Pelvic and Hindlimb Myology of the Basal Archosaur *Poposaurus gracilis* (Archosauria: Poposauroidea)

Emma R. Schachner,[1,2]* Phillip L. Manning,[1,3] and Peter Dodson[1,4]

[1]*Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania*
[2]*Department of Biology, University of Utah, Salt Lake City, Utah*
[3]*School of Earth, Atmospheric and Environmental Sciences, University of Manchester, Manchester, UK*
[4]*School of Veterinary Medicine, University of Pennsylvania, Philadelphia, Pennsylvania 19104*

ABSTRACT The discovery of a largely complete and well preserved specimen of *Poposaurus gracilis* has provided the opportunity to generate the first phylogenetically based reconstruction of pelvic and hindlimb musculature of an extinct nondinosaurian archosaur. As in dinosaurs, multiple lineages of basal archosaurs convergently evolved parasagittally erect limbs. However, in contrast to the laterally projecting acetabulum, or "buttress erect" hip morphology of ornithodirans, basal archosaurs evolved a very different, ventrally projecting acetabulum, or "pillar erect" hip. Reconstruction of the pelvic and hindlimb musculotendinous system in a bipedal suchian archosaur clarifies how the anatomical transformations associated with the evolution of bipedalism in basal archosaurs differed from that of bipedal dinosaurs and birds. This reconstruction is based on the direct examination of the osteology and myology of phylogenetically relevant extant taxa in conjunction with osteological correlates from the skeleton of *P. gracilis*. This data set includes a series of inferences (presence/absence of a structure, number of components, and origin/insertion sites) regarding 26 individual muscles or muscle groups, three pelvic ligaments, and two connective tissue structures in the pelvis, hindlimb, and pes of *P. gracilis*. These data provide a foundation for subsequent examination of variation in myological orientation and function based on pelvic and hindlimb morphology, across the basal archosaur lineage leading to extant crocodilians. J. Morphol. 272:1464–1491, 2011. © 2011 Wiley Periodicals, Inc.

KEY WORDS: Archosauria; extant phylogenetic bracket; myology; bipedalism; osteology

INTRODUCTION

Reconstructions of extinct archosaurian musculoskeletal anatomy have been a subject of interest for over a century (Dollo, 1888). However, research has been primarily dedicated to the myology of dinosaurian archosaurs, with particular attention focused on myological changes associated with the evolution of the avian fore and hindlimbs (e.g., Romer, 1923b; Walker, 1977; Hutchinson and Gatesy, 2000; Hutchinson, 2001a,b; Carrano and Hutchinson, 2002), and the anatomy of the ornithischian pelvic girdle (e.g., Romer, 1927; Galton, 1969; Norman, 1986; Dilkes, 2000). Historically, extant crocodilian myol-ogy has been used as a blueprint for most dinosaurian soft-tissue reconstructions; although this methodology is not very useful considering that crocodilian skeletal anatomy differs greatly from that of even basal crocodylomorphs (Clark et al., 2004). Hutchinson (2001a,b) noted that the osteological topography of extinct archosaurs is often more similar to that of modern birds than crocodilian taxa, limiting the utility of crocodilian anatomy as a template for restorations of extinct archosaurian myology. The extant phylogenetic bracket (EPB) method (Witmer, 1995) allows for parsimonious reconstructions of archosaurian musculature based on the concepts of phylogeny, outgroup analysis, and homology (Patterson, 1982). The EPB and another closely related method (Bryant and Russell, 1992) have been successfully used to reconstruct varying portions of the appendicular musculature of *Maiasaura peeblesorum* (Dilkes, 2000), *Tyrannosaurus rex* (Carrano and Hutchinson, 2002), *Neuquensaurus australis* (Otero and Vizcaíno, 2008), and *Plateosaurus engelhardti* (Fechner, 2009), and both the axial and appendicular musculature of dromaeosaurs (Jasinoski et al., 2006).

A virtually complete postcranial skeleton of *Poposaurus gracilis* (YPM 57100; Fig. 1A) was
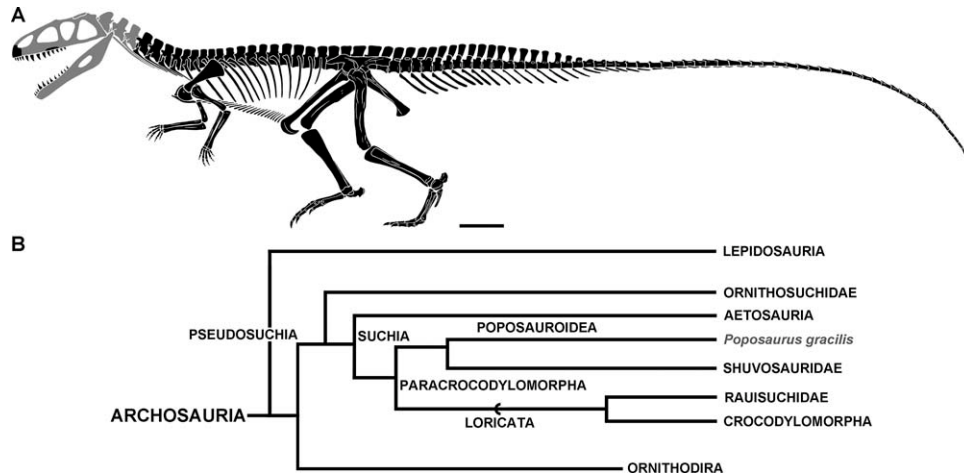
Fig. 1. **A**: Diagrammatic idealized reconstruction of the skeleton of *P. gracilis* (YPM 57100) in left lateral view. Known skeletal elements are shown in black, unknown elements are shown in gray. Scale bar = 20 cm. **B**: Phylogenetic framework followed for this study, demonstrating relationships of extant and extinct taxa to *Poposaurus*, based on Nesbitt (2011).

recently unearthed by a team from Yale University from Late Triassic sediments in the Chinle Formation of the Grand Staircase-Escalante National Monument of southern Utah (Benoit and Yarborough-Fitzgerald, 2004). This animal represents the most complete poposauroid skeleton known to date, and one of the most complete bipedal basal archosaurs yet discovered (Joyce and Gauthier, 2006; Gauthier et al., 2011). The exceptional preservation of this specimen has conserved the majority of the muscle attachment sites in the pelvic and hindlimb skeletal elements, enabling the use of this specimen in a phylogenetically based reconstruction of appendicular myology (Schachner and Dodson, 2009). *Poposaurus*, and other suchian archosaurs lie within the crocodile-line of the archosaur crown group (Fig. 1B; sensu Gauthier, 1986). Thus, understanding their biology is integral to providing insights to the larger evolutionary questions concerning the development of modern crocodilian anatomy and biology (Gower and Nesbitt, 2006). Similar to dinosaurs, multiple groups of basal archosaurs evolved a parasagittally erect limb posture (e.g., Benton and Clark, 1988), indicating that this anatomical state may be the plesiomorphic condition for Archosauria (Kubo and Benton, 2007). Extant crocodilians are quadrupeds with a semierect posture that appears to have evolved during the Jurassic, perhaps resulting from environmental pressures associated with living in an aquatic habitat (Kubo and Benton, 2007). They are, however, capable of a "high walk" gait, which mimics the parasagittally erect gait of extant mammals and birds, with the limbs rotated forward and adducted beneath the body (Brinkman, 1980; Gatesy, 1991). It has been demonstrated that Charig's (1972) hypothesized progression from sprawling, to "semierect" to the "improved" fully erect in archosaurs is an over simplification of

what was a complex nonlinear evolutionary sequence, particularly in basal archosaurs (e.g., Bonaparte, 1984; Hutchinson, 2006; Kubo and Benton, 2007; Padian et al., 2009). Reconstruction of the musculotendinous system in a bipedal basal archosaur provides a preliminary data set to begin detangling the evolutionary sequence of myological changes associated with the various postural shifts that occurred within basal archosaurs. The results of this study are also relevant to understanding the differences between the evolution of bipedal posture and locomotion of nondinosaurian archosaurs and the bipedal theropod lineage that eventually led to extant birds. This study aims to generate a reconstruction of the pelvic and hindlimb musculature of *P. gracilis*. A preliminary data set is generated for bipedal basal archosaurs that can be used as a starting point for basic biomechanical studies (see e.g., Hutchinson et al., 2005).

MATERIALS AND METHODS

Museum abbreviations. AMNH: American Museum of Natural History, New York, NY; FMNH: Field Museum of Natural History, Chicago, IL; MSM: Mesa Southwest Museum, Mesa, AZ; TMM: Texas Memorial Museum, Austin, TX; TTU-P: Museum of Texas Tech University, Lubbock, TX; UCMP: University of California Museum of Paleontology, Berkeley, CA; and YPM: Yale Peabody Museum, New Haven, CT.

A parsimonious reconstruction of extinct archosaurian myology requires strict adherence to the conservative methods of the EPB (Witmer, 1995). This methodology facilitates the assessment of the composition of the soft-tissue anatomy of extinct archosaurs by analyzing the morphology of homologous muscles in phylogenetically relevant extant taxa. Skeletal morphology is then used to avoid restoring features that diverge from those found in extant relatives (Rowe, 1986) and to reduce the amount of speculation in the model. This study follows the approach for applying the EPB method as outlined by Carrano and Hutchinson (2002). Extensive dissections and descriptions have provided soft-tissue data for various extant avian, and reptilian specimens that can be used to infer the myology of extinct

TABLE 1. Origin and insertion of pelvic and hindlimb muscles inferred in Poposaurus

Muscle	Origin	Insertion
IT 1, 2 + 3	Dorsal margin of the ilium (I)	Tibial cnemial crest (I)
AMB	Depression on the lateral surface of the proximal pubis (I)	Tibial cnemial crest (I)
FMT	Majority of the femoral shaft (I)	Tibial cnemial crest (I)
ILFB	Crest on the lateral postacetabular ilium (I)	Fibular tubercle (I)
IF	Supraacetabular crest and lateral preacetabular ilium (I)	Lateral surface of the proximal femur (I)
PIFI 2	Ventral aspect of the preacetabular process (II)	Proximolateral surface of the femur (I)
PIFI 1	Cranial margin of the ilium, dorsal to the pubic process (II)	Proximolateral surface of the femur (I)
PIT	Craniolateral surface of the ischium (II)	Proximal tibia (II)
FTI	Caudolateral surface of the postacetabular ilium (I)	Proximal tibia (I)
FTE	Caudolateral surface of the postacetabular ilium (I)	Proximal tibia (I)
ADD 1	Cranioventral ischial shaft (I)	Flange on the caudal surface of the femoral shaft (I)
ADD 2	Caudodorsal ischial shaft (II)	Caudal surface of the distal femoral shaft (I)
PIFE 1	Ventral surface of the pubic apron (II)	Caudal surface of the proximal femur (I)
PIFE 2	Lateral surface of the pubic boot (II)	Caudal surface of the proximal femur (I)
PIFE 3	Lateral surface of the ischial boot (II)	Caudal surface of the proximal femur (I)
ISTR	Medial surface of the ischium (II)	Lateral surface of the proximal femur (I')
CFB	Iliac brevis fossa (II)	Medial surface of the femur (I)
CFL	Caudal vertebral centra (I')	Medial surface of the femur (I)
Muscles to the Pes		
GL	Caudolateral femur just distal to the insertion of ADD2 (I)	Plantar surface of metatarsals I–IV with medial head (II)
GM	Proximal medial tibia (I)	Plantar surface of metatarsals I–IV with lateral head (II)
TA	Cranial surface of the proximal tibia (I)	Proximodorsal surface of metatarsals I–III (IV?; I)
POP	Proximal medial fibular shaft (I')	Distal lateral tibial shaft (I')
PL	Lateral fibula (I')	Calcaneal tuber (II)
PB	Lateral fibula (I)	Caudolateral surface of metatarsal V (I)
EDL	Lateral femoral condyle (I)	Distal end of the dorsal shaft of metatarsals I–IV (II)
EDB	Craniomedial surface of the tarsals (II)	Dorsal surface of the phalanges (II)
FDL	Caudal femur, distal to GL (I)	Ventral surface of phalanges and unguals (I)
FDB	Plantar aponeurosis (II')	Ventral surface of the phalanges (II')
EHL	Cranial surface of the distal fibula (II)	Dorsal surface of metatarsal I'
FHL	Caudolateral aspect of the femur (I')	Ventral surface of the distal phalanx and ungula of digit I (I')

archosaurs. A cautious approach must be undertaken when assigning muscles to specific skeletal features due to a weak correlation between archosaurian skeletal structure and the corresponding muscle attachments (McGowan, 1979, 1982; Bryant and Seymour, 1990; Dilkes, 2000; Carrano and Hutchinson, 2002).

Muscle attachment sites have been found to vary between individuals of the same species of ratite, and only ∼29% of the total number of muscle attachments could be unequivocally correlated with a specific feature on the surface of the bones in the appendicular skeleton of *Apteryx australis mantelli* (McGowan, 1979, 1982). However, it is also conceivable that size could play a factor, as muscle attachment sites tend to be clearer in larger vertebrates and *Apteryx* is a small bird. Also, the EPB for the Archosauria includes multiple members of Aves (both paleognaths and neognaths) and Crocodylia, with Squamates as an outgroup (Fig. 1B), providing a stronger myological framework (Supporting Information Table S1) for reconstructing the soft tissues of extinct archosaurs. As all extinct archosaurs lie within the same EPB, the same set of extant taxa is used to generate the data set for inferences of soft-tissue anatomy regardless of the extinct taxon (Bryant and Russell, 1992). Osteological topography from the selected extinct specimen is then used to modify the myological data set produced from the EPB so that the musculature and soft-tissue structures inferred for extinct archosaurs can be adapted to fit the skeletal architecture of the hindlimbs and pelvis of *Poposaurus* (Tables 1 and 2). The relationships among the various groups are derived from Gauthier (1986) and Nesbitt (2011; Fig. 1B).

Procedure

The reconstruction in this study is based on rigorous adherence to the EPB methodology (Witmer, 1995) to interpret the hindlimb myology of *Poposaurus*. The EPB has been thoroughly discussed elsewhere (see e.g., Carrano and Hutchinson, 2002) and has been used to reconstruct the pelvic musculature of *T. rex* (Carrano and Hutchinson, 2002), *M. peeblesorum* (Dilkes, 2000), and *P. engelhardti* (Fechner, 2009). Multiple specimens of *P. gracilis* were used to generate the data set for the pelvis and femoral muscle attachment sites for this study (FMNH UR357; TMM-4368; TTUP 9243; TTUP 10419; and TTUP 11203), but we relied primarily on the largely complete Yale specimen (YPM 57100). The data on muscle attachments on the hindlimbs were derived solely from this specimen (YPM 57100), as it was the only one with the distal hindlimbs preserved.

The morphology and patterns of the hindlimb musculature of extant archosaurs and squamates were determined through dissection of fresh and preserved specimens of *Alligator mississippiensis*, *Varanus niloticus*, *V. albigularis albigularis*, *Struthio camelus*, and *Dromaius novaehollandiae*. The following literature was also used to confirm the myological arrangement in select extant phylogenetically relevant taxa. Data on the musculature of *Sphenodon punctatum* were gleaned from Byerly (1925). The myology of squamates was derived from Gregory and Camp (1918), Romer (1922), Snyder (1954), Russell (1993), and Herrel et al. (2008). Data on crocodilians were from Romer (1923a,b), Reese (1915), Chiasson (1962), and Cong et al. (1998). Terminology for reptilian musculature

TABLE 2. Origin and insertion of nonmyological soft-tissue structures inferred in Poposaurus

Structure	Origin	Insertion
Plantar aponeurosis	Caudoventral surface of the pes (I′)	Cranioventral surface of the pes (I′)
Extensor retinaculum	Distal tibia (I′)	Distal fibula (I′)
Iliopubic ligament (ipl; Fig. 11)	Craniomedial and ventral surface of the preacetabular process (I)	Cranial and proximal surface of the pubis (I′)
Puboischiadic ligament (pil; Fig. 11)	Cranial and proximal surface of the ischium (I′)	Caudal and proximal surface of the pubis (I′)
Ilioischiadic ligament (iil; Fig. 11)	Tubercle on the distal postacetabular ilium (I)	Caudal and proximal surface of the ischium (I′)

follows Romer (1923a). For avian myology, data were obtained from George and Berger (1966), Hudson and Lanzillotti (1955), McGowan (1979, 1982), Vanden Berge and Zweers (1993), Gangl et al. (2004), and Verstappen et al. (1998). Terminology for avian musculature follows Vanden Berge and Zweers (1993).

The parasagittally erect bipedal posture of the hindlimb is inferred from the fully articulated specimen of *Poposaurus* (YPM 57100). Muscles are described moving proximally to distally, and superficially to a position of greater depth. Level II inferences have generally been accepted as the minimum requirement to conservatively reconstruct a muscle in an extinct animal (Carrano and Hutchinson, 2002), and thus only muscles with a Level II or lower designation (for at least one of their attachment sites) were reconstructed for *Poposaurus*. A Level II Inference denotes that the anatomical trait is present in only one of the extant groups, and that the skeletal morphology of the extinct taxon supports the reconstruction of the soft-tissue character. The origin and insertion sites were evaluated and reconstructed with independent levels of inferences (Tables 1 and 2).

The Muscle–Bone Interface and Osteological Correlates

The osteological correlates utilized by the EPB (Witmer, 1995) method are topographic variations in bone resulting from the attachment of muscles via tendinous, aponeurotic, and fleshy insertions. Studies on the nature of bone under external mechanical stress have concluded that these factors affect the mass, density, and structure of the bone throughout the life of the animal (Johnson, 1998). The majority of muscles insert onto bones through tendons in concentrated areas, allowing for the transfer of stress from the muscle to the bone. These sites in the periosteum are usually characterized by Sharpey's fibers, which are the collagenous tissues that anchor tendons to bone (Hall, 2005). The regions containing these structures are generally denser, rugose, or pitted, and are often interpreted as muscle and ligament scars (Dilkes, 2000). It should be noted that the size of a muscle scar gives no indication of the actual size of the muscle (McGowan, 1979, 1982; Bryant and Seymour, 1990) and thus physical muscle properties cannot be inferred from muscle attachment sites alone. More direct (fleshy) attachments are harder to discern, as they often insert onto macroscopically smooth areas or within a depression (Dilkes, 2000). An additional complication is that other connective tissue structures (e.g., cartilage and ligaments) of the musculoskeletal system produce osteological scarring similar to that of tendons (Haines and Mohuiddin, 1968). It is also the case that osteological correlates can result from indirect association with muscle attachments, forming a ridge or intermuscular line between muscles, or adjacent to the actual muscle attachment site (Hutchinson, 2001a). In addition, it is difficult to discern between the attachment sites of muscles, tendons, ligaments, and other connective tissues, thus making osteological correlates closer to the joints less definitive in their assignment (Carrano and Hutchinson, 2002).

RESULTS
Superficial Dorsal Group

M. triceps femoris. In all extant taxa, M. triceps femoris is composed of three distinct muscles: M. iliotibialis, M. ambiens, and M. femorotibialis. All three divisions converge to form a common insertion on the femoropatellar tendon, which inserts on the proximocranial aspect of the tibia (the cnemial crest; Figs. 2D,E, 3E,F, and 4F).

The morphology of M. triceps femoris in *Poposaurus* was similar to that of extant archosaurs: the three distinct muscles converge to form a single tendon that inserts on the cranial aspect of the tibia onto a rugose ridge. Proposed function: hip flexion and knee extension.

M. iliotibialis (IT). In *Sphenodon*, the origin of M. iliotibialis is from the craniodorsal margin of the ilium. In squamates, M. iliotibialis is composed of two distinct heads, which unite into a common insertion (Fig. 2D,E); the cranial division arises fleshily from the cranial portion of the lateral surface of the ilium directly beneath the dorsal margin, whereas the caudal division arises from a wide, broad and thin aponeurosis (tendinous sheet) that runs along most of the dorsal margin (Fig. 2A). In crocodilians, M. iliotibialis is composed of three distinct heads, all arising from the dorsal margin of the ilium (Fig. 3A). The various heads of M. iliotibialis merge with the other muscles of M. triceps femoris to insert on the cranial aspect of the tibia (Fig. 3E,F). Similar to crocodilians, the avian M. iliotibialis is composed of three heads: M. iliotibialis 1 (=M. iliotibialis cranialis or M. sartorius), M. iliotibialis 2 (=M. iliotibialis lateralis), and M. iliotibialis 3. In *Apteryx*, M. iliotibialis muscle arises from almost the entire dorsal margin of the iliac crest (Fig. 4A). In neognath birds, M. iliotibialis cranialis (=M. iliotibialis 1 or M. sartorius) has an aponeurotic origin from the neural spines of the caudal dorsal vertebrae and the cranial portion of the iliac crest and the medial dorsal ridge of the synsacrum. The lateral and caudal heads of M. iliotibialis arise by a thin aponeurosis from the iliac crest and a portion of the lateral face of the postacetabular ilium.

It is clear on the basis of the myology of the extant taxa that M. iliotibialis is a broad thin muscle composed of three heads that originated from
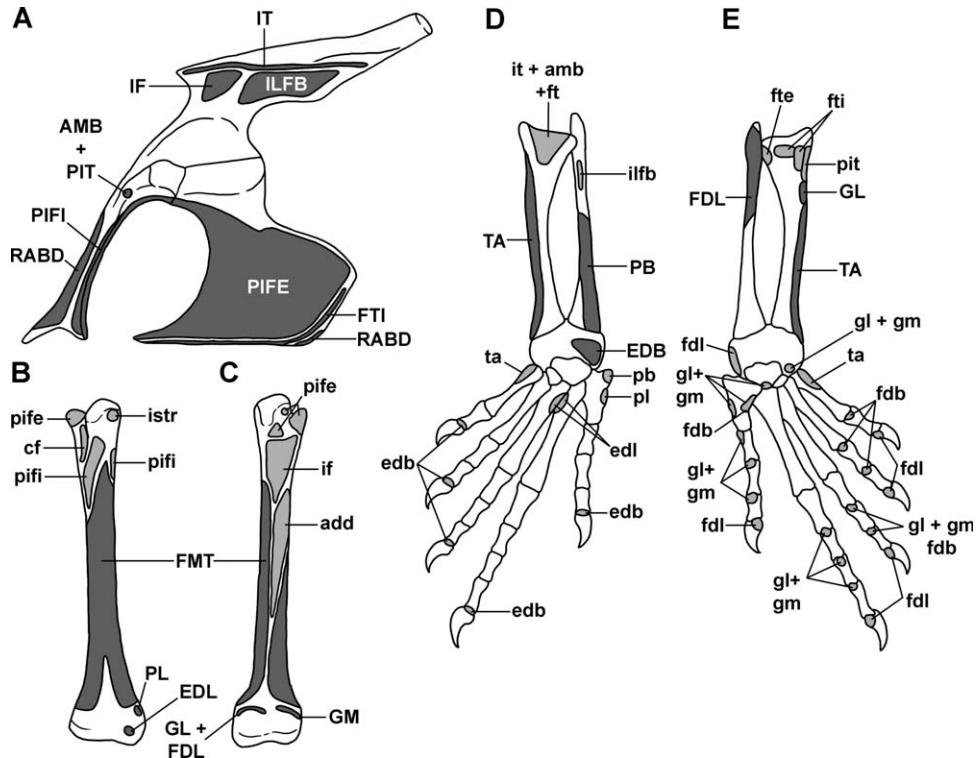
Fig. 2.   Diagrammatic images of the pelvis, hindlimb, and corresponding muscle attachments in *Iguana*; composite redrawn from Romer (1922) and Dilkes (2000). **A**: Left lateral view of the pelvis; **B**: dorsal view of the left femur; **C**: ventral view of the left femur; **D**: dorsal (extensor) view of the left crus and pes; and **E**: ventral (flexor) view of the left crus and pes. Muscle origin labels are capitalized; not all muscles are included. Muscle origins are indicated in dark gray, insertions in light gray. Images not drawn to scale. Abbreviations: ADD: M. adductor; AMB: M. ambiens; CF: M. caudofemoralis; EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDB: M. flexor digitorum brevis; FDL: M. flexor digitorum longus; FMT: M. femorotibialis; FT: M. femorotibialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; IF: M. iliofemoralis; ILFB: M. iliofibularis; ISTR: M. ischiotrochantericus; IT: M. iliotibialis; PB: M. peroneus brevis; PIFE: M. puboischiofemoralis externus; PIFI: M. puboischiofemoralis internus; PIT: M. puboischiotibialis; PL: M. peroneus longus; RABD: M. rectus abdominus; and TA: M. tibialis anterior.

the dorsolateral margin of the majority of the ilium in *Poposaurus* (Fig. 5A,B). There are very distinct longitudinal striations on the lateral surface of the cranial tip of the preacetabular process of the ilium that probably demarcate the origin site for M. iliotibialis 1. They continue caudally along the dorsal margin of the preacetabular process but become significantly finer and shallower, and disappear altogether above the supraacetabular crest. Directly dorsal to this crest and cranial to the lateral crest, there is a flat and slightly pitted depression that probably was the origin site for M. iliotibialis 2. There is no distinct indication demarcating the boundary between the origins of M. iliotibialis 2 and 3. The caudal margin of M. iliotibialis 3 probably extended caudally along the dorsal rim of the ilium, running parallel and dorsal to the lateral crest. There are fine striations along the dorsal rim of the ilium indicating muscle attachments. Proposed function: flexion, extension, and abduction of the hip; extension of the knee.

M. ambiens (AMB). In *Sphenodon*, M. ambiens arises from the lateral pubic tuberosity. In all lacer-

tilians, it takes an origin from the pubis, cranial and ventral to the acetabulum (usually with M. pubotibialis; Fig. 2A). The crocodilian M. ambiens is composed of two parts; the first head arises at the junction between the ilium and the preacetabular cartilage of the ischium, whereas the second head has an origin on the base of the pubis (Fig. 3A). In ratites, the origin of M. ambiens is variable, ranging from the pectineal process to the ventrolateral surface of the preacetabular ilium (Fig. 4A). In neognaths, when present, M. ambiens arises from the pectineal process, sometimes with a secondary caudal extension originating from the body of the pubis. In extant archosaurs, M. ambiens often has an accessory tendon that gives origin to one or more of the digital flexors.

There is no osteological evidence on the pubis of *Poposaurus* indicating that M. ambiens was composed of two heads like in crocodilians, and since the ancestral and avian condition is a single muscle, only one division will be reconstructed. In all extant taxa M. ambiens arises from a position cranioventral to the acetabulum (usually on the
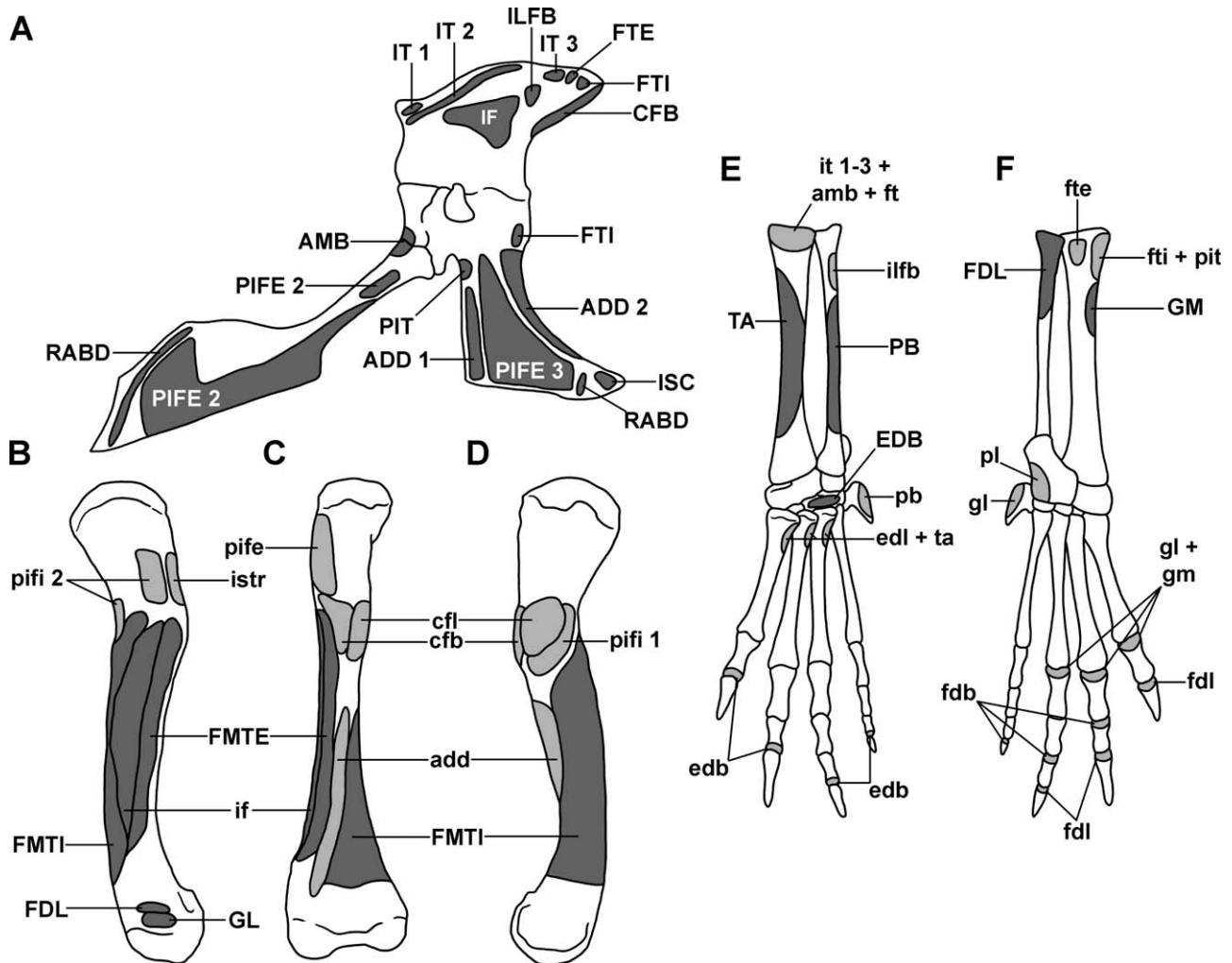
Fig. 3. Diagrammatic images of the pelvis, hindlimb, and corresponding muscle attachments in *Alligator*; composite redrawn from dissections, Romer (1923a) and Cong et al. (1998). **A**: Left lateral view of the pelvis; **B**: lateral view of the left femur; **C**: caudal view of the left femur; **D**: medial view of the left femur; **E**: dorsal (extensor) view of the left crus and pes; and **F**: ventral (flexor) view of the left crus and pes. Muscle origin labels are capitalized; not all muscles are included. Muscle origins are indicated in dark gray, insertions in light gray. Images not drawn to scale. Abbreviations: ADD 1–2: M. adductor 1–2; AMB: M. ambiens; CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDB: M. flexor digitorum brevis; FDL: M. flexor digitorum longus; FMTE: M. femorotibialis externus; FMTI: M. femorotibialis internus; FT: M. femorotibialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; IF: M. iliofemoralis; ILFB: M. iliofibularis; ISC: M. ischiocaudalis; ISTR: M. ischiotrochantericus; IT 1–3: M. iliotibialis 1–3; PB: M. peroneus brevis; PIFE 1–3: M. puboischiofemoralis externus 1–3; PIFI 1–2: M. puboischiofemoralis internus 1–2; PIT: M. puboischiotibialis; PL: M. peroneus longus; RABD: M. rectus abdominus; and TA: M. tibialis anterior.

pubis), so the plesiomorphic position for *Poposaurus* is at the base of the pubis just cranial to the acetabulum. On the lateral surface of the pubis, just distal to its proximal articular surface there is a sub-triangular depression that probably served as the origin site for M. ambiens (Fig. 6A,B). Proposed function: hip flexion and knee extension.

Mm. femorotibiales (FMT). In all lepidosaurs and crocodilians, M. femorotibialis has a fleshy origin from the dorsal surface of the femoral shaft that wraps around caudally to meet the insertion of M. adductor (Figs. 2B,C and 3B–D). There is usually only one head in lepidosaurs; however, a second division has been found in *Varanus*, although it is unclear if it is homologous to the secondary heads of archosaurs. Crocodilians possess two distinct heads to this muscle: M. femorotibialis internus and externus. The origin for M. femorotibialis internus is the larger of the two and occupies the majority of the femoral shaft (Fig. 3B–D). Most birds possess a M. femorotibialis with three heads (M. femorotibialis medialis, intermedius, and lateralis), although a few ratite taxa have further subdivided the muscle into four parts. In all avian taxa this muscle arises from the majority of the femoral shaft (Fig. 4B,C).
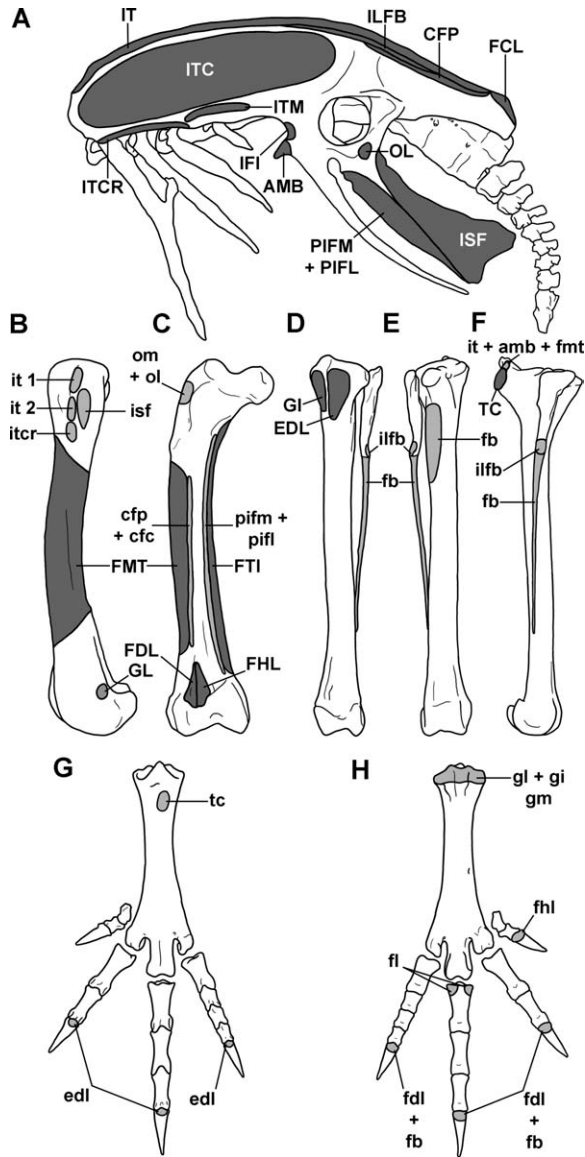
Fig. 4. Diagrammatic images of the pelvis, hindlimb, and corresponding muscle attachments in *Apteryx*, redrawn from McGowan (1979). **A**: Left lateral view of the pelvis, sacrum and pygostyle; **B**: lateral view of the left femur; **C**: caudal view of the left femur; **D**: cranial view of the left tibiotarsus and fibula; **E**: caudal view of the left tibiotarsus and fibula; **F**: lateral view of the left tibiotarsus and fibula; **G**: cranial (extensor) view of the left tarsometatarsus and pes; and **H**: caudal (flexor) view of the left tarsometatarsus and pes. Muscle origin labels are capitalized; not all muscles are included. Muscle origins are indicated in dark gray, insertions in light gray. Images not drawn to scale. Abbreviations: AMB: M. ambiens; CFC: M. caudofemoralis pars caudalis; CFP: M. caudofemoralis pars pelvica; FB: M. fibularis brevis; FCL: M. flexor cruris lateralis pars pelvica; FDL: M. flexor digitorum longus; FHL: M. flexor hallucis longus; FL: M. fibularis longus; FMT: M. femorotibialis; GI: M. gastrocnemius pars intermedia; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; IFI: M. iliofemoralis internus; ILFB: M. iliofibularis; ISF: M. ischiofemoralis; IT (1–2): M. iliotibialis (1–2); ITC: M. iliotrochantericus caudalis; ITCR: M. iliotrochantericus cranialis; ITM: M. iliotrochantericus medialis; OL: M. obturatorius lateralis; OM: M. obturatorius medialis; PIFL: M. puboischiofemoralis pars lateralis; PIFM: M. puboischiofemoralis pars medialis; and TC: M. tibialis cranialis.

There were plesiomorphically at least two heads to M. femorotibialis in *Poposaurus* and without any specific osteological topography indicating a third head, only two are reconstructed here. There is a long intermuscular line (=the posterior intermuscular line of Carrano and Hutchinson, 2002) running distally along the lateral aspect of the femoral shaft that demarcates the caudal boundary of the origin of M. femorotibialis externus (=lateralis; Fig. 7A–D). There is also a very subtle intermuscular line running along the cranial surface of the femoral shaft that probably divides the origin of the externus head from that of the internus (=medialis) head (Fig. 7A–D). The internal head originated from the femoral shaft, bounded by the external head laterally and the insertion of the adductor muscles caudally. Proposed function: extension of the knee.

M. iliofibularis (ILFB). M. iliofibularis arises from the lateral surface of the ilium, generally dorsal and slightly caudal to the acetabulum in all extant taxa (Figs. 2A, 3A, and 4A). Insertion in all taxa is on the lateral aspect of the fibula, just distal to the fibular head (Figs. 2D, 3E, and 4D–F).

As in all other archosaurs, M. iliofibularis in *Poposaurus* was positioned on the lateral surface of the ilium directly caudal to the origin of M. iliofemoralis, and slightly caudodorsal to the acetabulum. Unlike the relatively smooth surface of the dinosaurian ilium, the ilium of *Poposaurus* has a raised and rugose lateral crest that runs the length of the postacetabular process (Fig. 5A,B). There is a particularly rugose oval-shaped portion of the crest that is the probably origin site of M. iliofibularis. It is possible that the origin runs the length of the lateral crest; however, the rugose muscle scars are only present along the caudal half of the crest. The insertion of M. iliofibularis in *Poposaurus* was on an ovoid muscle scar on the craniolateral surface of the fibula approximately one-third of the way down the shaft (Fig. 8C,D). Proposed function: extension and abduction of the hip, flexion of the knee.

Deep Dorsal Group

M. iliofemoralis (=externus). *Sphenodon*, squamates, and crocodilians all share a common origin site for M. iliofemoralis on the ilium, just dorsal to the acetabulum (Figs. 2A and 3A). In birds, this muscle is divided into two parts: M. iliofemoralis externus in Carrano and Hutchinson (2002); IF and M. iliotrochantericus caudalis. The two heads arise from the majority of the lateral surface of the ilium just dorsal and caudal to the acetabulum (Fig. 4A,B). This muscle inserts on the proximolateral aspect of the femoral shaft in all taxa, except for the turtle in which insertion is on the major trochanter (Walker, 1977).
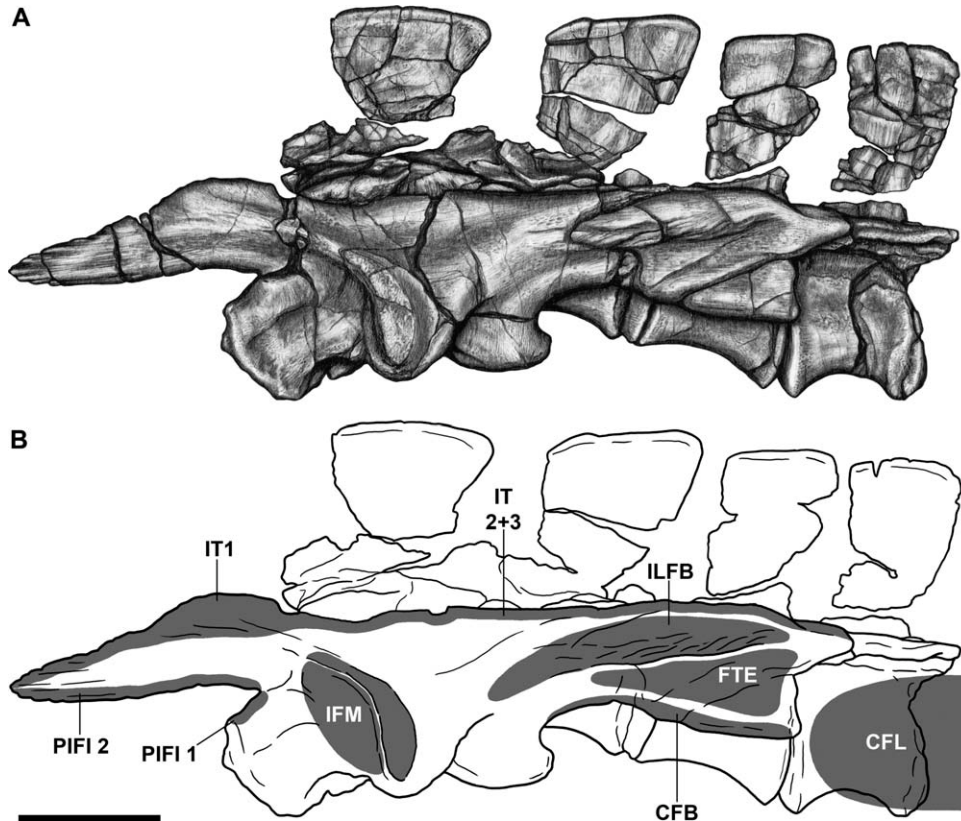
Fig. 5. Osteological correlates on the lateral surface of the ilium of *Poposaurus*. **A**: Illustration of the left ilium and sacral vertebrae in lateral view; **B**: diagrammatic image of the left ilium and sacral vertebrae with muscle origins indicated in gray. The muscle origins and insertions are indicated on the diagrammatic image in gray and muscle origin labels are capitalized; not all muscles are included. Scale bar = 5 cm. Abbreviations: CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; FTE: M. flexor tibialis externus; IFM: M. iliofemoralis; ILFB: M. iliofibularis; IT 1–3: M. iliotibialis 1–3; and PIFI 1–2: M. puboischiofemoralis internus 1–2.

The plesiomorphic origin for M. iliofemoralis is on the lateral surface of the ilium just dorsal to the acetabulum. In all extant archosaurs and dinosaurs, this surface is flat; however, in *Poposaurus* there is a very large and rugose supraacetabular crest (Fig. 5A,B). There is a large concavity cranial to the base of the supraacetabular crest that bears light striated muscle scars along its surface that is, along with the crest itself the probable origin of M. iliofemoralis. It is also possible that the concavity and the surface just dorsal to the crest represent a division in the muscle and that it had separated into two heads in *Poposaurus* that are either analogous or homologous to the two divisions found in dinosaurs and birds, and that extant crocodilians secondarily lost the second head. The insertion of M. iliofemoralis in *Tyrannosaurus* and *Maiasaura* has been reconstructed on a rugose ridge on the lateral surface of the proximal femur. The distal insertion of M. iliofemoralis in crocodilians, in conjunction with a rounded slightly rugose oval ridge on the proximolateral aspect of the femur of *Poposaurus*, makes this the probably insertion site for M. iliofemoralis (Fig. 7A,B). The

laterally projecting supraacetabular crest on the ilium (Fig. 5A,B) also precludes a more proximal insertion of this muscle in *Poposaurus*. Proposed function: abduction of the hip.

M. puboischiofemoralis internus (PIFI). M. puboischiofemoralis internus is made up of multiple divisions in all extant saurians. Most lepidosaurs have two divisions to this muscle; however, a few squamates have three. Crocodilians have two components to M. puboischiofemoralis internus muscle, whereas birds have subdivided it further to form three distinct muscles. This muscle both protracts the femur and rotates it laterally. It is unclear as to whether there were two or three divisions of M. puboischiofemoralis in *Poposaurus*, so with the aim of remaining conservative only two heads will be reconstructed.

M. puboischiofemoralis internus 1 (PIFI 1). The nomenclature for this muscle varies according to which taxonomic group is being described. The homologous avian name for this muscle is M. iliofemoralis internus (Rowe, 1986). For this reconstruction the saurian name M. puboischiofemoralis internus 1 is retained. The cranial division of this
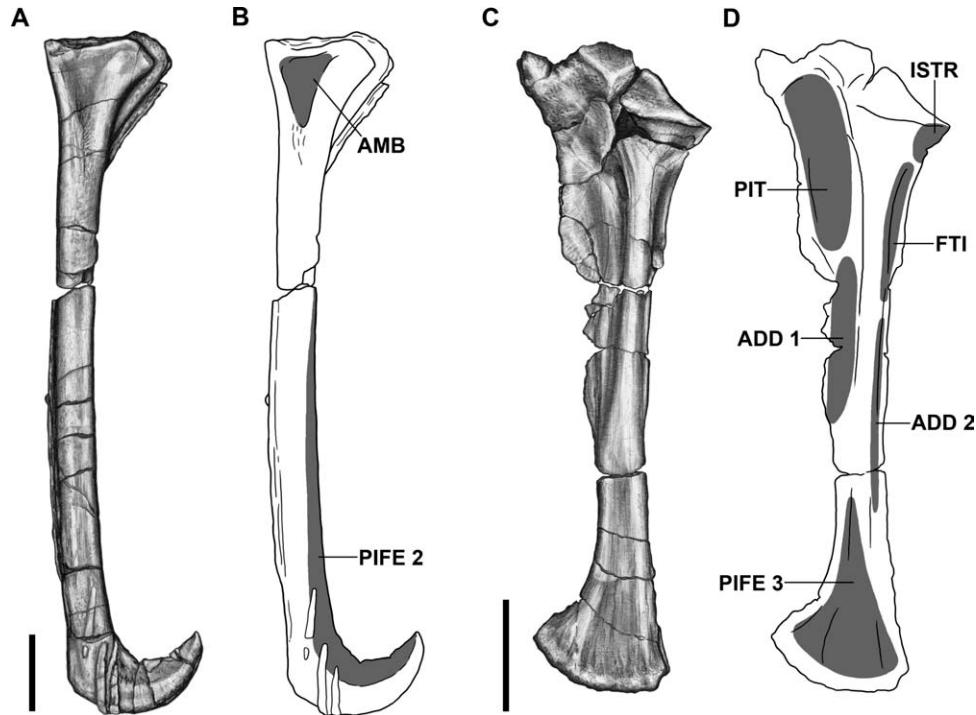
Fig. 6. Osteological correlates on the pubis and ischium of *Poposaurus*. **A**: Illustration of the left pubis in lateral view; **B**: diagrammatic image of the left pubis in lateral view; **C**: illustration of the left ischium in lateral view; and **D**: diagrammatic image of the left ischium in lateral view. Muscle origin labels are capitalized; not all muscles are included. Muscle origins are indicated in dark gray, insertions in light gray. Images not drawn to scale. Scale bar = 5 cm. Abbreviations: ADD 1–2: M. adductor 1–2; AMB: M. ambiens; FTI: M. flexor tibialis internus; ISTR: M. ischiotrochantericus; PIFE 2–3: M. puboischiofemoralis externus 2–3; and PIT: M. puboischiotibialis.

muscle arises on the dorsal side of the ischium in lepidosaurs and extends cranially around the pubis towards the femoroacetabular joint. In crocodilians, M. puboischiofemoralis internus 1 originates from the internal surface of the ischium and ilium as well as from portions of the ventral aspect of the sacral ribs. The avian M. iliofemoralis internus arises from the ventrolateral side of the presacral ilium and inserts on the dorsal surface of the proximal femoral shaft (Fig. 4A). In all extant taxa, M. puboischiofemoralis internus 1 inserts on the craniomedial aspect of the femur (Figs. 2B and 3B,D).

Similar to dinosaurs, the pelvis of *Poposaurus* is sufficiently different from lepidosaurs and even crocodilians so that M. puboischiofemoralis internus 1 probably also had a different morphology. There is a small depression on the medial aspect of the pubic process of the ilium that bears light striated muscle scars along its surface indicating a possible origin for M. puboischiofemoralis internus 1 (Fig. 5A,B). Insertion of this muscle in *Poposaurus* was on the lesser trochanter of the femur (a ridge that is probably not homologous to the lesser trochanter of theropods due to different muscle associations) just distal to the articular surface of the femoral head. Proposed function: hip flexion.

M. puboischiofemoralis internus 2 (PIFI 2). The second division of M. puboischiofemoralis internus is also assigned various different names depending on the taxonomic group. The avian homologues are Mm. iliotrochantericus cranialis and medius. In squamates, this muscle arises from the inner surface of the pubis. In crocodilians, M. puboischiofemoralis internus 2 originates from the bodies and ventral surfaces of the transverse processes of the six caudalmost lumbar vertebrae. In birds the two muscles have an origin on the ventrolateral surface and ventral margin of the ilium (Fig. 4A). In all extant taxa, insertion of M. puboischiofemoralis 2 is also on the dorsal (or lateral) side of the femur (Figs. 2B, 3B, and 4B).

The morphology of M. puboischiofemoralis internus 2 in lepidosaurs, crocodilians and birds is extremely divergent with no clear indication of how the origin shifted from the pubis (in lepidosaurs) to the dorsal vertebrae (in crocodilians) and the ilium (in birds). The confusion over the homology of the deep dorsal thigh musculature has complicated reconstructions of this muscle in dinosaurs; detailed discussions on the nature of M. puboischiofemoralis internus with respect to reconstructing the pelvic musculature can be found in Dilkes (2000) and Carrano and Hutchinson (2002). Recent reconstructions
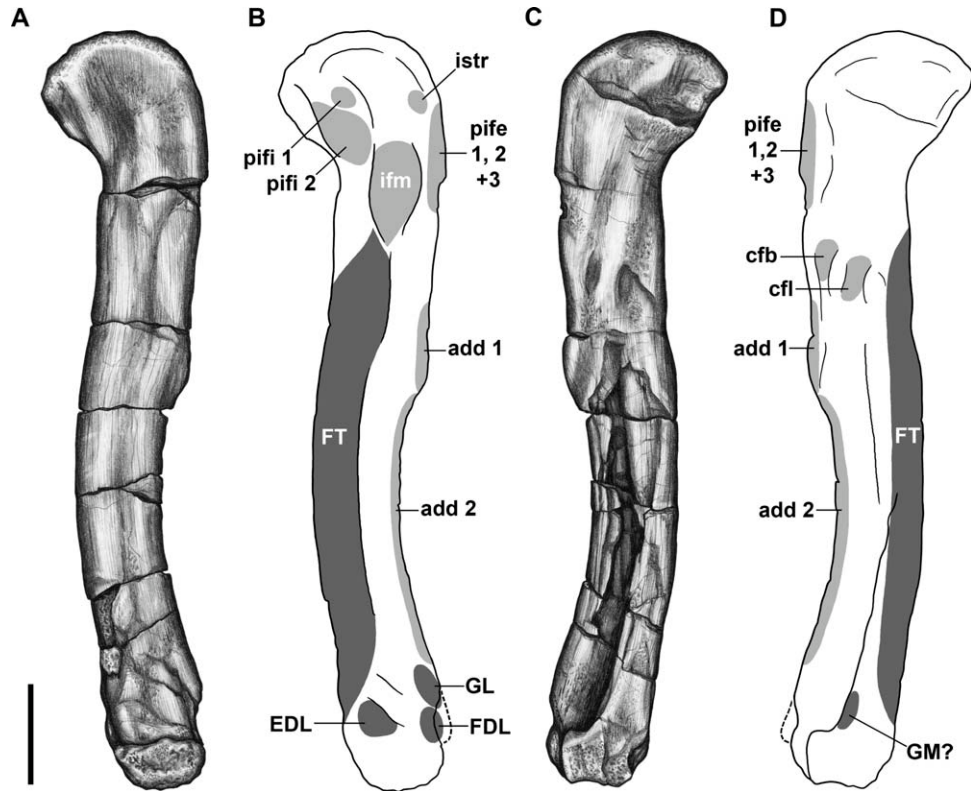
Fig. 7. Osteological correlates on the femur of *Poposaurus*. **A**: Illustration of the left femur in lateral view; **B**: diagrammatic image of the left femur in lateral view; **C**: illustration of the left femur in medial view; and **D**: diagrammatic image of the left femur in medial view. Muscle origin labels are capitalized; not all muscles are included. Muscle origins are indicated in dark gray, insertions in light gray. Images not drawn to scale. Scale bar = 5 cm. Abbreviations: ADD 1–2: M. adductor 1–2; CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; EDL: M. extensor digitorum longus; FDL: M. flexor digitorum longus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; IFM: M. iliofemoralis; ISTR: M. ischiotrochantericus; PIFE 1–2: M. puboischiofemoralis externus 1–2; and PIFI 1–2: M. puboischiofemoralis internus 1–2.

based on conclusions presented by Rowe (1986), are supported by the osteological topography and muscle scars found on the ilium of *Poposaurus*. M. puboischiofemoralis internus 2 (=Mm. iliotrochantericus cranialis and medius of birds and theropod dinosaurs) originated from the ventromedial surface of the elongated preacetabular process of the ilium. These surfaces of the preacetabular process are covered in longitudinal striations suggesting extensive muscle attachments for this muscle; however, the overall lack of significant scarring on the ventral surfaces of the caudalmost dorsal vertebrae does not preclude a vertebral origin, and a secondary head is also possible. There is no indication if this muscle has subdivided into two heads (as in *Tyrannosaurus* and in birds) so only one is reconstructed for *Poposaurus*. Insertion was just distal to the femoral articular head. In *Poposaurus*, there is an oval depression just caudal to the lesser trochanter and cranial to the insertion site of M. iliofemoralis that was the insertion site of M. puboischiofemoralis 2 (Fig. 7A,B). Proposed function: hip flexion.

Flexor Cruris (Ventral) Group

M. puboischiotibialis (PIT). In lepidosaurs, M. puboischiotibialis is a large fan shaped muscle that arises from the lateral pubic tuberosity, puboischiadic ligament, and the ventral symphysis of the ischium (Fig. 2A). M. puboischiotibialis in crocodilians is significantly reduced in comparison to squamates, originating from just the cranial margin of the ischium (Fig. 3A). This muscle is completely absent in birds. Insertion in all extant taxa possessing this muscle is on the proximoventral aspect of the tibia, just distal to the head (Figs. 2E and 3F). M. puboischiotibialis is absent in birds.

On the basis of the EPB, it is equivocal whether M. puboischiotibialis was present in basal archosaurs. In *Varanus*, one of the more ambulatory terrestrial lepidosaurs, this muscle is the single largest leg adductor; however, it is reduced in the more aquatic crocodilians. M. puboischiotibialis is absent in birds. The craniolateral surface of the ischium in *Poposaurus* has a large depression running distally for over half of its surface indicating an extensive muscular origin (Fig. 6C,D). Although
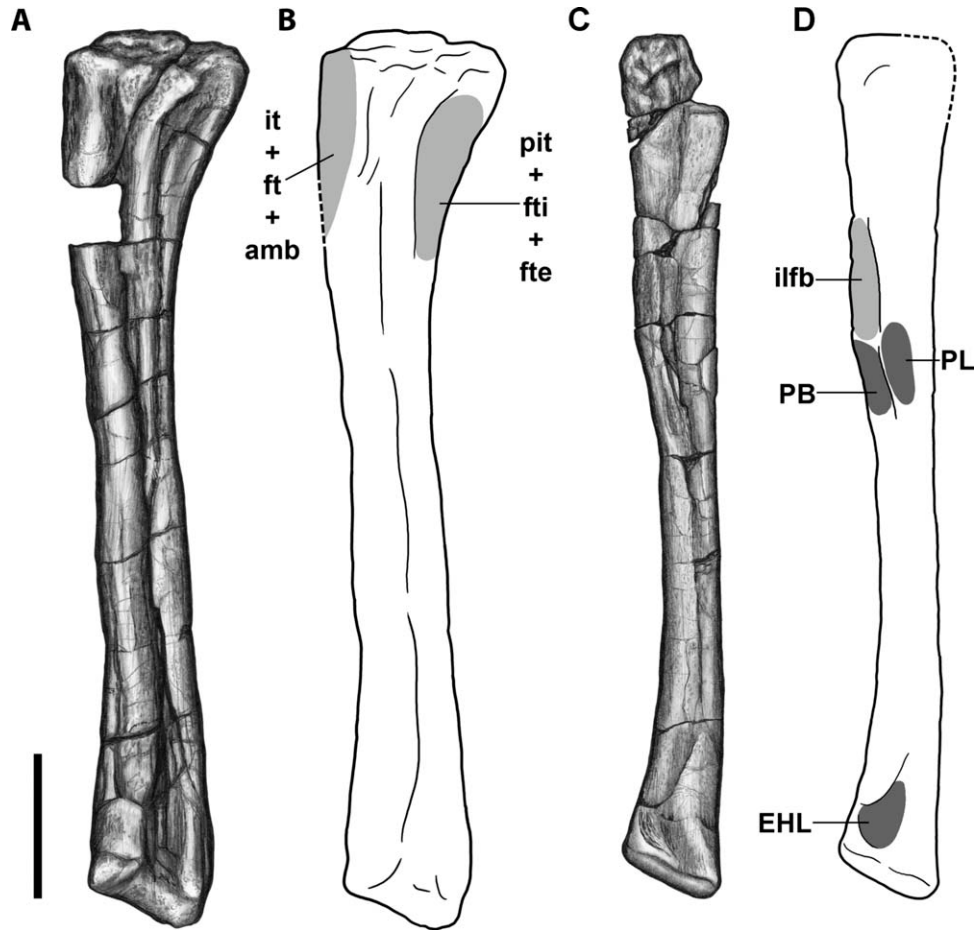
Fig. 8. Osteological correlates on the tibia and fibula of *Poposaurus*. **A**: Illustration of the left tibia in lateral view; **B**: diagrammatic image of the left tibia in lateral view; **C**: illustration of the left fibula in lateral view; and **D**: diagrammatic image of the left fibula in lateral view. The muscle origins and insertions are indicated on the diagrammatic images in gray and muscle origin labels are capitalized; not all muscles are included. Scale bar = 5 cm. Abbreviations: AMB: M. ambiens; EHL: M. extensor hallucis longus; FT: M. femorotibialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; ILFB: M. iliofibularis; IT: M. iliotibialis; PB: M. peroneus brevis; PIT: M. puboischiotibialis; PL: M. peroneus longus; and PT: M. pubotibialis.

this depression may be solely for the origin of M. adductor, there is a depression just distal to the articular surface of the ischium that is slightly deeper, possibly demarcating the origin of a separate and distinct M. puboischiotibialis (Fig. 6C,D). This muscle would have inserted onto the proximal tibia together with M. flexor tibialis internus and externus. There is a depression on the lateral surface of the tibia in *Poposaurus* (Fig. 8A,B) that indicates the insertion site of M. puboischiotibialis and the associated hip extensors. Proposed function: adduction and extension of the hip, flexion of the knee.

M. pubotibialis (PT). M. pubotibialis has an origin from the pubic tubercle in conjunction with M. puboischiotibialis in lepidosaurs. It inserts onto the tibia just medial to the cnemial crest. M. pubotibialis is also present in turtles with a similar arrangement. However, it is not present in any extant archosaurs, and as there are no muscle

scars on the pelvis of *Poposaurus* that can be associated with this muscle, it is not reconstructed here.

M. flexor tibialis internus (FTI 1, 2, 3, and 4). The homologies of the various divisions of M. flexor tibialis internus among the various extant taxa are not clear; however, Romer (1942) presents a well organized system that has been used for previous reconstructions of archosaur myology and will be followed here. *Sphenodon* has three distinct parts (=M. caudi-ischio-tibialis, M. ischio-tibialis posticus 1 and 2) that arise from the first six caudal vertebrae and the lateral tuberosity of the ischium. Lacertilians can have between two and four heads for this muscle, all originating primarily from the ilioischiadic ligament with a small attachment from the caudal aspect of the ilium (Fig. 2A). Crocodilians possess four heads, whereas birds have reduced this muscle complex to only one (M. flexor cruris medialis). One of the

crocodilian divisions arises from the caudodorsal aspect of the ilium, two have an ischial origin (this origin includes the ischial tuberosity and ilioischiadic ligament), whereas the fourth arises from the ilioischiadic fascia (Fig. 3A). In *Apteryx*, the single head of this muscle arises from the pygostyle with an accessory small aponeurotic origin from the caudal margin of the ischium. In *Struthio*, and neognath birds, the origin is completely from the caudal aspect of the ischium. In all of the extant taxa, the heads of M. flexor tibialis internus insert on the proximal half of the tibia (with the exception of *Apteryx* where it inserts on M. gastrocnemius; Figs. 2E and 3F).

It is not possible to unequivocally discern the number of divisions present in M. flexor tibialis internus in *Poposaurus*, but it is clear that the plesiomorphic origin was on the lateral side of the ischium. There is a shallow groove along the caudolateral surface of the ischium, approximately one-third of the way down the shaft that suggest an ischial origin for M. flexor tibialis internus in *Poposaurus* (Fig. 6C,D). It is possible that there was also a secondary origin from the ilioischiadic ligament, although this hypothesis is equivocal. In crocodilians two divisions of M. flexor tibialis internus arise from the postacetabular process of the ilium; however, this is not the case in either lepidosaurs or birds and there are no distinct scars on the postacetabular process of the ilium of *Poposaurus* that necessitate restoring a secondary origin of this muscle on the ilium. Insertion of M. flexor tibialis internus was on the lateral aspect of the tibia in association with M. puboischiotibialis and M. flexor tibialis externus. There is a depression on the lateral surface of the tibia in *Poposaurus* demarcating the insertion site for these muscles (Fig. 8A,B). Proposed function: hip adduction and extension, knee flexion.

M. flexor tibialis externus (FTE). M. flexor tibialis externus of archosaurs has been posited as homologous with the "semitendinosus" muscle of mammals (Carrano and Hutchinson, 2002). M. extensor tibialis of *Sphenodon* arises from the ischiadic tuberosity and the caudal vertebrae and inserts on the tibia. In squamates, this muscle arises from the ilioischiadic ligament and inserts on the proximolateral aspect of the tibia with an occasional slip to M. gastrocnemius. In crocodilians, M. flexor tibialis externus is a large muscle with an origin on the caudal margin of the iliac blade just dorsal to the iliac origin of M. flexor tibialis internus (Fig. 3A). It inserts on the proximal aspect of the tibia and on the gastrocnemius (Fig. 3F). The avian homologue is M. flexor cruris lateralis, which is often subdivided into a pars pelvica and pars accessoria and has varying origins and insertions depending on the taxon. The origin of M. flexor tibialis externus is variable, although it generally arises from the caudal iliac

crest and proximal caudal vertebrae (Fig. 4A). Insertion is equally as variable, with the most common state being an attachment to the tibiotarsus and M. gastrocnemius.

The phylogenetic data indicate an origin of M. flexor tibialis externus from the caudolateral surface of the ilium of *Poposaurus*. Just below the caudal half of the lateral crest on the postacetabular process, there is a shallow ovoid depression bearing very fine striations and indentations (Fig. 5A,B). This probably marks the origin of M. flexor tibialis externus. Insertion was via a tendon shared with M. flexor tibialis internus onto the depression on lateral surface of the tibia just distal to the articular head, in association with M. puboischiotibialis (Fig. 8A,B). Proposed function: Hip extension and adduction, knee flexion.

M. adductor femoris (ADD 1, 2). M. adductor femoris (=M. pubo-ischio-trochantericus in *Sphenodon*) is a large muscle in lepidosaurs arising from the puboischiadic ligament and the ischial symphysis. The crocodilian M. adductor femoris is composed of two heads, arising from the cranial and caudal aspects of the lateral margin of the ischium (Fig. 3A). The avian homologue (=Mm. puboischiofemoralis pars medialis and pars lateralis) also has two divisions although in some taxa they have secondarily fused into one muscle mass. The two heads arise from the ventral margin of the ischium (Fig. 4A). Insertion of M. adductor femoris is on the ventral (medial) surface of the femur just distal to the insertion of M. caudofemoralis and caudal to M. ambiens in almost all of the extant taxa (Figs. 2C, 3C,D, and 4C).

Poposaurus plesiomorphically had two heads to M. adductor femoris, both of which arose from the lateral margin of the ischium. There is a larger depression that runs the length of the cranioventral aspect of the ischium that served as the origin of M. adductor femoris 1 (Fig. 6C,D). The second head (M. adductor femoris 2) probably arose from a shallow groove running along the caudal aspect of the shaft of the ischium similar to that observed in extant crocodilians (Fig. 6C,D). Insertion of both heads was along the caudal surface of the femur. A slightly raised process midway down the shaft demarcates the insertion of M. adductor femoris 1 (Fig. 7A–D). The insertion of M. adductor femoris 2 continued distally along a vertically oriented ridge that runs along the caudal surface of the femoral shaft (Fig. 7A–D). Proposed function: adduction of the hip.

M. puboischiofemoralis externus (PIFE). In lepidosaurs there are three heads (although some taxa have only one) that arise from the pelvic symphysis (Fig. 2A) that are probably homologous to the crocodilian M. puboischiofemoralis externus 1, 2, and 3 (= M. pubofemoralis pars ventralis, M. ischiofemoralis anterior, and M. ischiofemoralis posterior). The cranialmost muscle arises from the

pubic symphysis and pubic tubercle to insert on the lesser trochanter of the femur (Fig. 2B,C). The second head arises from both the pubic and ischial symphyses to insert on and just caudal to the trochanter (Fig. 2B,C). The third head arises from the ischial symphysis to insert via a flat tendon on to the caudal aspect of the femoral shaft just proximal to the insertion of Mm. caudofemorales (Fig. 2B,C). The heads of M. puboischiofemoralis externus in crocodilians share a similar morphology. They arise sequentially from the pelvic symphysis and converge to insert at the caudal margin of the femur just distal to the head (Fig. 3A,C). In birds, this muscle (=M. obturatorius lateralis and medialis, or M. obturator externus and internus) has been reduced to two heads. The first head (lateralis) arises from the lateral surface of the ischium (Fig. 4A) surrounding the obturator foramen; the second head (medialis) arises from the medial aspect of both the ischium and pubis. Insertion is on the caudolateral aspect of the trochanter femoris (Fig. 4C).

The origin of M. puboischiofemoralis externus 1 was most probably on the ventral surface of the pubic apron in *Poposaurus*. As the pubes are fused for their entire lengths, the pubic apron extends proximally all the way up to where the pubes articulate with their corresponding pubic processes on the ilia providing a broad area for muscle attachments. The lateral surface of the pubic boot bears a distinct depression containing thin striated muscle scars that are oriented towards the acetabulum (Fig. 6A,B), suggesting the possibility of a lateral origin of M. puboischiofemoralis externus 2 on the distal pubis similar to that of crocodilians. Just proximal to the pubic boot, there is a vertically oriented shallow groove on the lateral margin of the pubic shaft that we interpret as a probably myological indicator of the cranial margin of this muscle. M. puboischiofemoralis externus 3 in *Poposaurus* retained the crocodilian morphology, arising from the lateral aspect of the distal ischium as evidenced by thin longitudinal muscle scars on the lateral surface of the ischial boot (Fig. 6C,D). There is a slightly raised ridge on the caudal surface of the femoral shaft just distal to its articular surface that is the probably insertion site for M. puboischiofemoralis externus (Fig. 7A–D). Proposed function: Flexion and adduction of the hip.

M. ischiotrochantericus (ISTR). Embryological data have indicated that this muscle is derived from M. iliofemoralis (Romer, 1923a). In all nonavian taxa surveyed, M ischiotrochantericus takes it origin from the inner surface of the ischium. In avian taxa the origin has shifted to the lateral surface (Fig. 4A). Insertion of M. ischiotrochantericus in all taxa is tendinous on the outer dorsal margin of the femur just distal to the head (Figs. 2B, 3B, and 4B).

Plesiomorphically M. ischiotrochantericus arises from the inner surface of the ischium in *Poposaurus*; there are fine striations on the caudomedial surface of the ischium just distal to its articulation with the ilium that indicate the origin of this muscle. Insertion was on the caudodorsal aspect of the femur just distal to the head (Fig. 7A,B). Proposed function: lateral rotation (supination) and retraction of the hip.

M. caudofemoralis brevis (CFB). In lepidosaurs and crocodilians, M. caudofemoralis brevis arises from approximately the first four caudal vertebrae, runs superficial to M. caudofemoralis longus, to insert on the femur just dorsal to the insertion of the longus head (Figs. 2B and 3C,D) . In crocodilians, there is also a secondary origin from the caudal margin of the ilium (Fig. 3A). M. caudofemoralis brevis (=M. caudofemoralis pars pelvica) of birds has lost the vertebral origin and arises solely from the lateral surface of the ilium (Fig. 4A). Insertion in all taxa is on the caudal margin of the femoral shaft (Figs. 2B, 3C,D, and 4C).

The phylogenetic data indicate that M. caudofemoralis brevis arose from the lateral surface of the ilium in *Poposaurus*. The postacetabular process is elongated with an expanded brevis shelf, the ventrolateral surface of which bears striated muscle scars that are probably associated with the origin of this muscle (Fig. 5A,B). It is possible that there was a secondary vertebral origin for M. caudofemoralis brevis in *Poposaurus*; however, there are no distinct muscle scars on the caudal vertebrae that can be unequivocally linked to the M. caudofemoralis brevis. Insertion was on a raised ridge on the caudomedial surface of the femur, just proximal to the insertion of M. adductor 1 (Fig. 7C,D). Proposed function: extension and adduction of the hip.

M. caudofemoralis longus (CFL). In lepidosaurs and crocodilians, M. caudofemoralis longus (=M. coccygeo-femoralis longus; Romer, 1923a) is the major femoral retractor, and makes up the majority of the muscle mass of the tail. In extant birds, this muscle (=M. caudofemoralis pars caudalis) has been significantly diminished in association with the reduction of the tail. In both lepidosaurs and crocodilians, M. caudofemoralis longus arises from the centra and ventral side of the transverse processes of a varying number of caudal vertebrae (the vertebral number varies depending on the taxon). The muscle runs cranially to insert on the femur, just distal to the lesser trochanter in lepidosaurs, and on the fourth trochanter in crocodilians (on the caudoventral surface of the femur; Figs. 2B and 3C,D). In all lepidosaurs and crocodilians, it sends a secondary long tendon distally to insert on the tibia just below the knee. In birds, M. caudofemoralis pars caudalis (=M. piriformis pars caudofemoralis) arises from the ventrolateral surface of the caudal vertebrae and pygostyle. It

merges with the tendon of M. caudofemoralis pars pelvica into a single insertion tendon that attaches to the proximocaudal aspect of the femur (Fig. 4C).

In *Poposaurus*, M. caudofemoralis longus arose from the bodies of the proximal caudal vertebrae and ventral aspects of the corresponding transverse processes (as in extant lepidosaurs and crocodilians). The proximal insertion was on the caudomedial aspect of the femur, on a low obliquely oriented ridge just medial to and in association with the brevis head. There is an oval depression that separates the insertion sites of the caudofemoral muscles on the medial aspect of the femur (Fig. 7C,D). The secondary tendon of M. caudofemoralis longus was lost in birds; however, it was reconstructed in basal nonavian theropods (see Carrano and Hutchinson, 2002) and it was probably present in *Poposaurus* as well, inserting on the caudal aspect of the proximal tibia, although no distinct scar can be attributed to its insertion. Proposed function: extension and adduction of the hip.

Muscles to the Pes

M. gastrocnemius (GL, GM). In both lepidosaurs and crocodilians, M. gastrocnemius has two heads, although in some lacertilian taxa it has been further subdivided into three. One head arises from the lateral aspect of the femoral condyle and the other variably from the caudomedial aspect of the distal femur and the medial aspect of the proximal tibia (Figs. 2C,E and 3B,F). In lepidosaurs the two heads, M. gastrocnemius pars profundus (=M. gastrocnemius externus of crocodilians) and pars fibularis (=M. gastrocnemius internus of crocodilians), merge with the tendon of M. flexor tibialis externus and run distally under the plantar aponeurosis to insert on the ventral aspect of the metatarsals with varying extensions onto the proximal phalanges (Fig. 2E). In crocodilians the long tendon of the external head runs over the calcaneum, sending attachments to the plantar aponeurosis, and inserts on the ventral surface of the metatarsals and with varying extensions to their corresponding proximal phalanges (Fig. 3F). The insertion tendon of the internal, or tibial head follows a similar path, inserting on the base of the first metatarsal with an extension to metatarsal V (Fig. 3F). The avian M. gastrocnemius is generally composed of three parts: pars lateralis, pars intermedia and pars medialis. The pars lateralis head has an origin from the lateral side of the proximocranial tibia, the pars medialis head from the medial aspect (Fig. 4D). The pars intermedia arises from the proximocaudal surface of the femur, in association with the insertion of the adductor muscles (Fig. 4B). All three heads merge into a single tendon that runs distally to insert onto the base of the tarsometatarsus (Fig. 4H).

On the basis of the phylogenetic data, *Poposaurus* had at least two divisions to M. gastrocnemius. M. gastrocnemius lateralis arose from the caudal aspect of the distal femoral shaft and lateral femoral condyle just distal to the insertion of the adductors (Fig. 7A,B). The medial head took its origin from the medial aspect of the proximal tibia just distal to its articular surface. There is a large depression just below the proximal articular head down and caudal to the origin of M. tibialis anterior that would have served as the origin of the lateral head of M. gastrocnemius. There was also a possible secondary femoral origin in *Poposaurus*. The caudomedial aspect of the femur bears subtle rugosities indicating soft-tissue attachments, but no specific boundary lines are visible. The two divisions of M. gastrocnemius then merged into a common tendon and ran distally through a deep groove on the enlarged calcaneal tubercle to the ventral aspect of the pes (Fig. 9A,B,E, and F). There are very distinct grooves running along the ventrolateral shaft of metatarsals I through IV that demarcate the insertion sites of M. gastrocnemius (Figs. 10C–F and 11E,F) in a manner very similar to that of extant crocodilians. The medial head probably inserted on both the plantar aponeurosis and digit V. Proposed function: flexion of the knee, extension of the ankle.

M. tibialis anterior (TA). In all lepidosaurs and crocodilians, M. tibialis anterior arises from shaft of the tibia. In *Sphenodon*, this muscle arises from the proximal cranial region of the tibia and runs distally to insert on the lateral surface of the tibiale, metatarsal I, and distal phalanx. M. tibialis of lacertilians is composed of one or two heads, depending on the taxon, and arises fleshily from the cranial and ventral sides of the tibial shaft (Fig. 2D,E). Insertion is on the base of metatarsal I (Fig. 2D,E) with the second division often inserting onto the plantar aponeurosis. In crocodilians, the single head of M. tibialis anterior arises from the proximal third of the cranial face of the tibia (Fig. 3E). It inserts in association with the tendon of M. extensor digitorum longus onto the dorsal surface of the first three metatarsals (Fig. 3E). The avian M. tibialis cranialis is composed of two heads, the larger arising from the lateral surface of the cnemial crest (Fig. 4F), and the smaller arising from the external femoral condyle. The two heads merge into a common tendon that inserts onto the cranioproximal end of the tarsometatarsus (Fig. 4G). There are some problems with the homology of M. tibialis anterior and M. extensor digitorum longus in birds (for a more detailed discussion on muscle homology, see e.g., Hutchinson, 2002); however, for this reconstruction the classical interpretation is retained.

The number of heads of M. tibialis anterior in *Poposaurus* is equivocal; however, the origin was very clearly on the craniolateral face of the cnemial
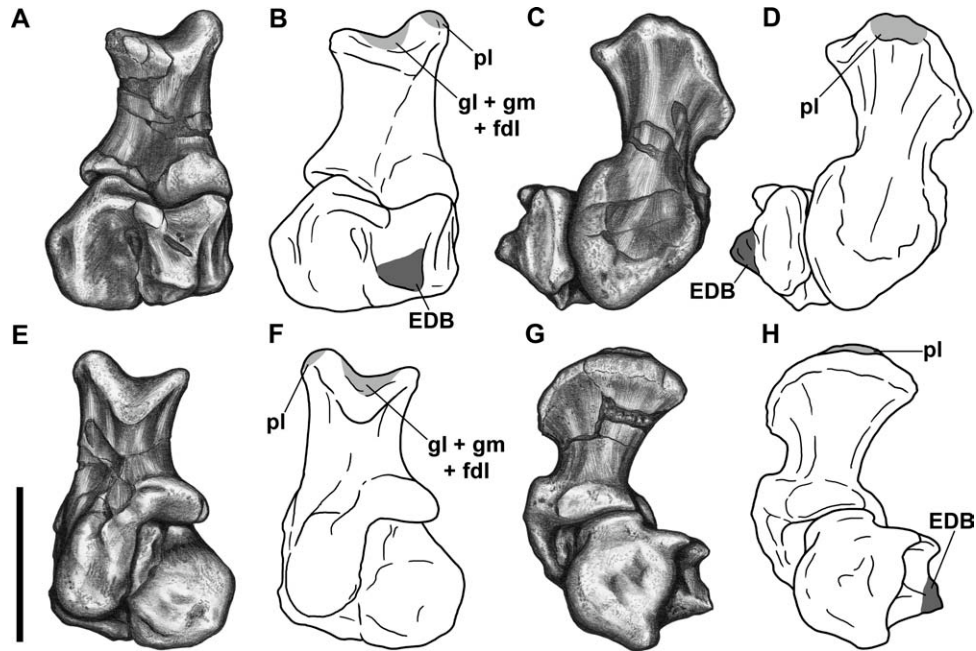
Fig. 9.   Osteological correlates on the calcaneum and astragalus of *Poposaurus*. **A**: Illustration of the left calcaneum and astragalus in dorsal view; **B**: diagrammatic image of the left calcaneum and astragalus in dorsal view; **C**: illustration of the left calcaneum and astragalus in lateral view; **D**: diagrammatic image of the left calcaneum and astragalus in lateral view; **E**: illustration of the left calcaneum and astragalus in caudal view; **F**: diagrammatic image of the left calcaneum and astragalus in caudal view; **G**: illustration of the left calcaneum and astragalus in medial view; and **H**: diagrammatic image of the left calcaneum and astragalus in medial view. The muscle origins and insertions are indicated on the diagrammatic images in gray and muscle origin labels are capitalized; not all muscles are included. Scale bar = 5 cm. Abbreviations: EDB: M. extensor digitorum brevis; FDL: M. flexor digitorum longus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; and PL: M. peroneus longus.

crest. There is a rugose depression in this region correlating with the origin of this muscle. A secondary head, (if present) would have been from the lateral femoral condyle; however, there is no way to know if the muscle scars on the femur were associated with this muscle or other distal limb muscles. Insertion was presumably onto the base of the first three metatarsals. There is a slight depression on the dorsal surface of each of the metatarsals corresponding to the insertion of M. tibialis anterior (Figs. 10A–D and 11A,B). It is possible that the insertion extended to the fourth metatarsal since there is a similar depression present on its dorsal surface as well (Figs. 10A–D and 11A,B). Proposed function: flexion of the ankle joint.

M. popliteus (POP). In both lepidosaurs and crocodilians M. popliteus runs obliquely from the proximal half of the medial shaft of the fibula to the shaft of the tibia. In birds, the M. popliteus originates on the caudomedial surface of the proximal fibula and runs obliquely to insert on the caudal surface of the tibia.

In *Poposaurus*, M. popliteus would have closely resembled that of all of the extant taxa, running from the proximomedial surface of the fibular shaft obliquely to the lateral surface of the shaft of the tibia. Proposed function: fibular rotation.

M. peroneus longus and brevis (PL, PB). There is only one head to M. peroneus in *Sphenodon*, arising from the proximolateral surface of the fibula and inserting on the lateral surface of the fibulare and terminal phalanx of digit V. In all other squamates and archosaurs there are two heads to this muscle: a longus head, and a brevis head (=Mm. fibulares longus et brevis). In squamates, the longus head arises on the lateral aspect of the external femoral condyle, whereas the origin of the brevis head is from craniolateral surface of the fibular shaft (Fig. 2B,D). The two heads insert either separately or via a common tendon onto the base of metatarsal V (Fig. 2D). In crocodilians both heads arise from the fibular shaft (morphologically similar to squamates; Fig. 3E). Insertion of the longus head is on the calcaneal tuber, while the brevis head inserts on the lateral aspect of the tarsals and proximal metatarsals (Fig. 3E,F). In both paleognath and neognath birds, the M. peroneus longus arises from the lateral aspect of the cnemial crest of the tibiotarsus and the knee joint capsule (although in some taxa it arises from the tibiotarsus and fibula). Insertion is on the caudal aspect of the tibiotarsus with a secondary extension to the insertion tendon of M. flexor perforatus digit III (Fig. 4H). In most avian taxa, M. pero-
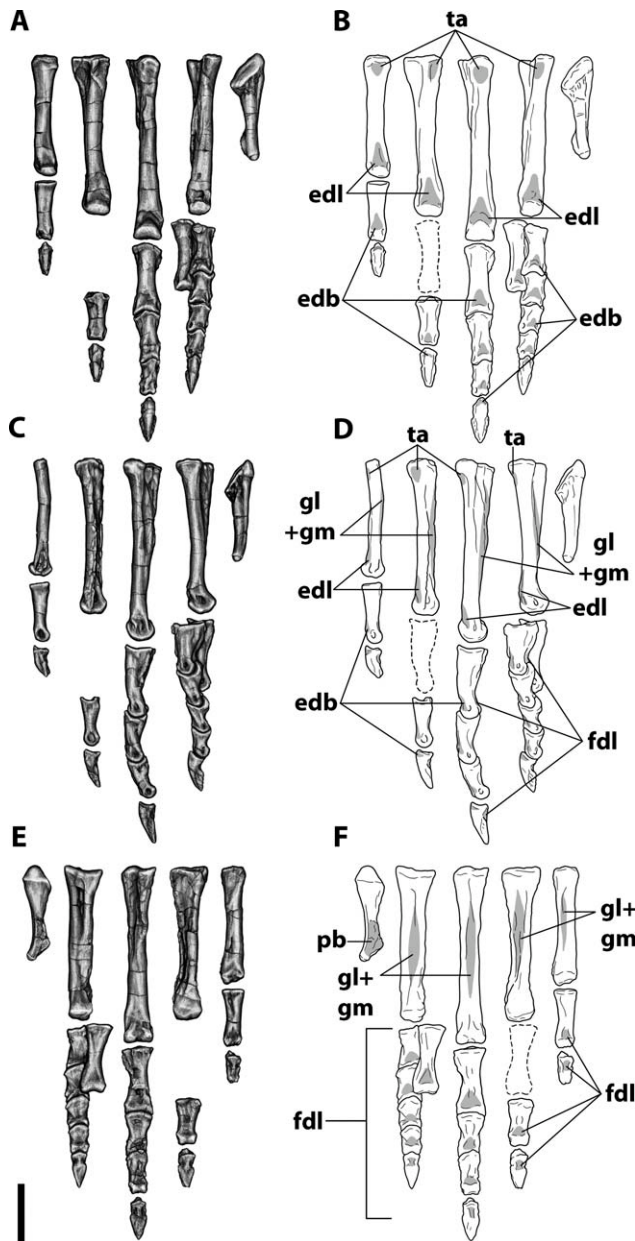
Fig. 10. Osteological correlates on the pes of *Poposaurus*. **A**: Illustration of the left pes in dorsal (extensor) view; **B**: diagrammatic image of the left pes in dorsal (extensor) view; **C**: illustration of the left pes in lateral view; **D**: diagrammatic image of the pes in lateral view; **E**: illustration of the left pes in ventral (flexor) view; and **F**: diagrammatic image of the pes in ventral (flexor) view. The first phalanx of digit II could not be removed from digit IV; dotted lines indicate proper placement of this phalanx. The muscle origins and insertions are indicated on the diagrammatic images in gray and muscle origin labels are capitalized; not all muscles are included. Scale bar = 5 cm. Abbreviations: EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDL: M. flexor digitorum longus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; PB: M. peroneus brevis; and TA: M. tibialis anterior.

neus brevis arises from the lateral surface of both the tibiotarsus and fibula (Fig. 4D–F), and travels distally to insert on the proximolateral aspect of the tibiotarsus (or on the tendon of M. flexor digitorum longus in *Apteryx*). M. peroneus brevis is absent in all other ratites.

The morphology of these muscles is extremely variable in the extant taxa; however, most taxa retain a fibular origin for at least one of the heads. Slight intermuscular lines are discernible on the fibulae of *Poposaurus* allowing for the identification of the most probably origin site for M. peroneus longus and brevis. The longus head inserted on the raised lateral ridge of the calcaneal tuber (Fig. 9A–H). The brevis head arose from an oval shaped rugosity on the lateral shaft of the fibula just distal to the origin of M. iliofibularis (Fig. 8C,D). Unlike dinosaurs and birds, metatarsal V is not lost in *Poposaurus*, and thus the insertion tendon of M. peroneus brevis probably retained the ancestral morphology and inserted on the fifth metatarsal. There is a very distinct and rugose muscle scar along the caudolateral margin of metatarsal V in *Poposaurus* supporting the reconstruction of this insertion site for M. peroneus brevis (Figs. 10E,F and 11D,E). Proposed function: flexion of the ankle joint.

M. extensor digitorum longus and brevis (EDL, EDB). In all extant lepidosaurs and crocodilians, M. extensor digitorum longus takes its origin from the dorsal aspect of the external femoral condyle (Fig. 2B). The insertion of this muscle is onto the proximodorsal surface of metatarsals III and IV in lepidosaurs and I–III (along with M. tibialis anterior) in crocodilians (Figs. 2D and 3E). M. extensor digitorum brevis arises from the dorsal surface of the tarsals to insert on the dorsal surfaces of the distal phalanges in all nonavian taxa (Figs. 2D,E and 3E,F). In *Apteryx*, M. extensor digitorum longus arises from the craniolateral surface of the tibial shaft just distal to the proximal articular head (Fig. 4D), and runs distally along the cranial face of the tarsometatarsus to insert tendinously on the dorsal surface of the distal phalanges (Fig. 4G). In Neognath birds, M. flexor digitorum longus arises from the lateral cnemial crest and the proximocranial surface of the tibiotarsus. It runs distally, passing through the Retinaculum extensorium tibiotarsi and Retinaculum extensorium tarsometatarsus to insert, after trifurcating, onto the proximodorsal aspect of the unguals. M. extensor digitorum brevis has been lost in birds.

M. extensor digitorum longus and brevis demonstrate extensive morphological variation in the extant taxa, probably due to the extreme modification of the avian foot relative to other extant archosaurs. The structure of the pes in *Poposaurus* is very similar to the crocodilian pes (e.g. five digits, enlarged calcaneal tuber) so its corresponding musculature was presumably more similar to crocodilians than to extant birds. The origin of this muscle is ambiguous; there are muscle scars on both the proximomedial aspect of the tibia and the
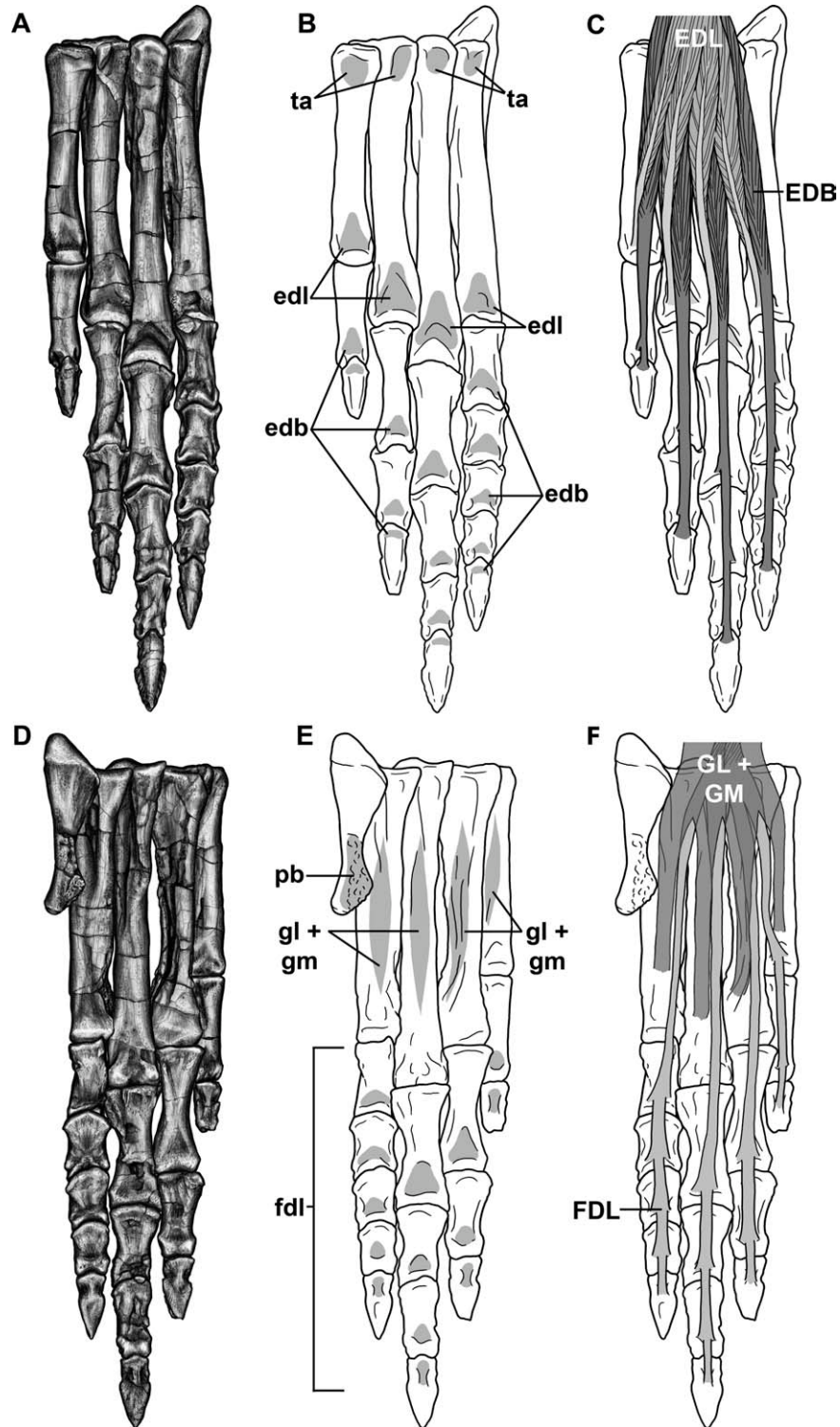
Fig. 11. Reconstruction of the pedal osteological correlates, musculature and tendons of *Poposaurus*. **A**: Illustration of the articulated pes in dorsal view; **B**: diagrammatic image of the articulated pes in dorsal view with pedal muscle attachment sites indicated in gray; **C**: diagrammatic image of the articulated pes in dorsal view with M. extensor digitorum longus and brevis restored; **D**: illustration of the articulated pes in ventral view; **E**: diagrammatic image of the articulated pes in ventral view with pedal muscle attachment sites indicated in gray; and **F**: diagrammatic image of the articulated pes in dorsal view with M. gastrocnemius and M. flexor digitorum longus restored. Articulation is an approximation based on the articulated state of the YPM 57100 specimen, the fusion of some of the phalanges, and the shape of the metatarsals. Abbreviations: EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDL: M. flexor digitorum longus; GL: M. gastrocnemius lateralis; GM: M. gastrocnemius medialis; PB: M. peroneus brevis; and TA: M. tibialis anterior.

lateral condyle of the femur so it is not possible to determine unequivocally the origin of M. extensor digitorum longus. There are distinct scars on the distal end of the dorsal shaft of metatarsals I through IV that are morphologically similar to those of extant crocodilians, that probably correspond to the insertion tendons of M. extensor digitorum longus (Figs. 10A,B and 11A,B). The phylogenetic data indicate that M. extensor brevis would arise from the extensor surface of the astragalus. There is a ridge that projects from the cranial face of the astragalus, just ventral to where it articulates with the fibula (Fig. 9A–D,G, and H) that probably served as the origin for M. extensor digitorum brevis in *Poposaurus*. There is a distinct depression (and sometimes accompanying ridge) just proximal to the distal articular surface of each phalanx indicating the insertion site of M. extensor digitorum brevis (Figs. 10A–D and 11A,B). Proposed function: flexion of the ankle and extension of the pedal digits.

M. flexor digitorum longus and brevis (FDL, FDB). M. flexor digitorum longus arises from the lateral femoral condyle in lepidosaurs and crocodilians, sometimes with an accessory origin from the proximal third of the fibula (or accessory fibers branching off of the first muscle; Figs. 2C,E and 3B,F). The two heads converge into a single insertion tendon that runs deep to the M. gastrocnemius to the ventral aspect of the pes. In lepidosaurs and crocodilians, M. flexor digitorum brevis takes its origin from the plantar aponeurosis. In *Apteryx* (and some other paleognaths), the M. flexor digitorum longus arises from the distocaudal (popliteal) aspect of the femur (Fig. 4C) and runs distally, giving off a branch to the hallux, which inserts on the terminal phalanx (Fig. 4H). The tendon then merges with the insertion tendon of M. peroneus brevis and inserts on the dorsal surface of the terminal phalanges of the three main digits (Fig. 4H). In all other birds, M. flexor digitorum longus arises variably from the proximocaudal tibia and fibula. M. flexor digitorum brevis has been lost in birds. Insertion of both muscles in all extant taxa is on the ventral surface of the terminal phalanges or unguals.

Analysis of the morphology of M. flexor digitorum longus in the extant taxa clearly indicates that this muscle arose from the caudolateral femur, just proximal to the condyle in association with the lateral head of the gastrocnemius. Although there are some muscle scars on the distal femur of *Poposaurus*, they do not permit the identification of the specific points of the origin of M. flexor digitorum longus (Fig. 7A,B). It is possible that there was a secondary origin from the proximal head of the fibula; however, there are no distinct scars supporting this reconstruction in *Poposaurus*. Insertion of M. flexor digitorum longus was onto the ventral surface of the phalanges

and flexor tubercles of the unguals in *Poposaurus* (Figs. 10C–F and 11D,E). *Poposaurus* does not have any of the osteological pedal reductions associated with extant birds so it is unlikely that it exhibited similar myological reductions, and thus M. flexor digitorum brevis was probably present as in other extant crocodilians, arising from the plantar aponeurosis and with an insertion on the ventral surfaces of the phalanges (Figs. 10C–F and 11D,E); however, the insertion site remains a Level II′ reconstruction because specific muscle scars cannot be directly connected to this muscle. Proposed function: extension of the ankle joint, flexion of the digits.

M. extensor hallucis longus (EHL). In all lepidosaurs and crocodilians M. extensor hallucis longus arises from the cranial aspect of the distal fibula. It inserts either on the dorsal aspect of the medial side of the tarsals or metatarsal I (depending on the taxon). In Aves, M. extensor hallucis longus arises from the cranial aspect of the distal tibiotarsus due to a reduction of the fibula. It inserts on the proximodorsal side of the ungual of the hallux.

In *Poposaurus*, there is no reduction of the fibula similar to extant birds, so this muscle probably arose from the cranial surface of the distal fibula. There is a slight depression on the fibular shaft just proximal to the distal articular head (Fig. 8C,D) that may have been the origin site of M. extensor hallucis longus. This muscle clearly inserts on the metatarsal or a phalanx of the hallux; however, there are no muscle scars that indicate the exact insertion site. Proposed function: extension of the hallux (digit I).

M. flexor hallucis longus (FHL). M. flexor hallucis longus shares an origin on the caudal aspect of the distal femur with M. gastrocnemius in both lepidosaurs and crocodilians. It inserts on the ventral surface of the terminal phalanges and ungual of the first digit. In birds, M. flexor hallucis longus arises from the external femoral condyle (Fig. 4C) and runs distally and ventrally to insert on the proximoventral aspect of the ungula of the hallux.

On the basis of the morphology of this muscle in the extant taxa it is clear that M. flexor hallucis longus arose from the caudolateral aspect of the femur in *Poposaurus*. Although there are many indicators of muscle attachments on the distal end of the femur, there is no distinct scar that can be clearly linked to the origin this muscle. Insertion was on the ventral surface of the distal phalanges and ungual of digit I. It is difficult to make a distinction between the osteological indicators for insertion sites for M. flexor digitorum longus and a possible insertion site for M. flexor hallucis longus, although clear insertion sites exist on the ventral aspect of the phalanges and ungual of digit I. Proposed function: flexion of the knee, extension of the ankle joint, and flexion of the hallux (digit I).

Nonmyological Soft-Tissue Structures (Table 2)

Plantar aponeurosis. A layered and complex plantar aponeurosis was present in all of the extant taxa examined indicating that a homologous structure was probably present on the ventral surface of the pes in *Poposaurus*. Fascia do not leave any osteological indicator; thus the lack of skeletal evidence for this soft-tissue structure on the pes of *Poposaurus* is not surprising. The plantar aponeurosis serves as a secondary insertion site for M. gastrocnemius in both extant lacertilians and crocodilians; this was probably also the case in the pes of *Poposaurus* as its pedal skeletal morphology is similar to that of crocodilians (i.e., five digits, enlarged calcaneum, calcaneal tuber).

Retinacula. The homologies of the various retinacula of the pedes of the extant taxa are beyond the scope of this study; however, all of the extant archosaurs exhibited at least one robust tibial retinaculum that restrains the digital extensors. In extant alligators there is a very large tibial retinaculum that runs distally across the cranial surface of the ankle just proximal to the joint, encompassing all of the extensor tendons. In both paleognath and neognath birds, the Retinaculum extensorium tibiotarsi is a broad and thick obliquely oriented tendinous retinaculum positioned just proximal to the ankle that serves to restrain the major extensors.

Although there are numerous muscle and soft-tissue attachment scars on the distal limb elements of *Poposaurus*, none can be unequivocally attributed to retinacula, so the location can only be approximated. On the basis of the phylogenetic data and the functional purpose of a retinaculum, the most probably location is at the junction between the articulation of the tibia and the tarsal bones. Because of the elongation of the poposaur pes relative to other archosaurs, particularly extant crocodilians, the functional significance of the tibial retinaculum in restraining the extensor tendons becomes of greater importance.

Pelvic ligaments. The pelvis of extant lepidosaurs and crocodilians is associated with a series of ligaments that act as structural support and attachment sites for the adjacent pelvic muscles. Romer (1922, 1923a, 1956; Hutchinson 2001a) originally contended that two of the main pelvic ligaments were lost in archosaurs due to their reduction in extant alligators; however, Hutchinson (2001a) determined that the primary semicircular ilio- and ischiopubic ligaments of Aves are probably homologous to those of extant crocodilians after they were reevaluated within an explicit phylogenetic framework.

Iliopubic ligament (ipl). In lepidosaurs this ligament runs from the cranioventral surface of the preacetabular process of the ilium ventrally to insert on the pubic tubercle (Fig. 12A). In crocodilians, there is fibrous band of connective tissue that has been hypothesized to be homologous to the lepidosaurian iliopubic ligament (Hutchinson, 2001a) that arises from the preacetabular ilium and attaches to the pubic tubercle (Fig. 12B). The avian iliopubic ligament is morphologically similar to the reptilian ligament, with an origin on the preacetabular process of the ilium and an insertion on the pubic tubercle (Fig. 12C). In both lepidosaurs and birds, this ligament runs ventral and superficial to the pubic musculature and serves as an origin site for some of the hypaxial musculature.

The preacetabular ilium is greatly expanded in *Poposaurus*, and the ventral surface serves as the origin site for the M. puboischiofemoralis internus 2. There are longitudinal scars on the ventral preacetabular ilium, but no discernable boundaries indicate a ligamental as opposed to myological origin site. On the medial surface of both ilia there is a rugose shelf that supported the epaxial musculature; however, in both birds and lepidosaurs, the iliopubic ligament serves as an origin for these muscles as well, so it is more probably that this inner shelf was the origin site for the iliopubic ligament as opposed to the ventral preacetabular ilium (Fig. 12E). This position on the ilium would also allow the ligament to run superficial to superficial and ventral to the Mm. puboischiofemoralis internus 1 and 2 as in all extant taxa.

Puboischiadic ligament (pil). In lepidosaurs, the puboischiadic ligament arises from the pubic tubercle and runs caudally to insert on the ischial tuberosity, linking the iliopubic ligament (cranially) to the ilioischiadic ligament (caudally; Fig. 12A). Contrary to Romer's (1922, 1923a, 1956) assertions that this ligament was lost in crocodilians, a small vestigial puboischiadic ligament of similar topography to that of lepidosaurs runs from the caudoproximal aspect of the pubis to the proximal ischium (Fig. 12B; Hutchinson, 2001a; Vivian Allen, pers. comm.). In crocodilians, this ligament serves as a proximal attachment site for the pelvic membrane. In birds, this ligament (=ligamentum ischiopubicum) is very short due to the retroverted pubis; it arises from the caudal surface of the pubic shaft and runs caudally to insert on the obturator tuberosity (Fig. 12C).

There is clear phylogenetic support for the presence of this ligament connecting the cranial surface of the ischium to the caudal surface of the pubis in *Poposaurus* (Fig. 12E). There are no obvious muscle scars or pelvic tuberosities that can be associated with either the origin or insertion of the puboischiadic ligament. The ventral surface of the pubis has a slight ridge just below the origin of M. ambiens, but there is no way to determine whether this is due to the presence of this muscle, this ligament or other adjacent soft tissues.

Ilioischiadic ligament (iil). This ligament arises from the ventral margin of the postacetabular
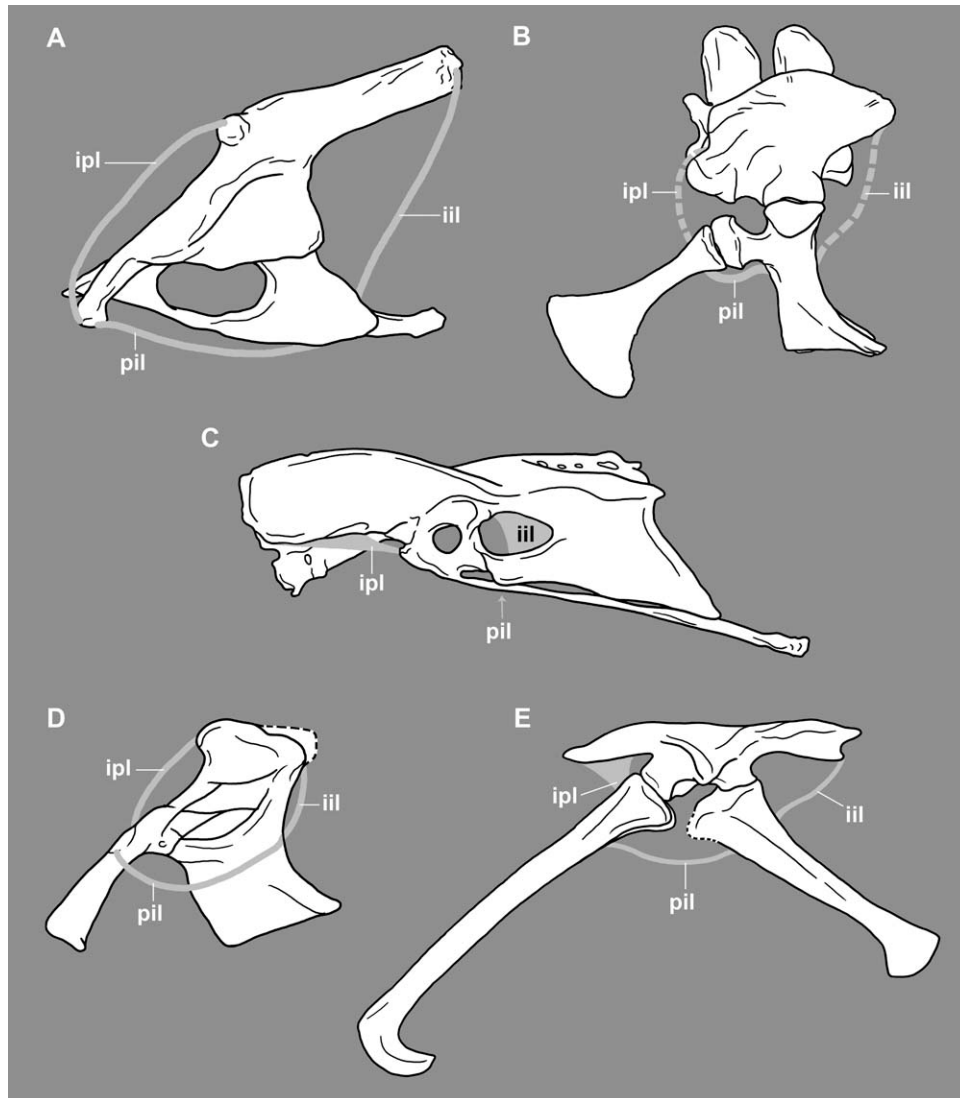
Fig. 12. Morphology of the pelvic ligaments. Diagrammatic images (in left lateral view) of **A**: the pelvis of *Varanus*; **B**: the pelvis of *Alligator*; **C**: the pelvis of *Meleagris gallapavo* (the turkey), redrawn from Baumel (1993); **D**: the pelvis of *Tropidosuchus*, redrawn from Hutchinson (2001a); and **E**: the pelvis of *Poposaurus*. Pelvic ligaments are indicated in gray. Vestigial ligaments are indicated by a dotted line. Images not to scale. Abbreviations: iil: ilioischiadic ligament (or dorsal margin of the membrane); ipl: iliopubic ligament; and pil: puboischiadic ligament.

ilium and inserts on the ischial tuberosity in all extant squamates (Fig. 12A) and serves as a partial origin site for the flexor cruris musculature. There is no such ligament in extant archosaurs; however, Hutchinson (2001a) identified dense fascia in crocodilians (Fig. 12B) and the ilioischiadic membrane of Neornithes (Fig. 12C) as possible homologous structures to the ilioischiadic ligament of squamates due to similar morphology, pelvic connections, and osteological correlates in fossil archosauriforms (Fig. 12D).

The postacetabular process of the ilium is elongated in *Poposaurus* and the brevis shelf serves as the origin site for the M. caudofemoralis brevis. The distal tip of the ventral surface of the postace-

tabular process is rounded into a distinct tubercle; the muscle scars associated with the adjacent muscles stop abruptly along its margin. This tubercle probably indicates the attachment site of the ilioischiadic ligament to the ilium (Fig. 12E). There are no discernable features on the dorsal surface of the ischium that can be attributed to the insertion site.

DISCUSSION
Comparisons With Reconstructions of Hindlimb Myology of Other Archosaurs

As a detailed review of the various reconstructions of tyrannosaur hindlimb and pelvic musculature
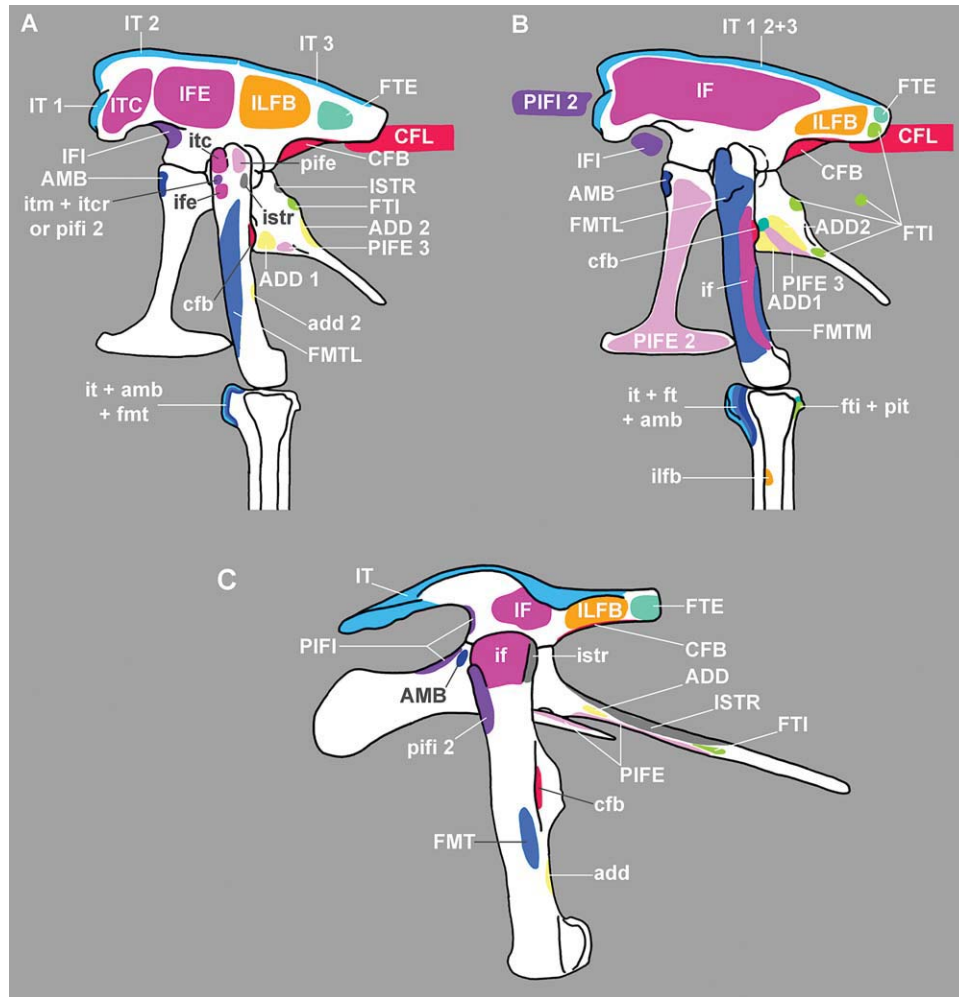
Fig. 13. Previous reconstructions of the pelvic and hindlimb musculature in extinct nonavian dinosaurs. All images are in left lateral view and are not to scale. **A**: *Tyrannosaurus* as reconstructed by Romer (1923b), image redrawn from Carrano and Hutchinson (2002); **B**: *Tyrannosaurus*, redrawn from Carrano and Hutchinson (2002); and **C**: *Maiasaura*, redrawn from Dilkes (2000). Muscle origin labels are capitalized; not all muscles are included. Abbreviations: ADD 1–2: M. adductor 1–2; AMB: M. ambiens; CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; FT: M. femorotibialis; FMT: M. femorotibialis; FMTL: M. femorotibialis lateralis; FMTM: M. femorotibialis medialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; IF: M. iliofemoralis; IFE: M. iliofemoralis externus; IFI: M. iliofemoralis internus; ILFB: M. iliofibularis; IT 1–3: M. iliotibialis 1–3; ITC: M. iliotrochantericus caudalis; ITCR: M. iliotrochantericus cranialis; ITM: M. iliotrochantericus medialis; ISTR: M. ischiotrochantericus; PIFE (2–3): M. puboischiofemoralis externus (2–3); PIFI (2): M. puboischiofemoralis internus (2); and PIT: M. puboischiotibialis.

have been completed elsewhere (Carrano and Hutchinson, 2002), it will not be repeated here. However, even considering that Romer's (1923b; Fig. 12A) reconstruction of saurischian pelvic musculature was based closely on the morphology of extant crocodilians as opposed to the entire EPB it is still of some relevance for comparison with the myology of *Poposaurus* (Fig. 13) due to this animal's close phylogenetic relationship with extant crocodilians. Another feature of Romer's work that is rarely discussed or completed in later myological reconstructions is a set of diagrammatic illustrations restoring the actual muscles. Diagramming the inferred muscles (Figs. 11C,F, 14B–D, and 15A,B) beyond the just the origin and insertion sites, while speculative, is

important in order to determine and demonstrate the spatial relationships of the muscles relative to one another, a feature that cannot be expressed in a figure showing attachment sites alone (Figs. 11A,B,D,E, 13A–C, and 14A) or with line segments. This can also be done via digital modeling (see e.g., Hutchinson et al., 2005, 2008; Hutchinson and Allen, 2008; Curtis et al., 2009; Sellers et al., 2009).

Because of the close phylogenetic relationship of the poposaur with extant crocodilians, the osteological topography of the hindlimb and pelvis indicates a more crocodilian than avian myological condition. Many of the avianlike soft-tissue modifications reconstructed in the pelvis of *Tyrannosaurus* (Fig. 13B) by Carrano and Hutchinson (2002)
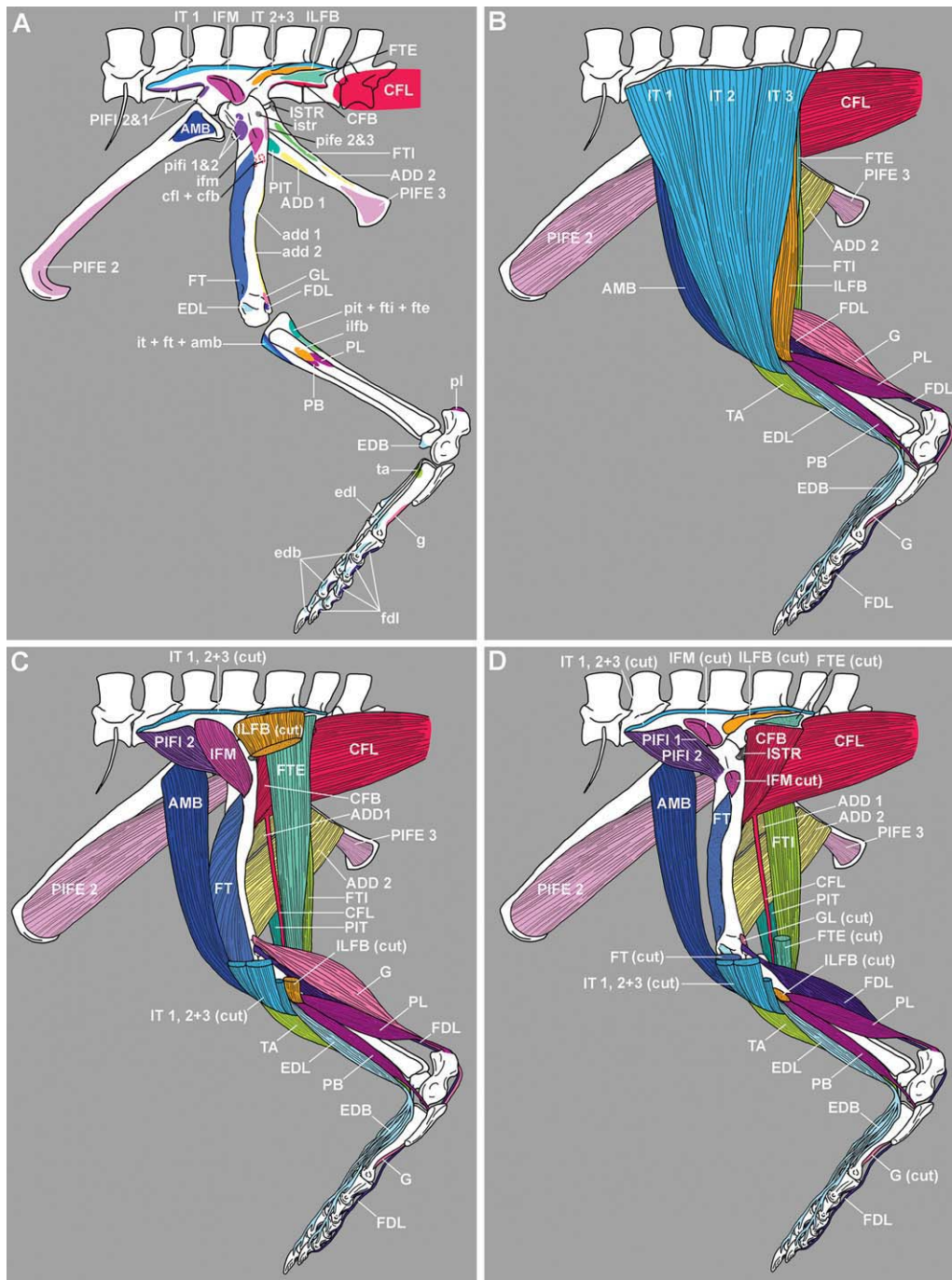
Fig. 14. Reconstruction of the pelvic and hindlimb musculature of *Poposaurus*. Exact size of origins and insertions are approximations based on osteological topography. Muscle size and fiber orientation are speculative and based on skeletal morphology and the EPB. Not all of the hindlimb muscles have been included. **A**: Reconstruction of the origins and insertions of the pelvic and hindlimb musculature in lateral view. **B**: Lateral view of the hindlimb and pelvis with superficial appendicular musculature restored. **C**: Same as B, but IT and ILFB have been cut. **D**: Same as C, but IF, FTE, FMT, and G have been cut. The muscle origin labels are capitalized. Abbreviations: ADD 1–2: M. adductor 1–2; AMB: M. ambiens; CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDL: M. flexor digitorum longus; FT: M. femorotibialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; G: M. gastrocnemius; GL: M. gastrocnemius lateralis; IFM: M. iliofemoralis; ILFB: M. iliofibularis; ISTR: M. ischiotrochantericus; IT 1–3: M. iliotibialis 1–3; PB: M. peroneus brevis; PIFE 2–3: M. puboischiofemoralis externus 2–3; PIFI 1–2: M. puboischiofemoralis internus 1–2; PIT: M. puboischiotibialis; PL: M. peroneus longus; and TA: M. tibialis anterior.
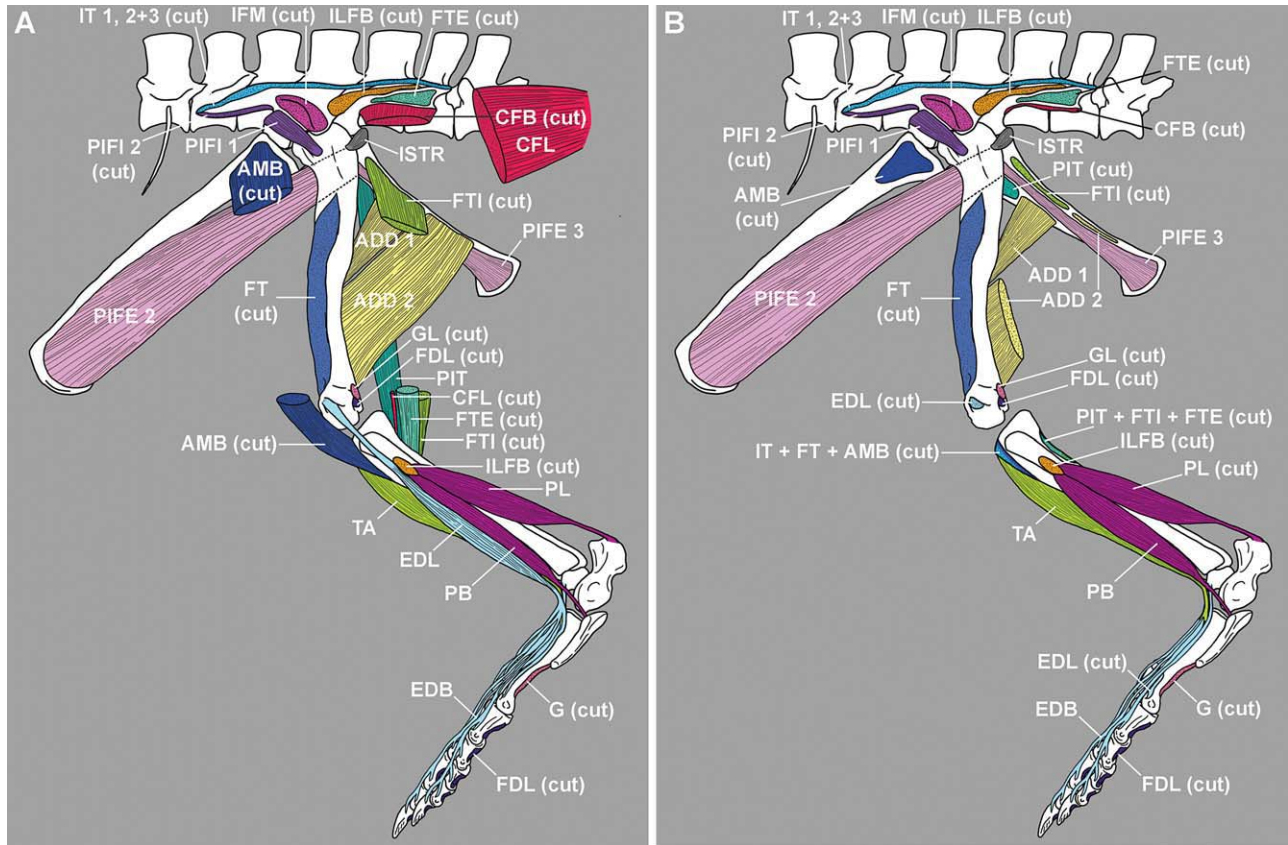
Fig. 15. Reconstruction of the pelvic and hindlimb musculature of *Poposaurus*. **A**: Lateral view of the hindlimb and pelvis with deep appendicular musculature restored; many of the superficial layers have been cut. **B**: Same as A, with the majority of the superficial musculature removed to show the deep musculature. The muscle origin labels are capitalized. Abbreviations: ADD 1–2: M. adductor 1–2; AMB: M. ambiens; CFB: M. caudofemoralis brevis; CFL: M. caudofemoralis longus; EDB: M. extensor digitorum brevis; EDL: M. extensor digitorum longus; FDL: M. flexor digitorum longus; FT: M. femorotibialis; FTE: M. flexor tibialis externus; FTI: M. flexor tibialis internus; G: M. gastrocnemius; GL: M. gastrocnemius lateralis; IFM: M. iliofemoralis; ILFB: M. iliofibularis; IT 1–3: M. iliotibialis 1–3; ISTR: M. ischiotrochantericus; PB: M. peroneus brevis; PIFE 2–3: M. puboischiofemoralis externus 2–3; PIFI 1–2: M. puboischiofemoralis internus 1–2; PIT: M. puboischiotibialis; PL: M. peroneus longus; and TA: M. tibialis anterior.

were not present in *Poposaurus* (Fig. 14A). There was evidence for the origin of M. puboischiotibialis on the proximal ischium, a reptilian muscle that has been lost in birds; neither Carrano and Hutchinson (2002) nor Dilkes (2000) found any evidence for this muscle in dinosaurs (Fig. 13A,C). Extensive and directional scarring on the expanded pubic and ischial boots suggests a more crocodilianlike origin for both M. puboischiofemoralis externus 2 and 3. It is interesting to note that the enlarged, caudally projecting pubic boot of *Poposaurus* is one of many features in the postcranial skeleton convergent with bipedal theropod dinosaurs. However, the unique caudodorsal "hooklike" distal symphysis of the pubes is quite distinct in *Poposaurus*. Similar convergent traits have also been identified in *Effigia okeeffeae* (Nesbitt, 2007) and *Shuvosaurus inexpectus*, (TTU-P 18418) other bipedal poposauroids.

The disparate nature of the origin of M. puboischiofemoralis internus 2 in extant archosaurs has resulted in some confusion in muscle homology and morphology in extinct archosaurs. On the basis of the presence of extensive muscle scarring on the ventral and lateral surfaces of the preacetabular process in *Poposaurus*, it seems probably that this muscle had at least one origin on the preacetabular ilium. It is equally parsimonious to reconstruct a double-headed muscle with a secondary crocodilianlike vertebral origin. However, the preacetabular process of extant crocodilians is smaller than that of all of the archosaurs examined for this study (Fig. 16), including other known obligate quadrupeds such as *Arizonasaurus* and aetosaurs (Fig. 16A,B). This raises the possibility that an iliac origin for M. puboischiofemoralis internus 2 is the plesiomorphic state for Archosauria and that the crocodilian vertebral origin is derived, resulting from the secondary loss of the elongated preacetabular ilium. This hypothesis warrants further investigation with the inclusion of more basal archosaurimorph taxa. The proposed preacetabular origin of this muscle in *Poposaurus* provides a scenario that would allow for a more parsimonious
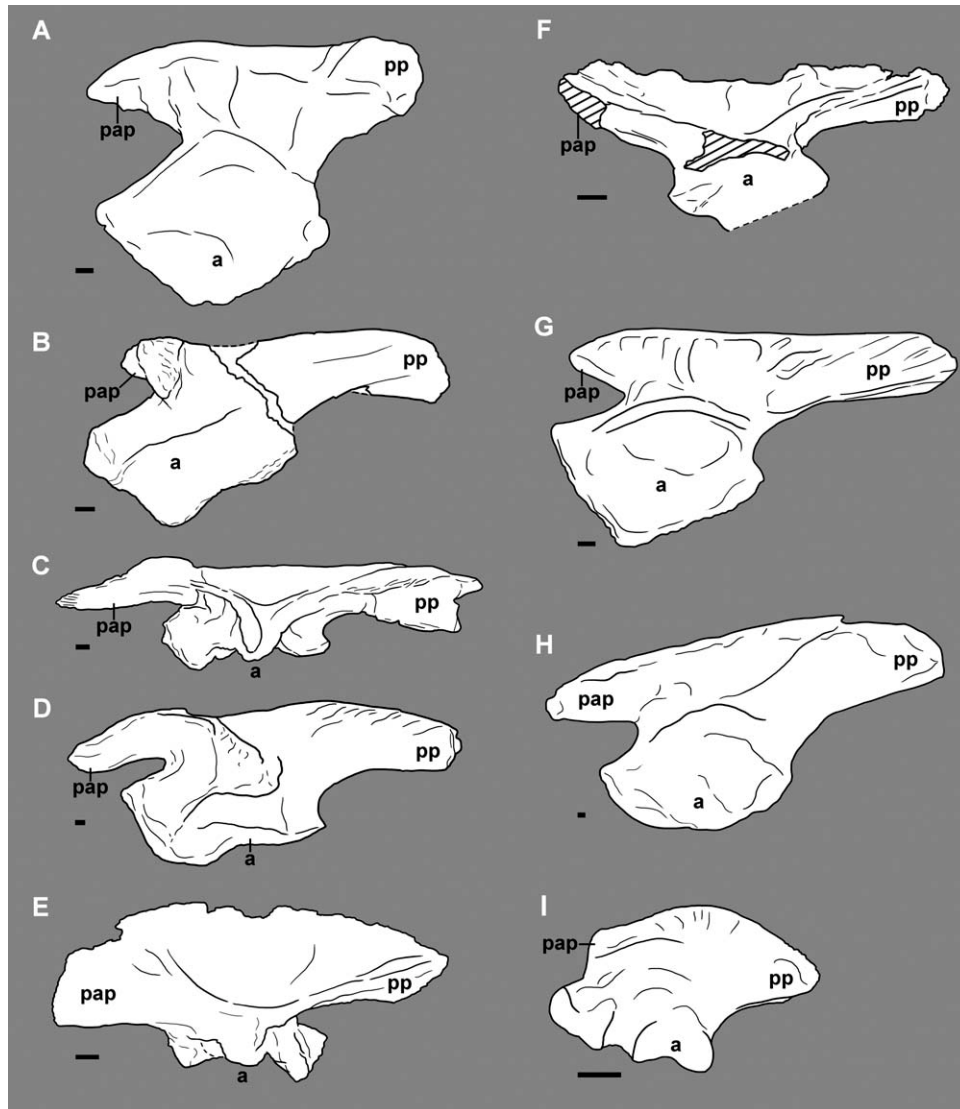
Fig. 16. Archosaurian ilia in lateral view. **A**: Left ilium of an aetosaur (UCMP 32422) redrawn from Nesbitt (2011); **B**: left ilium of *Arizonasaurus babbitti* (MSM 4590); **C**: left ilium of *P. gracilis* (YPM 57100); **D**: left ilium of *P. langstoni* (TMM 31025-12); **E**: left ilium of *S. inexpectus* (TTU-P 09003); **F**: partial distorted left ilium of *E. okeeffeae* (AMNH FR 30587); **G**: right ilium of *Bactrachotomus kuperferzellensis* redrawn (and flipped horizontally) from Gower and Schoch (2009); **H**: left ilium of *Dromicosuchus grallator* redrawn from Nesbitt (2010); and **I**: left ilium of *A. mississippiensis*. Scale bars = 1 cm. Abbreviations: a: acetabulum; pap: preacetabular process; and pp: postacetabular process.

evolutionary transition to the anatomical state found in both extant crocodilians and birds than the alternative hypothesis, a single vertebral origin, which was the ancestral morphotype proposed by Romer (1923b) for *Tyrannosaurus* (Fig. 13B). This hypothesis is also supported by musculotendinous reconstructions that have been generated for dinosaurian taxa as well. An iliac origin for M. puboischiofemoralis internus 2 is predicted for both *Tyrannosaurus* (Carrano and Hutchinson, 2002; Fig. 13A) and *Maiasaura* (Dilkes, 2000; Fig. 13C). Another significant morphological feature on the ilium of *Poposaurus* that had numerous effects on the myological reconstruction was the large,

laterally and ventrally projecting supraacetabular crest (Fig. 5A). All of the pelvic musculature that inserts onto the proximolateral femur was shifted distally because of the ventral projection of the supraacetabular crest (Figs.14A,C,D and 15A), and the difference in posture resulting from a ventrally articulating femoral head. This includes the insertions for M. puboischiofemoralis 1 and 2, M. iliofemoralis, M. ischiotrochantericus, and M. puboischiofemoralis 2, and 3.

The expanded distal ischium and ischial boot of *Poposaurus* are large relative to many other bipedal dinosaurs (Figs. 13 and 14A), and the corresponding attachment sites for the adducting
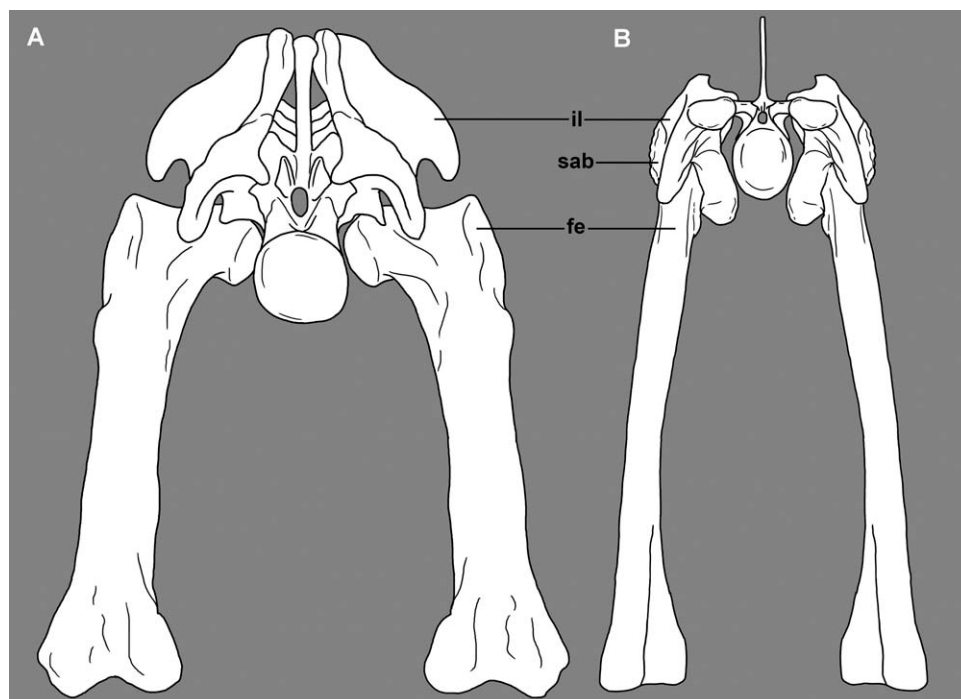
Fig. 17. Diagrammatic image demonstrating the differences between the "buttress erect" hip of a nonavian theropod dinosaur and the pillar erect hip of a poposauroid archosaur. The articulated sacrum, ilia, and femora in caudal view of **A**: *T. rex*, based on FMNH PR2081 (Brochu, 2003) and **B**: *P. gracilis*, based on YPM 57100. Images not to scale. il: ilium; sab: supraacetabular buttress; and fe: femur.

musculature were equally enlarged. The insertion sites for both M. adductor 1 and 2 occupied almost the entire distal half of the caudal aspect femoral shaft as evidenced by a distinct ridge (Figs. 7A–D, 14A, and 15A). The insertion sites on the caudal aspect of the femur were morphologically more similar to those observed in *Varanus* than any of the other extant taxa in that they ran along the length of the femur. It is possible that the adducting musculature for *Poposaurus* is different than that reconstructed for bipedal dinosaurs due to differences between the basal archosaurian and dinosaurian hip joints. One of the possible functional benefits of having enlarged adductors would be to reduce femoral torsion, although this hypothesis remains speculative and any direct biomechanical actions of the muscles have yet to be tested.

There are a few muscles that have been lost or reduced in the avian pes due to the fusion of the tarsometatarsus and various other modifications, and a lack of clear muscle scars in the pes of *Tyrannosaurus* preclude a Level II reconstruction of certain pedal musculature (Carrano and Hutchinson, 2002; Hutchinson et al., 2005). The more crocodilian morphology of the poposaur foot and osteological topography has allowed for a more detailed reconstruction of pedal myology with greater confidence (Figs. 11C,F, 14A–D, and 15A,B). The presence of muscle scars on the astragalus and phalanges indicate the presence of M.

extensor digitorum brevis (Figs. 9A–D,G,H, 11A–C, 14A–D, and 15A,B), a muscle lost in birds and with an indeterminate morphology in dinosaurs. The fifth metatarsal has been retained in *Poposaurus* and bears a distinct insertion scar for M. peroneus brevis on its caudolateral surface (Figs. 10E,F and 11D,E), suggesting a retention of the plesiomorphic insertion for this muscle as opposed to the more derived condition observed in dinosaurs and birds.

Pillar Erect Versus the Ornithodiran Hip Socket

Basal archosaurs evolved a parasagittally erect limb posture multiple times in both the pseudosuchian and ornithodiran lineages (Parrish, 1986, 1987; Benton and Clark, 1988; Sereno, 1991; Kubo and Benton, 2007). Ornithodiran archosaurs achieved this posture through a subvertical orientation of the acetabulum that articulates with an offset femoral head, termed "buttress-erect" (Fig. 17A). Basal archosaurs evolved a vertical ilium with a ventrally oriented acetabulum that articulated with a straight femur, termed "pillar-erect" (Fig. 17B; Bonaparte, 1984; Benton and Clark, 1988). Even without the laterally and ventrally projecting supraacetabular crest in *Poposaurus* this pelvic morphology forces all of the insertions of the pelvic musculature to shift distally on

the femoral shaft relative to dinosaurian archosaurs and even extant crocodilians. This type of pillar-erect hip morphology is not seen in any extant taxa and is not found in any taxa after the Late Triassic. The nature of this type of hip articulation limits femoral mobility in that if the femur is extended or flexed beyond a certain range it becomes dislocated from the acetabulum. Femoral abduction is also limited because of both the narrow width of the acetabulum and the presence of the supraacetabular crest laterally. It is unclear as to what effect this would have on locomotor capabilities, although on the basis of osteology alone, it is evident that the morphology of the acetabulum limited femoral range of motion. Distinct functional limits on ranges of motion could be determined using a digital model (e.g., Hutchinson et al., 2005; Sellers et al., 2009).

Functional and Evolutionary Implications

The ilium of *Poposaurus* is expanded both cranially and caudally relative to most other pseudosuchians (Fig. 16), increasing the surface area for the corresponding muscle attachments that flex the hip. This is also the case in other pseudosuchians that are hypothesized to have been obligate bipeds (e.g., *Effigia* and *Shuvosaurus*; Fig. 16D,E). This process is much shorter in quadrupedal taxa (e.g., the aetosaur; Fig. 16A), and almost absent in the alligator (Fig. 16H). The elongated preacetabular process provides for a larger attachment site for M. puboischiofemoralis internus 2 and M. iliotibialis 1 and 2; the postacetabular process for M. caudofemoralis brevis, M. iliotibialis 2 and 3, M. iliofibularis, and M. flexor tibialis externus (Figs. 5A,B, 14A–D, and 15A,B). These muscles would enable enhanced flexion and extension of both the hip socket and the knee. The enlargement and shifting of the origin for these muscles would also increase the moment arms for both hip and knee flexion and extension further enhancing bipedal locomotion in *Poposaurus*. This functional modification was also observed in *Tyrannosaurus* (Fig. 13B; Carrano and Hutchinson, 2002), and while analogous, is probably an anatomical adaptation associated with bipedalism in archosaurs.

The ankle morphology of crurotarsal archosaurs is significantly different than that of the ornithodiran lineage. Unlike ornithodirans, in which the ankle is a simple hingelike joint, crurotarsal archosaurs possess a rotary ankle joint with a calcaneum that has an enlarged and caudally projecting tuber (Fig. 9A–H; Sereno and Arcucci, 1990). In *Poposaurus* the calcaneal tuber is enlarged even relative to other basal archosaurs; whether or not this is due to the animals' obligate bipedal posture is unclear. The insertion tendons of M. gastrocnemius and M. flexor digitorum longus (Fig. 9A,B,E, and F) run through the groove in the caudal

aspect of the tuber, and M. peroneus longus inserts on the lateral aspect of the calcaneal tuber (Fig. 9A–H). The enlarged calcaneum shifts the muscle path of M. peroneus longus, M. flexor digitorum longus and M. gastrocnemius further from the ankle joint relative to forms with a smaller calcaneum, suggesting a relatively greater moment arm for all three muscles. The effects that this would have on the pedal mechanics and gait are unclear and deserve further study.

Integration of the Pelvic Musculoskeletal System into Lung Ventilation

Because of the presence of pelvic aspiration in both extant crocodilians and birds, albeit morphologically and functionally very different, Carrier and Farmer (2000a,b) have proposed a novel respiratory mechanism for basal archosaurs that involved aspects of the pelvic musculoskeletal system. The proposed mechanism, "cuirassal breathing," functions via an ischiotruncus muscle which, originating from the distal ischium, would run cranially and ventrally under the pubis to insert on the gastralia, with the pubis serving to orient and direct the muscular force of the ischiotruncus (Carrier and Farmer 2000a; Claessens, 2004). In association with M. rectus abdominus, M. ischiotruncus would actively function as a gastralial/abdominal aspiration pump (Claessens, 2004). Although the abdominal musculature is not reconstructed here, the expanded pubic boot and ischial boot in *Poposaurus* show rugosities along the ventral margin of the pubic boot indicating soft-tissue attachments that are not associated with any of the locomotor musculature of the hindlimb. The presence of gastralia in *Poposaurus*, as well as an elongated pubis, a well developed pubic boot, and a slightly expanded ischial boot (Fig. 6C,D), both with indications of soft-tissue attachments along their ventral surfaces, lend support to the hypothesis of a "cuirassal basket" breathing mechanism in basal archosaurs, or the gastralial aspiration pump proposed by Claessens (2004). This skeletal morphology is present in other bipedal basal archosaurs, and is convergent with theropod dinosaurs (Walker, 1964; Chatterjee, 1985; Nesbitt and Norell, 2006) suggesting at least, similarities in soft-tissue biology possibly resulting from the evolution of an obligate bipedal posture.

CONCLUSIONS

This is the first phylogenetically based reconstruction of the pelvic and hindlimb musculature of an extinct nondinosaurian archosaur. The results of this study demonstrate that *Poposaurus* had an overall appendicular myological arrangement similar to that of bipedal theropod dinosaurs. These similarities were due to both homology and

homoplasy. Differences between *Poposaurus* and dinosaurs in pelvic and pedal osteology, in association with its closer relationship to extant crocodilians than birds, resulted in a few myological differences in the data set, including evidence for the presence of a few muscles not previously reconstructed in dinosaurs. The results of this study do not contradict the "cuirassal basket" respiratory hypothesis as a respiratory mechanism for basal archosaurs as proposed by Carrier and Farmer (2000a,b) or gastralial aspiration pump (Claessens, 2004); however, these hypotheses warrant further investigation with respect to the functional morphology and biomechanics of pelvic and abdominal musculature in basal archosaurs. Finally, this data set can be used for future studies on the biomechanics of posture and gait in bipedal archosaurs, and when combined with similar studies on the anatomy of other taxa, to clarify the evolutionary history of bipedalism in crocodile-line archosaurs.

ACKNOWLEDGMENTS

LITERATURE CITED

Baumel JJ, Witmer LM. 1993. Osteologia. In: Baumel JJ, editor. Handbook of Avian Anatomy: Nomina Anatomica Avium, Second Edition. pp 45–132.
Benoit M, Yarborough-Fitzgerald V. 2004. Decay conditions of an Upper Triassic poposaur: Evidence from calcium carbonate nodules. J Vertebr Paleontol 24:38A.
Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, editor. The Phylogeny and Classification of the Tetrapods, Vol. 1. Oxford: Clarendon Press. pp 295–338.
Bonaparte JF. 1984. Locomotion in rauisuchid thecodonts. J Vertebr Paleontol 3:210–218.
Brinkman D. 1980. The hind limb step cycle of *Caiman sclerops* and the mechanics of crocodile tarsus and metatarsus. Can J Zool 58:2187–2200.
Brochu CA. 2003. Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution Computed Tomographic analysis of the skull. Soc Vertebr Paleontol Mem 7:1–138.
Bryant HN, Russell AP. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philos T Roy Soc B 337:405–18.
Bryant HN, Seymour KL. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. J Morphol 206:109–117.
Byerly TC. 1925. The myology of *Sphenodon punctatum*. Univ Iowa Stud Nat Hist 11:3–54.
Carrano MT, Hutchinson JR. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). J Morphol 253:207–228.
Carrier DR, Farmer CG. 2000a. The integration of ventilation and locomotion in archosaurs. Am Zool 40:87–100.
Carrier DR, Farmer CG. 2000b. The evolution of pelvic aspiration in archosaurs. Paleobiology 26:271–293.
Charig AJ. 1972. The evolution of the archosaur pelvis and hind-limb: An explanation in functional terms. In: Joysey KA, Kemp TS, editors. Studies in Vertebrate Evolution: Essays Presented to Dr. FR Parrington, FRS. Edinburgh: Oliver & Boyd. pp 121–155.
Chatterjee S. 1985. *Postosuchus*, a new thecodontians reptile from the Triassic of Texas and the origin of tyrannosaurs. Philos T Roy Soc B 309:395–460.
Chiasson RB. 1962. Laboratory anatomy of the alligator. Dubuque: WMC Brown. 61 pp.
Claessens LPAM. 2004. Dinosaur gastralia: Origin, morphology, and function. J Vertebr Paleontol 24:89–106.
Clark JM, Xu X, Forster CA, Wang Y. 2004. A middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. Nature 430:1021–1024.
Cong L, Hou L-H, Wu XC. 1998. The gross anatomy of *Alligator sinensis*. Fauvel [in Chinese with English summary]. Beijing: CIP, China; ISBN7-03-005979-4.
Curtis N, Jones MEH, Evans SE, O'Higgins P, Fagan MJ. 2009. Visualising muscle anatomy using three-dimensional computer models—An example using the head and neck muscles of *Sphenodon*. Palaeontol Electron 12.3(7T):1–18.
Dilkes DW. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Trans R Soc Edinb Earth Sci 90:87–125.
Dollo L. 1888. Sur la signification du "trochanter pendant" des dinosauriens. Bull Sci France Belgique 19:215–224.
Fechner R. 2009. Morphofunctional evolution of the pelvic girdle and hindlimb of Dinosauromorpha on the lineage to Sauropoda. PhD Dissertation. München: Ludwigs Maximilians Universität. 211 pp.
Galton PM. 1969. The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). Postilla 131:1–64.
Gangl D, Weissengruber GE, Egerbacher M, Forstenpointner G. 2004. Anatomical description of the muscles of the pelvic limb in the ostrich (*Struthio camelus*). Anat Hist Embryol 33:100–114.
Gatesy SM. 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. J Zool 224:577–588.
Gauthier J. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The Origin of Birds and the Evolution of Flight. San Francisco: Memoirs of the California Academy of Sciences 8. pp 1–47.
Gauthier JA, Nesbitt SJ, Schachner ER, Bever GS, Joyce WG. 2011. The bipedal stem crocodilian *Poposaurus gracilis*: Inferring function in fossils and innovation in archosaur locomotion. Bull Peabody Mus Nat Hist 52:107–126.
George JC, Berger AJ. 1966. Avian Myology. New York: Academic Press. 500 pp.
Gower DJ, Nesbitt SJ. 2006. The braincase of *Arizonasaurus babbitti*—Further evidence for the non-monophyly of 'rauisuchian' archosaurs. J Vertebr Paleontol 26:79–87.

Gower DJ, Schoch RR. 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vertebr Paleontol 29:103–122.

Gregory WK, Camp CL. 1918. Studies in comparative myology and osteology. No. III. Bull Am Mus Nat Hist 38:447–563.

Haines RW, Mohuiddin A. 1968. Metaplastic bone. J Anat 103:527–538.

Hall BK. 2005. Bones and Cartilage: Developmental and Evolutionary Skeletal Biology. London: Academic Press. 792 pp.

Herrel A, Vanhodydonck B, Porck J, Irschick DJ. 2008. Anatomical basis of differences in locomotor behavior in *Anolis* lizards: A comparison between two ecomorphs. Bull Mus Comp Zool 159:213–238.

Hudson GE, Lanzillotti PJ. 1955. Gross anatomy of the wing muscles in the family Corvidae. Am Midl Nat 53:1–44.a

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

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

Hutchinson JR. 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. Comp Biochem Phys A 133:1051–1086.

Hutchinson JR. 2006. Evolution of locomotion in archosaurs. Comptes Rendus Palé vol 5:519–530.

Hutchinson JR, Allen V. 2008. The evolutionary continuum of limb function from early theropods to birds. Naturwissenschaften 96:423–448.

Hutchinson JR, Miller C, Fritsch G, Hildebrandt T. 2008. The anatomical foundation for multidisciplinary studies of animal limb function: examples from dinosaur and elephant limb imaging studies. In: Endo H, Frey R, editors. Anatomical Imaging: Towards New Morphology. Tokyo: Springer-Verlag. pp 23–38.

Hutchinson JR, Gatesy SM. 2000. Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology 26:734–751.

Hutchinson JR, Anderson FC, Blemker SS, Delp SL. 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: Implications for stance, gait, and speed. Paleobiology 31:676–701.

Jasinoski SC, Russell AP, Currie PJ. 2006. An integrative phylogenetic and extrapolatory approach to the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. Zool J Linn Soc 146:301–344.

Johnson RB. 1998. The bearable lightness of being: bones, muscles, and spaceflight. Anat Rec (New Anat) 253:24–27.

Joyce W, Gauthier J. 2006. A nearly complete skeleton of *Poposaurus gracilis* from the Late Triassic of Utah. J Vertebr Paleontol 26:83A.

Kubo T, Benton MJ. 2007. Evolution of hindlimb posture in archosaurs: Limb stresses in extinct vertebrates. Palaeontology 50:1519–1529.

McGowan C. 1979. Hindlimb musculature of the brown kiwi, *Apteryx australis mantelli*. J Morphol 160:33–73.

McGowan C. 1982. The wing musculature of the brown kiwi, *Apteryx australis mantelli*, and its bearing on ratite affinities. J Zool Lond 197:173–219.

Nesbitt SJ. 2007. The anatomy of *Effigia okeeffeae* (Archosauria: Suchia), theropod-like convergence, and the distribution of related taxa. Bull Am Mus Nat Hist 302:1–84.

Nesbitt SJ. 2011. The early evolution of archosaurs: Relationships and the origin of major clades. Bull Am Mus Nat Hist 352:1–292.

Nesbitt SJ, Norell MA. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimd dinosaurs (Theropoda). Proc R Soc B 273:1045–1048.

Norman DB. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). Bull Inst R Sci Nat Belgique 56:281–372.

Otero A, Vizcaíno SF. 2008. Hindlimb musculature and function of *Neuquensaurus australis* (Sauropoda: Titanosauria). Ameghiniana 45:333–348.

Padian K, Li C, Pchelnikova J. 2009. The trackmaker of *Apatopus* (Late Triassic, North America): Implications for the evolution of archosaur stance and gait. Palaeontology 53:175–189.

Parrish JM. 1986. Locomotor adaptations in the hindlimb and pelvis of the thecodontia. Hunteria 1:1–36.

Parrish JM. 1987. The origin of crocodilian locomotion. Paleobiology 13:396–414.

Patterson C. 1982. Morphological characters and homology. In: Joysey KA, Friday AE, editors. Problems of Phylogenetic Reconstruction. New York: Academic Press. pp 21–74.

Reese AM. 1915. The Alligator and Its Allies. New York: The Knickerbocker Press (GP Putnam's Sons) of New York.

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

Romer AS. 1923a. Crocodilian pelvic muscles and their avian and reptilian homologues. Bull Am Mus Nat Hist 48:533–552.

Romer AS. 1923b. The pelvic musculature of saurischian dinosaurs. Bull Am Mus Nat Hist 48:605–617.

Romer AS. 1927. The pelvic musculature of ornithischian dinosaurs. Acta Zool Stockh 8:225–275.

Romer AS. 1944. The development of tetrapod limb musculature of Lacerta. J Morphol 71:251–298.

Romer AS. 1956. Osteology of the Reptiles. Chicago: University of Chicago Press.

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

Russell AP. 1993. The aponeurosis of the lacertilian ankle. J Morphol 218:65–84.

Schachner ER, Dodson P. 2009. Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (Archosauria: Suchia). J Vertebr Paleontol 29:177A.

Sellers WI, Manning PL, Lyson T, Stevens K, Margetts L. 2009. Virtual palaeontology: Gait reconstruction of extinct vertebrates using high performance computing. Palaeontol Electron 12.3 (13A):1–26.

Sereno PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Soc Vertebr Paleontol Mem 2:1–53.

Sereno PC, Arcucci AB. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. N Jb Geol Paläont Abh 180:21–52.

Snyder RC. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. Am J Anat 95:1–45.

Vanden Berge JC, Zweers GA. 1993. Myologia. In: Baumel JJ, editor. Handbook of Avian Anatomy: Nomina Anatomica Avian. Cambridge: Publications of the Nuttall Ornithological Club 23. pp 189–247.

Verstappen M, Aerts P, De Vree F. 1998. Functional morphology of the hindlimb musculature of the black-billed magpie, *Pica pica* (Aves, Corvidae). Zoomorphology 118:207–223.

Walker AD. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Phil T R Soc Lond B 248:53–134.

Walker AD. 1977. Evolution of the pelvis in birds and dinosaurs. In: Andrews SM, Miles RS, Walker AD, editors. Problems in Vertebrate Evolution. Linnean Society Symposium Series 4. London, UK: Academic Press. pp 319–358.

Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ, editor. Functional Morphology in Vertebrate Paleontology. Cambridge, UK: Cambridge University Press. pp 19–33.