematics of walking and increasing speed. J. Morph. 243, 173–185.

Reilly, S.M., Elias, J.A., 1998. Locomotion in Alligator mississipiensis: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. J. Exp. Biol. 201, 2559–2574.

Rewcastle, S.C., 1983. Fundamental adaptations in the lacertilian hind limb: a partial analysis of the sprawling limb posture and gait. Copeia 1983, 476–487.

Ribbing, L., 1938. Die Muskeln und Nerven der Extremitäten. Handb.Vergleich. Anat. Wirb. 5, 543–656.

Rieppel, O., 1989. The hind limb of *Macrocnemus bassanii* (Nopsca) (Reptilia, Diapsida): development and functional anatomy. J. Vert. Paleont. 9, 373–387.

Roberts, T.J., 2001. Muscle force and stress during running in dogs and wild turkeys. Bull. Mus. Comp. Zool. 156, 283–295.

Romer, A.S., 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. Bull. Am. Mus. Nat. Hist. 46, 517–606.

Romer, A.S., 1923a. The ilium in dinosaurs and birds. Bull. Am. Mus. Nat. Hist. 48, 141–145.

Romer, A.S., 1923b. Crocodilian pelvic muscles and their avian and reptilian homologues. Bull. Am. Mus. Nat Hist. 48, 533–552.

Romer, A.S., 1923c. The pelvic musculature of saurischian dinosaurs. Bull. Am. Mus. Nat. Hist. 48, 605–617.

Romer, A.S., 1942. The development of tetrapod limb musculature—the thigh of Lacerta. J. Morph. 71, 251–298.

Romer, A.S., 1956. Osteology of the Reptiles. Univ. Chicago Press, Chicago.

Rowe, T., 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. J. Morph. 189, 327–346.

Rowe, T., 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. J. Vert. Paleont. 9, 125–136.

Russell, A.P., 1988. Limb muscles in relation to lizard systematics: a reappraisal. In: Estes, R., Pregill, G. (Eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp. Stanford University Press, Stanford, CA, pp. 493–568.

Russell, A.P., 1993. The aponeuroses of the lacertilian ankle. J. Morph. 218, 65–84.

Sanders, A., 1870a. Notes on the myology of *Liolepis belli*. Proc. Zool. Soc. Lond. 1870 154–183.

Sanders, A., 1870b. Notes on the myology of *Platydactylus japonicus*. Proc. Zool. Soc. Lond. 1870 413–426.

Sanders, A., 1874. Notes on the myology of the *Phyrnosoma coronatum*. Proc. Zool. Soc. Lond. 1874 71–89.

Sarin, V.K. 2000. Mechanobiology of sesamoid formation, development, and ossification. Ph.D. Dissertation, Stanford University.

Sarin, V.K., Erickson, G.E., Giori, N.J., Bergman, A.G., Carter, D.R., 1999. Coincident development of sesamoid bones and clues to their evolution. Anat. Rec. 257, 174–180.

Sasso, C.D., Signore, M., 1998. Exceptional soft-tissue preservation in a theropod dinosaur from Italy. Nature 392, 383–387.

Sereno, P.C., 1991. Basal archosaurs: phylogenetic relationships and functional implications. J. Vert. Paleont. 11, 1–53.

Silver, F.H., Freeman, J.W., Horvath, I., Landis, W.J., 2001. Molecular basis for elastic energy storage in mineralized tendon. Biomacromolecules 2, 750–756.

Snyder, R.C., 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. Am. J. Anat. 95, 1–24.

Snyder, R.C., 1962. Adaptations for bipedal locomoton of lizards. Am. Zool. 2, 191–203.

Streicher, J., Müller, G.B., 1992. Natural and experimental reduction of the avian fibula: developmental thresholds and evolutionary constraint. J. Morph. 214, 269–285.

Surahya, S., 1989. Atlas Komodo: Studi Anatomi den Kedudukannya Dalam Sistematic Hewan. Gadjah Mada University Press, Yagyakarta.

Tarsitano, S., 1981. Pelvic and hindlimb musculature of archosaurian reptiles. Ph.D. Dissertation, City University, New York.

Urist, M.R., 1980. Heterotopic bone formation. In: Urist, M.R. (Ed.), Fundamental and Clinical Bone Physiology. JB Lippincott & Co, Philadelphia,.

Vanden Berge, J.C., 1982. Notes on the myology of the pelvic limb in Kiwi (*Apteryx*) and in other birds. Auk 99, 309–315.

Vanden Berge, J.C., Storer, R.W., 1995. Intratendinous ossification in birds: a review. J. Morph. 226, 47–77.

Vanden Berge, J.C., Zweers, G.A., 1993. Myologia. In: Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. (Eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. Second Ed. Publ Nutall Ornithol Club 23, Cambridge, MA, pp. 189–250.

Verstappen, M., Aerts, P., deVree, F., 1998. Functional morphology of the hindlimb musculature of the black-billed magpie, *Pica pica* (Aves, Corvidae). Zoomorphology 118, 207–233.

Walker, A.D., 1972. New light on the origin of birds and crocodiles. Nature 237, 257–263.

Walker, A.D., 1977. Evolution of the pelvis in birds and dinosaurs. In: Andrews, S.M., Miles, R.S., Walker, A.D. (Eds.), Problems in Vertebrate Evolution. Linn. Soc. Symp. Ser. 4, 319–358

Walker, W.F., 1973. The locomotor apparatus of testudines. In: Gans, C., Parsons, T. (Eds.), The Biology of the Reptilia, vol. 4. Academic Press, New York, pp. 1–100.

Watson, M., 1869. On the mechanism of perching in birds. J. Anat. 3, 379–384.

Witmer, L.M., 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason, J.J. (Ed.), Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge, pp. 19–33.

Witmer, L.M., 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. J. Vert. Paleontol. 17, 1–73.

Wortham, R.A., 1948. The development of the muscles and tendons in the lower leg and foot of chick embryos. J. Morph. 83, 105–148.

Zaaf, A., Herrel, A., Aerts, P., deVree, F., 1999. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). Zoomorphology 119, 9–22.

Zug, G.R., 1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. Misc. Publ. Mus. Zool. Univ. Mich. 142, 1–98.