

Adductors, abductors, and the evolution of archosaur locomotion

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Abstract.—Living crocodylians (Crocodylia) and birds (Neornithes) differ in many aspects of hind-limb anatomy and locomotor function. How did this disparity evolve? We integrate information from fossils with functional descriptions of locomotion in living crocodylians and birds, using a phylogenetic perspective. We then outline the major changes in three-dimensional control of the hip joint along the line from the ancestral archosaur to birds. Our analysis reveals that most aspects of hip morphology and function in *Alligator* are ancestral for Archosauria. Femoral protractors and retractors are located cranial and caudal to the hip, respectively. Similarly, femoral adductors and abductors are located ventral and dorsal to the hip. Transformations of this ancestral pattern on the line to birds involved modifications in osteology, myology, and neural control. In some cases, homologous muscles changed function by acquiring new activity patterns. In others, activity was conserved, but origins and/or insertions were altered. Fossil theropods document the stepwise evolution of a novel mechanism of limb adduction/abduction involving long-axis rotation of the femur. This mechanism accounts for the conspicuous absence of significant musculature ventral and dorsal to the hip joint in extant birds.

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Introduction

Extant crocodylians and birds are the sole survivors of the diverse clade Archosauria, which also includes numerous extinct Mesozoic groups, such as pterosaurs, non-avian dinosaurs, and their many relatives (formerly termed “thecodontians”). Crown-group crocodylians (Crocodylia) and birds (Neornithes) have diverged markedly since the separation of their respective lineages roughly 250 m.y. ago. One example of this disparity is the anatomy and function of the hindlimb and pelvis. Extant crocodylians are quadrupedal and plantigrade and have a more abducted (“sprawling”) limb posture than most birds. A large muscle, *M. caudofemoralis longus*, originates from the base of the long tail and inserts on the prominent fourth trochanter of the femur (Romer 1923a). During walking, this muscle retracts the entire limb through a large arc (Gatesy 1990). In contrast, extant birds are bipedal and digitigrade and have a more adducted (“erect”) limb posture. Their small tails are associated with an extremely reduced (or absent) fourth trochanter and *M. caudofemoralis pars caudalis* (= *longus*). The

femur moves little during walking; most limb rotation occurs at the knee, which is flexed by “hamstring” muscles (Gatesy 1990, 1999a,b).

Studies of extinct taxa have revealed some details of the evolutionary history of these different limb retraction patterns (Romer 1923a; Colbert 1964; Charig 1972; Walker 1977; Tarsitano 1983; Padian and Olsen 1989; Gatesy 1995; Carrano 2000). Other aspects of hind-limb function, however, have received less attention. Adduction and abduction are often discussed (e.g., Charig 1972; Parrish 1986; Welles 1986; Sennikov 1989), but long-axis rotation is rarely even mentioned (but see Brinkman 1980; Gatesy 1991; Blob 1998; Carrano 1998). During locomotion the hindlimb is moved three-dimensionally, yet the functional importance of neural control and the interaction of multiple muscles are seldom considered, even in living archosaurs. Most studies analyze simplified static “snapshots” of locomotion rather than a complete temporal sequence in three dimensions.

The different ways by which extant archosaurs stand and move poses the question, How did this disparity evolve? Herein, we present anatomical, electromyographic, and

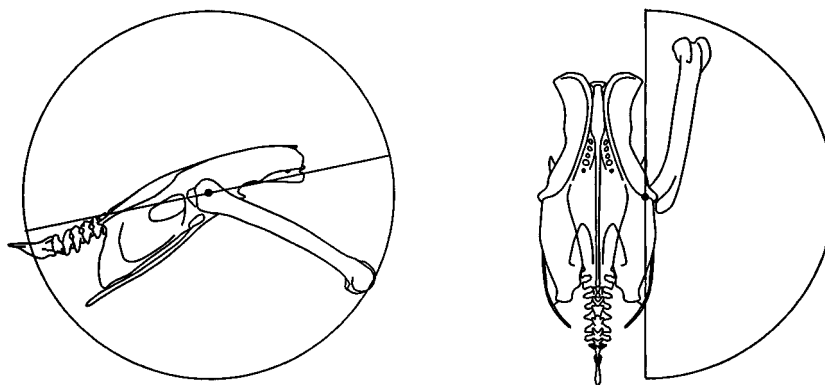


FIGURE 1. Global axis system for describing femoral motion. The potential range of movement of the femur in *Numida* (pelvis, tail, and femur in right lateral and dorsal views) can be visualized as a hemisphere centered on the femoral head with an equator parallel to the sacrum.

biomechanical data from the hindlimbs of walking crocodylians (*Alligator*) and birds (*Numida*). Our functional analysis emphasizes the different muscular mechanisms by which living archosaurs produce the full complement of forces and motion required for three-dimensional limb control about the hip. We then integrate morphological data from fossils to reconstruct the history of these mechanisms and their implications for archosaur locomotor evolution.

Materials and Methods

We describe the three-dimensional motion of the femur at the hip joint using a global axis system. The potential range of femoral mobility can be visualized as a hemisphere centered at the acetabulum, with a radius equal to femoral length and an equator oriented parallel to the sacral vertebrae. Within this hemisphere, any femoral position can be delineated by three angles; we use retraction, abduction, and long-axis rotation (Gatesy 1991). The retraction angle is the smallest three-dimensional angle between the femoral and sacral axes (Fig. 1). Contours of equal retraction form semicircles of latitude spanning from 0° retraction (pointing cranially), through 90° retraction (perpendicular to the sacral axis), to 180° retraction (pointing caudally). Movement leading to a decrease in retraction angle is femoral "protraction." Retraction and protraction of the femur in three dimensions are functionally equivalent to extension and flexion of the hip joint in the sagittal plane.

The abduction angle is the smallest three-dimensional angle between the femoral axis and the sagittal plane of the pelvis (Fig. 2A). Contours of equal abduction form circles of latitude spanning from 0° abduction (parallel to the sagittal plane) to 90° (perpendicular to the sagittal plane). Femoral "adduction" is motion toward the sagittal plane that decreases the abduction angle; thus "abduction" over 90° is technically adduction. Together, retraction angle and abduction angle delineate the location of the distal femur on the surface of the hemisphere. For example, the cylinder representing the femur in Figure 2B is retracted 45° and abducted 30°. Its proximal end is at the center of the hemisphere and its distal end is located at one of the two intersections between the retraction and abduction latitudes.

The third component of femoral motion is long-axis rotation. Medial and lateral long-axis rotation are used as relative, rather than absolute, terms of directional rotation. Such rotation does not change the position of the femur on the hemisphere's surface but affects all elements distal to the knee joint (Fig. 2C). The effect of long-axis rotation depends on the position of the phalanges with respect to the femur. If the knee joint is relatively extended, the phalanges lie close to the femoral axis and rotation primarily causes the toes to spin. For example, medial femoral rotation causes the foot to "toe in," whereas lateral rotation of the femur causes the foot to "toe out." However, if the knee is relatively flexed, the phalanges

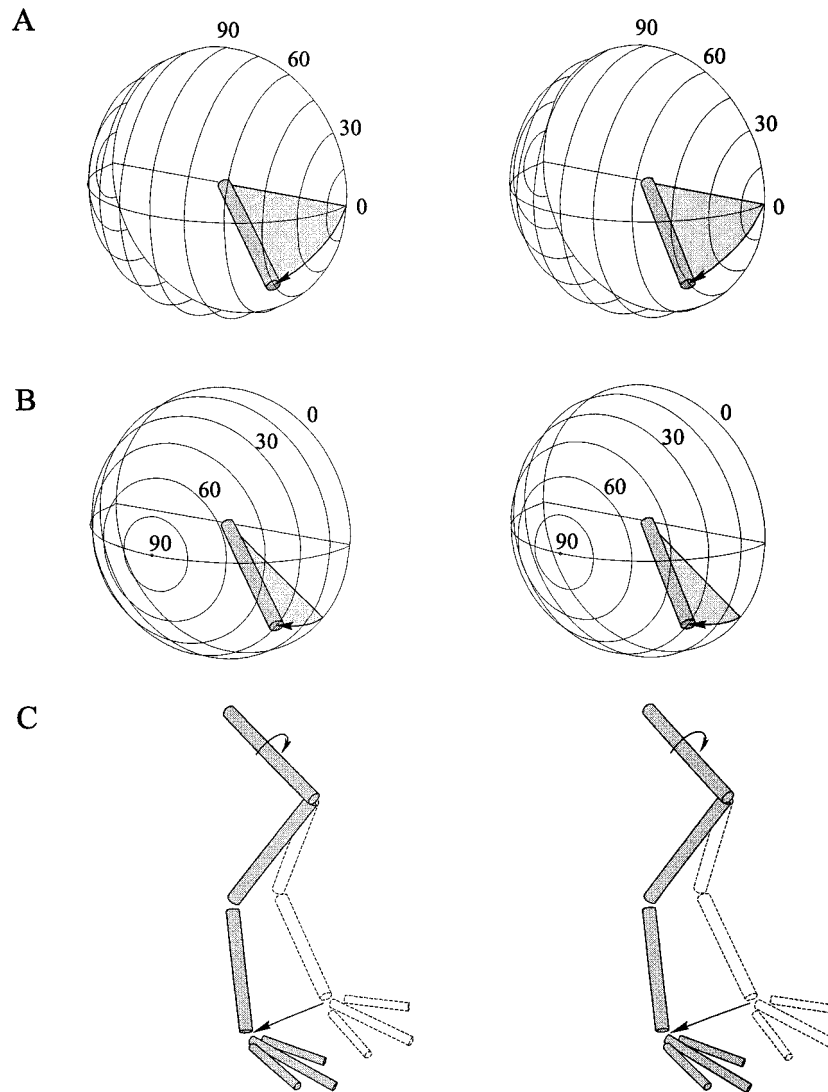


FIGURE 2. Explanations of hip joint angles in the global axis system. A, Stereo diagrams of femoral retraction angle. The cylinder represents a right femur in craniolateral view, retracted 45° from the sacral axis. Semicircular lines of latitude mark 15° increments of retraction. B, Stereo diagrams of femoral abduction angle. The femoral cylinder is abducted 30° from the sagittal plane of the pelvis. Circles of latitude mark 15° increments of abduction. C, Stereo diagrams showing the consequences of long-axis rotation of the femur on distal limb elements. With the knee flexed to 90° , 30° of medial rotation causes a dramatic abduction of the foot. The femur itself is not abducted.

lie far from the femoral axis and rotation primarily causes the toes to translate mediolaterally. Medial rotation of the femur abducts the lower limb, moving the phalanges away from the sagittal plane. In contrast, lateral femoral rotation adducts the lower limb and phalanges toward the midline (Fig. 2C). Therefore, a slight amount of long-axis femoral rotation with a strongly flexed knee can dramatically alter the position of the foot

when in the air, or can allow it to produce mediolateral forces against the ground.

Kinematic and electromyographic data from extant archosaurs are taken primarily from studies of the American alligator, *Alligator mississippiensis*, and the helmeted guinea fowl, *Numida meleagris*, walking and running on a treadmill. High-speed X-ray films were analyzed to quantify three-dimensional limb motion (see Gatesy 1991, 1999a for de-

tails). Electromyograms (EMGs) were recorded using fine-wire bipolar electrodes surgically implanted in anesthetized animals (as in Gatesy 1997, 1999b). Additional EMG data were either recorded for the present study or taken from published accounts of walking chicks (*Gallus*) (Jacobson and Hollyday 1982). Most alligator and guineafowl EMGs are based on data from at least two individuals in which electrode placement was verified by postmortem dissection. Muscles for which EMGs are limited to a single individual are marked by an apostrophe; unsampled muscles are denoted by an asterisk. Limb excursions and muscle activity are referenced to the stance phase (foot on tread) and swing phase (foot off tread) of the stride cycle. We use the term "control" to refer to muscles that resist, but do not prevent, joint movements; e.g., femoral "abductor" muscles that are active while the femur is adducting control adduction.

Anatomical nomenclature follows traditional reptilian nomenclature (e.g., Romer 1923a) or *Nomina Anatomica Avium* (Vanden Berge and Zweers 1993) terminology for birds. To clarify the historical discussion regarding these muscles, Romer's (1923a) original spellings and hyphenations for *M. pubo-ischio-femoralis internus*, *M. pubo-ischio-femoralis externus*, and *M. pubo-ischio-tibialis* are retained throughout. This nomenclature emphasizes the evolutionary separation of these muscles from the avian *M. puboischiofemoralis medialis* and *M. puboischiofemoralis lateralis*, which are entirely different muscles. Muscle homologies will be discussed in their own section later in the paper.

Hindlimb Function in Extant Archosaurs

Alligator.—The hip joint of *Alligator* comprises a slightly offset femoral head articulating with a relatively large acetabulum (Parrish 1986). This configuration allows a wide range of femoral motion, although acetabular ligaments further limit hip joint mobility. The hip abduction angle can reach 90°. In the stance phase of slowly walking *Alligator*, the femur retracts through an arc of 60–80°, abducts an additional 15–25°, and medially rotates slightly (Gatesy 1991; Reilly and Elias 1998). *M. caudofemoralis longus* accomplishes much of this

femoral retraction and medial rotation (Gatesy 1997), but abduction is mediated by other thigh muscles.

In *Alligator*, a stance phase hindlimb applies a force on the substrate that is opposed by a ground reaction force (GRF). The GRF is oriented roughly vertically in the transverse plane (Blob 1998). Because the foot is lateral to the acetabulum during the stance phase, the GRF vector creates an abduction moment about the hip joint. Femoral abduction is controlled by muscles originating from the lateral surface of the ischium below the acetabulum. These muscles include the two heads of *M. adductor femoris* (ADD1 and ADD2*), which insert on the caudal femoral shaft (Fig. 3A). The ADD1 is active during the stance phase (Gatesy 1997) to pull the limb medially, thereby countering abduction by the GRF (Fig. 4A). Other ventral muscles, *M. pubo-ischio-tibialis*, the third head of *M. pubo-ischio-femoralis externus* (PIFE3'), and possibly the ADD2* assist the ADD1 (Gatesy 1997). The GRF can be directed lateral to the hip joint during stance because the alligator is quadrupedal. At least one contralateral limb (fore and/or hind) balances the tendency of the body to collapse away from the supportive hindlimb (Fig. 4A).

During the swing phase of *Alligator*, the limb is lifted and brought forward to recover its position for the start of the next stance phase (Gatesy 1991; Reilly and Elias 1998). *M. iliofemoralis* (IF) originates from the lateral ilium above the hip joint and inserts on the lateral femoral shaft (Fig. 3A). The IF exhibits activity throughout the swing phase and thus actively abducts the limb during swing, potentially with some assistance from *M. iliofibularis* (Gatesy 1997). In turn, two muscle groups protract the limb (Fig. 3A). The first, *M. pubo-ischio-femoralis internus*, has two heads (PIFI1* and PIFI2). The PIFI2 originates from the "lumbar" vertebrae cranial to the hip joint and inserts on the proximal lateral femur. During swing the PIFI2 actively protracts the limb; the PIFI1* may function similarly (Gatesy 1997). The second, *M. pubo-ischio-femoralis externus* (PIFE), has two heads originating from the cranial (PIFE1') and caudal (PIFE2) surfaces of the pubis. Both insert on the caudolateral proximal femur ("greater trochan-

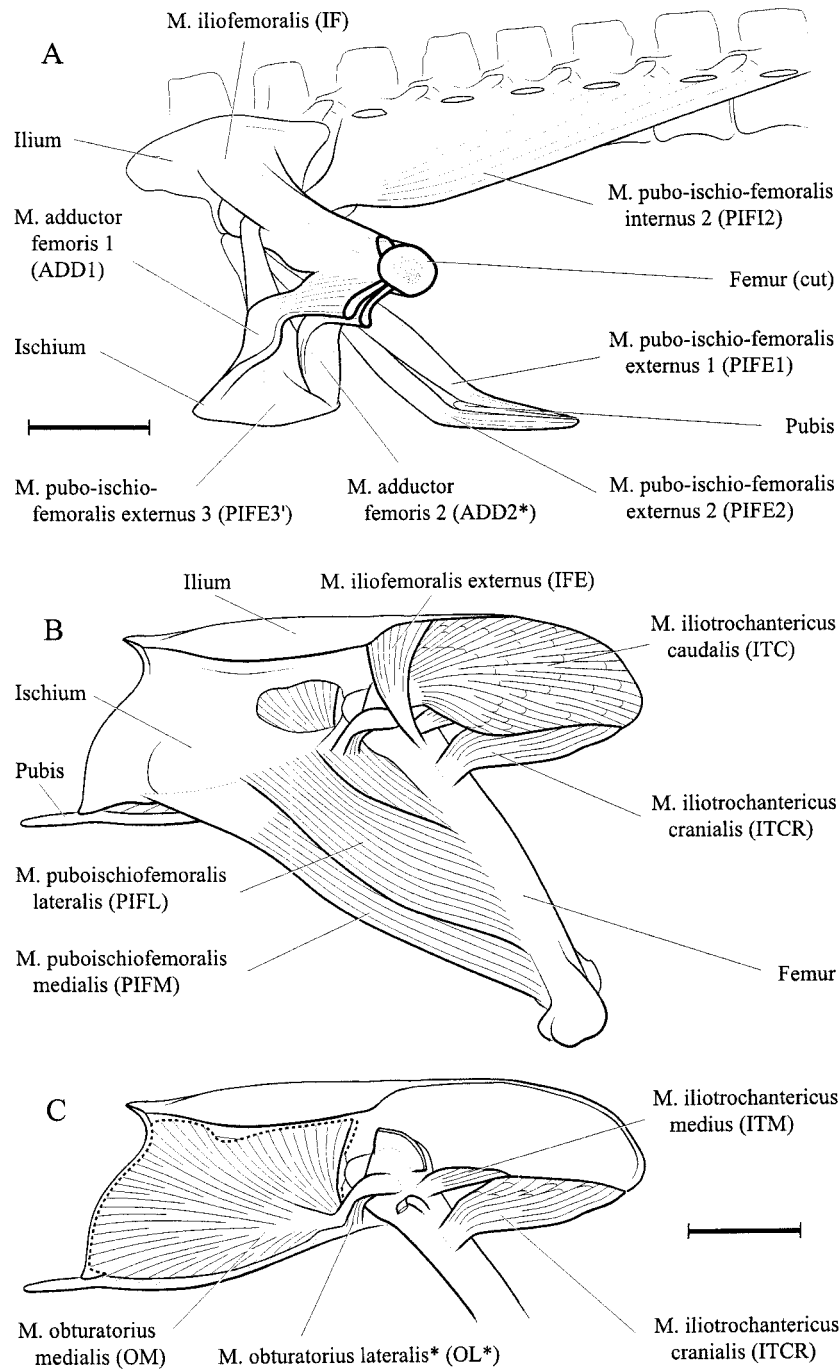


FIGURE 3. Thigh musculature of representative extant archosaurs in right lateral view. Only muscles discussed in detail in the text are shown. A, In this dissection of *Alligator*, the distal end of the highly abducted femur has been removed. Superficial structures have been excised to show the IF, ADD, PIFI, and PIFE muscle groups. Scale bar equals 1 cm. B, A dissection of *Numida* reveals the IFE, PIF, and iliotrochantericus muscle groups. C, Removal of the ischium and part of the ilium (dashed line) exposes the large OM. Scale bar, 2 cm. The deep dorsal thigh muscle *M. iliofemoralis internus* (IFI*; "cuppedicus" of Rowe 1986) is omitted, but we do not focus on it in this paper.

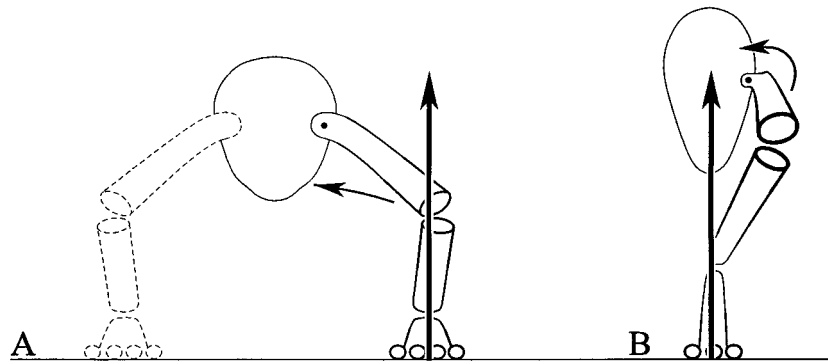


FIGURE 4. Diagrammatic representations of archosaur hindlimbs during midstance, shown in anterior view. For simplicity, the ground reaction force (GRF) is shown as a vertical arrow of equal magnitude in both forms. A, In *Alligator*, the GRF is directed lateral to the hip joint (dot), thereby tending to abduct the femur (GRF data from Blob 1998). Abduction is controlled by activation of the ventrally located *M. adductor femoris 1* (ADD1) and other muscles originating on the ischium (curved arrow). Adduction forces from muscles can counter abduction by the GRF, but will not prevent the body from collapsing because they cannot control pelvic roll away from the supportive limb. An additional stance fore- and/or hindlimb (dotted) is needed to achieve static equilibrium and hence stabilize the body. B, In most birds the GRF is directed medial to the hip joint (dot), thereby tending to adduct the femur. Adduction is controlled by *Mm. ilioprochantericus caudalis et medius* (ITC and ITM; curved arrow), which medially rotate the relatively horizontal femur to abduct the lower limb elements by the mechanism shown in Figure 1D. Unlike *Alligator*, *Numida* can balance statically on one leg.

ter"). The PIFE1' and PIFE2 are active during swing and thus are important for limb protraction (Gatesy 1997), but also appear to rotate the femur laterally. In addition, active heads of the PIFI and PIFE adduct the whole limb in late swing, returning the femur to a near-sagittal orientation for the next stance phase.

Numida.—Anatomical, kinematic, biomechanical, and electromyographic data from terrestrially locomoting *Numida* reveal major differences in limb control from that of *Alligator*. Some osteological specializations of the hip joint in *Numida* are relevant. In contrast to the crocodylian condition, the medially offset femoral head extends into the relatively small acetabulum, creating a tight ball-and-socket joint. The large antitrochanter articulates with the proximal femur (the fossa articularis antitrochanterica), limiting femoral abduction to about 60° while permitting substantial protraction/retraction and long-axis rotation. Soft tissues (hip joint muscles and ligaments) passively limit abduction further, to about 30°.

During stance, slowly walking *Numida* retract the femur only 5–10°, with only slight adduction and medial rotation (Gatesy 1999a). *M. caudofemoralis pars caudalis* (= longus) does not play an important role in generating

or controlling these movements, especially at lower speeds, when it is not active (Gatesy 1990). The GRF is oriented roughly vertically in the transverse plane, because lateral forces are relatively low (Clark and Alexander 1975). The foot is placed near the midline, thereby positioning the GRF vector medial to the hip joint. Thus the GRF imparts an adduction moment about the hip. It is limb adduction (rather than abduction as in *Alligator*) that must be controlled, especially when the body is balanced on only one limb (Fig. 4B). Two muscles oppose this adduction moment (Fig. 3B,C). *M. ilioprochantericus caudalis* (ITC) originates from the preacetabular ilium and inserts on the cranio-lateral rim of the trochanteric crest. *M. ilioprochantericus medius* (ITM) originates ventral to the ITC from the edge of the ilium, and inserts distal to it on the lateral proximal femur. Both muscles are active during stance, producing forces to rotate the femur medially about its long axis (Gatesy 1994, 1999b). Medial rotation does not abduct the femur. Rather, medial rotation of the relatively horizontal femur draws the lower leg (distal to the knee) laterally, thereby countering adduction of the lower leg by the GRF (Figs. 2C, 4B). This rotation-based abduction mechanism loads the femur in torsion (Carrano 1998; Carrano and

TABLE 1. Archosaurian muscle homologies used in this study. Modified from Romer 1923a, 1927a, 1942 and Rowe 1986. Boldface indicates active during stance (plain text: active during swing); a ~ denotes muscles also active during stance at lower speeds; an apostrophe indicates muscle EMG data from only one individual; an asterisk denotes that muscle EMG data are not available but predicted activity is shown. PIFL activity data are not available for *Numida*, but the PIFL is active during stance in *Gallus* (Jacobson and Hollday 1982).

Muscle homologies	
<i>Alligator</i>	<i>Numida</i>
M. adductor femoris 1 (ADD1)	M. puboischiofemoralis medialis (PIFM)
M. adductor femoris 2 (ADD2*)	M. puboischiofemoralis lateralis (PIFL)
M. iliofemoralis (IF) and M. iliofemoralis externus (IFE~)	M. iliotrochantericus caudalis (ITC)
M. pubo-ischio-femoralis internus 1 (PIFI1*)	M. iliofemoralis internus (IFI*)
M. pubo-ischio-femoralis internus 2 (PIFI2)	M. iliotrochantericus cranialis (ITCR) and
	M. iliotrochantericus medius (ITM)
M. pubo-ischio-femoralis externus 1 (PIFE1')	M. obturatorius lateralis (OL*)
M. pubo-ischio-femoralis externus 2 (PIFE2)	M. obturatorius medialis (OM)
M. pubo-ischio-femoralis externus 3 (PIFE3')	(absent)

Biewener 1999). The ITC and ITM simultaneously control pelvic roll (Gatesy 1999b) by opposing the tendency of the pelvis to fall during single-leg support. The "adductor" muscles of *Numida*, M. pubo-ischio-femoralis medialis (PIFM) and lateralis (PIFL) (recorded in *Gallus* [Jacobson and Hollyday 1982]) have attachments and activity similar to those of the ADD1 of *Alligator* (Fig. 3B). However, the more caudolateral position of the PIFM and PIFL relative to the hip joint indicates that they help to stabilize the hip joint and retract the femur during stance (rather than controlling abduction as in *Alligator*).

During swing, walking *Numida* protract and laterally rotate the femur (Gatesy 1999a). The hip is flexed by swing activity of M. iliotrochantericus cranialis (ITCR), which originates cranial to the ITM and inserts distal to it on the proximal femur (Fig. 3C). Other muscles extending from the ilium to the tibia assist the ITCR in flexing the hip. M. iliofemoralis externus (IFE) is a diminutive muscle that originates above the acetabulum and inserts on the distal midpoint of the lateral trochanteric crest (caudal to the ITM; Fig. 3B). It is also active during swing (and stance at lower speeds), yet its tiny size and frequent absence preclude its importance as an abductor in most neornithines (Gatesy 1999b). M. obturatorius medialis (OM) is a large pennate muscle that originates from the medial pubis, ischium, and pubo-ischadic fenestra (Fig. 3B). It tapers into a tendon as it passes through the obturator foramen to its insertion on the prox-

imal lateral trochanteric crest, caudal to the ITC. The OM is active during swing, laterally rotating the femur to adduct the lower limb for the next stance phase (as suggested by Gatesy [1999b]). Although the OM originates behind the hip joint, it does not retract the femur (contra Perle 1985), because its insertion is proximal and lateral, with no moment arm for retraction.

As we have outlined above, *Alligator* and *Numida* use disparate mechanisms to produce their three-dimensional locomotor movements. These mechanisms may seem too different to compare meaningfully. However, our summary of extant archosaurs lacks a historical emphasis. For the remainder of the paper we adopt a phylogenetic perspective to study the evolution of homologous structures and functions.

Muscle Homologies

The muscle homologies we use for our analysis of musculoskeletal evolution (Table 1) are primarily based on Romer (1923a, 1927a, 1942). Deep dorsal thigh muscle homologies remain controversial (Walker 1977; Carrano 2000) but we follow Rowe (1986).

We focus on four muscle groups: (1) M. adductor femoris (ADD). The division of the adductor muscle group into two parts constitutes an archosaurian synapomorphy (also see Romer 1923a). On the basis of their topological similarity, ADD1 and ADD2 of basal archosaurs are equivalent to the PIFM and PIFL of birds (ADD1/PIFM is medial to ADD2/

PIFL). (2) *M. iliofemoralis* (IF). Following Rowe's (1986) interpretation, the IF has two homologues in Neornithes: the IFE and ITC. (3) *M. pubo-ischio-femoralis internus* (PIFI). The two heads (PIFI1+2) in Crocodylia are homologous with three heads (*M. iliofemoralis internus* [IFI] + ITM + ITCR) in Neornithes. The PIFI1 corresponds to the IFI, whereas the PIFI2 is homologous with the ITM and ITCR in Neornithes (Rowe 1986). (4) *M. pubo-ischio-femoralis externus* (PIFE). Two pubic (PIFE1+2) and one ischial (PIFE3) heads in Crocodylia are related to one medial (OM) and one lateral (OL) head in Neornithes.

Romer (1923a, 1927a) never completely resolved the relationship of the non-avian PIFE1–3 to the avian OM and OL musculature. Using data from innervation and muscle development, Romer (1927a) inferred that the PIFE3 was lost, whereas the PIFE1+2 was equivalent to the OM+OL of Neornithes. We elaborate on Romer's hypothesis, proposing that the PIFE2 shifted medially between the pubis and ischium to become the OM, whereas the PIFE1 reduced and moved laterally onto the proximal pubic shaft to become the OL. This evolutionary scenario requires three steps: (1) movement of the PIFE2 off the caudal pubic apron into the medial pubo-ischiadic fenestra, (2) movement of the PIFE1 onto the proximal lateral pubis as it reduced, and (3) loss of the PIFE3. The extent of division of some of these muscles varies within Neornithes (George and Berger 1966; Raikow 1975; Gatesy 1994), but character optimization indicates that all were ancestrally divided in Neornithes (Rowe 1986; McKittrick 1991). Data from fossils are consistent with these hypotheses of homology, as we demonstrate below.

Musculoskeletal Evolution

A clearer perception of muscle homologies does not by itself resolve how archosaur locomotion evolved. As paleontologists have long recognized, the addition of osteological, soft-tissue, and trackway data from extinct archosaurs greatly clarifies locomotor evolution. To reconstruct the evolutionary history of archosaur thigh muscles, we followed the methods of character optimization outlined by Maddison et al. (1984) and formalized for soft-

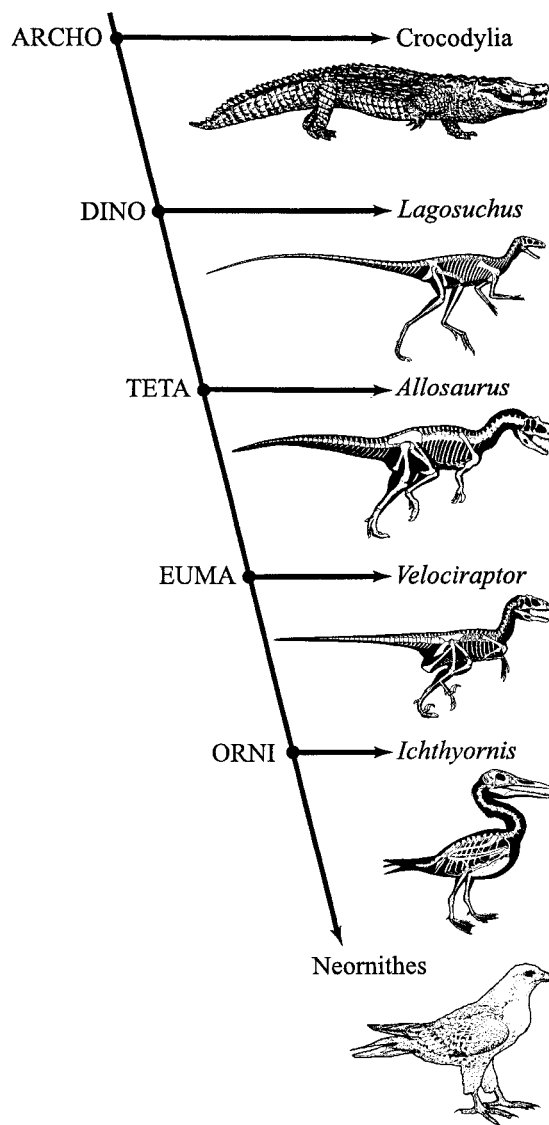


FIGURE 5. Phylogenetic framework used in this study for character optimization. ARCHO = Archosauria, CROC = Crocodylia, DINO = Dinosauromorpha, EUMA = Eumaniraptora, ORNI = Ornithurae, TETA = Tetanurae. Sources of pictures: Crocodylian modified from Grenard 1991, *Lagosuchus* (= *Marasuchus*) modified from Sereno and Arcucci 1994, *Allosaurus*, *Velociraptor*, and *Ichthyornis* modified from Chatterjee 1997, and falcon modified from Proctor and Lynch 1993.

tissue reconstruction by Bryant and Russell (1992) and Witmer (1995). We mapped osteological and correlated soft-tissue character data on a phylogenetic framework (Fig. 5), based on studies by Gauthier (1986), Gauthier et al. (1988), Sereno (1991, 1999), Chiappe (1996), Novas (1996), Forster et al. (1998),

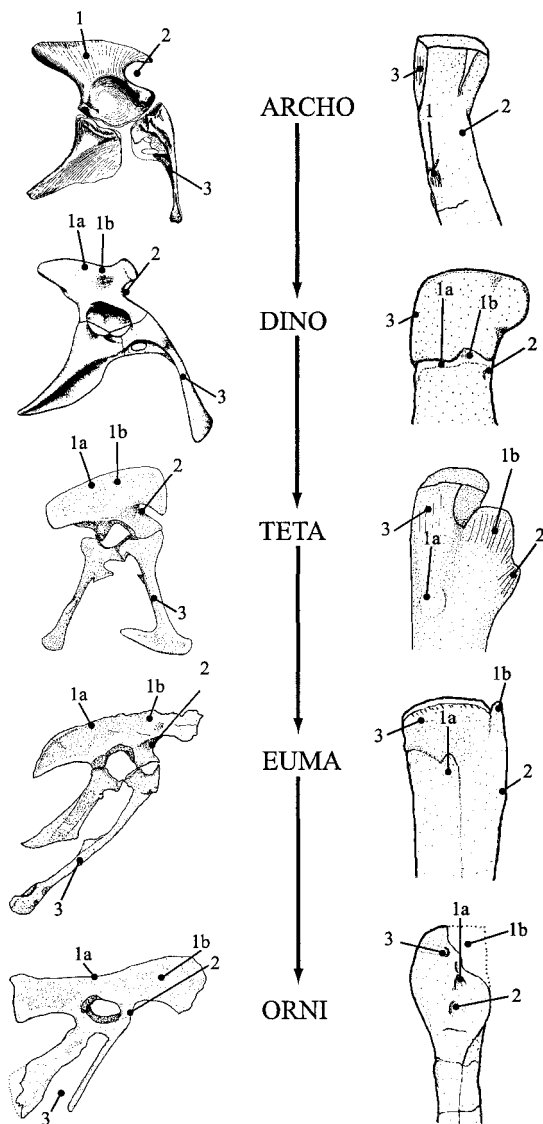


FIGURE 6. Musculoskeletal evolution on the archosaurian line to birds. Right pelvis (left column) and femora (right column) of taxa that are representative of the ancestral morphology in lateral view, from top to bottom: *Stagonolepis* (pelvis modified from Walker 1961) and *Aetosauroides* (femur of Fundación "Miguel Lillo" [San Miguel de Tucumán, Argentina] specimen number PVL 2073); *Lagosuchus* (= *Marasuchus*; pelvis modified from Sereno and Arcucci 1994; femur of Fundación "Miguel Lillo" [San Miguel de Tucumán, Argentina] specimen number PVL 3871); *Allosaurus* (pelvis modified from Molnar et al. 1990; femur of Museum of the Rockies [Bozeman, Montana] specimen number MOR 698); *Velociraptor* (left pelvis and femur [reversed] of Geological Institute of Mongolia [Ulan Bataar, Mongolia] specimen number IGM 100/985); and *Patagopteryx* (pelvis and femur of Museo Argentino de Ciencias Naturales [Buenos Aires, Argentina] specimen number MACN-N 11). Not to scale. Solid circles approximate centroids of muscle attachments. Numbers correspond to muscle groups

Holtz (in press), and Padian et al. (1999). The data supporting these inferences are presented in more detail elsewhere (Hutchinson in press a,b), but we summarize them here (Fig. 6).

M. adductor femoris (ADD).—Ischial morphology in basal archosaurs is similar enough to the crocodylian condition to infer the presence of the ADD1 on the cranioventral edge of the ischium (e.g., the obturator process), cranial to the PIFE3. The ADD2 would have originated from the lateral ischial shaft, caudodorsal to the PIFE3 as in *Alligator* (Fig. 3A). The neornithine ADD homologues (PIFM and PIFL) have origins in similar positions but are not separated by the PIFE3. This difference is related to the loss of the PIFE3 and the ischial obturator process, and to the lateral shift of other thigh-muscle origins. The femoral insertions of the ADD/PIF did not change appreciably on the lines to Crocodylia or Neornithes (Romer 1923a). Rugosities (often called the adductor ridge or crest) on the caudal femoral shaft between the fourth trochanter and popliteal fossa are commonly present in archosaurs (Gauthier et al. 1988; Makovicky and Sues 1998; Hutchinson in press b).

Three evolutionary alterations moved the PIFM+L origins caudally and laterally with respect to the hip joint: (1) increased retroversion of the ischia in Eumaniraptora and especially Ornithurae, (2) a posterior widening of the pelvis in maniraptorans, and (3) the loss of the ischial symphysis in basal birds (Hutchinson in press a). These changes were most prominent in ornithurine birds (Chiappe 1996), shifting PIFM+L function from femoral adduction to femoral retraction. Along the same lineage, the remaining stance phase adductors (the PIFE3 and *M. pubo-ischio-tibialis*) were also lost (Romer 1923a). This prompts the question, Were stance phase femoral adductors no longer important in basal

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(also see Table 1): 1 = *M. iliofemoralis* (IF), 1a = *M. iliofemoralis externus* (IFE), 1b = *M. iliotrochantericus caudalis* (ITC), 2 = *M. pubo-ischio-femoralis internus* 2 (PIFI2) or *Mm. iliotrochanterici cranialis et medius* (ITCR and ITM), 3 = *M. pubo-ischio-femoralis externus* 2 (PIFE2) or *obturatorius medialis* (OM). Other muscle groups from Table 1 are omitted for clarity.

birds? We hypothesize that stance phase femoral abduction became more important than adduction quite early on the line to Neornithes. This abduction was controlled by at least part of the IF muscle group.

M. iliofemoralis (IF).—The origin of the IF was located dorsal to the acetabulum in Reptilia ancestrally (Romer 1923a; Rowe 1986). It shifted cranially with the preacetabular ilium in dinosaurs (especially theropods [Carrano 2000]), correlated with an increase in sacral vertebral count. A preacetabular iliac concavity became pronounced in some maniraptorans (especially birds), demarcated from the postacetabular ilium by a supratrochanteric iliac process (Hutchinson in press a). By this point, the centroid of the IF origin was markedly cranial to the acetabulum, a feature inherited by neornithines (Figs. 3B, 6).

The IF insertions are well marked in archosaurs. Many basal archosaurs show muscle scars on the lateral shaft of the distal femur that correspond topologically to the distally positioned IF insertion of Crocodylia (Figs. 3A, 6) (Walker 1977). A trochanteric shelf for the IF insertion is present in basal dinosauromorphs (e.g., *Lagosuchus* and *Lewisuchus* [Novas 1996; Hutchinson in press b]). The caudal part of this structure remained near its ancestral position, whereas the cranial portion was expanded proximally into a large, blade-like lesser trochanter in dinosaurs (Fig. 6). The trochanteric shelf corresponds to the IFE insertion of Neornithes. Parts of the shelf were expanded into a posterior trochanter (sensu Ostrom 1976) and/or lateral ridge (sensu Norell and Makovicky 1999) in many maniraptorans, including basal birds (Forster et al. 1998), but the entire trochanteric shelf was reduced in Ornithurae (Chiappe 1996). Considering these features, we propose that the split of the IF into the IFE and ITC, as well as the IFE insertion on the lateral surface of the proximal femur, was established quite early in dinosauromorph evolution. The IFE insertion remained relatively unchanged as the homologue of the ITC moved its insertion.

Along the line of descent from Dinosauria to Maniraptora, the lesser trochanter expanded more proximally and shifted cranially (Fig. 6) as the proximal femur was rotated medially

(Carrano 2000). The lesser trochanter shifted close to the greater trochanter (i.e., opposite the femoral head), fusing with it to form a trochanteric crest in many maniraptorans, especially in basal birds (Ostrom 1976; Gauthier 1986; Chiappe 1996). Prominent Sharpey's fibers (mineralized collagen strands) are longitudinally oriented on the lesser trochanter in non-maniraptoran dinosaurs. These fibers corroborate the presence of a muscular attachment running from the preacetabular ilium to the lateral side of the trochanter (Walker 1977). These fibers are restricted to a semicircular, dorsally convex scar on the proximal trochanteric crest in Ornithurae and other birds, but their orientation is at a marked angle to the longitudinal axis of the femur (Hutchinson in press b). The fibers and scar mark the ITC insertion in Neornithes and hence other ornithurine birds. Thus the ITC insertion on the lesser trochanter (or trochanteric crest) moved proximally and cranially on the line to crown-group birds, whereas the IFE insertion on the trochanteric shelf remained distal and caudal to the ITC insertion (Fig. 6).

As we will further explain below, these morphological changes suggest at least three functional changes in the IF group: (1) a shift of ITC activity from swing phase to stance phase abduction within Dinosauromorpha; (2) altering the function of the ITC from abduction to medial rotation within Maniraptora; and (3) reduction of role of the IFE in stance phase abduction in Ornithurae. Stance phase adduction by the ADD was thus ultimately replaced by medial rotation (leading to lower limb abduction) by the ITC, although additional muscles were important for protraction and medial rotation.

M. pubo-ischio-femoralis internus (PIFI).—The PIFI ancestrally originated medial to the ilium (PIFI1+2) and from the proximal ischium (PIFI1). The origins of the PIFI homologues (the IFI, ITM, and ITCR) are on the lateral ilium in Neornithes, so they must have shifted laterally on the line to Neornithes. A ventrolateral, preacetabular iliac fossa (the "cuppedic fossa") in many Tetanurae appears to indicate the shift of at least part of the PIFI muscle group (Fig. 6). The fossa extended laterally onto the ilium in Maniraptora (Norell and Ma-

kovicky 1999) including basal birds, but was strongly reduced in *Patagopteryx* and Ornithurae (Chiappe 1996). Perhaps the lateral shift of the PIFI origins was complete in Ornithurae (Hutchinson in press a).

The insertion of the PIFI2 seems to have changed little from its ancestral position on the proximal lateral femur. Scars are present in this region in basal archosaurs (e.g., phytosaurs, aetosaurs, poposaurs, and crocodylomorphs), and the insertions in Neornithes are in similar positions. An accessory trochanter near the base of the lesser trochanter in many Tetanurae (Fig. 6) (Makovicky and Sues 1998) is in roughly the same position as the ITM and ITCR (= PIFI2) of Neornithes (Hutchinson in press b). This trochanter may mark the position of the PIFI2 insertion, which remained distal to the ITC insertion while the ITC (and the lesser trochanter) moved proximally. A transverse groove and scar in this position in *Rahonavis*, Enantiornithes, and ornithurine birds suggest that the modern neornithine insertion(s) were present in basal birds (Fig. 6), yet no scars unambiguously show when the PIFI2 split into the ITM and ITCR (Hutchinson in press b). The insertion of the PIFI1 and IFI is similar in Crocodylia and Neornithes (proximal to the fourth trochanter on the medial femur, near the femoral neck), and muscle scars in most basal birds corroborate its consistent presence there. Because EMGs and other data are lacking for the PIFI1 and IFI, their functions remain unclear.

The sequence of functional evolution of the PIFI2 is also ambiguous. The ITCR (= PIFI2 *partim*) retains its plesiomorphic protractive function in *Numida* and other birds (Gatesy 1994). However, it is unequivocal that the function of ITM portion of the PIFI2 shifted from swing phase protraction (and active adduction of the lower leg) in basal archosaurs to stance phase medial rotation (and controlling lower leg adduction) in Neornithes (see Gatesy 1999b for motor pattern data). The adoption of a well-flexed hip joint within birds may relate to this transformation, but unfortunately the lack of unequivocal anatomical data from fossils hinders detailed inferences about the number and sequence of changes in the PIFI2.

M. pubo-ischio-femoralis externus (PIFE).—The origin of the PIFE was mainly on the concave lateral surface of the pubo-ischiadic plate in basal archosaurs, segregated into pubic (PIFE1 and PIFE2) and ischial (PIFE3) parts. The PIFE1 and PIFE2, respectively, arose from the cranial and caudal faces of the pubic apron, whereas the PIFE3 origin was from the “obturator process” (cranioventral ischium, between the ADD1+2). As the ventrolateral surfaces of the pubo-ischiadic plate separated within Dinosauromorpha, so did the PIFE origins (Fig. 6), but this separation had already begun in more basal reptiles. The PIFE1+2 origins shifted distally with the pubic apron in Tetanurae, and the PIFE3 eventually disappeared with the obturator process within Aves, especially Ornithurae (Hutchinson in press a).

The pubes were cranially oriented from basal Archosauria through Tetanurae. Maniraptorans changed their pubes radically, at first to a near-vertical position in basal taxa (Serenio 1999; Holtz in press), and later to a well-retroverted position within birds (e.g., in Ornithurae and related taxa [Chiappe 1996]). The arc of pubic retroversion from ancestral Archosauria to Neornithes is roughly 90°. This retroversion would also have moved the PIFE1+2 origins from cranioventral to the acetabulum to caudoventral to the acetabulum (Fig. 6), eventually eliminating any PIFE moment arm for femoral protraction (Romer 1927b; Charig 1972; Walker 1977).

When and how the ancestral PIFE1 and PIFE2 became the OL and OM of Neornithes is not certain. The loss of the pubic symphysis, boot, and apron, the more elongate and blade-like form of the ischium, and the apparent formation of a lateral pubo-ischiadic membrane in some basal birds (e.g., *Patagopteryx* and Ornithurae) are similar enough to the neornithine condition to infer the medial origin of the OM in these taxa (Hutchinson in press a). As the pubic apron was reduced distally within Tetanurae, bringing the PIFE1+2 origins with it, a portion of the PIFE1 may have remained on the proximal pubic shaft to later become the OL of Neornithes.

The ancestral insertions of the PIFE probably were in a common region on the proximal

caudolateral femur (“greater trochanter”), because the proximal femur of basal archosaurs lacks the internal trochanter and intertrochanteric fossa (the ancestral insertion for Reptilia) and it is morphologically similar to the crocodylian insertion area (Hutchinson in press b). Fossils reveal that this insertion shifted laterally as the femoral head inflected medially within Tetanurae (Fig. 6), rotating through an arc of roughly 45° (Carrano 2000). This twisting of the proximal femur increased the PIFE moment arm for lateral femoral rotation, thus enhancing the capability of the PIFE1+2 to produce this motion during the swing phase. Therefore, an increase in the capacity of the PIFE1+2 to rotate the femur laterally preceded the retroversion of the pubes and the concomitant loss of PIFE1+2 protraction ability. In *Rahonavis*, Enantiornithes, and Ornithurae, a slight groove runs craniolaterally from the caudal edge of the trochanteric crest to a scar near the center of the trochanteric crest, adjacent to the ITC insertion. If we are correct in our homology assumptions, then the PIFE1 (= OL) insertion would have remained on the caudolateral side of the femur while the PIFE2 (= OM) insertion moved laterally with the greater trochanter. Neornithines retain these plesiomorphic insertions.

Functional Evolution

Finally, we combine the experimental functional data with our inferences about musculoskeletal evolution to reconstruct the pattern of functional evolution on the line to Neornithes (Figs. 5, 6). Our inferences are strongest (least speculative) for skeletal morphology, followed by osteological restrictions of joint mobility, osteological correlation of soft tissues, muscle activity, muscle function, and kinematics. We reconstruct five ancestral conditions (following Gatesy [in press]) along the line to crown-group birds (including *Numida*): ARCHO (ancestral archosaur), DINO (ancestral dinosauriform), TETA (ancestral tetanurine theropod), EUMA (ancestral eumaniraptoran coelurosaur), and ORNI (ancestral ornithurine bird). The optimization of motor pattern data from thigh muscles follows Gatesy (1999b). Our inferences about ancestral morphologies were based on the preceding

section; for more detailed discussion, see Hutchinson in press a,b.

ARCHO.—The quadrupedal ARCHO appears to have been morphologically and functionally similar to *Alligator*. The craniomedially oriented femoral head was not well offset from the proximal femur (Parrish 1986; Sennikov 1989). The acetabulum was large relative to the femoral head, permitting a wide range of abduction/adduction, flexion/extension, and long-axis rotation that was partly limited by acetabular ligaments. The antitrochanter of ARCHO was a small structure that was poorly differentiated from the remainder of the acetabulum. It was in the caudoventral corner of the acetabulum, facing dorsolaterally (Novas 1996). These features did not impose many constraints on hip joint mobility relative to Neornithes.

Muscle function in ARCHO can be reconstructed from optimization of muscle motor patterns (see Gatesy 1999b) combined with the musculoskeletal data discussed in the previous section. In ARCHO, the ADD1+2 would have opposed abduction during stance, keeping the abduction angle below 90°. In the swing phase, the IF of ARCHO would have abducted the limb while the PIFI1+2 and PIFE1+2 protracted it and rotated the femur laterally. The PIFI1+2 and PIFE1+2 would also have produced some ancillary whole-limb adduction during late swing. Despite the more erect posture and specialized osteology of many non-dinosauriform archosaurs, including some taxa along the line to Crocodylia (Charig 1972; Walker 1977; Parrish 1986; Sereno 1991), their ADD, IF, PIFI, and PIFE musculature may have worked in a manner comparable to that in *Alligator*. Fossil archosaur trackways reveal a similar pattern of movement in most non-dinosauriform archosaurs (Padian and Olsen 1984), corroborating this inference. The large tail and fourth trochanter of ARCHO suggest that the caudofemoral musculature was proportionately large and important in stance phase femoral retraction (Tarsitano 1983; Gatesy 1990).

DINO.—Some osteological changes in DINO are noteworthy. The expanded, ventrolaterally projecting supra-acetabular crest limited abduction to about 70°. Because the femoral

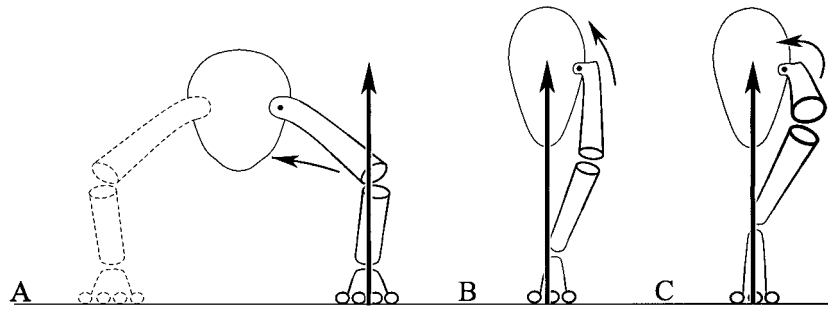


FIGURE 7. Diagrammatic representations of stance-phase postural support in archosaurs. A, C, *Alligator* and *Numida*, respectively, from Figure 4. B, Bipedal dinosauromorph during midstance, shown in anterior view. For simplicity, the ground reaction force (GRF) is shown as a vertical arrow. In most bipedal dinosauromorphs the GRF presumably was oriented medial to the hip joint (dot), because the foot is near the midline of the body. Abduction of the relatively vertical femur by the M. iliofemoralis (IF; or ITC and IFE) muscle group (curved arrow) was likely needed to counter adduction by the GRF. Unlike *Alligator*, but like *Numida* and most other extant birds, extinct theropods could balance statically on one leg.

head is not fully offset medially, the supra-acetabular crest also limited mediolateral rotation. The acetabulum is partly open to accommodate the femoral head, further limiting abduction. Thus the hip joint shows some specializations for erect posture and parasagittal gait. Other specializations in the distal hindlimbs, and the reduction of the forelimbs, indicate that DINO was bipedal and digitigrade and had erect posture, as is generally agreed (Charig 1972; Padian and Olsen 1989; Sennikov 1989; Sereno 1991; Novas 1996). An erect biped has no supportive contralateral forelimb to prevent collapse of the body away from the supportive hindlimb. Therefore, an erect biped cannot balance statically on one leg if the foot is placed lateral to the hip joint. However, DINO could have stood on one leg and maintained static equilibrium (Fig. 7B) because the position of the foot would have been medial to the hip joint, and thus abduction by the IF muscle group could balance the adduction moment induced by the GRF (Welles 1986). Fossil trackway data confirm that the feet were placed near the body midline in all known bipedal dinosauromorph tracks (Padian and Olsen 1989; Wade 1989).

The adduction function of the ADD would have been de-emphasized in favor of more hip extension, because the posture of DINO was more erect and the gait was more parasagittally restricted. Furthermore, the ischial origins were placed farther behind the hip joint. Nonetheless, some adduction function would

still have remained. The origin of bipedalism in DINO is correlated with a proximal shift of the IF insertion and a division of the IF into the ITC and IFE. We have proposed that the ITC activity changed from swing to stance phase in DINO. Thus the ITC would have exerted an abduction moment countering the GRF adduction moment, and also controlling pelvic roll (Fig. 7) (also suggested by Romer 1923b; Colbert 1964; Walker 1977; Welles 1986). A similar function is ascribed to the hominid gluteus medius and minimus muscles (McLeish and Charnley 1970; Lovejoy 1973; Stern and Susman 1981). The IFE of DINO may have had stance phase activity as well as plesiomorphic swing phase activity. Note that the prominent supra-acetabular crest of DINO would also have maintained the distance of the IFE and ITC lines of action from the hip joint, and thus maintained their moment arms for abduction.

TETA.—In *TETA*, the medially offset femoral head maintained a limit on abduction at roughly 70° , even though the supra-acetabular crest was slightly reduced. The acetabulum was still widely open, which allowed more long-axis rotation of the femur relative to extant birds (although again, soft tissues could have limited this range). The ITC origin and insertion expanded more cranially, possibly adding hip protraction function if some swing phase activity persisted (Carrano 2000). Stance phase femoral abduction continued to be emphasized. The medial inflection of the

femoral head brought the greater trochanter (and its PIFE2 insertion) from the caudolateral side of the femur to the lateral side (as in Neornithes). This change would have increased the lateral rotation moment arm of the PIFE2. Some protraction function remained, however, because the pubes (and PIFE1+2 origins) were still in front of the hip joint. Therefore, the PIFE2 moment arm for lateral femoral rotation had attained its derived "neornithine" condition, but PIFE1+2 function still involved swing phase protraction and thus was not completely in its most derived state.

EUMA.—*EUMA* had many changes relative to *TETA*, most of which arose in a stepwise pattern within Tetanurae. The iliac antitrochanter was more dorsally positioned and ventrolaterally oriented, intermediate between the morphology of *ARCHO* and *Neornithes*. This change occurred concomitant with further reduction of the supra-acetabular crest and a constriction of the acetabulum. The hip joint still would have limited abduction to roughly 70°.

The *ADD* origins were more laterally placed in *EUMA*, because the ischial symphysis was reduced and the postacetabular pelvis was widened. This would have shifted the *ADD* function to more hip extension and less femoral adduction during stance. The proximal femur of *EUMA* has a trochanteric crest (or a nearly complete one) formed by the fusion of the greater and lesser trochanters, which indicates a fully proximal insertion of the *ITC*, as in *Neornithes*. Therefore, the abduction function of *ITC* could have shifted into more medial rotation function, because the *ITC* had little or no moment arm for abduction but had a large moment arm for medial rotation (enhanced by the cranial shift of the *ITC* origin). Indeed, a change in *ITC* function from abduction to medial rotation might account for the formation of the trochanteric crest. However, this possible shift depends on the orientation of the femur, which may not have been as strongly protracted as in *Neornithes*. In any case, the PIFE2 (= *OM*) and *ITC* moment arms for long-axis rotation were roughly equal in *EUMA* (as in *Neornithes*), suggesting the acquisition of some derived aspects of long-axis rotational capacity.

One major change in *EUMA* was the retroversion of the pubes. Pubic retroversion moved the origins of the PIFE1+2 caudally, essentially eliminating the ability of these muscles to protract the femur. However, the PIFE2 (= *OM*) could still have rotated the femur about its long axis, because of its insertion on the lateral surface of the greater trochanter, as in *Neornithes*. Thus although the protractive ability of the PIFE2 was lost, the ability of the PIFE2 to laterally rotate the femur was maintained. Other features of *EUMA* are intermediate between those of basal taxa and *Neornithes*. The tail and fourth trochanter of the femur are reduced along with caudofemoral retraction (Gatesy 1990, 1995), and the hindlimb proportions are similar to those in many basal birds (Gatesy and Middleton 1997; Carrano 1998).

Additional evidence supports the inference that hip (and knee) flexion increased in *EUMA*. The reduced or absent supra-acetabular crest may indicate that (1) the *ITC* was oriented less vertically, and hence the shelf was not necessary to keep the muscle lateral to the hip joint, and (2) resisting femoral abduction was less important in *EUMA*. In these characteristics *EUMA* is more similar to extant birds than to *DINO*. Basal birds such as *Archaeopteryx* inherited this complement of features from *EUMA* relatively unchanged.

ORNI.—*ORNI* was strikingly similar to *Numida* and other *Neornithes*. The antitrochanter is large, caudodorsally positioned above the acetabulum, and ventrolaterally facing. The small acetabulum tightly encloses the spherical femoral head, limiting abduction to about 60°. Distally in the limb, the femoral condyles, their fibular and tibial articulations, and the ossified patella and hypotarsus of the knee and ankle are all morphologically quite similar to *Neornithes* (also see Chiappe 1996). All of these features are correlated with increased hip and knee flexion as well as increased ankle extension in *ORNI*, including *Neornithes* (Hutchinson in press b).

The pubes and ischia of *ORNI* are well retroverted and lack symphyses or aprons, consistent with the inference that the *OM* (= PIFE2) and PIFM+L (= *ADD*1+2) were in their most derived positions. The large tro-

chanteric crest and expanded ilium also are characteristics almost identical in Neornithes, suggesting similar ITC and IFE (= IF), ITM+ITCR (= PIFI2), and IFI (= PIFI1) attachments and moment arms. The more oblique orientation of the Sharpey's fibers at the ITC insertion supports the inference that the hip joint of ORNI was more strongly flexed than in basal taxa. The ITM may have shifted from swing to stance phase activity in ORNI (if not earlier), supplementing medial femoral rotation by the ITC. Finally, the reduced tail, the pygostyle (Gatesy 1990, 1995), and the hindlimb proportions (Gatesy and Middleton 1997; Carrano 1998) of ORNI are much the same as in Neornithes. In fact, no substantial differences in hindlimb morphology separate ORNI and Neornithes (Chiappe 1996; Hutchinson in press b). These similarities with crown-group birds compel us to reconstruct ORNI as fundamentally similar to *Numida* in femoral orientation and control, unlike ARCHO, DINO, TETA, or even EUMA in several key aspects.

Summary of Motor Pattern Evolution.—Muscle function can be retained through time or undergo modification via alteration in motor pattern, anatomical reorientation, or both. Instances of each of these evolutionary patterns are found in the four muscle groups we studied. For example, the ITCR of *Numida* appears to have changed little from its crocodylian homologue, the PIFI2, despite having shifted its origin from the dorsal vertebrae to the ilium. Both muscles shorten to protract the limb during the swing phase. In contrast, the ITM runs in parallel with the ITCR in *Numida*, but the ITM has changed in activity from swing to stance. The ITM no longer acts to protract the limb like the PIFI2. Rather, the ITM assists the ITC in producing a force to rotate the femur medially during stance, thereby preventing hip adduction and pelvic collapse.

Alternatively, the PIFM of *Numida* retains its ancestral stance phase motor pattern but has undergone a functional shift due to anatomical reorientation. The ancestral PIFM homologue (the ADD1) ran primarily in the transverse plane from the ischium (medial) to the femoral shaft (lateral). This arrangement was well suited for producing an adductive force

but less effective at retraction. Transformation of the relative position of the origin and insertion led to the PIFM running primarily in the sagittal plane from the ischium (caudal) to the femur (cranial). In extant birds the ischium is directed caudally and deflected laterally, allowing the PIFM to produce a retractive force on the relatively horizontal femur with almost no adductive component.

Finally, both the anatomy and activation of the ITC in *Numida* are derived relative to its crocodylian homologue, the IF. The ITC's origin has moved cranially, whereas its insertion on the femur has shifted proximally and cranially. The IF was active during swing to elevate the limb, but the ITC fires during stance to assist the ITM, as discussed above. It is important to note that although we know such a modification took place, the specific order of changes in IF anatomy and motor pattern is ambiguous. The simplest sequence we can propose involves three steps: (1) splitting of the IF (swing activity) into the ITC and IFE (both swing activity), (2) ITC activity changing from swing to stance, and (3) the IFE adding a stance burst at lower speeds. Obviously, more convoluted scenarios can be hypothesized but are less parsimonious (more speculative). We postulate that the switch of IF activity from swing to stance was related to the origin of striding bipedalism in dinosauro-morphs.

Evolution of Hip Adduction/Abduction.—Although birds such as *Numida* have relatively planar overall limb motion (the so-called parasagittal gait), a closer look reveals that this classical depiction is oversimplified. Birds not only need to adduct/abduct the limbs during forward locomotion and maneuvering, but they must also produce mediolateral forces in order to balance. In this study we have begun to unravel the evolutionary history of this three-dimensional control system. Ancestral archosaurs had several muscle groups positioned around the hip joint. This condition persists in Crocodylia, which have limb protractors cranially, retractors caudally, adductors ventrally, and abductors dorsally. Such an organization was retained in dinosaurs, including basal theropods.

We propose that on the line to Neornithes,

whole-limb adduction and abduction were replaced by femoral long-axis rotation as the primary mechanism of mediolateral limb control. *Numida* exemplifies a derived design that almost entirely lacks muscles above and below the acetabulum. Instead, two large pinnate muscles (the ITC cranially and the OM caudally) control long-axis rotation of the femur. Cranial migration of the ancestrally dorsal IF musculature gave rise to an ITC capable of medial femoral rotation. When active during stance, the ITC allows the toes to push laterally against the substrate and prevent pelvic collapse. An abductor of the whole limb was thus transformed into an abductor of the limb distal to the knee.

The antagonist of the ITC is the OM, which laterally rotates the femur in swing, thereby adducting the distal limb. Retroversion of the avian pubis has long interested morphologists, especially paleontologists (Romer 1927b; Galton 1969; Walker 1977; Perle 1985; Chatterjee 1997; Ruben et al. 1997; Rasskin-Gutmann and Buscalioni in press). We do not speculate on the proximate cause(s) for this dramatic re-orientation but focus on its consequence. As the pubis rotated through about 90°, the PIFE1+2 lost their protractive function (Romer 1927b; Galton 1969; Perle 1985) but retained their ability to rotate laterally. The OL (= PIFE1) was strongly reduced in birds, whereas the OM (= PIFE2) remained large and shifted its origin caudally. Fossils illuminate the stepwise nature of the transformations that led to this novel mechanism in *Numida* and other birds.

Paleontological data also reveal how the hip joint and its mediation of hip abduction angle evolved, supporting the inference that extant birds retain a similar osteological limit on hip abduction angle as basal dinosauromorphs did (roughly 60–70°). The osteological structures that limited abduction evolved within Dinosauroomorpha, but a similar quantitative limit on abduction was maintained on the line to crown-group birds. For example, the femoral head became medially offset in TETA, the supra-acetabular crest was strongly reduced and the acetabulum became relatively more constricted in EUMA, and the antitrochanter enlarged and shifted dorsally in ORNI, but

none of these taxa could abduct their hip past about 60–70°. Nonetheless, the possibility of a large hip-abduction angle does not necessitate a large hip-abduction angle. Living birds constrain femoral abduction with soft tissues, and data from fossil trackways strongly support the hypothesis that this constraint on abduction is an ancient dinosaurian plesiomorphy (Padian and Olsen 1989).

Conclusions

Our reconstruction of hypothetical ancestors on the line to crown-group birds reveals that significant anatomical and functional transitions are distributed across many nodes in a protracted sequence, rather than being concentrated at one or two. Although we dealt only with ARCHO, DINO, TETA, EUMA, and ORNI, changes appear to have evolved in an incremental fashion. Inclusion of intermediate nodes between these ancestors would likely reveal an even more gradual transformation series. Dichotomizing archosaurian locomotion into “birdlike” and “not birdlike” categories obscures the interesting and complex underlying details of this continuum. For example, EUMA appears to be more similar to ORNI than to TETA in some aspects of hindlimb function, even though EUMA was not a bird.

This analysis highlights the benefits of integrating data from multiple sources (neontological and paleontological, anatomical and functional) to help decipher the evolution of archosaur locomotion. Experimental studies of living birds and crocodylians yield kinematic, kinetic, and motor-control data unattainable from extinct organisms. However, Neornithes and Crocodylia have diverged too far to permit adequate comparison without the inclusion of data from extinct forms. Fossils are important for calibrating evolutionary polarity (Gauthier et al. 1988; Witmer 1995; Hutchinson in press a) and can reveal intermediate character states not observable in living taxa. Without such data, we would be unable to appreciate the plesiomorphic nature of crocodylian hindlimb function or to make strong inferences about the sequential derivation of neornithine locomotion.

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