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Hip joint articular soft tissue of basal Dinosauromorpha: evolutionary and biomechanical implications for Saurischia

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ABSTRACT

Dinosauromorphs evolved a wide diversity of femoral and pelvic morphologies, suggesting highly divergent articular soft tissue anatomies among major clades. However, poor preservation of joint soft tissues in fossil taxa has thus far hampered functional inferences. We reconstruct the soft tissue anatomy of basal dinosauromorph hip joints using osteological correlates derived from extant sauropsids and infer trends in femoral and acetabular character transitions leading to theropods and sauropodomorphs. Femora and pelves of 107 dinosauromorphs and outgroup taxa were digitized using 3D imaging techniques. Key transitions were estimated using maximum likelihood ancestral state reconstruction. We found that the hip joints of extinct dinosauromorphs possess soft tissue morphologies beyond the spectrum of variation exhibited by extant archosaurs. Early evolution of the Dinosauriformes hip joint is characterized by the retention of a prominent femoral hyaline cartilage cone in post-neonatal individuals, but the cartilage cone is independently reduced within the theropod and sauropodomorph lineages. The femur of Dinosauriformes possessed a fibrocartilage sleeve on the femoral metaphysis, which surrounded a hyaline cartilage core. The acetabulum of basal Dinosauriformes possesses distinct labrum and antitrochanter structures on the supraacetabulum. Sauropodomorphs evolved thick hyaline cartilage on the femoral head for maintaining hip congruence, whereas theropods relied on acetabular soft tissues such as ligaments and articular pads. In particular, the rostrolaterally ossified hip capsule of basal theropods permitted mostly parasagittal femoral movements. These data indicate that the dinosauromorph hip joint underwent mosaic evolution within the saurischian stem-lineage, and that sauropodomorphs and sauropods underwent both convergence and divergence in articular soft tissues, reflective of transitions in body size, locomotor posture, and joint loading.

INTRODUCTION

The evolution of Dinosauromorpha is characterized by a suite of anatomical features in the appendicular limbs, culminating in the drastically divergent locomotor behaviors of birds, sauropods, and multiple clades of ornithischians (Allen et al., 2009; Hutchinson and Allen, 2009; Sander et al., 2011; Maidment and Barrett, 2012). Numerous musculoskeletal transitions in the hind limbs of extinct dinosauromorphs distinguish their morphologies from those of crocodylians, the only extant clade of archosaurs aside from birds (Huxley, 1870; Romer, 1923; Galton, 1969; Parrish, 1986, 1987; Gatesy and Middleton, 1997; Wilson and Carrano, 1999; Hutchinson, 2001a, b; Benson and Choiniere, 2013; Maidment and Barrett, 2014). Numerous studies explored the functional significance of musculoskeletal hind limb characters during the evolution of dinosauromorph locomotion, including cursorial bipedality (non-dinosaurian dinosauromorphs, Nesbitt et al., 2009; herrerasaurids, Grillo and Azevedo, 2011; basal ornithischian, Bates et al., 2012a), cursorial quadrupedality (silesaurids, Nesbitt et al., 2010; Maidment and Barrett, 2012), graviportal bipedality (large theropods, Hutchinson et al., 2005; Bates et al., 2012b; basal sauropodomorphs, Mallison, 2010b, c), graviportal quadrupedality (sauropods, Wilson and Carrano, 1999; Yates and Kitching, 2003; Carrano, 2005; ornithischians, Mallison 2010a), knee-driven bipedality (avialans, Gatesy and Middleton, 1997; Carrano, 1998), and flight (theropods, Gatesy and Dial, 1996; Clarke et al., 2006; Heers and Dial, 2015; Chatterjee and Templin, 2007). Moreover, the rich evolutionary history of dinosaurs features multiple, independent transitions in body size, including gigantism (Dinosauria, Benson et al., 2014; sauropods, Sander et al., 2011; theropods, Christiansen and Fariña, 2004; Lee et al., 2014a) and miniaturization (ornithischians, Butler et al., 2010; sauropods, Stein et al., 2010; non-avian theropods, Turner et al., 2007; avialans, Hainsworth and Wolf, 1972). Throughout these

transitions, the hip joint served as an important load-bearing articulation in bipeds and quadrupeds of all body sizes. Therefore, new anatomical data on hip joint soft tissues should elucidate patterns in hind limb functional morphology and evolution of the dinosaurian lineage.

However, our understanding of archosaurian, and for that matter, most reptile hip joint anatomy remains hindered by the lack of articular soft tissues in the fossil record (Holliday et al., 2010; Bonnan et al, 2010, 2013; Tsai and Holliday, 2015). Joint soft tissues such as epiphyseal cartilages, fibrocartilaginous pads, and joint ligaments provide constraints to the mobility (Carter and Wong, 2003; Hall, 2005), load-bearing ability (Carter et al, 1998; Carter and Beaupre, 2007) and growth (Haines, 1942) of limb elements. Archosaurs retain the basal tetrapod joint morphology, wherein a single layer of epiphyseal cartilage maintains joint articulation at its superficial surface and facilitates longitudinal bone growth at its metaphyseal growth plate surface (Haines 1938, 1941). With the exception of Neoaves, extant archosaurs retain thick layers of articular soft tissues in the hip, even at skeletal maturity (Cracraft, 1971; Firbas and Zweymüller, 1971; Fujiwara et al., 2010; Tsai and Holliday, 2015). Thick layers of epiphyseal cartilage have also been inferred for extinct dinosaurs, in particular saurischians (sauropods, Cope, 1878; Marsh, 1896; Hay, 1908; theropods, Hutchinson et al., 2005; Gatesy et al., 2009; Holliday et al., 2010). These observations suggest that articular soft tissues played crucial mechanical and physiological roles in the evolution of dinosaurian hind limbs and likely influenced the bony morphologies seen in clades as morphologically disparate as sauropods and birds.

Thus far, there has been little concerted effort to investigate the evolution of archosaur hip joints (but see Kuznetsov and Sennikov, 2000; Tsai and Holliday, 2015). Among hip joint soft tissues, joint ligaments and articular pads have never been reported in fossil archosaurs,

whereas calcified cartilage (Norman, 1980; Nicholls and Russell, 1985; Wilson and Sereno, 1998; Mallison, 2010b) and desiccated epiphyseal cartilage (Schwarz et al., 2007) are occasionally found on the ends of fossil long bones. However, when preserved in fossils the cartilage conforms to the shape of the subchondral bone and thus offers little information on articular surface morphology in-vivo. Moreover, although the anatomy of extant archosaur hip joints have received some attention in the comparative literature (Stolpe, 1932; Haines, 1938; 1942; Kuznetsov and Sennikov, 2000), homologies of hip joint soft tissues, as well as the anatomical relationship of soft tissues and their osteological correlates, remain unresolved. These uncertainties have led to substantial disagreements in osteological character description and soft tissue reconstructions of fossil saurischian hip joints (Kurzanov, 1981; Osmólska, 1972; Rowe, 1989; Brochu, 2003; Butler et al., 2011).

Here, we investigate the sequence of evolutionary transitions in the hip joint from basal dinosauromorphs along the sauropod and theropod lineages. We infer the presence and topology of joint soft tissues using phylogenetically informed osteological correlates (Tsai and Holliday, 2015), identify the polarity and sequence of discrete character transitions using maximum likelihood ancestral state reconstruction (Schluter et al., 1997; Pagel, 1999), and test the homology of osteological characters based on reconstructed soft tissues. This study establishes the basic comparative framework of hip joint anatomical structures, such as cartilage caps, ligaments, and articular pads, within the dinosaurian lineage, and forms the basis for subsequent work on archosaur locomotor mechanics and joint biology.

MATERIALS AND METHODS

Osteological correlates and anatomical reference axes

Anatomical abbreviations used in this study are summarized in Table 1 and illustrated in Fig. 1. In order to characterize the shift of cartilaginous and ligamentous attachments within the dinosauromorph lineage, nomenclature for osteological correlates follows the prescribed homology in Tsai and Holliday (2015). We used cartilage correction factors (CCFs) described by Holliday et al. (2010) for *Alligator*, juvenile *Struthio*, and adult *Struthio* to scale the thickness of dinosauromorph femoral epiphyseal cartilage, and based the inference on similarity in growth plate morphology. Additionally, although crocodylians and birds form the Extant Phylogenetic Bracket (EPB; Witmer, 1995) for Dinosauromorpha, the inclusion of non-archosaurian archosauromorphs in this analysis requires a broader range of phylogenetic comparison beyond extant archosaurs. The identification of topologically and histologically similar tissues in outgroup diapsids, such as lepidosaurs, further supports the inference of tissue homology within Archosauromorpha (Tsai and Holliday, 2015).

We used reference axes (Fig. 1c; modified from Tsai and Holliday, 2015) to account for evolutionary shifts in femoral condylar orientation among dinosauromorphs, theropods (Hutchinson, 2001b), and sauropodomorphs (Martínez and Alcober, 2009; Yates et al., 2010). The mediolateral plane (red) passes through the distal condyles and intersects the femoral long axis. The craniocaudal plane (blue) is perpendicular to the mediolateral plane and intersects the latter at the femoral long axis. The anatomical capital-trochanteric plane (green) passes through the femoral head and the greater trochanter. In all archosauromorphs examined in this study, the acetabulum faces laterally. Therefore, the craniocaudal and dorsoventral axes of the whole animal, as well as the mediolateral axis through both acetabulae, describe the orientation of acetabular soft tissue structures.Throughout this study the proximal attachments of ligaments are denoted as the origins, whereas the distal attachments are denoted as the insertions.

Data collection

We studied a broad phylogenetic range of archosauromorph taxa (N = 107 taxa; Table 1S), including 101 dinosauromorphs, and scored discrete osteological characters on the proximal femur and acetabulum. Outgroup archosauromorph comparisons potentially allow robust inferences of soft tissue transitions leading to each terminal taxon in Dinosauromorpha. Fossil specimens were studied by observation and digital photography (Sony DSC-F828). Many specimens (N = 83 taxa) were reconstructed as surface models using 3D imaging techniques including photogrammetry, computed tomography (CT), and laser scans. Photogrammetric models were generated using the freely available, open source package Bundler (http://www.cs.cornell.edu/~snavely/bundler/) and PMVS (Patch-based Multi-view Stereo Software, http://www.di.ens.fr/pmvs/) using techniques modified from Falkingham (2012) and Mallison and Wings (2014). Taxa included in the character analysis were selected based on quality of preservation and completeness of hip joint elements in the referred individuals. In order to maintain the broad phylogenetic scope of the current study, we sampled only taxa represented by adult or large subadult individuals and excluded young juvenile and neonates from the comparative analysis. The inclusion of subadults in this analysis is merited because many archosaurs, including most nonavian dinosaurs, attain reproductive maturity well ahead of skeletal maturity defined as effective cessation of somatic growth (Erickson, 2005; Erickson et al., 2007; Lee and Werning, 2008). Because terminal skeletal maturity is seldom preserved in the archosaurian fossil record, many extinct archosaur taxa were defined based on character states exhibited by locomotor competent and reproductively mature individuals that were nevertheless undergoing active bone growth prior to death (Hone et al., 2016). For taxa represented by multiple individuals (e.g., *Coelophysis*), we scored only consistent osteological character states

on individuals inferred as adults or subadults. For taxa represented only by a single holotype individual (e.g., *Carnotaurus*) the individual is assumed to be an adult or subadult, unless it was a young juvenile or neonate individual in its description. Nevertheless, young juvenile and neonate individuals were scored to assess ontogenetic transitions in hip joint character states. Institutional abbreviations are summarized in Table 2S.

Ancestral state reconstruction of hip joint soft tissues

We identified 14 characters based on osteological correlates of putatively homologous hip joint cartilages, ligaments, and articular pads in extant diapsids (Table 2; Tsai and Holliday, 2015). These osteological characters serve as proxies for the presence, orientation, thickness, and shapes of articular soft tissues.

We used maximum likelihood ancestral state reconstruction to optimize the polarity of character state transitions in the osteological correlates (Schluter et al., 1997; Pagel, 1999). Composite phylogenetic trees were constructed using Mesquite (V2.73; Maddison and Maddison, 2015) based on published studies, with branch lengths based on estimated divergence date between sister clades and sister taxa (See Fig. 1S for references). We constructed a consensus phylogenetic tree (Fig. 2a), in which Silesauridae is considered as a non-dinosaurian Dinosauriformes (Brusatte et al., 2010b; Nesbitt, 2011), Herrerasauridae as a basal theropod (Sues et al., 2011), *Eoraptor* as the basal-most sauropodomorph (Martínez and Alcober, 2009), and *Archaeopteryx* as the basal-most avialan (Turner et al., 2012). Additionally, we analyzed four additional tree topologies based on modifications of the consensus tree to account for contentious phylogenetic placement of Silesauridae as stem-ornithischians (Fig. 2b; Langer and Ferigolo, 2013), Herrerasauridae as the basal-most saurischian lineage (Fig. 2c; Novas et al.,

2010), *Eoraptor* as a basal theropod (Fig. 2d; Sues et al., 2011) and *Archaeopteryx* as a stem-deinonychosaur (Fig. 2e; Xu et al., 2011; Godefroit et al., 2013).

Discrete characters were analyzed using the Trace Character History function of Mesquite using the maximum likelihood reconstruction method (Schluter et al., 1997; Pagel, 1999). Relative likelihood of character states at each node was estimated on the composite phylogeny of Saurischia using a marginal probability reconstruction of Markov k-state 1 parameter model (Mk1; Lewis, 2001). This method prescribes equal likelihood for the directions of character state transition (i.e., a character gain from 0 to 1 is as likely as a reversal from 1 to 0). Because hip joint osteological characters of basal archosaurs are highly variable (Nesbitt, 2011), character gains and losses in basal Dinosauria is assumed to occur with little directional bias.

The ancestral state at each given node is estimated using the likelihood decision threshold (T), set to 2.0 by default in Mesquite. For each node, a particular character state was considered significant and preferred over the other character state if its likelihood value is higher by at least two log units than that of the other character state (following Maddison and Maddison, 2015). If the relative likelihoods of character states do not differ significantly at a particular node, the ancestral state at that node was inferred to be equivocal. Relative likelihood values for the derived state of each character were noted as RL in the text, with statistical significance indicated by an asterisk (*). We focused on the results from the consensus phylogenetic tree (Fig. 2a), and report results from the four alternative trees only if they returned significantly different character state estimations from the consensus tree. We then reconstructed hip joint articular soft tissues based on the sequence of transitions in osteological correlates for focal taxa along the sauropod and theropod lineages.

Overview of hip joint osteological correlates

Extinct archosaurs exhibit a wide range of osteological characters in the hip joint, many of which are not present in extant birds and crocodylians. In a generalized dinosaurian hip joint, the inner acetabular wall is unossified, resulting in a ring-shaped bony acetabulum (Fig. 3c-i). This "perforated acetabular" (Kuznetsov and Sennikov, 2000; Nesbitt, 2011) morphology is the osteological correlate for the acetabular membrane. The dorsal portion of the bony acetabulum (the supraacetabulum) possesses craniocaudally distinct soft tissue attachments (Fig. 4). The acetabular labrum, a fibrous articular pad, occupies the cranial supraacetabulum. The antitrochanter cartilage, which consists of a fibrocartilaginous articular surface and a hyaline cartilage core, occupies the caudal acetabulum. The labrum's attachment can be distinguished from the antitrochanter by its striated surface texture, as well as a distinctive ridge separating the two surfaces in well preserved specimens. The antitrochanter's fibrocartilage surface peripherally attaches to the cortical bone surface on the ischial peduncle of the ilium and the ilial peduncle of the ischium and envelops the hyaline cartilage core at its center (Fig. 5). The antitrochanter's hyaline cartilage core is an extension of the ilial-ischial synchondrosis and attaches to the calcified cartilage-covered growth plates on the two peduncles. In most Mesozoic fossils examined, the thin layer of calcified cartilage is weathered away. Nevertheless, the growth plate surface can be identified by the exposed trabecular bone immediately deep to the calcified cartilage layer. The combined osteological correlate for both antitrochanter fibro- and hyaline cartilage is here termed the bony antitrochanter. The antitrochanter of saurischian-line archosaurs is reconstructed as a simple articular pad as in extant birds and lepidosaurs, rather than the complex meniscus structure in crocodylians (Tsai and Holliday, 2015), due to the early

phylogenetic split between ornithodirans and pseudosuchians (Nesbitt, 2011), and because the crocodylian meniscus has few unambiguous osteological correlates.

The hip joint of fossil archosauromorphs possesses three distinct joint capsular ligaments. The iliofemoral ligament is homologous with the avian "pubofemoral" ligament (*sensu* Baumel and Raikow, 1993). The iliofemoral ligament originates on the supraacetabular rim (supraacetabular crest *sensu* Nesbitt, 2011) and inserts on the craniolateral metaphyseal surface of the femur, lateral to the extent of the fibrocartilage sleeve of the femoral head (Fig. 6). The femoral attachment of the iliofemoral ligament presents as a shallow depression in silesaurids (Fig. 6b, i) but is less distinct in dinosaurs. The two ventral joint ligaments are homologous with the ligamentum capitis femoris in birds (Cracraft, 1971; Tsai and Holliday, 2015). Specifically, the pubofemoral ligament originates on the pubic acetabular rim and is homologous with the avian ligamentum teres. The ischiofemoral ligament is homologous with the avian posterior acetabular ligament and originates on the ischial acetabular rim. Because an unossified inner acetabular wall is thought to be associated with the internal shift of the pubofemoral and ischiofemoral ligaments, the origins of these two ligaments is here inferred to be located on the inner pubic and ischial acetabular rims in dinosauromorphs with a perforated acetabulum. In contrast, dinosauromorphs that retain an ossified inner acetabular wall possess pubofemoral and ischiofemoral ligaments that originate on the outer pubic and ischial acetabular rim. The pubofemoral and ischiofemoral ligaments unite distally to form the ligamentum captis femoris and insert onto fovea capitis on the proximal femur.

The epiphyseal cartilage on the saurischian proximal femur consists of a hyaline cartilage core and a peripheral fibrocartilage sleeve. The hyaline core attaches to the entire proximal growth plate surface (*facies articularis antitrochanterica*, *sensu* Hutchinson, 2001a), which

includes both the femoral head (capital) and trochanteric regions (Fig. 7). The fibrocartilage sleeve attaches to a collar of metaphyseal cortical bone surrounding the growth plate and proximally overlap the capital extent of the femoral head and part of the femoral neck (trochanteric region), forming a layered fibro-hyaline cartilage structure in these regions (Fig. 6a-h, 7b-f). A prominent metaphyseal line distinguishes the metaphyseal collar from the growth plate proximally, whereas a prominent ridge distinguishes the metaphyseal collar from the bony diaphysis distally (Fig. 6b-g, i-n). A patch of exposed trabecular bone distal to the metaphyseal-diaphyseal junction is the osteological correlate for an articular bursa ventral to the hip joint capsule.

Discrete character evolution

1. Pelvis, acetabular perforation: (0) unperforated or incompletely perforated, (1) fully perforated.

Basal dinosauromorphs retained unperforated acetabula, in which the bony inner acetabular wall is lined by hyaline cartilage. Multiple lineages of dinosaurs convergently evolved perforated acetabula, a condition characterized by an unossified and ligamentous inner acetabular wall. Up to three independent acquisitions of perforated acetabula occurred within ornithischians, theropods, and sauropodomorphs. Because the perforated acetabulum is the osteological correlate for internalized pubofemoral and ischiofemoral ligaments (Tsai and Holliday, 2015), these results suggest multiple convergent evolutions of the ligamentum captis femoris within Dinosauria.

Among extant sauropsids, presence of the acetabular membrane is associated with an intracapsular origin of the pubofemoral and ischiofemoral ligaments. Tsai and Holliday (2015) further suggested that the acetabular membrane prevents compression of these two ventral joint

ligaments between the femoral and acetabular articular surfaces, therefore serving a function analogous to the mammalian acetabular notch. Here we infer that the amount of acetabular perforation is associated with the extent of internal shift in the pubofemoral and ischiofemoral ligaments. An unperforated or incompletely perforated acetabulum indicates that the two ventral ligaments are largely capsular in origin, whereas a fully perforated acetabulum indicates that the two ventral ligaments form the intracapsular dual origins of the ligamentum capitis femoris. Acetabular perforation is difficult to assess in specimens missing pubes and ischia. Therefore, the acetabulum is scored as "fully perforated" only if the ilial portion of the inner acetabular wall is emarginated (ilium: ventral acetabular flange absent, *sensu* Martínez et al., 2011).

Dinosauromorphs ancestrally possess an incompletely perforated acetabulum (RL~0.01*), indicating that the ventral joint ligaments function largely as external capsular ligaments, as in lepidosaurs (Tsai and Holliday, 2015). Although Sereno and Arcucci (1994) reconstructed the acetabulum of *Marasuchus* as possessing a small perforation at the puboischial junction, both of the ventral elements were described by Bonaparte (1975) as damaged. Therefore, *Marasuchus* is inferred here as possessing an unperforated acetabulum as in *Lagerpeton*. Silesaurids have been described by Dzik (2003) and Nesbitt et al. (2010) as possessing an unperforated acetabulum, and the "perforated" morphology on the puboischial margin of *Asilisaurus* (Fig. 3a) was due to breakage (Nesbitt, personal communication). It is unclear if a fully perforated acetabulum is the basal condition for dinosaurs (RL~0.18) or saurischians (RL~0.21), because the ancestral state for these nodes are ambiguous. Basal theropods possess a fully perforated acetabulum (RL~0.99*), as does the basal ornithischian *Lesothosaurus*. In contrast, basal sauropodomorphs retained an incompletely perforated acetabulum (RL~0.03*), with a single transition to a fully perforated condition in the common

ancestor of *Efraasia* and more derived sauropodomorphs (RL~0.99*). Basal sauropodomorphs such as *Panphagia* possess incompletely perforated inner acetabular walls, in which the ventral rim of the ilium forms a distinct indentation (Fig. 3b). This indentation receives the ventral acetabular ligaments during femoral adduction and corresponds to the acetabular membrane in taxa with perforated acetabula. Alternative placement of Silesauridae as basal ornithischians (Fig. 2b) resolves the ancestral state for Saurischia with the presence of an incompletely perforated acetabulum (RL~0.04*). In contrast, alternative placement of Herrerasauridae (Fig. 2c, RL~0.91*) and *Eoraptor* (Fig. 2d, RL~0.92*) both resolve the ancestral state for Saurischia with the presence of a completely perforated acetabulum. These results indicate that uncertainties in the phylogenetic placement of basal dinosauriformes affect the status of acetabular perforation as a synapomorphy of Dinosauria. Nevertheless, as much as three convergent acquisitions of perforated acetabula likely occurred within ornithischians, theropods, and sauropodomorphs. Because the perforated acetabulum is the osteological correlate for internalized pubofemoral and ischiofemoral ligaments, these results suggest multiple convergent evolutions of the ligamentum captis femoris within Dinosauria.

Although it is not known whether the acetabular membrane forms a physical restriction for the medial insertion of the femoral head in dinosaurs, the femoral heads of extant archosaurs never insert medially beyond the inner acetabular rim and into the pelvic cavity (Stolpe, 1932; Kuznetsov and Sennikov, 2000). Therefore we refrained from inferring medial insertion of the femoral head beyond the inner acetabular rim as suggested by Chatterjee and Templin (2007) and Makovicky and Zanno (2011). Instead, we used the acetabular membrane as the indicator of functional acetabular depth.

2. Pelvis, medial reduction of the supraacetabular rim. (0) laterally expanded, (1) medially reduced.

Basal dinosauromorphs possessed laterally expanded dorsal outer rim of the acetabulum, here termed the supraacetabular rim. The supraacetabular rim provides attachment for the acetabular labrum on its ventral surface (the acetabular "ceiling") and provides origin for the iliofemoral ligament on its apical edge. Medial reduction of the supraacetabular rim shifts the origin of the iliofemoral ligament medially and decreases the area of contact between the acetabular labrum and the femoral neck (trochanteric region of the *facies articularis antitrochanterica*) when the femur is held in a retracted or vertical position relative to the craniocaudal axis of the sacrum.

Lagerpetids and silesaurids possess laterally expanded supraacetabular rims, but sauropodomorphs and multiple lineages of theropods independently reduced the rim. Among basal sauropodomorphs, plateosaurids (*Ruehleia* + *Plateosaurus*, RL~0.99*, Fig. 3c) and the common ancestor of *Sarahsaurus* and more derived sauropodomorphs (RL~0.99*, Fig. 3d, 4a, b) possess reduced supraacetabular rims, but it is unclear if the two lineages independently reduced the supraacetabular rim (RL~0.81). Basal theropods maintained a laterally expanded supraacetabular rim in the stem lineage, but derived taxa in several averostran (Ceratosauria + Tetanurae) lineages independently reduced the rim. All alternative tree topologies yielded similar patterns in character state transitions as the consensus phylogenetic tree. Overall, medially reduced supraacetabular rims evolved independently in sauropodomorphs and multiple lineages of theropods.

3. Pelvis, orientation of the supraacetabular rim. (0) laterally oriented, (1) ventrolaterally oriented.

Basal dinosauromorphs possess laterally oriented supraacetabular rim, a morphology retained by sauropodomorphs. However, theropods underwent a single transition to a ventrolaterally oriented supraacetabular rim before multiple, independent reversions to a laterally oriented configuration. Ventrolateral orientation of the supraacetabular rim indicates an ossified craniodorsal hip joint capsule. A ventrolaterally oriented supraacetabular rim increases the depth of the bony acetabulum dorsally and orients the acetabular labrum ventromedially. Moreover, because the iliofemoral ligament originates on the supraacetabular rim, ventral orientation of the rim signifies partial ossification of the ligament at its origin. These transitions allow the entire proximal femur to insert deeper into the acetabulum during femoral retraction. A ventrolaterally oriented supraacetabular rim also forms a bony constraint to the femur laterally, thus restricting abduction and long axis rotation at the hip joint.

Basal dinosauromorphs possess a laterally oriented supraacetabular rim (RL~0.01*, Fig. 3a), and this morphology is retained in Saurischia (RL~0.02*) and Sauropodomorpha (RL~0.01*, Fig. 3b-d). The ancestral state of Theropoda is ambiguous (RL~0.51). Both Herrerasauridae (RL~0.99*, Fig. 3e) and Neotheropoda (*Tawa* + more derived theropods, Fig. 4c) possess ventrolaterally oriented supraacetabular rims, but *Eodromaeus* possesses a laterally oriented rim. The ventrolaterally oriented supraacetabular rim is retained among the basal theropod lineage and underwent two unambiguous reversions to the laterally oriented state in *Carnotaurus* and Avetheropoda (Allosauroidea + Coelurosauria, RL~0.01*, Fig. 4d). It is unclear whether the ventrolaterally oriented supraacetabular rim in Megalosauroidea (RL~0.99*) signifies a retention of the basal Neotheropoda morphology or a secondary reversion, because the ancestral state of Orionides (Megalosauroidea + Avetheropoda) is equivocal (RL~0.75). Alternative placement of Herrerasauridae (Fig. 2c; RL~0.05) and *Eoraptor* (Fig. 2d; RL~0.11*)

resolves the ancestral state reconstructed for Theropoda as retaining a laterally oriented supraacetabular rim. We infer that, whereas sauropodomorphs retained the laterally oriented supraacetabular rim of basal dinosauromorphs, basal theropods underwent a transition to a ventrolaterally oriented rim, before multiple, independent reversions to a laterally oriented configuration.

4. Pelvis, Expansion of the bony antitrochanter. (0) unexpanded, (1) expanded.

The bony antitrochanter consists of the rostrolaterally facing growth plate surfaces of the ilioischial joint, which supported the synchondrosis between the ilium and the ischium in life. Basal dinosaurs (Thulborn, 1972; Novas, 1994; Butler, 2010) and sauropodomorphs (Wilson, 2002; Langer, 2003) possess unexpanded bony antitrochanters, in contrast to the expanded morphology seen in extant birds (Stolpe, 1932; Baumel and Witmer, 1993), maniraptorans (Allen et al., 2009; Maryańska, 2002; Turner et al., 2012), and some ornithischians (Romer, 1927; Maidment and Barrett, 2012). The bony antitrochanter is expanded if its subchondral growth plates form a distinct articular surface caudal to the sub-circular outline of the acetabular fossa in lateral view. Since the fibrocartilaginous surfaces of the antitrochanter contacts the fibrocartilaginous surface of the femoral neck, expansion of the bony antitrochanter indicates an increase in the femoral neck-antitrochanter articulation at the caudal acetabulum.

Basal dinosauromorphs possess unexpanded antitrochanters (RL~0.01*), and this morphology is maintained throughout sauropodomorphs (Fig. 3b-d). Basal theropods also retain unexpanded antitrochanters, and this character state is maintained in the stem theropod lineage (Fig. 3e-g). Maniraptorans underwent several independent transitions among each terminal clade, resulting in laterally expanded antitrochanters in Therizinosauria, Oviraptorosauria (Fig. 3h), Deinonychosauria, and Avialae. Alternative placement of *Archaeopteryx* as a stem-

deinonychosaur complicates the character transition at each node within Deinonychosauria considerably. Under the alternate topology, the ancestral state of most nodes within Deinonychosauria remain unresolved, with only one unequivocal transition to the expanded antitrochanter at Velociraptorinae (*Deinonychus* + *Velociraptor*, RL~0.99*). These results suggest that an expanded antitrochanter evolved multiple times within the maniraptoran radiation, likely correlated with independent convergences in avian-like load bearing femoral postures.

5. Pelvis, shape of the ischial peduncle of the ilium. (0) flat, (1) cranially concave.

The ilial part of the bony antitrochanter is formed by the ischial peduncle of the ilium. In basal dinosauromorphs and theropods, the ischial peduncle is largely planar and oriented craniolaterally. In contrast, the ischial peduncle of large sauropods is cranially concave and forms a cranially oriented "U" shape in ventral view (Fig. 4b, dotted outline). This morphology first appeared in Anchisauria (RL~0.99*) and is retained throughout Sauropoda. No other dinosauromorphs possess cranially concave ischial peduncles. Based on osteological correlates of supraacetabular soft tissues, the plesiomorphic craniolaterally oriented bony antitrochanters supported a hyaline cartilage core, encapsulated by a fibrocartilage surface. In contrast, the cranially oriented, U-shaped antitrochanters of anchisaurian sauropodomorphs incorporated the acetabular labrum as part of the articular surface. All alternative tree topologies yielded similar patterns in character state transitions as the consensus tree.

6. Pelvis, co-ossification of the antitrochanter. (0) open synchondrosis, (1) co-ossified (fused or tightly sutured).

The antitrochanter of archosauromorphs exhibits a diverse range of ossification patterns, likely associated with ontogeny, phylogeny, and load bearing function. Most dinosauromorphs

possess an open synchondrosis at the bony antitrochanter, such that the ischial and ilial peduncles were bridged by a hyaline cartilage antitrochanter. Although extant birds possess fully co-ossified bony antitrochanters at skeletal maturity, evolutionary inference of a co-ossified antitrochanter in non-avian archosaurs remains elusive due the multiple instances of its gain among phylogenetically disparate taxa, as well as the late onset of its fusion during ontogeny.

Among extant archosaurs, crocodylians maintain an open synchondrosis between the ischial and ilial peduncles throughout life, even as large adults (Tsai and Holliday, 2015). In contrast, birds possess a synchondrosis as juveniles but completely fuse the bony antitrochanter at skeletal maturity (Hertel and Campbell, 2007). Antitrochanter ossification is difficult to investigate in fossils due to two confounding issues. First, most taxa are represented by small numbers of individuals for which ontogenetic status cannot be consistently inferred. Second, in contrast to birds, non-avian dinosaurs achieve sexual maturity prior to skeletal maturity (Erickson et al., 2007; Lee and Werning, 2008; Hone et al., 2016), such that many specimens represent animals still undergoing active bone growth. The current analysis addresses these caveats by only considering specimens inferred to be adults or subadults. We infer a co-ossified bony antitrochanter for a taxon if any individual possesses ischial and ilial peduncles that are either fused or articulate via immobile, deeply interdigitated sutures. Conversely, we identify an open synchondrosis if the ilium and ischium is naturally disarticulated, without visible breakage in the peduncles. Admittedly, this method potentially introduces errors in taxa for which the terminal adult morphology is not known. Therefore, the following data should be considered as a minimal estimate in the actual number of saurischian-line archosaur taxa with co-ossified antitrochanters.

Basal dinosauromorphs possess an open synchondrosis at the bony antitrochanter (RL~0.01*, Fig. 3a). The bony antitrochanters of sauropodomorphs retained the open synchondrosis (Fig. 3b-d, 5a). In contrast, theropods maintained an unfused bony antitrochanter in the crownward stem lineage but underwent four independent transitions to the co-ossified state according to the consensus phylogenetic tree (Fig. 2a). The bony antitrochanter is co-ossified in *Herrerasaurus*, *Coelophysis*, Ceratosauria (RL~0.99*, Fig. 3e, 5b), and avialans (RL~0.99*). In *Herrerasaurus* only the largest individual studied (MCZ 4381, Fig. 3e) possesses a co-ossified bony antitrochanter, whereas all *Coelophysis* specimens in this analysis possess co-ossified bony antitrochanters, including the smallest individual studied (YPM 41197). Ceratosauria possess fully co-ossified bony antitrochanters (RL~0.99*). The ilium and ischium of *Elaphrosaurus* are mechanically separated at the ischium's ilial peduncle in the display mount, but full fusion of the bony antitrochanter is nevertheless observable. Bonaparte et al. (1990) described the bony antitrochanter of *Carnotaurus* as "partially fused", but because the bony antitrochanter is obscured due to plaster reconstruction, it was not coded for this taxon. Large, presumably adult *Ceratosaurus* possess fully co-ossified bony antitrochanters (USNM 4735, Gilmore, 1920; Carrano and Sampson, 2008), but juveniles, represented by TPI 1010, possess an open synchondrosis that articulates via a sharply convex, rugose ischial peduncle and a deeply concave ilial peduncle. This morphology suggests a tightly interdigitated, immobile bony antitrochanter. However, because the convex-concave articulation is unobservable for taxa possessing co-ossified bony antitrochanters, the articular morphology of the peduncles is not scored in this study. Nevertheless, convex-concave articulation between the ilium and ischium is widespread across Avetheropods, as evident in *Siats*, *Ornitholestes*, Ornithomimosauria, Tyrannosauroidea, and *Falcarius* (Fig. 5d). Among *Tyrannosaurus*, the largest individual

(FMNH PR 2081) possesses incipient fusion of at the bony antitrochanter (Fig. 5c), but the peduncles are not extensively co-ossified. The convex-concave articulation is absent in Megalosauroidea and Maniraptora. The bony antitrochanter is co-ossified in all avialans, including both *Archaeopteryx* and one specimen of *Patagopteryx* (MACN N-11) included in this analysis. However, it is not known if *Archaeopteryx* and more derived avialans independently evolved a co-ossified antitrochanter, because the ancestral state for Avialae is unresolved (RL~0.87). Alternative placement of *Archaeopteryx* reconstructs two independent gains of antitrochanter co-ossification in avialans and *Archaeopteryx* itself but otherwise did not alter the sequence of character transitions within theropods.

These results indicate that, regardless of the condition achieved by adults at full skeletal maturity, most dinosauromorphs possess an open synchondrosis at the bony antitrochanter during much of their lifespan, bridged by a hyaline cartilage core similar to those observed in juvenile birds. However, evolutionary inference of a co-ossified antitrochanter in the theropod lineage remains elusive due the multiple instances of its gain among phylogenetically disparate taxa (see Discussion). Additional data on the ontogenetic data on basal theropods will provide further insights on the evolution of antitrochanter ossification.

7. Femur, Femoral head deflection: (0) craniomedially deflected; (1) medially deflected.

Within Dinosauria, sauropodomorphs, theropods, and ornithischians independently evolved medially deflected femoral heads. Femoral head deflection is here defined as the angle between the capitular-trochanteric axis of the proximal femur and the mediolateral axis of the distal condyles, hereafter abbreviated the proximodistal angle. A craniomedially deflected femoral head possesses a proximodistal angle of ~45°, whereas a medially deflected femoral head possesses a proximodistal angle close to 0° (Fig. 1c). Although distinction between these

two character states is possible in most specimens examined, the precise angle of deflection is difficult to quantify due to unavoidable taphonomic distortions, such as torsion and flattening. Therefore, femoral head deflection is analyzed as a discrete binary character and only coded for taxa represented by well-preserved femora.

Basal dinosauromorphs possess craniomedially deflected femoral heads (RL~0.01*). In sauropodomorphs, a medially deflected femoral head evolved by the common ancestor of plateosaurids and more derived taxa (RL~0.95*), whereas in theropods the transition occurred at Avetheropoda (RL~0.99*). All alternative tree topologies yielded similar patterns in character state transitions as the consensus tree. *Lesothosaurus*, the only ornithischian included in the current study, possesses a medially deflected femoral head. These results support Carrano (2000) that the medially deflected femoral head evolved independently in sauropodomorphs, theropods, and ornithischians.

8. Femur, surface texture of the proximal femoral growth plate: (0) smooth; (1) rugose.

Silesaurids, sauropodomorphs, and multiple lineages of theropods independently evolved thick layers of epiphyseal hyaline cartilage on the proximal femur, as indicated by the presence of rugose growth plate surface textures. Among extant tetrapods, growth plate rugosities are present in "incompletely ossified" joints of immature birds, lepidosaurs, and mammals (Haines, 1942; 1975) and are associated with the presence of a thick epiphyseal hyaline cartilage layer that differs significantly from the contour of the subchondral growth plate surface (Snover and Rhoudin, 2008; Holliday et al., 2010; Tsai and Holliday, 2015). Numerous studies have noted rugosities on the subchondral surfaces of large saurischians (sauropods, Marsh, 1896; theropods, Gilmore, 1920; Brochu, 2003), rhynchosaurs (this study), and phytosaurs (Zeigler et al., 2003), suggesting the presence of thick hyaline cartilage layers in these taxa. The current study uses

growth plate rugosities as the osteological correlate for thick hyaline cartilage. Although Marsh (1896) noted the similarity between rugose subchondral surfaces of dinosaurs with the ossifying growth plates of juvenile mammals and birds, this study does not employ growth plate rugosities as an ontogenetic indicator, because many extinct saurischians retain growth plate rugosities throughout ontogeny, even as large-bodied, presumably adult individuals (Brochu, 2003; Tidwell et al., 2005).

Basal dinosauromorphs possess smooth subchondral growth plates on the proximal femur (RL~0.02*, Fig. 6a, 7a, j), but this morphology is independently lost in silesaurids (Fig. 7k), sauropodomorphs, and multiple lineages of theropods. Among sauropodomorphs, *Eoraptor* retains the smooth growth plate morphology, whereas plateosaurids (RL~0.99*) and the common ancestor of *Mussaurus* and sauropods (RL~0.96*) possess highly rugose growth plate surfaces. It is unclear whether the plateosaurid morphology (Fig. 6j, 7l) and that of the more derived sauropodomorphs (Fig. 6k, 7m) resulted from a single or two independent acquisition (RL~0.80), because *Adeopapposaurus* possesses a smooth growth plate similar to *Eoraptor* and basal dinosauromorphs. Nevertheless, growth plate rugosities are maintained throughout Sauropoda.

Theropods retained the smooth proximal femoral growth plate in basal dinosauromorphs (Fig. 6e, l, m, 7e) but underwent multiple transitions to a more rugose surface morphology. When present in theropods, growth plate rugosities typically possess lower amplitudes than in sauropodomorphs, resulting in a more subtle morphology. Rugose growth plates are present in the larger individuals of *Ceratosaurus* (Fig. 7o) and *Allosaurus* but not in smaller, presumably juvenile individuals. Rugose growth plate is absent in basal Tyrannosauroidea (RL~0.01*) but present in *Alioramus* and more derived tyrannosaurids (RL~0.93*, Fig. 7f). Lastly, although the stem Maniraptoriformes lineage maintained smooth growth plates on the proximal femur,

Ornithomimus, *Anzu* (Fig. 7q), and *Deinonychus* possessed rugose growth plates. All alternative

tree topologies yielded similar patterns in character state transitions as the consensus

phylogenetic tree. These results indicate that silesaurids, sauropodomorphs, and multiple

lineages of theropods independently evolved thick layers of epiphyseal hyaline cartilage.

Estimates of epiphyseal cartilage thickness are noted in the discussion (see below).

9. Femur, concentration of irregular rugosities on the femoral head: (0) absent; (1) present.

The femoral heads of large sauropodomorphs possess highly pronounced, cauliflower-

like irregular rugosities (Fig. 6d, k, 7d, l, m). In contrast, the femoral heads of theropods and

basal dinosauromorphs lack concentrated rugosities, instead possessing an overall smooth

surface texture or largely uniformly distributed rugosities. The presence of capital-trochanteric

polarity indicates regional differences in hyaline cartilage thickness: the more rugose capital

region of the growth plate would possess a significantly thicker hyaline cartilage layer than the

smoother trochanteric region. In particular, the highly convoluted rugosities on the femoral head

of *Diplodocus*, *Tornieria*, and *Apatosaurus* possess amplitudes up to 20 mm, greater than the

thickness of all known epiphyseal cartilages among extant tetrapods. Because it is unlikely that

the cartilaginous articular surface possess similarly convoluted surface texture as the growth

plate, the articular cartilage of large sauropods must have exceeded 20 mm in thickness.

Irregularly rugose femoral head growth plates are observed in plateosaurids (RL~0.99*)

and the common ancestor of *Mussaurus* and sauropods (RL~0.99*), indicating that both lineages

possess thick hyaline cartilage on the femoral head. The absence of femoral head rugosities in

Adeopapposaurus (Martínez, 2009) complicates inferences on the origin of thick hyaline

cartilage within Sauropodomorpha (RL~0.75). Therefore, it is unclear whether femoral head

rugosities originated once at the common ancestor of plateosaurids and other sauropodomorphs,

with one reversal at *Adeopapposaurus*, or rather the rugose morphology independently evolved in the two clades. All alternative tree topologies yielded similar patterns in character state transitions as the consensus tree.

10. Femur, transphyseal striations: (0) absent, (1) present.

Some saurischians possess rugosities on the subchondral surface contact the metaphyseal line peripherally and excavate parallel striations which span across the growth plate and the metaphyseal collar (Fig. 7f, g, l, m, o). These transphyseal striations are oriented perpendicular to the capital-trochanteric axis of the proximal femur and give the metaphyseal junction a "wavy" appearance. Transphyseal striations in saurischians are the osteological correlates for highly integrated attachments between the fibrocartilage, hyaline cartilage, and subchondral growth plate across the metaphysis of the proximal femur.

Basal dinosauromorphs lack transphyseal striations (RL~0.01*) but underwent multiple transitions to the derived morphology along the lineages leading to sauropodomorphs and theropods. Among sauropodomorphs, it is unclear whether transphyseal striations evolved independently in plateosaurids (RL~0.99*) and anchisaurians (RL~0.98*), or rather if this character shared a common origin (RL~0.81), because *Adeopapposaurus* lack transphyseal striations. In theropods, the transphyseal striations are present in *Ceratosaurus* (Fig. 7o), Allosauroidea (RL~0.91*), Tyrannosauridae (RL~0.98*, Fig. 7f), *Ornithomimus*, and *Anzu*. Although transphyseal striations were not observed on other ornithomimosaurs and oviraptorosaurs, their absence may be partly due to poor preservation of the metaphyseal boundary in most specimens. Transphyseal striations are wholly absent in Paraves (RL~0.01*), even in well preserved specimens. These results indicate that sauropodomorphs and multiple lineages of theropods independently gained transphyseal striations.

The absence of transphyseal striations among extant archosaurs makes inferring soft tissues in extinct dinosaurs difficult. Nevertheless, we hypothesize that the striations in dinosaurs indicate uneven fronts of endochondral and perichondral ossifications along the metaphyseal line. Specifically, the wavy morphology on the growth plate provides insertion for correspondingly protrusions on the hyaline cartilage core; whereas continuation of the wavy morphology on the metaphysis provides insertion for corresponding protrusions of the fibrocartilage sleeve. The presence of transphyseal striations in saurischians thus indicates highly integrated attachment morphology between the fibrocartilage, hyaline cartilage, and subchondral growth plate across the metaphyseal junctions.

11. Femur, fovea capitis: (0) indistinct, (1) planar or concave.

The fovea capitis is the femoral insertion point of the ligamentum capitis femoris. The fovea is located on the capital-medial surface of the proximal femoral growth plate, between the anatomical femoral head and the posteromedial tuber (*sensu* Nesbitt, 2011). Among extant archosaurs, the ligamentum capitis presents a continuum of attachment topology across phylogeny and ontogeny. In crocodylians and skeletally immature birds, the ligamentum capitis inserts onto the relatively thick epiphyseal cartilage layer but does not progress into the subchondral growth plate. This morphology is indicated by an indistinct fovea that follows the convex contour of the subchondral surface. In contrast, the ligamentum capitis of skeletally mature birds inserts past the relatively thin epiphyseal cartilage layer and excavates a distinctively planar or concave fovea on the otherwise convex femoral growth plate. The depth of the fovea capitis is therefore the osteological correlate for the ligamentum capitis' depth of insertion into the subchondral growth plate and serves as an additional indicator in the relative thickness of the epiphyseal cartilage on the femoral head. Among dinosaurs, distinctively

concave or planar foveae are rarely observed in coelurosaurian theropods, suggesting the evolution of deeper insertion of the ligamentum capitis on the femoral head in these taxa.

Within the saurischian lineage, the fovea capitis ranges from indistinct in sauropodomorphs (Fig. 7d, m), planar in tyrannosaurids (Fig. 7f), and deeply convex in extant birds. These observations indicate that the insertion depth of the ligamentum capitis, as well as the thickness of the epiphyseal hyaline cartilage, varies across extinct saurischians. In order to account for the ontogenetic influence and diagenetic alteration on the proximal femur, the current analysis simplified fovea morphology into two discrete states: indistinct, in which the fovea follows the convex contour of the remaining subchondral surface; or distinct, in which the fovea can clearly be distinguished by a planar surface or concavity.

Basal dinosauromorphs possess an indistinct fovea capitis (RL~0.01*), and this morphology is maintained throughout sauropodomorphs. Theropods underwent several transitions to the derived character state in tyrannosaurids (RL~0.99*, Fig. 7f), *Nothronychus*, some oviraptorosaurs (Fig. 6o, 7q), and Euornithes. These results indicate that multiple theropod lineages independently evolved deeper insertion of the ligamentum capitis on the subchondral growth plate of the femoral head.

12. Femur, ischiofemoral ligament sulcus: (0) shallow, (1) deep.

The ischiofemoral ligament originates on the inner rim of the ischial acetabulum and merges with the pubofemoral ligament distally to form the ligamentum capitis femoris. The ligamentum capitis femoris inserts onto the fovea capitis on the femoral head. In most dinosauromorphs, the ischiofemoral ligament excavates a sulcus on the capital-medial metaphyseal collar of the proximal femur. The sulcus varies considerably in depth, ranging from a shallow, indistinct indentation in basal dinosauromorphs (Nesbitt et al., 2009), basal

sauropodomorphs (Novas, 1996; Müller et al., 2015), and birds (Tsai and Holliday, 2015) to a deep, distinct groove in most non-avian theropods (*Syntarsus*, Rowe, 1989; *Gallimimus*, Osmólska et al., 1972). The sulcus is the osteological correlate for the passage taken by the ischiofemoral ligament but does not provide attachment for any intrinsic or capsular ligaments. The width of the ischiofemoral ligament sulcus can be visualized when the femur is oriented in caudomedial view, and indicates the diameter of the ligament itself.

The current analysis describes the ischiofemoral ligament sulcus depth as a binary character, the continuous spectrum of sulcus depth, width, and angle, suggesting that the ischiofemoral ligament varies considerably in thickness and course within Dinosauromorpha. Nevertheless, basal dinosauromorphs possess a shallow but distinct ischiofemoral ligament sulcus (RL~0.01*, Fig. 7a, j). Basal sauropodomorphs such as *Plateosaurus* (SMNS F 14-91294, Fig. 7l) and basal sauropods such as *Patagosaurus* (MACN CH 1986) retained the dinosauromorph morphology, whereas derived sauropods such as *Diplodocus* (DMNH 462, Fig. 6k) and *Camarasaurus* (YPM 4625, DNM 4514, Fig. 7d, m) completely reduced the sulcus. In theropods, the common ancestor of *Tawa* and more derived taxa acquired a deeply excavated ischiofemoral ligament sulcus (RL~0.99*), but the stem lineage underwent several reversions in Maniraptora (e.g., *Anzu* among oviraptorosaurs, Fig. 7q; Euornithes, RL~0.04*). All alternative trees yielded similar patterns in character state transitions as the consensus phylogenetic tree.

13. Femur, cartilage cone trough: (0) absent, (1) present.

The cartilage cone is a convex extension of the epiphyseal hyaline cartilage core that inserts into the metaphyseal growth plate (Carter et al., 1998). Presence of a cartilage cone on the proximal femur can be identified by a capital-trochanterically oriented trough on the growth plate (Tsai and Holliday, 2015). In extant archosaurs, the cartilage cone results from the

relatively slower progression of endochondral ossification compared to perichondral ossification during the neonatal period (Carter et al., 1998). The cartilage cone disappears as the two forms of ossification synchronize (Carter et al., 1998) and is entirely absent in juvenile crocodylians and birds (Tsai and Holliday, 2015).

In many fossil archosauromorphs, the osteological correlate of the cartilage cone persists in post-neonatal individuals. The cartilage cone is inferred to be present in non-archosaurian archosauromorphs (e.g., *Erythrosuchus*: Nesbitt, 2011, *Hyperodapedon*, juvenile *Trilophosaurus*), stem-suchians (e.g., poposauroids, *Prestosuchus*), silesaurids (Ezcurra, 2006; Nesbitt, 2011), sauropodomorphs (*Gyposaurus = Massospondylus,* Galton and Cluver., 1976; *Saturnalia*, Langer, 2003; *Pampadromaeus*, Müller et al., 2015), theropods (e.g., *Staurikosaurus*, Galton, 1977; *Coelophysis*, Padian, 1986), and ornithischians (*Lesothosaurus*, Sereno, 1991). Although the cartilage cone tends to be shallower and less distinct in dinosaurs than in silesaurids, the depth and distinctiveness of the cartilage cones are highly subject to the degrees of taphonomic breakage, deformation, and subsequent preparation of the fossil material. Moreover, the cartilage cone's depth is expected to be ontogenetically variable because endochondral ossification progresses continuously during growth. These factors limit the current analysis to distinguishing the cartilage cone morphology as a binary discrete character. The cartilage cone is coded as "present" in a taxon if a capital-trochanterically oriented trough is retained in post-neonatal individuals.

Basal dinosauromorphs lack a cartilage cone on the proximal femur (RL~0.02*, Fig. 7j), but Dinosauriformes evolved a cartilage cone (RL~0.99*). In particular, silesaurids possess a deep, highly distinct trough on the growth plate surface (Fig. 6i, 7j); whereas dinosaurs possess a shallow, indistinct trough that gradually fades into the convex contours of the proximal femur

(Fig. 7n, o). Sauropodomorphs and theropods independently reduced, and ultimately lost the cartilage cone on the proximal femur during the evolution of crown lineages. Among sauropodomorphs, the cartilage cone is present in plateosaurids and *Adeopapposaurus* but is absent in the common ancestor of *Ammosaurus* and more derived sauropodomorphs (RL~0.99*). Among theropods, the cartilage cone is present early in the stem lineage but underwent two independent losses. Basal herrerasaurids such as *Staurikosaurus* possess the cartilage cone (Fig. 7n), but the cone is absent in *Herrerasaurus* (Fig. 7e). Basal neotheropods retain very shallow cartilage cones (RL~0.99*, Fig. 6l, 7n), but the cone is absent in Orionides (RL~0.99*). All alternative tree topologies yielded similar patterns in character state transitions as the consensus tree, and indicate that sauropods and theropods independently reduced, and ultimately lost, the cartilage cone during the evolution of crown lineages.

14. Femur, metaphyseal collar: (0) unexpanded, (1) expanded.

The metaphyseal collar is a raised surface of cortical bone surrounding the proximal femoral growth plate. The metaphyseal collar is the bony attachment for the fibrocartilage sleeve and therefore serves as the osteological correlate for the extent of fibrocartilage on the metaphysis. The metaphyseal collar can be distinguished proximally from the growth plate by a prominent metaphyseal line and distally from the diaphysis by a patch of exposed trabecular bone, indicative of the synovial bursa. Basal dinosauromorphs possess unexpanded metaphyseal collar, indicating that that the fibrocartilage sleeve possesses limited bony attachment on the metaphysis. The metaphyseal collar is expanded in Dinosauriformes, but reverted to the unexpanded state within at least two lineages of maniraptoran theropods. The morphological similarity between the proximal femur of birds and non-avian pennaraptorans suggest that bird-like composite fibro-hyaline cartilage evolved prior to the first occurrence of Avialae.

Among extant sauropsids, the metaphyseal collar is most conspicuous in crocodylians and indicates an expanded bony attachment for the fibrocartilage sleeve. In contrast, birds, lepidosaurs, and turtles possess fibrocartilage sleeves with smaller attachment to the bony metaphysis and possess indistinct metaphyseal collars (Tsai and Holliday, 2015). The presence of a distinct metaphyseal collar indicates a crocodylian-like fibrocartilage attachment on the proximal femur, in which the fibrocartilage sleeve possesses substantial bony attachments on the bony metaphysis. An unexpanded metaphyseal collar indicates smaller bony attachments for the fibrocartilage sleeve.

Basal dinosauromorphs possess an unexpanded metaphyseal collar (RL~0.08*), a condition shared by basal archosaurs. This indicates that the fibrocartilage sleeve possesses limited bony attachment on the metaphysis. However, an incipient metaphyseal collar is present in *Dromomeron* as a small patch of cortical bone between the growth plate and the bursal attachment surface (Fig. 6a). Dinosauriformes possess expanded metaphyseal collars (RL~0.99*). In particular, silesaurids expanded the collar on the capital and entire medial periphery of the proximal femoral growth plate (Fig. 6b, 7b), whereas basal saurischians expanded the collar only on the capital periphery of the growth plate (*Plateosaurus*, Fig. 6c; *Coelophysis*, Fig. 6e). Among dinosaurs, sauropodomorphs expanded the collar both laterally and medially, surrounding the femoral head in a C-shaped "cuff" in proximal view (Fig. 6d, k, 7d). This morphology indicates that the fibrocartilage sleeve is particularly well developed on the periphery of the thick hyaline cartilage cap on the capital growth plate surface. In an exceptionally well preserved *Camarasaurus* femur (YPM 4625, Fig. 7d), the fibrocartilage sleeve is partially calcified on the capital metaphyseal collar, thereby providing support for the current soft tissue inferences in other sauropodomorphs.

In theropods, the metaphyseal collar is only expanded on the craniolateral surface of the proximal metaphysis, whereas the caudomedial surface is excavated the ischiofemoral ligament sulcus (see character 12). Avetheropods greatly expanded the metaphyseal collar on the craniolateral metaphyseal surface as a prominent shelf, bordered by a right-angled ridge (Fig. 6f, m). The metaphyseal collar retains its expanded morphology throughout Avetheropoda, but underwent one or more reversion in Maniraptora (RL~0.85) to the unexpanded condition. The unexpanded metaphyseal collar of maniraptorans is inferred not to be homologous with those of basal dinosauromorphs but instead signifies a trend towards the avian-like proximal femoral articular cartilage (Wess et al., 1997). As in birds, the fibrocartilage sleeve of non-avian maniraptorans possesses little attachment to the bony metaphysis but rather expands proximally and integrates with the hyaline cartilage core to form a composite cartilage articular surface (Wess et al., 1997; Tsai and Holliday, 2015). It is therefore inferred that bird-like proximal femoral epiphyseal cartilage first evolved in non-avian theropods. All alternative tree topologies yielded similar patterns in character state transitions as the consensus tree.

Summary

Overall, results of this study indicate that most saurischian dinosaurs construct the entire ventral half of their femoral heads using a fibrocartilage sleeve, similar to crocodylians. However, because basal dinosauriformes, stem-archosaurs (*Trilophosaurus*, rhynchosaurs, phytosaurs), and stem-suchians (aetosaurs, basal loricatans) lack expanded metaphyseal collars, the crocodylian morphology does not reflect the ancestral archosaur condition. Rather, dinosaurs and crocodylians independently evolved expanded fibrocartilage attachments on the metaphyseal cortical bone. In contrast, secondary reduction of the metaphyseal collar occurred in the

maniraptoran lineage, and indicates the evolution of a composite fibro-hyaline cartilage epiphysis on the proximal femur, a morphology retained by extant birds.

DISCUSSION

Dinosauromorphs underwent multiple, iterative convergences and divergences in hip joint anatomy, reflecting a spectrum of locomotor adaptations. The loss of articular soft tissues in the fossil record have traditionally hindered inferences of joint loading, range of motion, and kinematics (Holliday et al., 2010; Bonnan et al., 2013). In this study, we examine the evolutionary transitions of several key anatomical features in basal dinosauromorphs and their implications on the origin of dinosaur locomotor posture. A summary of key morphological features and evolutionary trends in the Dinosauromorph hip joint is provided in Fig. 9.

Evolution of the cartilage cone in non-dinosaurian Dinosauromorpha

Our results support previous inferences that non-dinosaurian dinosauromorphs were able to assume adducted hind limb postures (Dzik, 2003; Nesbitt et al., 2009; 2010) as part of their locomotor repertoire. However, our reconstructed epiphyseal and ligament topologies show that that the hip joints of lagerpetids, *Marasuchus*, and silesaurids were capable of a greater range of mediolateral and axial rotation than reconstructed by previous studies. The basal dinosauromorph hip joint is exemplified by lagerpetids and *Marasuchus*, in which the inner acetabular walls are unperforated, indicating that the ventral joint ligaments remain as capsular ligaments in their origin. The height of the acetabulum is relatively tall compared to the dorsoventral and mediolateral diameters of the proximal femur, similar to extant lepidosaurs and crocodylians, suggesting that a substantial amount of soft tissue maintained hip articulation in lagerpetids and *Marasuchus*. Basal dinosauromorphs possess smooth, convex femoral growth plates similar to crocodylians and adult birds. For a 135 mm *Dromomeron* femur, the proximal hyaline cartilage

layer is estimated to be 3.2 ±1.1 mm thick (mean ± sd based on cartilage cap estimates in Holliday et al., 2010) based on the adult *Struthio* cartilage correction factor; and 4.3 ±1.1 mm thick based on the *Alligator* cartilage correction factor. Due to the basal phylogenetic position of *Dromomeron* within Dinosauromorpha, femoral cartilage reconstructions based on *Struthio* <u>and *Alligator* are equally preferred, such that</u> the two alternative reconstruction schemes are presented here as the maximal and minimal estimates of proximal femoral articular cartilage thickness in *Dromomeron*.

The craniomedially deflected proximal femur of lagerpetids and *Marasuchus* allows the femoral head to insert deep into the acetabulum during femoral retraction. Because the metaphyseal shelf is slightly expanded on the craniolateral femoral metaphysis, the fibrocartilage sleeve in this region may buttress the hyaline cartilage core on the femoral head region against axial compression and translational shear during femoral protraction and retraction. The laterally expanded supraacetabular rim indicates that the pliant, fibrous acetabular labrum is able to undergo maximal contact with the entire proximal femur when the femur is adducted and retracted. However, because basal dinosauromorphs possess a hyaline cartilage-covered, osseous inner acetabular wall, load-bearing articulation between the proximal femur and the inner acetabular wall is still potentially possible during femoral abduction. Overall, these results suggest that basal dinosauromorphs were able to adopt a more abducted femoral posture than dinosaurs during locomotion.

Silesaurids retain basal dinosauromorph morphology in the acetabulum but possess a lepidosaur-like proximal femoral epiphysis, in which a thick, highly convex cartilage cap inserts onto the proximal femoral growth plate via a cartilage cone. The subchondral surface of silesaurid proximal femora is terminally planar and possesses an angled junction with the

femoral head (Fig. 6b, 7b). A deeply excavated cartilage cone trough spans the capital-trochanteric axis of the proximal growth plate, indicating the presence of a well-developed cartilage cone. The trough is present in all silesaurid femora studied and has even been reported in a particularly large-bodied individual as well (Barrett et al., 2015), indicating that silesaurids retain the cartilage cone in postnatal juveniles and adults. The silesaurid epiphyseal morphology is unlike either extant crocodylians or birds, because both clades retain the cartilage cone only as neonates. Instead, the silesaurid growth plate indicates a lepidosaur-like epiphyseal cartilage shape (Haines, 1942). In particular, post-natal juvenile lepidosaurs retain a prominent cartilage cone on the metaphyseal surface of the cartilage cap (Buffrénil et al., 2004). The articular surface of the cartilage cap on the proximal femur is convex in lepidosaurs, allowing congruent articulation with the acetabulum. Since silesaurids possess similar subchondral morphology to lepidosaurs, we reconstruct the epiphyseal cartilage shape of silesaurids based on that of extant lepidosaurs, in which a semi-ellipsoid, convex epiphyseal cartilage cap inserts into the metaphysis via a cartilage cone. We reconstruct the apex of the silesaurid cartilage cap as situated capital relative to the midpoint of the proximal femur in lateral view (Fig. 8a), because the well-developed metaphyseal shelf on the capital region indicates that prominent fibrocartilage sleeve supported thicker hyaline cartilage on the femoral head (Fig. 6b, 7b). Thickness of the proximal epiphyseal cartilage of a 137 mm *Asilisaurus* femur is estimated as 13.6 mm, half the capital-trochanteric length of the proximal growth plate.

It is not known if silesaurids calcified the hyaline cartilage core like lepidosaurs do (Haines, 1941). Calcification centers have never been described at the ends of silesaurid limb bones. It is possible that remnants of calcification centers have been removed from the ends of silesaurid long bones via diagenesis or preparation, but it is more likely that silesaurids retain

uncalcified epiphyseal cartilage caps throughout life, as in other archosauriformes. In support of the latter hypothesis, silesaurids possess an expanded metaphyseal collar on the proximal femur. This indicates that silesaurs possess a prominent fibrocartilage sleeve on the medial periphery of the hyaline cartilage core (Fig. 8a). In contrast, lepidosaurs possess only a modest fibrocartilage sleeve on the periphery of the epiphyseal calcification center and lack an expanded metaphyseal shelf. The fibrocartilage sleeve has been inferred to function as mechanical support for the epiphyseal hyaline cartilage core in extant archosaurs (Tsai and Holliday, 2015). These lines of evidence indicate that, although silesaurids possess a cartilage cone and a lepidosaur-like epiphyseal cartilage cap, they nevertheless maintain a hyaline, uncalcified cartilage core, surrounded by an extensive fibrocartilage sleeve.

Like basal dinosauromorphs, silesaurids are capable of greater range of hip abduction and axial rotation than inferred by previous studies (Dzik, 2003). Silesaurids retain a laterally expanded supraacetabular rim, suggesting that the epiphyseal cartilage articulates with the supraacetabular labrum dorsally in parasagittal locomotor posture (Fig. 8a). However, an abducted femoral posture remains mechanically possible because the pubofemoral and ischiofemoral ligaments are capsular in origin. Overall, results of this study support previous inferences that basal dinosauromorphs were able to assume adducted hind limb postures (Dzik, 2003; Nesbitt et al., 2009; 2010) but retain the capacity for mediolateral and axial femoral rotation. Results of this study provide the means of hip joint articulation for further *in silico* modeling of hip joint postural mechanics using quantitative techniques (e.g., muscle moment arm analysis, Bates and Schachner, 2011).

Hip joint evolution in basal dinosaurs is characterized by independent reduction and eventual loss of the cartilage cone-metaphyseal trough articulation, as well as independent

modifications of the two ventral capsular ligaments into the ligamentum capitis femoris. Although the cartilage cone is ubiquitously present among silesaurids, it is variably present in basal theropods, sauropodomorphs, and ornithischians. Among basal dinosaurs, the cartilage cone is frequently present post-neonatal individual, though shallow or absent in large conspecific adults. The presence of cartilage cones in locomotor patent subadults indicate that basal dinosaurs retain similar function of the epiphyseal hyaline cartilage as non-dinosaurian dinosauriformes, and were able to use uncalcified hyaline cartilage as load bearing tissues on par with subchondral bones.

Early evolution of the graviportal hip joint of Sauropodomorpha

Hip joint evolution in basal sauropodomorphs is characterized by few concerted transitions in both the femur and the acetabulum, followed by subsequent stasis in soft tissue anatomy throughout Sauropoda (Fig. 9). Key characteristics of the sauropod hip joint include a highly cartilaginous, medially deflected femoral head, a fully perforated acetabulum, a reduced supraacetabular rim, and a cranially concave ischial peduncle of the ilium. These key characteristics of the sauropod hip joint appeared within a relatively short time (~220-190 MYA) during the early evolution of sauropodomorphs. In particular, small basal sauropodomorphs possess markedly different growth plate morphology compared to their larger relatives, suggesting an association between epiphyseal soft tissue and the evolution of gigantism in the sauropod lineage. Basal sauropodomorphs retain a shallow indentation on the proximal femoral growth plate, homologous with the cartilage cone trough in silesaurs and basal theropods. The shallowness of this trough indicates that the cartilage cone is not as prominent in sauropodomorphs as it is in silesaurids. Although a shallow cartilage cone is present in some individual of *Plateosaurus* (absent in SMNS F 14-91294, Fig. 7l), it is unequivocally lost in

Anchisauria. The loss of the cartilage cones in derived sauropodomorphs coincides with the acquisition of highly rugose growth plate surfaces on the proximal femur and indicates a major transition in joint loading in the sauropod lineage. Using the cartilage cap reconstruction of juvenile *Struthio*, a 590 mm *Plateosaurus* femur would possess an 18.6 (±4.9) mm thick cartilage cap on its proximal end. In contrast, cartilage reconstruction based on *Alligator* estimates a 18.9 (±6.6) mm cartilage cap. The two alternative reconstruction schemes are presented here as the minimal- and maximal estimates of proximal femoral articular cartilage thickness in *Plateosaurus*. Large-bodied sauropodomorphs possess absolutely thicker layers of epiphyseal cartilage than silesaurids in both minimal and maximal estimates. Given the marked disparity in body size between large sauropodomorphs and silesaurids, the cartilage cap of large sauropodomorphs is expected to experience much greater absolute magnitudes of compressive and shear forces during stance and locomotion. Compared to a cone-trough articulation, an irregularly rugose articulation is hypothesized provide greater traction between the hyaline cartilage and the subchondral growth plate, thus prevent slippage and avulsion of the thick cartilage cap (Carter, 1987; Carter et al., 1998)

The supraacetabular rim is reduced in all but the most basal sauropodomorphs (Fig. 3b, c, d). The reduction of the supraacetabular rim coincides with medial deflection of the femoral head, as well as the evolution of thick hyaline cartilage on the femoral head. In sauropods, the mediolateral depth of the supraacetabulum is generally similar to the capital-trochanteric extent of the highly convoluted rugosities on the femoral head growth plate. The congruence in osteological correlates suggest that the supraacetabulum articulates solely with the thick epiphyseal cartilage layer of the femoral head when the femur is held vertically, and that the

femoral neck, though still possessing a hyaline cartilage growth plate surface, does not articulate with the supraacetabulum during vertical femoral posture.

Basal sauropodomorphs possess an incompletely perforated acetabulum (Fig. 3b), indicative of capsular ventral joint ligaments (Fig. 8b). However, incipient perforations of the acetabulum in basal sauropodomorphs indicate that the ventral joint ligament can enter the acetabulum during femoral adduction, without the risk of compression between the articular surfaces. The inner acetabular rim is particularly expanded in sauropods, such that the inner rim's circumference approaches that of the outer rim. This results in a shallow, dish-shaped acetabular fossa. The inner acetabular rim is covered by a ligamentous acetabular membrane, forming a pliant surface against capital extant of the femoral head.

As in other diapsids, sauropodomorphs are inferred to possess a common femoral insertion for the pubofemoral and ischiofemoral ligament on the fovea capitis. The fovea capitis located entirely on the epiphyseal hyaline cartilage and does not leave a pit on the subchondral surface. Nevertheless, the location of the fovea can be estimated in basal sauropodomorphs as the subchondral surface between the anatomical femoral head and the posteromedial tuber. The ligamentum capitis femoris (i.e., the conjoined portion of the two ventral joint ligaments) is inferred to be relatively shorter in sauropodomorphs more basal than *Mussaurus*, because the ischiofemoral ligament's passage can be traced using the ischiofemoral ligament sulcus on the caudomedial surface of the femoral neck (e.g., *Plateosaurus*, Fig. 7c).

Evolution of the obligate parasagittal hip joint in basal Theropoda

The hip joint evolution of theropods is best characterized by differential combinations of character state transitions, which suggest unique locomotor adaptations in each clade. The basal theropod hip joint morphology (e.g., *Coelophysis*, Fig. 8c) indicates a highly constrained

locomotor posture in which the femur cannot undergo axial rotation but is instead "locked" into protraction and retraction. The basal theropod morphology is termed the "obligate parasagittal" hip joint.

Basal theropods retained the cartilage cone trough on the subchondral growth plate of the proximal femur, although the trough is considerably shallower and less distinct compared to those of silesaurids. The shallowness of the trough indicates a reduction in the cartilage cone's insertion into the metaphysis. Reduction of the cartilage cone in theropods is not associated with a gain in growth plate rugosities, as the case of sauropodomorphs. The smooth growth plate texture indicates that basal theropods possess relatively thin epiphyseal cartilage compared to sauropodomorphs. Using the cartilage cap reconstruction of adult *Struthio*, a 240 mm *Coelophysis* femur would possess a cartilage cap 5.6 ± 2.0 mm in thickness on its proximal end. In contrast, cartilage reconstruction based on *Alligator* reconstructs a 7.6 ± 2.0 mm cartilage cap. The two alternative reconstruction schemes are presented here as the minimal- and maximal estimates of proximal femoral articular cartilage thickness in *Coelophysis*. The articular surface on the proximal femur is reconstructed here as a convex surface, in which the reconstructed epiphyseal cartilage fills in the cartilage cone trough, because the proximal femur of taxa bracketing basal theropods (basal dinosauromorphs and tetanurans) possess convex subchondral and articular surfaces.

In basal theropods, the loss of femoral axial rotation is facilitated by both musculoskeletal transitions as well as shifting roles of ancestral hip joint soft tissues. The femoral head inserts into the acetabulum craniomedially and is confined laterally by the ventrolaterally oriented supraacetabular rim (Fig. 8c). This morphology indicates that the iliofemoral ligament no longer functions to constrain femoral lateral rotation as in basal dinosauromorphs. Instead, the

iliofemoral ligament stabilizes the proximal femur laterally during hip protraction and retraction. Moreover, the proximal femur of basal theropods possesses a distinct metaphyseal collar, which forms the ventral half of the capital and lateral portion of the femoral head. This morphology indicates that the fibrocartilage sleeve attaches extensively to the metaphysis, such that the entire ventral half of the femoral head consists of a fibrocartilaginous articular surface. This capital expansion of the fibrocartilage sleeve is inferred to prevent avulsion of the hyaline cartilage core from the subchondral growth plate of the femoral head during femoral protraction and retraction. Additionally, whereas the hyaline cartilage on the apical proximal femur articulates with the labrum on the acetabular "ceiling", the fibrocartilage sleeve on the trochanteric region articulates with the unexpanded, craniolaterally facing antitrochanter. The craniomedially deflected femoral head allows the distal condyles to remain perpendicular to the craniocaudal axis of the animal during femoral protraction and retraction. Lastly, the amount of femoral head displacement is inferred to be constrained by the intrinsic joint ligaments. We reconstructed the ventral joint ligaments within the hip joint capsule based on the presence of a fully perforated inner acetabular wall. In particular, the ischiofemoral ligament is inferred to function as an internal constraint to femoral head displacement during femoral retraction. During femoral retraction, the fovea capitis is displaced craniad relative to the ischium, suggesting that the ischiofemoral ligament is stretched during this posture. Overall, our results show that transitions in hip joint soft tissue morphology in basal theropods facilitated the evolution of a obligate parasagittal hip posture, as inferred by Carrano (2000).

CONCLUSION

The evolutionary history of Dinosauromorpha is characterized by multiple, iterative convergences and divergences in hip joint anatomy. Both theropods and sauropodomorphs

independently evolved intrinsic hip joint ligaments, which constrained femoral head movement during hip excursion. Moreover, theropods and sauropodomorphs independently modified the fibrocartilage sleeve to provide mechanical support for thick layer of femoral hyaline cartilage. Among saurischians, sauropodomorphs underwent swift, concerted evolutionary transitions in femoral and acetabular soft tissues within the basal lineage ("prosauropods"), culminating in the highly conserved sauropod morphology. The sauropod hip joint is characterized by a highly cartilaginous femoral head and a reduction in the femoral neck-antitrochanter articulation. In contrast, basal theropods evolved a highly constrained femoral posture in which abduction and axial rotation is greatly reduced, before undergoing several clade-specific combinations of character transitions among major radiations. The theropod hip joint is characterized by a thinner layer of hyaline cartilage on the femoral head and the retention of femoral neck-antitrochanter articulation. These data indicate highly divergent locomotor adaptations within Dinosauromorpha, worthy of additional phylogenetic and functional analyses.

LITERATURE CITED

Allen, V., H. Paxton, and J. R. Hutchinson. 2009. Variation in center of mass estimates for extant sauropsids and its importance for reconstructing inertial properties of extinct archosaurs. The Anatomical Record 292:1442–1461.

Barrett, P. M., S. J. Nesbitt, and B. R. Peecook. 2015. A large-bodied silesaurid from the Lifua member of the Manda beds (Middle Triassic) of Tanzania and its implications for body-size evolution in Dinosauromorpha. Gondwana Research 27: 925–931.

Bates, K. T., R. B. J. Benson, and P. L. Falkingham. 2012. A computational analysis of locomotor anatomy and body mass evolution in Allosauroidea (Dinosauria: Theropoda). Paleobiology 38:486–507.

Bates, K. T., S. C. R. Maidment, V. Allen, and P. Barrett. 2012. Computational modeling of locomotor muscle moment arms in the basal dinosaur *Lesothosaurus diagnosticus*: assessing convergence between birds and basal ornithischians. Journal of Anatomy 220:212–232.

Bates, K. T., E. R. Schachner. 2012. Disparity and convergence in bipedal archosaur locomotion. Journal of the Royal Society, Interface 9:1339–1353.

Baumel, J., and R. Raikow. 1993. Arthrologia. pp. 133–188. in Publications of the Nuttall Ornithological Club. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed., Vol. 23.

Baumel J., and L. Witmer. 1993. Osteologia. pp. 45–132. in Publications of the Nuttall Ornithological Club. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed., Vol. 23.

Benson, R. B. J., and J. N. Choiniere. 2013. Rates of dinosaur limb evolution provide evidence for exceptional radiation in Mesozoic birds. Proceedings of the Royal Society B: Biological Sciences 280:20131780.

Benson, R. B. J., N. E. Campione, M. T. Carrano, P. D. Mannion, C. Sullivan, P. Upchurch, and D. C. Evans. 2014. Rates of Dinosaur Body Mass Evolution Indicate 170 Million Years of Sustained Ecological Innovation on the Avian Stem Lineage. PLoS Biology 12:e1001853.

Bonaparte, J. F. 1975. Nuevos materiales de *Lagosuchus talampayenis* Romer (Thecodontia-Pseudosuchia) y su significado en el origen de los Saurischia: Chañarense inferior, Triásico medio de Argentina. Acta Geologica Lilloana 13:1–90.

Bonaparte, J. F., F. Novas, and R. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Contributions in Science. Natural History Museum of Los Angeles County 416:1–42.

Bonnan, M. F., J. L. Sandrik, T. Nishiwaki, D. R. Wilhite, R. M. Elsey, and C. Vittore. 2010. Calcified cartilage shape in archosaur long bones reflects overlying joint shape in stress-bearing elements: Implications for nonavian dinosaur locomotion. The Anatomical Record 293:2044–2055.

Bonnan, M. F., D. R. Wilhite, S. L. Masters, A. M. Yates, C. K. Gardner, and A. Aguiar. 2013. What Lies beneath: Sub-articular long bone shape scaling in eutherian mammals and saurischian dinosaurs suggests different locomotor adaptations for gigantism. PLoS ONE. 8. e75216. doi: 10.1371/journal.pone.0075216.

Brochu, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Journal of Vertebrate Paleontology 22:1–138.

Brown J., J. Rest, J. Garcia-Moreno, M. Sorenson, and D. Mindell. 2008. Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. BMC Biology 6:6.

Brusatte, S. L., M. J. Benton, J. B. Desojo, and M. C. Langer. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). Journal of Systematic Palaeontology 8:3–47.

Brusatte, S. L., S. J. Nesbitt, R. B. Irmis, R. J. Butler, M. J. Benton, and M. A. Norell. 2010. The origin and early radiation of dinosaurs. Earth-Science Reviews 101:68–100.

Buffrénil, V., I. Ineich, and W. Bohme. 2004. Comparative data on epiphyseal development in the family varanidae. Journal of Herpetology 39:328–335.

Butler, R. J. 2010. The anatomy of the basal ornithischian dinosaur *Eocursor parvus* from the lower Elliot Formation (Late Triassic) of South Africa. Zoological Journal of the Linnean Society 160:648–684.

Butler, R. J., J. Liyong, C. Jun, and P. Godefroit. 2011. The postcranial osteology and phylogenetic position of the small ornithischian dinosaur *Changchunsaurus parvus* from the Quantou Formation (Cretaceous: Aptian–Cenomanian) of Jilin Province, north-eastern China. Palaeontology 54:667–683.

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

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

Carrano, M. T. 2005. The evolution of sauropod locomotion; pp. 229–249 In: K. C. Curry Rogers and J. Wilson (eds.), The sauropods: evolution and paleobiology. University of California Press, Berkeley. Berkeley, CA.

Carrano, M. T., and S. D. Sampson. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 6:183–236.

Carrano, M. T., R. B. Benson, and S. D. Sampson. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10:211–300.

Carter, D. R. 1987. Mechanical loading history and skeletal biology. Journal of Biomechanics 20:1095–1109.

Carter, D. R., B. Mikic, and K. Padian. 1998. Epigenetic mechanical factors in evolution of long bone epiphyses. Zoological Journal of the Linnean Society 123:163–178.

Carter, D. R., and M. Wong. 2003. Modeling cartilage mechanobiology. Philosophical Transactions of the Royal Society B: Biological Sciences 358:1461–1471.

Carter, D. R., and G. S. Beaupré. 2007. Skeletal function and form: mechanobiology of skeletal development, aging, and regeneration: Cambridge University Press. Cambridge.

Chatterjee, S., and R. J. Templin. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. Proceedings of the National Academy of Sciences 104:1576–1580.

Christiansen, P., and R. A. Fariña. 2004. Mass prediction in theropod dinosaurs. Historical Biology 16:85–92.

Clarke, J. A., C. P. Tambussi, J. I. Noriega, G. M. Erickson, and R. A. Ketcham. 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. Nature 433:305–308.

Clarke, J. A., Z. Zhou, and F. Zhang. 2006. Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. Journal of Anatomy 208:287–308.

Cope, E. 1878. On the saurians recently discovered in the Dakota Beds of Colorado. American Naturalist 12: 71–85.

Cracraft, J. 1971. The functional morphology of the hind limb of the domestic pigeon, *Columba livia*. Bulletin of the American Museum of Natural History144:175–268.

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology 23:556–574.

Erickson, G. M. 2005. Assessing dinosaur growth patterns: a microscopic revolution. Trends in Ecology and Evolution 20:677–684.

Erickson, G. M., K. C. Rogers, D. J. Varricchio, M. A. Norell, and X. Xu. 2007. Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition. Biology Letters 3:558–561.

Ericson, P. G., C. L. Anderson, T. Britton, A. Elzanowski. U. S. Johansson, M. Källersjö, J. I. Ohlson. T. J. Parsons, D. Zuccon. and G. Mayr. 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biology Letters 2:543–547.

Ezcurra, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28:649–684.

Ezcurra, M. D., T. M. Scheyer and R. J. Butler. 2014. The Origin and early evolution of Sauria: Reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS ONE 9:e89165.

Falkingham, P. L. 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. Palaeontologia electronica 15:1-15.

Firbas, W. and K. Zweymüller. 1971. Über das Hüftgelenk der Ratiten. Gegenbaurs Morphologisches Jahrbuch 116:91–103.

Fujiwara, S. I., H. Taru, and D. Suzuki. 2010. Shape of articular surface of crocodilian (Archosauria) elbow joints and its relevance to sauropsids. Journal of Morphology 271:883-896.

Galton, P. M. 1969. The pelvic musculature of the dinosaur Hypsilophodon (Reptilia: Ornithischia). Postilla:1–64.

Galton, P. M., and M. A. Cluver. 1976. *Anchisaurus capensis* (Broom) and a revision of the Anchisauridae (Reptilia, Saurischia). Annals of the South African Museum 69:121–159.

Galton, P. M. 1977. On *Staurikosaurus pricei,* an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. Paläontologische Zeitschrift 51:234–245.

Gatesy, S.M., M. Bakder, and J. R. Hutchinson. 2009. Constraint-based exclusion of limb poses for reconstructing theropod dinosaur locomotion. Journal of Vertebrate Paleontology 29:535–544.

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

Gatesy, S.M., and K. M. Middleton. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. Journal of Vertebrate Paleontology 17:308–329.

Gervais, P. 1872. Ostéologie du *Sphargis luth*. Nouvelles Archives du Muse um d'Histoire Maturelle 8: 199–228.

Gilmore, C. W. 1920. Osteology of the carnivorous Dinosauria in the United State National museum: with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bulletin of the United States National Museum 110:1–159.

Godefroit, P., A. Cau, H. Dong-Yu, F. Escuillié, W. Wenhao, and G. Dyke. 2013. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. Nature 498:359–362.

Grillo, O. N., and S. A. Azevedo. 2011. Pelvic and hind limb musculature of *Staurikosaurus pricei* (Dinosauria: Saurischia). Anais da Academia Brasileira de Ciências 83:73–98.

Haines, R. W. 1938. The Primitive form of epiphysis in the long bones of tetrapods. Journal of Anatomy 72:323–343.

Haines, R. W. 1941. Epiphyseal structure in lizards and marsupials. Journal of Anatomy 75:282–294.

Haines, R. W. 1942. Evolution of epiphyses and of endochondral bone. Biological Reviews 17:262–292.

Haines, R. W. 1975. The histology of epiphyseal union in mammals. Journal of Anatomy 120:1-25.

Hainsworth, F. R., and L. L. Wolf. 1972. Power for hovering flight in relation to body size in hummingbirds. American Naturalist 106: 589–596.

Hall, B. K. 2005. Bones and cartilage: developmental and evolutionary skeletal biology: Academic Press.

Hartman. S., D. Lovelace, and W. Wahl. 2005. Phylogenetic assessment of a maniraptoran from the Morrison Formation. Journal of Vertebrate Paleontology 25, Supplement to No. 3: 67A–68A.

Hay, O. 1908. On the habits and pose of the sauropodus dinosaurs, especially of *Diplodocus*. American Naturalist 42:672–681.

Heers, A. M., and K. P. Dial. 2015. Wings versus legs in the avian bauplan: Development and evolution of alternative locomotor strategies. Evolution 69:305–320.

Hertel, F., and K. E. Campbell. 2007. The antitrochanter of birds: form and function in balance. Auk 124: 789–805.

Holliday, C. M., R. C. Ridgely, J. C. Sedlmayr, and L. M. Witmer. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. PLoS ONE 5(9): e13120. doi: 10.1371/journal.pone.0013120.

Hone, D. W. E., A. A. Farke, and M. J. Wedel. 2016. Ontogeny and the fossil record: what, if anything, is an adult dinosaur? Biology Letters 12. doi: 10.1098/rsbl.2015.0947.

Hutchinson, J. R., and Allen, V. 2009. The evolutionary continuum of limb function from early theropods to birds. Naturwissenschaften 96:423–448.

Hutchinson, J. R., F. C. Anderson, S. S. Blemker, and S. L. Delp. 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model. Paleobiology 31:676–701.

Hutchinson, J. R. 2001. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zoological Journal of the Linnean society 131:169–197

Hutchinson, J. R. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zoological Journal of the Linnean society 131:123–168.

Huxley, T. 1870. Further evidence of the affinity between the dinosaurian reptiles and birds. Quarterly Journal of the Geological Society Scientific Memoirs III:12–13.

Kurzanov, S. 1981. An unusual theropod from the Upper Cretaceous of Mongolia. Joint Soviet-Mongolian Paleontological Expedition 15:39–49.

Kuznetsov, A. N., and A. G. Sennikov. 2000. On the Function of a Perforated Acetabulum in Archosaurs and Birds. Paleontological Journal 34:439–448.

Langer, M. C., and J. Ferigolo. 2013. The Late Triassic dinosauromorph *Sacisaurus agudoensis* (Caturrita Formation; Rio Grande do Sul, Brazil): anatomy and affinities. Geological Society, London, Special Publications 379:353–392.

Langer, M. C., S. J. Nesbitt, J. S. Bittencourt, and R. B. Irmis. 2013. Non-dinosaurian Dinosauromorpha. Geological Society, London, Special Publications 379.

Langer, M. C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). PaleoBios. 23:1–30

Lee, A. H., and S. Werning. 2008. Sexual maturity in growing dinosaurs does not fit reptilian growth models. Proceedings of the National Academy of Sciences 105:582–587.

Lee, M. S. Y., A. Cau, D. Naish, and G. J. Dyke. 2014. Sustained miniaturization and anatomical innovation in the dinosaurian ancestors of birds. Science 345:562–566.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50:913–925.

Maddison, W. P., and D. R. Maddison. 2015. Mesquite: a modular system forevolutionary analysis. Version 3.02. http://mesquiteproject.org

Maidment, S. C., and P. M. Barrett. 2012. Does morphological convergence imply functional similarity? A test using the evolution of quadrupedalism in ornithischian dinosaurs. Proceedings of the Royal Society B: Biological Sciences 279:3765–3771.

Maidment, S. C., and P. M. Barrett. 2014. Osteological correlates for quadrupedality in ornithischian dinosaurs. Acta Palaeontologica Polonica 59:53–70.

Makovicky, P. J., and L. E. Zanno. 2011. Theropod diversity and the refinement of avian characteristics. In: G. Dyke, G. Kaier (eds.), Living Dinosaurs: the evolutionary history of modern birds. Oxford, UK. John Wiley & Sons, Ltd. pp. 9–39.

Mallison, H. 2010. CAD assessment of the posture and range of motion of *Kentrosaurus* aethiopicus Hennig 1915. Swiss Journal of Geosciences 103:211–233.

Mallison, H. 2010. The digital *Plateosaurus* I: body mass, mass distribution, and posture assessed using CAD and CAE on a digitally mounted complete skeleton. Palaeontologia Electronica 13 (2, 8A): 26.

Mallison, H. 2010. The digital *Plateosaurus* II: an assessment of the range of motion of the limbs and vertebral column and of previous reconstructions using a digital skeletal mount. Acta Palaeontologica Polonica 55:433–458.

Mallison, H. and O. Wings. 2014. Photogrammetry in paleontology—a practical guide. J Paleontol Tech 12:1–31.

Marsh, O. 1896. The dinosaurs of North America. USGS 16th Ann Rep 1894–1895:133–244.

Martínez, R. N. 2009. *Adeopapposaurus mognai*, gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. Journal of Vertebrate Paleontology 29:142–164.

Martínez, R. N., and O. A. Alcober. 2009. A Basal Sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the Early Evolution of Sauropodomorpha. PLoS ONE 4:e4397.

Martínez, R. N., P. C. Sereno, O. A. Alcober, C. E. Colombi, P. R. Renne, I. P. Montañez, and B. S. Currie. 2011. A Basal Dinosaur from the Dawn of the Dinosaur Era in Southwestern Pangaea. Science 331:206–210.

Maryańska, T., and H. Osmólska, Wolsan M. 2002. Avialan status for Oviraptorosauria. Acta Palaeontologica Polonica 47:97–116.

Müller, R. T., M. C. Langer, S. F. Cabreira, and S. Dias-da-Silva. 2015. The femoral anatomy of *Pampadromaeus barberenai* based on a new specimen from the Upper Triassic of Brazil. Historical Biology:1–10.

Nesbitt, S. J., R. B. Irmis, W. G. Parker, N. D. Smith, A. H. Turner, and T. Rowe. 2009. Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. Journal of Vertebrate Paleontology 29:498–516.

Nesbitt, S. J., C. A. Sidor, R. B. Irmis, K. D. Angielczyk, R. M. Smith, and L. A. Tsuji. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. Nature. 464: 95–98.

Nesbitt, S. J. 2011. The early evolution of Archosaurs: Relationship and the origin of major clades. Bulletin of the American Museum of Natural History 352: 1–292.

Nicholls, E. L., and A. P. Russell. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). Palaeontology 28:643–677.

Norman, D. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). Institut Royal des Sciences Naturelles de Belgique Memoire 178:1–103.

Novas, F. E., M. D. Ezcurra, S. Chatterjee, and T. Kutty. 2010. New dinosaur species from the Upper Triassic upper Maleri and lower Dharmaram formations of Central India. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 101:333–349.

Novas, F. E. 1994. New Information on the Systematics and Postcranial Skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. Journal of Vertebrate Paleontology 13:400–423.

Novas, F. E. 1996. Dinosaur monophyly. Journal of Vertebrate Paleontology 16:723–741.

Osmólska, H., E. Roniewicz, and R. Barsbold. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp.(Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 27:103–143.

Padian, K. 1986. On the type material of Coelophysis Cope (Saurischia: Theropoda) and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation). The Beginning of the Age of Dinosaurs Cambridge University Press, Cambridge:45–60.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology 48:612–622.

Parrish, J. M. 1986. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. Hunteria 1: 1–35.

Parrish, J. M. 1987. The Origin of Crocodilian locomotion. Paleobiology 12:396–414.

Phillips, M. J. G. C. Gibb, E. A. Crimp, and D. Penny. 2010. Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. Systematic Biology 59:90–107.

Romer, A. S. 1923. The pelvic musculature of saurischian dinosaurs. Bulletin of the American Museum of Natural History 48: 605–617.

Romer, A. S. 1927. The development of the thigh musculature of the chick. J Morph. 43: 347–385.

Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology 9:125–136.

Sander, P. M., A. Christian, M. Clauss, R. Fechner, C. T. Gee, E-M. Griebeler, H-C. Gunga, J. Hummel, H. Mallison, S. F. Perry, H. Preuschoft, O. W. M. Rauhut, K. Remes, T. Tütken, O. Wings, and U. Witzel. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. Biological Reviews 86:117–155.

Schluter, D., T. Price, A. Ø. Mooers, and D. Ludwig. 1997. Likelihood of ancestor states in adaptive radiation. Evolution:1699–1711.

Schwarz, D., O. Wings, and C. Meyer. 2007. Super sizing the giants: first cartilage preservation at a sauropod limb joint. Journal of the Geological Society of London 164:61–65.

Sereno, P. C., and A. B. Arcucci. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. Journal of Vertebrate Paleontology 14:53–73.

Sereno, P. C. 1991. *Lesothosaurus*, "fabrosaurids," and the early evolution of Ornithischia. Journal of Vertebrate Paleontology 11:168–197.

Snover, M. L., A. G. J. Rhoudin. 2008. Comparative Ontogenetic and Phylogenetic Aspects of chelonian chondro-osseus growth and skeletochronology. In: J. Wyneken (eds.), Biology of Turtles. Boca Raton, FL: CRC Press. p 22–39.

Stein, K., Z. Csiki, K. C. Rogers, D. B. Weishampel, R. Redelstorff, J. L. Carballido, and P. M. Sander. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Proc Nat Acad Sci. 107: 9258–9263.

Stolpe, M. 1932. Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. Journal of Ornithology 80: 161–247.

Sues, H-D., S. J. Nesbitt, D. S. Berman, and A. C. Henrici. 2011. A late-surviving basal theropod dinosaur from the latest Triassic of North America. Proceedings of the Royal Society B: Biological Sciences 278:3459–3464.

Thulborn, R. 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus* australis. Palaeontology 15:29–60.

Tidwell, V., K. Stadtman, and A. Shaw. 2005. Age-related characteristics found in a partial pelvis of *Camarasaurus*. In: V. Tidwell, K. Carpenter (eds.), Thunder-lizards: the Sauropodomorph Dinosaurs. Bloomington, IN. Indiana University Press. pp 180–186.

Tsai, H. P., and C. M. Holliday. 2015. Articular soft tissue anatomy of the archosaur hip joint: Structural homology and functional implications. Journal of Morphology 276: 601–630.

Turner, A. H., D. Pol, J. A. Clarke, G. M. Erickson, and M. A. Norell. 2007. A basal dromaeosaurid and size evolution preceding avian flight. Science 317: 1378–1381.

Turner, A. H., P. J. Makovicky, and M. A. Norell. 2012. A Review of Dromaeosaurid Systematics and Paravian Phylogeny. Bulletin of the American Museum of Natural History: 1–206.

Wess, T. J, L. Wess, and P. M. Hocking. 1997. The structure of avian cartilage: A combined X-ray and biochemical analysis. Journal of Comparative Pathology 116: 145–155.

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Journal of Vertebrate Paleontology: Society of Vertebrate Paleontology Memoirs 4(18): 1–79.

Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society 136: 215–275.

Wilson, J. A., and M. T. Carrano. 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology 25: 252–267.

Wilson, J. A. 2005. Overview of sauropod phylogeny and evolution. In: K. A. Curry Rogers, J. A. Wilson (eds.), The Sauropods: Evolution and Paleobiology. Berkeley, CA. University of California Press: pp. 15–49.

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

Xu, X., Q. Ma, and D. Hu. 2010. Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins. Chinese Science Bulletin 55: 3971–3977.

Xu, X., H. You, K. Du, and F. Han. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. Nature 475: 465–470.

Yates, A. M., and J. W. Kitching. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. Proceedings of the Royal Society of London B: Biological Sciences 270: 1753–1758.

Yates, A. M., M. F. Bonnan, J. Neveling, A. Chinsamy, and M. G. Blackbeard. 2010. A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. Proceedings of the Royal Society of London B: Biological Sciences 277 (1682): 787–794.

Zeigler, K. E., A. B. Heckert, and S. G. Lucas. 2003. An illustrated atlas of the phytosaur (Archosauria, Parasuchidae) postcrania from the Upper Triassic Snyder Quarry (Petrified Forest Formation, Chinle Group): New Mexico Museum of Natural History and Science. Bulletin 24: 89–103.

Table 1. Anatomical abbreviations.

att	antitrochanter	l. ilf	iliofemoral ligament
brs	bursa	l. isf	ischiofemoral ligament
cc	calcified cartilage	l. pf	pubofemoral ligament
cd. med	medial condyle		
cd. lat	lateral condyle	m. istr	*m. ischiotrochantericus*
c. mp	metaphyseal collar	mb. act	acetabular membrane
cn	cartilage cone	pb	pubis
fm	femur	ppi	pubic peduncle of ilium
fov	fovea capitis	pcf	peripheral collagen fiber
fc	fibrocartilage	pd. pb	pubic peduncle of ilium
gp	growth plate	pd. is	ischial peduncle of ilium
hc	hyaline cartilage		
hcc. att	Antitrochanter hyaline cartilage core	r. cp	capital region
il	ilium	r. tr	trochanteric region
is	ischium	s. a	articular surface
lab	acetabular labrum	sc. isf	ischiofemoral ligament sulcus
l. cf	ligamentum capitis femoris	tr. cn	cartilage cone trough

Table 2. Osteological correlates of hip joint soft tissues.

Soft tissue structure	Osteological correlates
Iliofemoral ligament: Origin	Craniodorsal acetabular rim (pubic peduncle of ilium).
Iliofemoral ligament: Insertion	Craniolateral metaphyseal collar of the proximal femur.
Acetabular labrum	Ventral side of supraacetabular rim (cranial portion of acetabular roof).
Acetabular membrane	Unossified inner acetabular wall (the inner acetabular foramen).
Antitrochanter fibrocartilage	Laterally oriented surface of the bony antitrochanter; surface of antitrochanter hyaline cartilage core.
Antitrochanter hyaline cartilage core	Growth plate surfaces of the ilio- and ischial peduncles (archosaur).
Pubofemoral ligament: Origin	Cranioventral (pubic) rim of the inner acetabular foramen.
Ischiofemoral ligament: Origin	Caudoventral (ischial) rim of the inner acetabular foramen.
Ischiofemoral ligament: Passage	Ischiofemoral ligament sulcus on the proximal femoral metaphysis.
Ligamentum capitis femoris: Insertion (confluence of pubofemoral and ischiofemoral ligaments)	Cranial surface of the posteromedial tuber (plesiomorphic); flat or concave surfaces on the femoral head (Aves and some coelurosaurs).
Expanded metaphyseal attachment for fibrocartilage sleeve	Striated, elevated cortical bone surface on the metaphysis.
Hyaline cartilage core	Calcified cartilage-covered growth plate overlying subchondral trabecular bone.
Thick layer of hyaline cartilage	Irregularly rugose growth plate surface.
Extension of the cartilage cone into the metaphyseal growth plate	Longitudinal groove on the proximal femoral growth plate surface.
Synovial bursa	Exposed patch of metaphyseal trabecular bone surrounded by cortical bone.

Figure 1. **A.** 3D surface model of a *Liliensternus* right pelvis (MB.R 2175, all elements except pubis are mirrored) in lateral view. **B.** Schematic representation of acetabular soft tissues (black dotted inset in A), excluding joint ligaments. **C**. 3D surface model of the associated *Liliensternus* right femur (mirrored) in cranial, medial, and proximal views. Relative orientation between the femoral head-greater trochanter axis (green labels) and the mediolateral axis of the distal condyles (red labels) determines the orthogonal reference planes used to describe anatomical structures, shown as dotted lines in proximal views of each femur. The cranio-trochanteric plane in represented in green, mediolateral plane in red, craniocaudal plane in blue. **D.** Schematic representation of proximal femoral soft tissues (black dotted inset in **C**), excluding joint ligaments. Tissue nomenclature and color schemes are labeled according to homology inferences in Tsai and Holliday (2015).

Figure 2. Simplified topologies of phylogenetic trees used in this study. **A.** The consensus phylogenetic tree based on published studies (Archosauromorpha, Ezcurra et al., 2014; Archosauriformes, Brusatte et al., 2010a; Nesbitt, 2011; Dinosauromorpha, Langer et al., 2013; Sauropodomorpha, Wilson, 2005; Martínez and Alcober, 2009; Theropoda, Carrano et al., 2012; Paraves, Hartman et al., 2005; Turner et al., 2012; Xu et al., 2010; Aves, Clarke et al., 2005; Erickson et al., 2006; Brown et al., 2008; Phillips et al., 2010). **B.** Alternate placement of Silesauridae as stem ornithischians (Langer and Ferigolo, 2013). **C.** Alternate placement of Herrerasauridae as the sister taxon to Theropoda + Sauropodomorpha (Novas et al., 2010). **D.** Alternate placement of *Eoraptor* as a basal theropod, rather than as a basal sauropodomorph (Sues et al., 2011). **E.** Alternate placement of *Archaeopteryx* as a stem-deinonychosaur, rather than as the basal-most avialan (Xu et al., 2011; Godefroit et al., 2013).

Figure 3. Osteological correlates of dinosauromorph acetabulae in left lateral view. **A.** *Asilisaurus* (NMT RB 159). Pubis and ischium mirrored from contralateral elements. Scale is 12.3 mm. **B.** *Panphagia* (PVSJ 874). Scale is 12.8 mm **C.** *Plateosaurus* (GPIT 1), scale is 80 mm. **D.** *Diplodocus* (CM94). Ischium mirrored from the contralateral element. Scale is 200 mm. **E.** *Herrerasaurus* (MCZ 438). Scale is 23.8 mm. **F.** *Piatnitzkysaurus* (MACN CH 895). Ischium mirrored from contralateral element. Scale is 70 mm. **G**. *Allosaurus* (UMNH VP 2560). Scale is 127 mm. **H.** *Khaan* (IGM 100-1002). Articulated pelvis and femur mirrored from contralateral elements. Scale is 29 mm. **I.** *Utahraptor* (BYU 7510-10073). Ilium mirrored from contralateral element. Scale is 50 mm.

Figure 4. Osteological correlates of the acetabular labrum and antitrochanter. All pelves shown in left ventral view. **A.** *Sarahsaurus* (TMM 43646). Scale is 29 mm **B.** *Apatosaurus* (YPM 1987). Scale is 135 mm. **C.** *Dilophosaurus* (TMM 43246). Scale is 25 mm. **D.** *Allosaurus* (UMNH VP 8119). Ilium mirrored from the contralateral element. Scale is 35 mm. **E.** *Tyrannosaurus* (FMNH PR 2081). Scale is 126 mm. **F.** *Bambiraptor* (FIP 001). Scale is 8.4 mm.

Figure 5. Osteological correlates of the antitrochanteric cartilages. All pelves shown in left lateral view. Soft tissue attachments are preceded by an asterisk (*). **A.** *Apatosaurus* (3D model of FMNH 25112, photograph of CM 83). Scale is 260 mm. **B.** Coelophysoidae (Reconstructed based on 3D surface models of *Coelophysis* UCMP 129618 and *Liliensternus* M.Br. 2175). Scale is 23 mm. **C.** *Tyrannosaurus* (FMNH PR 2081). Scale is 173 mm. **D.** *Falcarius* (UMNH VP 12368 ilium, 12375 ischium, 12539 pubis). Scale is 40 mm.

Figure 6. Osteological correlates of the proximal femur in lateral/cranial (A-H) and capital (I-P) views. Soft tissue attachments are preceded by an asterisk (*). **A.** *Dromomeron* (GR 218). Scale is 6.3 mm. **B.** *Silesaurus* (PEFO 34343, mirrored). Scale is 15.1 mm. **C.** *Plateosaurus* (SMNS F 14-91294). Scale is 60 mm. **D.** *Alamosaurus* (TMM 41541). Scale is 163.1 mm. **E.** *Coelophysis* (UCMP 129618). Scale is 20.3 mm. **F**. *Allosaurus* (UMNH VP 8119). Scale is 79.4 mm. **G.** *Falcarius* (UMNH VP 12361) Scale is 26.0 mm. **H.** *Deinonychus* (MCZ 4371). Scale is 27.7 mm. **I.** *Eucoelophysis* (GR 195, mirrored). Scale is 13.6 mm. **J**. *Plateosaurus* (SMNS F 14-91294). Scale is 60 mm. **K**. *Diplodocus* (DMNH 462). Scale is 107.1 mm. **L.** *Liliensternus* (MB.R. 2175, mirrored). Scale is 28.8 mm. **M**. *Piatnitzkysaurus* (MACN CH 895). Scale is 39.6 mm. **N**. *Coelurus* (YPM 2010). Scale is 10.8 mm. **O**. *Anzu* (CM 78000). Scale is 41.4 mm. **P.** *Deinonychus* (MCZ 4371). Scale is 27.7 mm. Foveae capitis of *Eucoelophysis*, *Plateosaurus*, and *Diplodocus* are obscured by the thick hyaline cartilages inferred for these taxa.

Figure 7. Osteological correlates of the proximal femur in medial/caudal (A-H) and proximal (I-P) views. Soft tissue attachments are preceded by asterisk (*). **A**. *Dromomeron* (GR 218). Scale is 6.3 mm. **B**. *Asilisaurus* (NMT RB159, mirrored). Scale is 10.9 mm. **C**. *Plateosaurus* (SMNS F 14-91294). Scale is 60 mm. **D.** *Camarasaurus* (YPM 4625, mirrored). Scale is 157.0 mm. **E**. *Herrerasaurus* (PVSJ 373). Scale is 24.7 mm. **F**. *Tyrannosaurus* (FMNH PR 2081). Scale is 155.0 mm. **G**. *Ornithomimus* (RAM 6794). Scale is 23.9 mm. **H.** *Anzu* (CM 78000). Scale is 38.8 mm. **I**. *Velociraptor* (IGM 100/986, modified from Norell and Makovicky, 1999). Scale is 13.4 mm. **J**. *Dromomeron* (GR 218). Scale is 6.3 mm. **K.** *Silesaurus* (PEFO 34343, mirrored). Scale is 12.6mm. **L**. *Plateosaurus* (SMNS F 14-91294). Scale is 60 mm. **M**. *Camarasaurus* (DNM 4514, mirrored) Scale is 162.4 mm. **N**. *Staurikosaurus* (MCZ 1669). Scale is 13.2 mm. **O**. *Ceratosaurus* (UMNH VP 5728). Scale is 65.1 mm. **P**. *Coelurus* (YPM 2010). Scale is 14.9 mm. **Q**. *Anzu* (CM 78000). Scale is 38.8 mm. Foveae capitis of *Asilisaurus*, *Plateosaurus*, and *Camarasaurus* are not shown due to the thick hyaline cartilage attachment in these taxa.

Figure 8. Hip joint soft tissue reconstructions of dinosauriformes. All elements represent the left side. Acetabular sectional planes are marked by red dotted line. Femur is shown articulated but not sectioned. Tissues are labeled and color-coded based on inferred homology in Tsai and Holliday (2015). Cut surfaces of bones and ligaments are marked by † before the labels. **A**. *Asilisaurus*. Caudal section is shown in cranial view. **B**. *Plateosaurus*. Acetabular membrane is removed in medial view. Femur is shown articulated with the pelvis in medial view. C. Coelophysoidae, reconstructed based on *Coelophysis* and *Liliensternus*. Magnified region of the proximal femur is indicated by red dotted box. Acetabular membrane is removed in medial view. Femur is shown articulated with the pelvis in medial view. Cranial section is shown in caudal view.

Figure 9. Evolutionary history of the hip joint characters in the dinosauromorph stem lineage based on the consensus phylogenetic tree (Fig. 2a). All character states are inferred to be absent in outgroup dinosauromorphs, here represented by *Lagerpeton*. Presence of character states are represented by +. Absence of character states are represented by -. Ambiguous character states are represented by ? and are highlighted in gray. Silhouettes of taxa depicted here are provided by S. Hartman, J. Headden, and N. Tamura.