**ARCHOSAUR HIP JOINT ANATOMY AND ITS SIGNIFICANCE IN BODY
SIZE AND LOCOMOTOR EVOLUTION**

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APPROVAL PAGE

The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

**ARCHOSAUR HIP JOINT ANATOMY AND ITS SIGNIFICANCE IN BODY SIZE
AND LOCOMOTOR EVOLUTION**

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Table of Contents

LIST OF FIGURES AND ILLUSTRATIONS.....	vi
LIST OF TABLES.....	viii
ABSTRACT.....	1
CHAPTER 1: Introduction: The evolving view of saurischian locomotion.....	2
CHAPTER 2:	15
INTRODUCTION.....	15
MATERIALS AND METHODS	19
RESULTS.....	24
DISCUSSION	36
CONCLUSION	52
CHAPTER 3: Articular soft tissue anatomy of the archosaur hip joint: Structural homology and functional implications.....	79
INTRODUCTION.....	79
MATERIALS AND METHODS	82
RESULTS.....	86
DISCUSSION	114
CONCLUSION	137
CHAPTER 4: Convergence and disparity in saurischian dinosaur hip joints associated with gigantism.....	159
INTRODUCTION.....	159
MATERIALS AND METHODS	162
RESULTS.....	171
DISCUSSION	175
CONCLUSION	187
CHAPTER 5: Summary.....	212
LITERATURES CITED.....	215
VITA.....	239

LIST OF FIGURES AND ILLUSTRATIONS

Figure 1-1. Simplified phylogeny of Saurischia and its successive diapsid outgroups.

Figure 2-1. Evolutionary relationships of the tetrapod epiphyseal region and their anatomical nomenclature.

Figure 2-2. Orthogonal reference planes used to describe anatomical structures on the proximal femur of extant archosaurs.

Figure 2-3. Schematic representation of hip joint tissues homology in Diapsida.

Figure 2-4. Gross morphology of lepidosaur acetabular soft tissues.

Figure 2-5. Microstructure of lizard supraacetabular tissues.

Figure 2-6. Gross morphology of the crocodylian acetabulum and microstructure of the acetabular labrum.

Figure 2-7. Morphology of the *Alligator* antitrochanter region.

Figure 2-8. Gross morphology and microstructure of avian acetabular soft tissues.

Figure 2-9. Gross morphology and microstructure of the lizard proximal femoral epiphyseal region.

Figure 2-10. Gross morphology and microstructure of the crocodylian proximal femoral epiphyseal region.

Figure 2-11. Gross morphology and microstructure of the avian proximal femoral epiphyseal region.

Figure 2-12. Irregular rugosities on the growth plate surface (green arrow) are the osteological correlates of thick hyaline cartilage.

Figure 2-13. Evolutionary history of the hip joint characters in sauropsids, with emphasis on archosaurs.

Figure 3-1. Orthogonal reference planes used to describe articular structures on the proximal femur of *Tyrannosaurus*, and exemplary theropod. Tissues nomenclature and color schemes are labeled according to homology inferences in Table 2-1 and Figure 2-3.

Figure 3-2. Simplified topologies of phylogenetic trees used in this study.

Figure 3-3. Osteological correlates of the acetabulum.

Figure 3-4. Osteological correlates of the acetabular labrum and antitrochanter.

Figure 3-5. Osteological correlates of the antitrochanteric cartilages.

Figure 3-6. Osteological correlates of the proximal femur in lateral/cranial and capital views.

Figure 3-7. Osteological correlates of the proximal femur in medial/caudal and proximal views.

Figure 3-8. Hip joint soft tissue reconstructions of the silesaurid *Asilisaurus* and the basal sauropodomorph *Plateosaurus*.

Figure 3-9. Hip joint soft tissue reconstructions of the sauropod *Apatosaurus* and the basal theropod *Coelophysis*.

Figure 3-10. Hip joint soft tissue reconstructions of the theropods *Tyrannosaurus* and *Deinonychus*.

Figure 4-1. Discrete osteological correlates and continuous hip joint metrics taken from the hip joints of saurischians, as exemplified by the theropod *Allosaurus* and the sauropod *Apatosaurus*.

Figure 4-2. Phylogenetic generalized reduced major axis regressions of hip joint linear dimensions vs. log femur length in the sauropod lineage using the “default” tree.

Figure 4-3. Phylogenetic generalized reduced major axis regressions of hip joint surface area dimensions vs. log femur length in the sauropod lineage using the “default” tree.

Figure 4-4. Phylogenetic generalized reduced major axis regressions of hip joint linear dimensions vs. log femur length in the theropod lineage using the “default” tree.

Figure 4-5. Phylogenetic generalized reduced major axis regressions of hip joint surface area dimensions vs. log femur length in the theropod lineage using the “default” tree.

Figure 4-6. Simplified phylogenetic tree showing major evolutionary transitions in saurischian body size and hip joint anatomy.

Figure 4-7. Hip joint soft tissue reconstructions of representative gigantic saurischians, the sauropod *Apatosaurus* and the theropod *Tyrannosaurus*.

LIST OF TABLES

Table 2-1. Synonyms of anatomical structures the epiphyseal region used in this study and selected literature. Quotation marks are included as used by the authors.

Table 2-2. Anatomical abbreviations.

Table 2-3. Sauropsid specimens and techniques used to investigate hip joint anatomy.

Table 2-4. Osteological correlates of hip joint soft tissues in extant sauropsids.

Table 2-5. Prescribed homologies among hip joint ligaments illustrated in figure 3.

Table 3-1. Anatomical abbreviations.

Table 3-2. Archosauromorph taxa studied and imaging techniques used to investigate hip joint anatomy.

Table 3-3. Institutional abbreviations.

Table 3-4. Osteological correlates of hip joint soft tissues in fossil archosaurs.

Table 3-5. Reconstructed thicknesses of the proximal femoral epiphyseal cartilage among Dinosauromorpha based on cartilage correction factors proposed by Holliday et al. (2010). Cartilage thickness is estimated based on similarities in subchondral growth plate surface textures.

Table 4-1. Results of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the sauropod lineage using the “default” phylogenetic tree.

Table 4-2. Results of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the theropod lineage using the “default” phylogenetic tree.

Table 4-3. P-values of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the sauropod lineage using alternative tree topologies.

Table 4-4. P-values of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the theropod lineage using alternative tree topologies.

Table 4-5. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using the “default” tree (Fig. 3-2a).

Table 4-6. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of Silesauridae (Fig. 3-2b).

Table 4-7. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of Herrerasauridae (Fig. 3-2c).

Table 4-8. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of *Eoraptor* (Fig. 3-2d).

Table 4-9. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using the “default” tree (Fig. 3-2a).

Table 4-10. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of Silesauridae (Fig. 3-2b).

Table 4-11. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of Herrerasauridae (Fig. 3-2c).

Table 4-12. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of *Eoraptor* (Fig. 3-2d).

Table 4-13. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of *Archaeopteryx* (Fig. 3-2e).

ABSTRACT

Archosaurs (crocodylians, birds and their extinct relatives) underwent numerous evolutionary transitions in appendicular skeletal morphology and body size, reflecting a diverse suite of postural and behavioral adaptations. Among archosaurs, saurischians (sauropodomorph and theropod dinosaurs) evolved a wide diversity of hip joint morphology and locomotor postures, as well as spanning seven orders of magnitude in body size. The very largest saurischians possess incongruent hip joints in which the subchondral surfaces differ in shape and size, suggesting that large volumes of soft tissues mediate hip articulation during locomotion. Nevertheless, the two extant archosaur clades (birds and crocodylians) possess highly divergent hip joint morphologies, and the homologies and functions of their articular soft tissues, such as ligaments, cartilage, and tendons, are poorly understood. The lack of hip joint anatomical data in extant taxa and the poor preservation of joint soft tissues in extinct taxa hinder functional inferences of archosaur hip joints, thus complicating our attempts to understanding the posture, locomotor behavior, ecology, and evolution of this diverse clade. In this study, I first described the soft tissue anatomies and their osteological correlates in the hip joint of archosaurs and their sauropsid outgroups, and infer structural homology across the extant sauropsids using dissection, imaging, and histology. This study provides new insight into soft tissue structures and their osteological correlates in the archosaur hip joint. Secondly, I used maximum likelihood ancestral state reconstruction and osteological correlates to infer major trends in hip joint soft tissue transitions of within sauropodomorphs and theropods, and test the integration between femoral and acetabular anatomy. Results of this study indicate that sauropodomorph hip joints underwent few concerted transitions, followed by subsequent stasis in soft tissue anatomy throughout Sauropoda. In contrast, the theropod hip joint is characterized by mosaic evolution within the stem lineage, such that the avian-like hip joint independently evolved in multiple theropod clades. Lastly, I tested the relationships among hip joint dimensions, morphological characters, body mass, and locomotor postures of sauropodomorph and theropod dinosaurs. Using 3D imaging techniques, discrete and continuous characters were analyzed using phylogenetically corrected correlation to reveal trends in body size evolution. Giant theropods and sauropods convergently evolved highly incongruent bony hip joints. In sauropods, the femoral head is capped a thick layer of hyaline cartilage, and functioned to resist massive axial compressive loads. In contrast, theropods covered their femoral head and neck with thinner hyaline cartilage, and maintained the femoral neck-antitrochanter articulation to accommodate shear forces during femoral abduction and axial rotation. Additionally, sauropods used femoral head hyaline cartilage to maintaining joint congruence, whereas theropods relied primarily on acetabular articular pads. These data indicate that the archosaur hip joint underwent divergent transformations in soft tissue morphology reflective of body size, locomotor posture, and joint loading.

CHAPTER 1

Introduction: The evolving view of saurischian locomotion

Archosaurs, the sauropsid clade which includes crocodylians, birds, and extinct forms such as nonavian dinosaurs, underwent numerous evolutionary transitions in appendicular anatomy and body size. During the last 250 million years, archosaurs evolved highly divergent locomotor behaviors, ranged seven orders of magnitude in body size, filled virtually all terrestrial ecological niches, and survived multiple mass extinctions. The two extant archosaur clades, crocodylians and birds, differ drastically in body plan, locomotor behavior, and ecology. Extant crocodylians are quadrupedal, semi-aquatic predators, but employ a wide range of hindlimb adduction during terrestrial locomotion (Reilly and Elias, 1998). In contrast, birds occupy a wide spectrum of ecological niches, but maintained obligate bipedality with a unique, proximally knee-driven step cycle during terrestrial locomotion (Stolpe, 1932; Firbas and Zweymuller, 1971). The great disparity in hindlimb anatomy and locomotor behavior between birds and crocodylians are merely two examples within the range of morphological diversity exhibited by the archosaur locomotor apparatus. Archosaurs underwent multiple, independent transitions between quadrupedality and bipedality (stem archosaurs: Sereno, 1991; Nesbitt et al., 2010; pseudosuchians: Nesbitt, 2007; Bates and Schachner, 2012; dinosaurs: Senter, 2007; Dilkes, 2001; Yates and Kitching, 2003), as well as variably adducted hindlimb postures (Walker, 1964; Charig, 1972). These morphological transitions reflect a diverse suite of postural and behavioral adaptations, and contributed to the vast radiation of archosaurs throughout the Mesozoic and beyond.

Within Archosauria, dinosaurs exhibit the most dramatic range of body size and locomotor adaptations. Dinosaurs include the largest and smallest known taxa among archosaurs, and evolved a wide diversity of hip joint morphology and locomotor postures (Benson et al., 2014). The ancestral locomotor posture of dinosaurs has been the subject of contrasting studies, because postural inferences differ for the two immediate outgroups to Dinosauria: the quadrupedal Silesauridae (Nesbitt et al., 2010) and the otherwise bipedal assemblages of non-dinosaurian dinosauromorphs (Nesbitt et al., 2009). Nevertheless, the earliest dinosaurs were small, terrestrial bipeds less than 10 kg in body mass (Sereno et al., 1993; Martínez et al., 2011), with multiple lineages independently evolved large body size (Sauropodomorpha: Sander et al., 2004; Theropoda: Christiansen and Fariña, 2004; Ornithischia, Yannan et al., 2011). Moreover, dinosaurs evolved a diversity of appendicular skeletal morphologies indicative of an equally diverse range locomotor behavior, including graviportal quadrupedality in sauropods (Carrano, 2005), thyreophorans (Coombs, 1978), and ceratopsians (Fujiwara, 2009); cursorial bipedality in theropods and ornithopods (Carrano, 1999); graviportal bipedality in gigantic theropods (Hutchinson et al., 2005); as well as facultative bipedality in gigantic ornithopods (Maidment et al., 2014). The extreme body size and highly disparate locomotor behaviors of dinosaurs have made them focal taxa for researchers in functional morphology, ecology, and evolution (Carrano, 2000) as well as the center of fascination among the general public.

The multiple, independent transitions in locomotor behavior and body size suggests that the dinosaur hip joint experienced substantial selective pressure. In all terrestrial, limbed vertebrates, the hip joint functions as the immediate load-bearing

structure between the hindlimb and the body trunk. Additionally, the cartilaginous growth plates of the hip joint are centers of longitudinal bone growth for the femur and the pelvic girdle. Therefore, hip joint morphology is expected to be intimately associated with evolutionary transitions in joint loading, bone growth, locomotor posture, and body size.

Unlike mammals, archosaurs lack secondary mineralization centers in their appendicular joints, instead possess a single layer of epiphyseal cartilage that serves as both the articular surface and the growth plate (Haines, 1942a). Among extant archosaurs, birds possess thin layers of epiphyseal cartilages at skeletal maturity, allowing congruent articulation between terminal ends of limb bones (Goetz et al., 2008). In contrast, crocodylians maintain thick layers of epiphyseal cartilage that contribute significantly to the size and shape of joints (Fujiwara et al., 2010; Holliday et al., 2010). This morphological dichotomy among extant archosaurs complicates inferences of the ancestral archosaurian condition, as well as the sequence of evolutionary transitions along either stem lineage. Moreover, the evolution and functional biology of sauropsid joints remains largely unknown because few comparative studies have focused on the same appendicular joint across different lineages (But see Haines, 1942). Instead, previous comparative studies used generic model joints that characterize each “grade” (i.e., the primitive tetrapod vs. mammalian condition: Haines, 1939; Carter et al., 1998). In particular, despite the hip joint’s role in vertebrate terrestrial locomotion, its soft tissue anatomy has not been the focus of comparative studies on non-mammalian vertebrates (But see Martin et al., 1994; Kuzenetsov and Sennikov, 2000). Because the functions of extant archosaur hip joints are not well understood, inferences of locomotor behavior and evolution in nonavian dinosaurs and other extinct archosaurs are hampered. The

insufficiency of knowledge in joint anatomy limits the biological applicability of joint range of motion (e.g., Senter, 2007; Hutson and Hutson, 2012; 2013; VanBuren and Bonnan, 2013) and inferred limb stress (Kubo and Benton, 2007; Bonnan et al., 2010) studies based on bony morphology alone. Lastly, the vast diversity of osteological joint morphology present in fossil archosaurs suggests an equally diverse suite of soft tissue attachments (Kuznetsov and Sennikov, 2000; Hutchinson, 2001a, b), which can severely impact inferences of character homology and phylogenetic reconstructions (e.g., Romer, 1956; Nesbitt, 2012).

Among dinosaurs, saurischians exhibit the most extreme disparity in body size and locomotor adaptations. Saurischians include the gigantic, long-necked sauropodomorphs and the bipedal theropods (Seeley, 1887). Sauropodomorphs include the largest terrestrial animals (*Argentinosaurus*, ~70 tons: Mazzetta et al., 2004) of all time, whereas theropods include the most massive (*Tyrannosaurus*, ~6 tons: Hutchinson et al., 2007) and the most diminutive bipeds (bee hummingbirds, ~2 grams: Hainsworth et al., 1972). Sauropodomorphs were ancestrally small, bipedal animals, but underwent a multiple evolutionary increases in body size preceding Sauropoda (Yates, 2004). Nevertheless, Sauropoda mostly maintained gigantic (>5 tons) body size throughout Late Jurassic and Cretaceous, with few instances of secondary miniaturization (Sander et al., 2011; Stein et al., 2010). Although sauropods consist entirely of obligate quadrupeds, the evolution of graviportal quadrupedality in sauropods is preceded by the various degrees of facultative bipedality in basal sauropodomorphs (Yates et al., 2009). The evolution of gigantism within sauropodomorphs, as well as the continued presence of sauropods in the Jurassic and Cretaceous ecosystems, has led to substantial interest in the anatomical and

physiological adaptations that permitted the evolutionary success of the sauropods, such as metabolism, growth strategy, and appendicular morphology (Sander et al., 2011). The evolutionary history of theropods is characterized by the retention of bipedality, the sustained decrease in body size along the avian stem lineage, as well as multiple, independent evolution of gigantism within many clades. Among theropods, gigantic body size (>5 ton) evolved in Ceratosauria (Sertich et al., 2013), Megalosauria (Hendrickx and Mateus, 2014), Allosauroidea (Calvo, 1998), Tyrannosauridae (Hutchinson et al., 2007), Ornithomimosauria (Lee et al., 2014b), Therizinosauria (Barsbold, 1976), and Oviraptorosauria (Xu et al., 2007). The independent evolution of gigantism in theropods have generated substantial interest in the effect of body size on the evolution of avian-like hindlimb morphology (Hutchinson 2001a, b) and the correlated evolution of large body size and hyper-carnivory (Zanno and Makovicky, 2013) and herbivory (Zanno and Makovicky, 2011). In contrast, the sustained trend of theropod miniaturization in the stem-avian lineage has been inferred to associate with the evolution of avian-like growth rate and life history strategies within nonavian theropods (Erickson, 2005) as well as the survival of ornithuromorph birds across the Cretaceous-Palaeogene extinction event (Hone et al., 2008). The numerous, iterative transitions in body size and locomotor posture among saurischians provide an excellent model for investigating the evolutionary relationship between hip joint anatomy and function.

The rich fossil record of dinosaurs throughout much of the Mesozoic has led to reasonably well resolved phylogenetic relationship within Saurischia (Fig. 1-1). In particular, the distinction of Sauropodomorpha and Theropoda as distinct monophyletic clades remain supported since its original proposal by Marsh (1878). However, the

disputed phylogenetic placement of several taxa complicates the tree topology at different parts of the saurischian lineage. The evolutionary relationship between dinosaurs and the highly derived Silesauridae remains in dispute, with Brusatte (2010) and Nesbitt (2011) considering Silesauridae as non-dinosaurian dinosauiromorphs whereas Langer and Ferigolo (2013) considering it as stem-ornithischian dinosaurs. Similarly, Herrerasauridae, a basal radiation of carnivorous dinosaurs, have been alternatively reconstructed as basal theropods (Sues et al., 2011) and as stem-saurischians, with Theropoda and Sauropodomorpha forming a monophyletic group (Novas et al., 2010). Moreover, *Eoraptor*, a small, basal saurischian, has been alternatively interpreted as the basal-most sauropodomorph (Martinez and Alcober, 2009) and as a basal theropod (Sues et al., 2011). Lastly, the recent influx of maniraptoran discoveries has helped to constrained much of the tree topology among the most bird-like of theropods. Therizinosauria, a previously enigmatic group of herbivorous dinosaurs, are now recognized as maniraptorans, contrasting previous interpretations as basal saurischians or sauropodomorphs. Similarly, Oviraptorosaurs are now widely recognized as the sister clade of Paraves (Foth et al., 2014), rather than sister group to Therizinosauria (Turner et al., 2007) or secondarily flightless birds (Maryńska et al., 2002). However, recent discoveries of paravians have also introduced numerous uncertainties in the phylogenetic relationship between Dromaeosauridae, Troodontidae, and Avialans. In particular, although *Archaeopteryx* has long been recognized as the first avialan, its phylogenetic position fluctuates between the avian stem-lineage (Turner et al., 2012) and the side branch of Deinonychosauria (Xu et al., 2011; Godefroit et al., 2013) depending on the inclusion of new, bird-like paravian theropods in the analysis (e.g., *Xiaotingia*: Xu et al.,

2011). The uncertain phylogenetic placements of basal Dinosauriformes influence reconstructions of the early evolutionary scenario of dinosaurs, such as the sequence of anatomical transitions leading to the ecological diversity in sauropodomorphs, theropods, and ornithischians. In contrast, the fluctuating phylogenetic relationship among the maniraptorans impacts studies on avian origin, such as the evolution of powered flight (Heers and Dial, 2015) and the early divergence of crown group Aves during the Mesozoic (O'Connor et al., 2011).

Numerous attempts have been made to reconstruct the posture and behavior of extinct saurischians. Immediately following the first discovery of reasonably complete, associated fossils of the sauropod *Cetiosaurus*, Owen (1841) inferred a semi-aquatic lifestyle for sauropods, a view which persisted throughout much of the 19th and 20th century, with Hay (1908) and Tornier (1909) inferring a highly abducted, lizard-like limb posture for the sauropod *Diplodocus*. The aquatic “whale-lizard” reconstruction received little support at the time of its proposal (Holland, 1910) and subsequent studies on musculoskeletal anatomy and trackways (Romer, 1923; Wilson and Carrano, 1999; Wilhite, 2003) eventually re-interpreted sauropods as terrestrial quadrupeds. Nevertheless, substantial questions on sauropod locomotor behavior remain difficult to approach due to their unique appendicular joint morphology. Large sauropods possess incongruent joints, in which the terminal ends of long bones fit poorly together. Moreover, the bony ends of limb elements possess highly convoluted, irregular rugosities, a feature which resembles the cartilaginous, “unfinished” growth plates in juvenile birds and mammals, leading to inferences of enormous layers of epiphyseal cartilage (Owen, 1841; Cope, 1878; Marsh, 1896). Hay (1908) suggested that the highly cartilaginous sauropod limb joints were

poorly adapted for bearing compressive loads. Therefore, he argued that sauropods were primarily aquatic in habit. Subsequent overwhelming evidence of terrestrial lifestyle in sauropods (Coombs, 1975; Henderson, 2004) led to new questions in the articular soft tissue anatomy of sauropod joints, as well the function of these soft tissues in maintaining joint congruence, facilitating limb growth, and transmitting the loads imposed by the enormous body mass of these animals during quadrupedal locomotion (Holliday et al., 2010; Bonnan et al., 2013) and occasional rearing, tripodal postures (Mallison et al., 2011).

Similarly, views of theropod locomotor posture have gone through a series of changes since the initial description of *Megalosaurus* (Buckland, 1824). Though originally inferred as mammal-like quadrupeds (Owen, 1841), subsequent discoveries of associated theropod materials were characterized by highly disparate fore- and hindlimb lengths, supporting their reconstruction as obligate bipeds (Wagner, 1859; Phillips, 1871). Early reconstructions of theropod bipedality were heavily influenced by the tripodal postures seen in lizards and kangaroos (Osborn, 1917; Knight, 1946). Under this reconstruction, the vertebral column is often oriented at 45 degree or greater relative to the ground, and the tail drags against the substrate during stance. This reconstruction pervaded museum exhibits and popular portrayals of theropods in the public consciousness until the 1980s, wherein new studies on hindlimb musculoskeletal anatomy (Charig, 1972; Parrish, 1986) and trackways (Wade, 1989) suggested that theropods held their backs horizontally during locomotion, with the tail acting as counterbalance to the head and body trunk. This updated view on theropod locomotor posture contributed the “dinosaur renaissance” of the 1980-90s, during which dinosaurs

were reconstructed as active, dynamic organisms on par with mammals and birds in their metabolic and behavioral repertoires. Subsequent work reconstructing hindlimb musculoskeletal anatomy (Hutchinson and Gatesy, 2000; Carrano, 2000) showed that numerous features associated with the avian body plan, such as the highly flexed femoral posture relative to the substrate and the primarily knee-driven locomotor cycle (Carrano, 1998) arose incrementally in theropods along the avian stem lineage. These studies further refined the anatomical reconstruction of theropod locomotor behavior and the evolutionary origin of avian locomotion.

However, significant outstanding questions remain in theropod locomotor mechanics. Like sauropods, gigantic theropods possess incongruent joint surfaces, in which substantial amount of empty space is present between the proximal femur and the acetabulum. The largest theropods also possess rugosities on the terminal ends of their long bones (Gilmore, 1920; Brochu, 2003), suggesting the presence of a considerable amount of epiphyseal cartilage during life. The role of thick epiphyseal cartilage in the evolution of theropod gigantism, such as load bearing and bone growth, has received little attention (Holliday et al., 2010). Moreover, the contribution of cartilage also confounded inferences on theropod hip articulation and hindlimb range of motion (Hutchinson et al., 2005; Paul, 2005). For example, Hutchinson et al. (2005) assumed the hip joint of *Tyrannosaurus* as a uniaxial hinge, in which the axis of rotation is determined by aligning the centers of the bony femoral head and the acetabulum. This method ignores the potential effects of differential cartilage thickness and type at different portions of the hip joint, and cannot account for additional range of potential hip motion in theropods such as hip abduction and femoral axial rotation. Overall, the lack of skeletal

congruence between the terminal ends of saurischian limb bones, as well as the inference of thick layers of articular cartilage, complicates our ability to understand the function of saurischian appendicular joints, such as loading, and growth, and articulation during evolutionary shifts in body size and locomotor postures.

This dissertation research provides the soft tissue anatomical basis for osteological characters in the archosaur hip joint, infers the evolutionary transformations leading to extant avian morphology, and infers morphological adaptations during independent, repeated transitions of body size and locomotor postures in the saurischian lineage. These new insights into hip joint anatomy will allow biologically plausible reconstruction of hind kinematics in both extant and extinct archosaurs, and improve upon model-based investigations on limb musculoskeletal biomechanics and locomotor behavior.

In chapter one, I investigate the gross anatomy and microstructure of hip joint soft tissues in extant archosaurs and their sauropsid outgroup. This study provides the first detailed description of the hip joint anatomy of crocodylians, and compares it with previous studies on birds (e.g., Firbas and Zweymuller, 1971; Baumel and Raikow, 1993), lepidosaurs (Snyder, 1954), and turtles (Walker, 1973; Wyneken, 2003). Finally, histological similarities, topological congruence, and osteological correlates of articular soft tissues are used to propose structural homologies across the hip joints of extant diapsids (Patterson, 1982). Results from this study allow inferences about hip joint soft tissue anatomy in fossils to be made by identifying osteological correlates of these soft tissues.

In chapter two, I investigate the sequence of evolutionary transitions in the hip joint of saurischian-line dinosauromorphs. This study infers the presence and topology of joint soft tissues in fossil saurischians and their outgroup archosauromorphs using the phylogenetically informed osteological correlates proposed in chapter one, identifies the polarity and sequence of discrete character transitions using maximum likelihood ancestral state reconstruction (Schluter et al., 1997; Pagel, 1999), and tests the homology of osteological characters based on reconstructed soft tissues. This study establishes the basic comparative framework of hip joint anatomical characters, such as cartilage caps, ligaments, and articular pads, within the dinosaur lineage leading to sauropods and birds, and forms the basis for subsequent work on archosaur locomotor mechanics, joint biology, and systematics.

In chapter three, I investigate the crown-ward transitions in both discrete and continuous hip joint characters using a comprehensive sample of fossil saurischians and outgroups archosaurs. Discrete characters and osteological correlates of articular soft tissues noted in chapter two were combined with continuous characters, which included both linear and area measurements of the subchondral surfaces. Dimensional congruence between the femoral and acetabular subchondral surfaces serve as proxies for the amount of soft tissues once present in the hip joint. Phylogenetic comparative methods are used to test if gigantic theropods and sauropods independently acquired highly cartilaginous hip joints. In both sauropods and theropods, the largest taxa maintained hip joint congruence using much thicker layers of articular soft tissues compared to extant vertebrates. However, whereas gigantic sauropods maintained hip congruence primarily using the highly cartilaginous femoral head, gigantic theropods maintained hip

congruence using substantial contributions from the acetabular labrum, the antitrochanter cartilage, and the femoral neck articular surface. These findings inform the first reconstruction of dinosaur hip joint anatomy, as well as the mechanical (e.g., articulation, load bearing) and physiological (e.g., bone growth, joint maintenance) adaptations in the largest animals ever to walk the earth.

This dissertation will form the necessary basis for future studies on archosaur locomotor behavior, ecology, and evolution. Knowledge on archosaur joint anatomy will further expand our understanding of vertebrate joint biology, thus answer critical questions on the adaptive response of the vertebrate joint during major shifts in Earth's environments and ecosystems.

Figure 1-1. Simplified time-calibrated phylogeny of Saurischia and its successive diapsid outgroups. Major radiations within Theropoda and Sauropodomorpha are emphasized. Silhouettes of taxa (phylogenies) depicted here are provided by S. Hartman, T. M. Keesey, N. Kelley, A. A. Farke, B. McFeeters, S. Werning, G. E. Lodge, E. Willoughby, M. Martyniuk, and Benchill (Wikipedia user). Silhouettes are not to scale.

CHAPTER 2

Articular soft tissue anatomy of the archosaur hip joint: Structural homology and functional implications

INTRODUCTION

Archosaurs (crocodylans, birds and their extinct relatives) underwent numerous evolutionary transitions in appendicular skeletal morphology and body size, reflecting a diverse suite of postural and behavioral adaptations. Archosaur hindlimbs were loci of morphological evolution during the iterative independent transitions of posture, such as quadrupedality and bipedality (Stem archosaurs: Sereno, 1991; Nesbitt et al., 2010; Pseudosuchia: Nesbitt, 2007; Bates and Schachner, 2012; Ornithischia: Senter, 2007; Dilkes, 2001; Sauropodomorpha: Yates and Kitching, 2003). Modifications of hindlimb morphology correlate with body size evolution in archosaurs, including phylogenetic trends towards gigantism (Pseudosuchia: Farlow et al., 2005; Dinosauria: Carrano, 2006; Theropoda: Christiansen and Fariña, 2004; Sauropodomorpha: Sander et al., 2004) and miniaturization (Theropoda: Turner et al., 2007; Lee et al., 2014; Sauropodomorpha: Stein et al., 2010) among different lineages. Therefore, Archosauria provides an excellent model for investigating the evolutionary relationship between hindlimb anatomy and locomotor postures.

The hindlimb anatomy of extant archosaurs is well documented in the comparative literature (Birds: Romer, 1927; Berge, 1970; 1982; Raikow, 1985; McKittrick, 1991; Berge and Zweers, 1993; crocodylans: Romer, 1932; Cong et al., 1998). These studies provide the foundation for research on archosaur hindlimb muscle homology and evolutionary transformations (Archosauria: Romer, 1923; 1956;

Pseudosuchia: Parrish, 1986; 1987; Ornithischia: Maidment and Barrett, 2011; Theropoda; Hutchinson, 2001a; b; Sauropodomorpha: Langer, 2003), muscle functions (Birds: Berge and Storer, 1995; Picasso, 2010; crocodylians: Otero et al., 2010; Ornithischia: Maidment et al., 2013; Sauropodomorpha; Mallison, 2010; Theropoda: Hutchinson and Gatesy; 2000; Hutchinson, 2005), muscle activation patterns (Gatesy, 1997; 1999b), limb kinematics (Birds: Gatesy, 1999a; crocodylians: Reilly and Elias 1998; Dinosauria; Hutchinson and Allen, 2009; Carrano, 2010; Bates et al., 2012), and limb scaling (Ornithischia: Maidment et al., 2012; Sauropoda: Bonnan, 2007; Theropoda: Gatesy, 1991). However, few studies have explored the soft tissues articulating the bony limb elements in birds (Cracraft, 1971; Firbas and Zweymüller, 1971), crocodylians (Fujiwara et al., 2010; Holliday et al., 2010), or outgroups (lizards: Buffrénil et al., 2004; turtles: Snover and Rhodin, 2008). Articular cartilage, fibrocartilaginous pads, capsular ligaments, and the ligamentum capitis femoris facilitate smooth, gliding motion between long bones, transmit locomotor- and muscle-induced loads between limb segments (Carter and Beaupre, 2001; Carter and Wong, 2003), limit joint excursion (Girgis et al., 1975; Kivlan et al., 2013), maintain pressurized synovial fluid (MacConaill, 1932; Ferguson et al., 2000), and provide proprioceptive feedback (Johansson et al., 1991).

The majority of research on joint soft tissues focuses on mammalian joints, which maintain only a thin layer of articular cartilage (Walmsley, 1915; Simon, 1970; Enlow, 1980; Moss and Moss-Salentijn, 1983; Eckstein et al., 1997; Carter, 2001). Additionally, mammals possess secondary centers of mineralization within the epiphyseal cartilage, dividing the articular surface from the growth plate (Moodie, 1908; Haines, 1941; 1942a; 1975). Secondary centers are also present in the epiphyses of lepidosaurs (Haines, 1941;

1969; Buffrénil et al., 2004) and some lissamphibians (Haines, 1938; Erismis and Chinsamy, 2010). The secondary center eventually fuses with the metaphysis at skeletal maturity, obliterates the growth plate, and terminates longitudinal growth (Haines, 1941; 1942; Buffrénil et al., 2004). Archosaurs (Haines, 1942a; Wess et al., 1997; Buffrénil et al., 2004) and turtles (Snover and Rhodin, 2008) lack secondary mineralizing centers and instead possess a single layer of epiphyseal cartilage that serves as both the articular surface and the growth plate throughout life. Haines (1938; 1939) inferred the epiphyseal morphology of turtles and archosaurs as the plesiomorphic tetrapod condition. Within extant archosaurs, birds possess thin layers of epiphyseal cartilage at skeletal maturity. The thinner layers of articular cartilage in skeletally mature birds and mammals form more congruent articulation between limb bones, because the bony subchondral surfaces match their overlying, cartilaginous articular surface in shape (MacLatchy and Bossert, 1996; Goetz et al., 2008). In contrast, crocodylians maintain thick layers of epiphyseal cartilage that contribute significantly to the size and shape of joints (Fujiwara et al., 2010; Holliday et al., 2010). Thick layers of joint soft tissue have been hypothesized in some fossil archosaurs, which exhibit incongruent, rugose joint surfaces (Cope, 1878; Hay, 1908; Osborn, 1898). This is particularly apparent in the hip joint of large saurischians, where the bony acetabulum can be twice as wide in linear dimension as the proximal femur (circumference: Hutchinson et al., 2005; craniocaudal diameter: Tsai et al., 2012). Calcified cartilage (Norman, 1980; Nicholls and Russell, 1985; Wilson and Sereno, 1998; Mallison, 2010) and desiccated epiphyseal cartilage (Schwarz et al., 2007) are occasionally observed on the end of fossil archosaur long bones. However, since these

structures largely conform to the subchondral shape when preserved in fossils, they offer little information on articular cartilage morphology during life.

The evolution and functional biology of sauropsid joints remains largely unknown because, despite interests in the functional anatomy of appendicular joints (e.g., the ligamentum capitis of the hip joint: Chandler and Kreuscher, 1932; Kivlan et al, 2013; the meniscus of the knee joint: Haines, 1942), few comparative studies have focused on the same appendicular joint across different lineages. Instead, previous comparative studies used generic model joints that characterize each “grade” (i.e., the primitive tetrapod vs. mammalian condition: Haines, 1942; Carter et al., 1998; but see Fujiwara et al., 2010; Holliday et al., 2010). Despite the hip joint’s role in both bipedal and quadrupedal locomotion in archosaurs, its soft tissue anatomy has not been the focus of many studies (Martin et al., 1994; Kuzenetsov and Sennikov, 2000). Because the function and homology of extant archosaur hip joints are not well understood, inferences of locomotor behavior and evolution in fossil archosaurs are hampered. The insufficiency of knowledge in archosaur joint anatomy limits the biological applicability of joint range of motion (Carpenter and Smith, 2001; Carpenter, 2002; Paul, 2005; Senter and Robin, 2005; Senter, 2007; Hutson and Hutson, 2012; 2013; Liparini, 2013; VanBuren and Bonnan, 2013) and inferred limb stress (Kubo and Benton, 2007; Bonnan et al., 2010) studies based on bony morphology alone.

Here I investigate the gross anatomy and microstructure of hip joint soft tissues in extant archosaurs (birds and crocodylians) and their sauropsid outgroups (lizards and turtles). I provide the first detailed description of the hip joint anatomy of crocodylians, compare my observations to those of previous studies on birds (Owen, 1874; Firbas and

Zweymuller, 1971; Baumel and Raikow, 1993; Martin et al., 1994; Hertel and Campbell, 2007), lepidosaurs (Snyder, 1954), and turtles (Walker, 1973; Wyneken, 2003), and identify patterns of similarity among the groups (Patterson, 1982). I identify histological similarities, topological congruence, and osteological correlates of soft tissues traceable in the fossil record to better understand the evolution of the hips within Sauropsida.

MATERIALS AND METHODS

Definitions: Anatomical definitions and orthogonal reference axes:

Anatomical abbreviations used in this study are summarized in Table 2-2 and illustrated in Fig. 2-1. Anatomical terminology differs among neonatologists and paleontologists regarding structures on the end of long bones. Most neontological studies describe the secondary mineralized centers within the epiphyseal hyaline cartilage of mammals, lepidosaurs, and anurans as “epiphyses” and the subchondral growth plate as the “diaphyseal” (Parson, 1905) or “metaphyseal” surfaces (Barreto et al., 1993; Carter et al., 1998; Leunig et al., 2000; Cardoso, 2009). Haines (1969) and Maisano (2002) referred to the mineralization center simply as “secondary center” and the surrounding tissue as “epiphyseal cartilage”. This scheme was followed by Holliday et al. (2010), which distinguished between the cartilaginous epiphyses and its underlying bony metaphysis. In contrast, most paleontological studies on tetrapods lacking secondary centers of calcification (e.g., fossilized dinosaurs) tend to refer to the subchondral growth plate as an “epiphysis” or “epiphyseal surface” (Horner et al., 2001; de Ricqlès et al., 2003a, b; Bonnan et al., 2010; 2013). These contrasting definitions complicate inferences of homology in soft tissue structures in sauropsid joints. This study employs a unifying

set of definitions based on common developmental processes of tetrapod limb bones (Table 2-1).

Limb bones initiate as condensations of mesenchymal cells into a cartilaginous precursor, and undergo subsequent perichondral and endochondral ossification. These processes reduce the cartilaginous anlagen to the *chondroepiphysis*, which provides articulation between adjacent long bones superficially via the *articular surface*, and continuation of longitudinal growth on the *metaphyseal growth plate surface*. In lepidosaurs and mammals, the *secondary center* develops inside the chondroepiphysis, separating the articular and growth plate surfaces, whereas in archosaurs and turtles, the uncalcified chondroepiphysis remains continuous between the articular and growth plate surfaces. The *metaphyseal collar* is the cortical bone which links the diaphysis with the chondroepiphysis (Fig 1-1).

The archosaur hip joint underwent substantial evolutionary modification associated with changes in femoral orientation, such as the evolution of parasagittal locomotion in pseudosuchians (Walker, 1964; Charig, 1972; Chatterjee, 1985; Jones et al., 2000; Weinbaum, 2013), the evolution of protracted femoral posture in theropod dinosaurs (Gatesy, 1991; 2002; Gatesy and Middleton, 1997; Hutchinson 2001a, b, 2006; Allen et al., 2013), and the reversion to sprawling posture in crocodyliforms (Parrish, 1987; Pol, 2013). Moreover, during theropod evolution, the ancestrally cranial surface of the proximal femur enlarged medially, a transition that Hutchinson (2001b) attributed to the medial deflection of the femoral head relative to the distal condyles. In order to account for differences in femoral posture and condylar orientation across Sauropsida, I use a set of reference axes (Fig. 2-2). The mediolateral plane (red) passes through the

distal condyles and intersects the femoral midshaft long axis. The craniocaudal plane (blue) is perpendicular to the mediolateral plane and intersects the latter at the femoral midshaft long axis. Additionally, an anatomical capital-trochanteric plane (green) passes through the femoral head and the greater trochanter. In all sauropsids 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, are used to describe the orientation of acetabular soft tissue structures. Lastly, throughout this study the proximal attachment of ligaments will be noted as the origins, whereas the distal attachment will be noted as the insertions.

Specimens:

A sample of extant and recently extinct sauropsids was used in this study to investigate hip joint soft tissue homologies in Archosauria including wild-caught, free-range farmed, salvaged, and museum specimens. Specimens used are summarized in Table 2-3. The crocodylian sample (n= 22) included wet specimens of *Alligator mississippiensis* supplied by the Rockefeller Wildlife Refuge (Grand Chenier, LA) catalogued under the MU vertebrate collection (MUVc), as well as osteological specimens of *Crocodylus*, *Gavialis*, and *Tomistoma* from the Field Museum of Natural History (FMNH), and National Museum of Natural Sciences of Taiwan (NMNH). The crocodylian specimens range from a late-stage embryo (MUVc-AL 114. Stage 28 in Ferguson, 1985) to large adults (MUVc-AL 711. SVL~350cm).

The avian specimens (n= 16) included MUVc's commercially obtained and salvaged wet specimens and osteological specimens from MUVc and the Los Angeles County Museum of Natural History (LACM). The domestic chicken *Gallus gallus* was

chosen for histological analysis based on the basal position of Galloanseriforms within Neornithes (Livezey and Zusi, 2007). Additionally, the chickens used in histological analysis are heritage lines obtained from the Vikon Farms Company (Arkadelphia, AR). Compared to modern boiler breeds, heritage chickens have not been artificially selected for increased muscle mass and elevated growth rates, minimizing the potential effect of growth hypertrophy on joint morphology (Schmidt et al., 2009). The lepidosaur sample (n= 19) included wet specimens of iguanids, varanids, and *Gekko gecko* from MUV, wet specimens of *Sphenodon punctatus* from FMNH, and osteological specimens from FMNH and LACM herpetology collections. Turtles used in this analysis (n= 7) included osteological specimens from FMNH and LACM, as well as salvaged specimens of an adult and a juvenile *Chelydra serpentina* collected in Columbia, MO. The phylogenetic placement of turtles within amniotes is contentious, with competing hypotheses based on molecular and morphological evidence (summarized in Carroll, 2013). Turtles are used as the outgroup to Diapsida (Lepidosauria+Archosauria, Werneburg and Sanchez-Villagra, 2009).

Dissection:

Fresh frozen and fixed specimens were dissected by hand. Fixed specimens were either preserved in 10% Neutral Buffered Formalin or 70% ethanol. Dissection at each stage was photographed for visualization of muscle attachments, tendinous insertions, and cartilage attachment using a Nikon D90 DSLR camera, a Sony DSC-F828 camera, or a Nikon SMZ-1000 dissection microscope fitted with a Nikon DS-Fi1 digital camera. Select dissected specimens were further processed for histology.

Imaging:

Photographs of select specimens were combined into 3D surface models via photogrammetry (OSM-bundler, PMVS; Falkingham, 2012). This method allows the production of virtual surface models for documenting osteological correlates of soft tissue attachments. The hindlimb of a subadult American alligator (AL102) was scanned using a GE LightSpeed VCT computed tomography scanner at 0.625 cm slice thickness, allowing visualization of skeletal articulation. The hip joint of this individual was further dissected of extrinsic soft tissues, formalin fixed, and saturated with Lugol's Iodine (I₂KI) using techniques modified from Metscher (2009), Jeffery et al. (2011), and Tsai and Holliday (2011) to enhance visual contrast between soft tissues. The specimens were then scanned on a Siemens Inveon MicroCT scanner at a slice thickness of 83 microns. The articulated hindlimb of a juvenile American alligator (AL100) was also subjected to the iodine-enhanced Micro CT (μ CT) process to visualize the joint capsule tissues. All scans were imported as DICOM files into Amira v5.2 (Visage Imaging) for segmentation and analysis. Soft tissue structures were segmented for qualitative analysis of cartilage topology with respect to neighboring structures. The alligator hindlimb muscle model and the comparative sauropsid osteological photogrammetry models used in this paper will be made available online at figshare [<http://figshare.com/>] and Morphobank [<http://www.morphobank.org/>].

Histology:

Dissected hip joints of *Alligator*, *Ctenosaura*, and *Gallus* were fixed in 10% neutral buffered formalin and decalcified. Smaller specimens were fixed in-situ, whereas larger specimens were disarticulated by excising the capsular and intrinsic joint ligaments. The proximal femur and acetabulum were variably sectioned prior to

embedding in order to access the deeper portions of the tissues. Typically, the left hip was sectioned parasagittally and the right sectioned transversely. The acetabulum of MUV-AL 103, a subadult alligator (SVL~130cm), was dissected further to separate its regionally distinct soft tissues for separate histological sections. Each specimen was embedded in paraffin, serially sectioned on a rotary microtome, and mounted on glass slides. Slides were alternately stained using Masson's Trichrome, Hematoxylin and Eosin (H&E), or Picrosirius Red (PSR) in order to study the connective tissue microstructures. Slides were viewed and photographed using either an Aperio Scanscope CS scanner with ImageScope software or an OlympusBX41TF microscope with an Olympus DP71 camera.

RESULTS

Acetabulum:

The three pelvic bones of turtles and lepidosaurs form a synchondrosis, which may ossify as a bony medial acetabular wall (Fig. 2-3). In contrast, the medial acetabular wall of archosaurs is unossified and bound by a thick membrane, a condition termed “perforated acetabulum” (Romer, 1956; Kuzenetsov and Sennikov, 2000). The turtle acetabulum consists of a continuous, hyaline cartilage-covered acetabular surface. In contrast, the diapsid acetabulum is covered by hyaline cartilage only on the ventral surface (the “floor”, or cotyloid cavity *sensu* Vialleton, 1924. Fig. 2-4c, e). The dorsal portion of the acetabulum (the supraacetabulum) possesses two distinct cranial and caudal soft tissue regions, both of which articulate with the proximal femur during locomotion. The cranial acetabular rim consists of a pliant, fibrocartilaginous acetabular labrum that attaches to the ventral surface of the iliofemoral ligament. The labrum

expands internally to form the dorsal articular surface (the “ceiling”) of the acetabulum. The caudal acetabular region consists of the antitrochanter, a fibrous structure that lines the caudodorsal acetabular rim in lizards and the ilioischial junction in archosaurs and *Sphenodon*. These tissues are histologically distinct from extrinsic capsular ligaments and the hyaline surface of the acetabulum.

In lepidosaurs, the acetabular labrum attaches to the ventral surface of the iliofemoral ligament and consists of loose connective tissues surrounded by longitudinally oriented, wavy collagen fibers (Fig. 2-4c, 2-5b). A bony groove along the medial wall of the acetabulum separates the labrum’s attachment site dorsally from the hyaline cartilage-covered acetabular surface ventrally (Fig. 2-4d, f). The lepidosaurian antitrochanter is distinct fibrocartilaginous pad on the caudodorsal edge of the acetabulum. In *Sphenodon*, the antitrochanter attaches primarily on the caudal ilial acetabular surface and forms a meniscus-like, ligamentous attachment to the ischial acetabular surface (Fig. 2-4e). This ligamentous connection continues past its ischial attachment point as the ischiofemoral ligament and forms part of the ventral synovial capsule. The antitrochanter’s ilial attachment of *Sphenodon* presents a V-shaped notch on skeletal specimens, whereas its ischial attachment is indistinct from the hyaline cartilage-covered acetabular surface (Fig. 2-4f). In lizards, the antitrochanter is located exclusively on the ilial portion of the acetabulum. The antitrochanter leaves a continuous grooved border distinguishing it from the labrum cranially and hyaline cartilage ventrally. The overall microstructure of the lizard antitrochanter resembles elastic cartilage, as it consists of a highly cellular, cartilaginous core, embedded by randomly oriented fibers

bundles and encapsulated by longitudinally oriented, wavy collagen fibers along the periphery (Fig. 2-5c).

In crocodylians, the acetabular foramen is medially enclosed by a thick, fibrous inner acetabular membrane, which experiences substantial mediolateral displacement during ex-vivo femoral excursions (Kuzenetsov and Sennikov, 2000). The entire lunate surface is formed by the acetabular labrum and the antitrochanter (Fig. 2-6c, d). The cranioventral portion of the acetabulum is constructed by a large mass of structural cartilage (*cartilago acetabularis*, Cong et al., 1998) and consists of a hyaline cartilage core encapsulated by fibrocartilage. The acetabular cartilage forms the junction between the three pelvic bones, including the mobile puboischial synchondrosis (Claessens and Vickaryous, 2012). The acetabular labrum attaches to the ventral surface of the supraacetabular ridge on the ilium, occupies almost half of the volume of the bony acetabulum, and extends externally with the iliofemoral ligament. The bony attachment of the acetabular labrum is distinguished from the hyaline cartilage-covered acetabular surface by small perforating vascular canals. Histologically, the alligator labrum is comprised of loose connective tissue and longitudinally oriented, wavy collagen fibers as in the lizards studied (Fig. 2-6f).

Caudally, the crocodylian antitrochanter consists of a pair of semilunate, overlapping fibrocartilaginous acetabular menisci (Fig. 2-6d, 2-7a). The menisci originate on the hyaline cartilage synchondrosis between the ilium and ischium, and they can be distinguished on skeletal specimens by the craniolaterally-oriented, calcified cartilage-covered growth plate surfaces on the ilial and ischial peduncles. The superficial meniscus originates on the caudal edge of the ilial acetabular rim and inserts onto the ischial

acetabular surface. The deep meniscus originates from a small notch on the ilial acetabular surface of the ilioischial junction, lies under the superficial meniscus, and inserts onto the synovial membrane on the caudodorsal acetabular rim. The deep meniscus continues past this attachment point as the caudal ligamentum capitis femoris (Fig. 2-6c). Histologically, the acetabular menisci resemble ligaments, with longitudinally-oriented collagen fibers embedded in minimal amounts of cartilage matrix (Fig. 2-7c, d). The deep meniscus in particular consists of circumferentially-oriented collagen fiber bundles which pass parallel to its semilunate superficial contour, similar to collagen fibers found in the tetrapod knee meniscus (Fig. 2-7d; Haines, 1942b; Eleswarapu et al., 2011). Overall, the crocodylian supraacetabular soft tissues reduce the volume of acetabular cavity and increase congruence between the acetabulum and proximal femur.

The crocodylian pelvis remains unfused throughout the life and maintains patent growth plates between each bone. Each pelvic element articulates with its neighbor via a synchondrosis comprised of a hyaline cartilage core encapsulated by a peripheral sleeve of fibrocartilage. In skeletal specimens, the hyaline cartilage attachment is distinguishable by its calcified cartilage lining and subchondral trabecular bone, whereas the fibrocartilage attachment has increased striations on the cortical bone peripheral to the growth plate. The growth plate surfaces increase in rugosity during ontogeny, a feature likely reflective of the absolutely larger volume of hyaline cartilage in the acetabulum of large adults (Fig. 2-12c).

In lepidosaurs and crocodylians, the craniocaudal length of the acetabulum is similar to the capital-trochanteric length of the proximal femur, such that the crocodylian

and lepidosaurian hip joint is craniocaudally congruent (Tsai et al., 2013). However, because the acetabulum contains large volume of supraacetabular soft tissues, its dorsoventral length is nearly twice the corresponding mediolateral length of the proximal femur. The influence of supraacetabular soft tissues thus makes up for the dorsoventral incongruence observed in the bony hip joint of non-avian diapsids.

In birds, the inner acetabular membrane is taut and prevents the femoral head from displacing medially through the acetabular foramen. The acetabulum is bordered craniodorsally by the acetabular labrum and caudodorsally by the large, laterally expanded bony antitrochanter (Fig. 2-8c). Firbas and Zweymuller (1971) reported that large palaeognaths (“ratites”) possess thick acetabular labra, whereas the avian wet specimens examined here (galloanseriformes, *Buteo*, *Cathartes*, *Corvus*) possess relatively small, fibrous labra that contributes little to acetabular depth (Fig. 2-8c, e). The craniodorsal acetabular rim marks the attachment of the avian acetabular labrum. However, the surface textures of labral versus synovial hyaline cartilage attachments within the acetabulum are indistinct, presented as a continuous surface of smooth, calcified cartilage surface on the acetabular “ceiling” (Fig. 2-8d).

The avian antitrochanter is a laterally expanded bony buttress on the caudodorsal rim of the acetabulum, formed by lateral expansion of the ilioischial junction (Fig. 2-8d). In skeletally immature birds, the antitrochanter is a mass of hyaline cartilage, attaching to the laterally oriented peduncular surfaces of the ilium and ischium. The antitrochanter hyaline cartilage is bordered superficially by a layer of fibrocartilage and internally by a calcified cartilage-lined growth plate (Fig. 2-8g). In skeletally mature birds, fusion between the ilial- and ischial peduncles ossifies the antitrochanter into a robust bony

structure. In the skeletally mature antitrochanter, the entire articular surface is fibrocartilaginous, and the underlying hyaline cartilage is reduced to a thin layer (Fig. 2-8c). Firbas and Zweymuller (1971) identified a meniscus on the antitrochanter of ratites, but I have not found such a structure in dissections of *Struthio* and neornithine species.

Joint ligaments:

The hip joints of birds, crocodylians, and *Sphenodon* possess both extrinsic and intrinsic ligaments, whereas the hip joints of turtles and lizards lack intrinsic joint ligaments. In turtles, three distinct, non-overlapping joint ligaments originate on the acetabular rim of each pelvic bone and distally to the metaphysis of the proximal femur. In lizards and *Sphenodon*, the iliofemoral ligament originates broadly from the ilial acetabular rim and excavates a notch on the craniodorsal edge of the acetabulum (Fig. 2-4b, d, f). The iliofemoral ligament tapers distally to a narrow insertion on the lateral femoral metaphysis. Caudodorsally, the tendinous insertion of *m. ischiotrochantericus* partially merges with the joint capsule and inserts onto the lateral metaphysis, caudal to the iliofemoral ligament insertion (Fig. 2-4b, c). The pubofemoral ligament originates from the pubic acetabular rim and is more robust than the ischiofemoral ligament. The origin of the ischiofemoral ligament differs between lizards and *Sphenodon*. In lizards the ischiofemoral ligament originates on the ischial acetabular rim and is not attached to the antitrochanter (Fig. 2-4c). On the other hand, in *Sphenodon*, the ligament originates from the ischial acetabular surface at the caudal attachment site of the antitrochanter (Fig. 2-4e). The pubofemoral and ischiofemoral ligaments form part of the ventral synovial capsule, and fuse near the puboischial junction to form the ligamentum capitis femoris. The ligamentum capitis inserts onto a bony protuberance on the medial metaphyseal

junction, such that the attachment site includes both the medial metaphyseal collar and the secondary center (Fig. 2-9b, g). For the current study, the femoral attachment of the ligamentum capitis is termed the fovea capitis following the avian terminology (Baumel and Witmer, 1993). Apart from the joint ligaments, the lepidosaurian hip joint is bound by a thin synovial membrane cranially and caudally.

The crocodylian iliofemoral ligament originates dorsally from the acetabular labrum on the acetabular crest and inserts on the lateral bony metaphyseal collar. The *m. ischiotrochantericus* tendon partially merges with the synovial capsule and inserts caudodorsally to the iliofemoral ligament (Fig. 2-6b). Within the synovial capsule, the cranial crus of the ligamentum capitis originates on the acetabular “floor” of the pubic peduncle of the ischium, near the ventral attachment of the inner acetabular membrane at the inner acetabular rim. The caudal crus of the ligamentum capitis originates as a continuation of the deep meniscus and inserts onto joint capsule on the caudodorsal acetabular rim. The two crura fuse to form the ligamentum capitis femoris, which inserts onto the fibrocartilage on the cranial surface of the “posteromedial tuber” (*sensu* Nesbitt, 2011; Fig. 2-6c, 2-10a). The fovea capitis is usually continuous with the convex contour of the posteromedial tuber, though in one specimen of *Crocodylus plaustris* (FMNH 51691) the fovea is a flattened surface (Fig. 2-10g). The cranial crus of the ligamentum capitis is shorter and more robust than the caudal crus. Extrinsically, the ventral joint capsule consists only of a thin synovial membrane and lacks the clearly defined pubofemoral and ischiofemoral ligaments seen in lepidosaurs.

Previous studies on avian hip joint capsular ligaments differ in interpretation. Cracraft (1971) described the hip joint capsule of *Columba* as possessing “one or two”

ligamentous bands on the cranial and caudoventral acetabular rim, whereas the dorsal portion is the weakest area of the capsule. Baumel and Raikow (1993) described the generalized avian hip joint as possessing three capsular ligaments: the pubofemoral, iliofemoral, and ischiofemoral ligaments. The pubofemoral ligament originates on the pubic peduncle of the ilium and inserts onto the craniolateral surface of the femoral metaphyseal collar. This ligament is robust and well-distinguished from the rest of the joint capsule. The iliofemoral ligament originates on the dorsal acetabular rim and inserts onto the trochanteric extent of the articular surface. The ischiofemoral ligament originates on the ventral and caudal acetabular rim and inserts onto the caudal femoral metaphyseal collar. In my dissections of galloanseriformes, *Buteo*, *Cathartes*, and *Corvus*, I was able to distinguish the pubofemoral ligament from the rest of the synovial capsule. However, the cranial and caudal borders of the ischiofemoral ligament are less distinct in these taxa; instead, the ligament appears to arise from a local, gradual thickening of the caudoventral synovial capsule. Nevertheless, my results agree with previous studies in that the avian hip joint capsule can be characterized as robustly supported by joint ligaments cranially and ventrally, but is thinner and lacks embedded ligaments dorsally.

Within the synovial capsule of the avian hip joint is a single ligamentum capitis femoris (Fig. 2-11a). The ligamentum capitis originates on the inner acetabular rim, and is partially confluent with the inner acetabular membrane's pubic and ischial attachments. Distally, the ligamentum capitis inserts on the concave fovea capitis on the femoral head via successive layers of fibrocartilage and calcified cartilage (Fig. 2-11b, c). The ligamentum capitis was also observed by Cracraft (1971) in *Columba* and was reported to possess two craniocaudally distinct origins, termed the ligamentum teres and the posterior

acetabular ligament, respectively. Craniocaudal division of the ligamentum capitis is present in *Struthio* (Fig. 2-8b), in which the posterior acetabular ligament inserts proximocaudally relative to the ligamentum teres (*sensu* Cracraft, 1971). In juvenile birds, the fovea capitis is indistinct on the bony subchondral surface; whereas in skeletally mature birds, the fovea usually presents as a single, deeply excavated fovea on the subchondral surface (Fig. 2-11e). However, in one *Emeus crassus* and one *Rhea pennata*, the femoral head possesses two distinct, concave foveae (Fig. 2-11f, g), supporting the dual-origin morphology of the ligamentum captis as identified by Cracraft (1971). The fovea for the ligamentum teres is a shallow indentation, whereas the fovea for the posterior acetabular ligament is deeper, elongated, and oriented caudally relative to the femoral head.

Proximal femur:

The chondroepiphysis of a generalized sauropsid proximal femur is comprised of a hyaline cartilage core, surrounded peripherally by a fibrocartilaginous sleeve at the metaphyseal junction (Fig. 2-1b). In turtles, the fibrocartilaginous sleeve is small and unexpanded, which may account for its omission in previous anatomical description despite being figured in these studies (Suzuki, 1963; Snover and Rhodin, 2008). In all turtles except for *Dermochelys*, the hyaline cartilage core is avascular and reduced to a thin layer at adulthood, resulting in smooth subchondral growth plate surfaces and high level of congruence between the femoral head and the acetabulum. *Dermochelys* uniquely possesses thick, vascularized epiphyseal hyaline cartilage at the ends of most limb and girdle elements. The attachments of these thick chondroepiphyses leave irregularly rugose growth plate surfaces, covered by calcified cartilage and perforated by large,

widely spaced vascular canals. The femur of *Dermochelys* possesses a smoother growth plate surface but nevertheless retains patent vascular canals. In contrast, other long bones of this taxon, such as the humerus, possess highly rugose growth plate surfaces, indicative of thick hyaline cartilage (Fig. 2-12a).

In diapsids, the fibrocartilage sleeve is particularly prominent at the capital and trochanteric regions and attaches the epiphyseal hyaline cartilage to the bony metaphyseal collar. In skeletally mature lizards, fusion of the secondary center to the metaphysis obliterates the growth plate, whereas juvenile lizards retain bony ends of metaphyseal growth plates that are anatomically homologous with those at the ends of archosaur long bones. The metaphyseal growth plates of juvenile lizards are largely flat in mediolateral view and possess irregular rugosities, dominated by a prominent trough along the capital-trochanteric axis of the proximal femur (Fig. 2-9c, 2-12b). This trough corresponds to a bony ridge on the internal surface of the secondary center, here termed the cartilage cone following Carter et al. (1998). This cone-trough articulation contributes to the immobile synchondrosis between the secondary center and the metaphyseal growth plate. The fibrocartilage sleeve binds the chondroepiphysis to the bony metaphyseal collar along the periphery of the growth plate. In skeletally mature lizards, the fibrocartilage sleeve forms plate-like calcifications, termed apophyseal centers (*sensu* Haines, 1969), along the medial and lateral metaphyseal collars, eventually fusing to both the ossified epiphyseal center and the metaphysis (Fig. 2-9b).

In a pre-hatching *Alligator* embryo, perichondral ossification of the metaphyseal collar precedes endochondral ossification, such that the chondroepiphysis extends deep into the bony metaphyseal collar as a massive cartilage cone (Fig. 2-10f). However,

locomotor competent juveniles and adults lack the cone-trough articulation between the chondroepiphysis and the metaphyseal growth plate. In juvenile and adult *Alligator*, the fibrocartilage sleeve attaches broadly to the chondroepiphysis and the bony metaphyseal collar, leaving longitudinally-oriented striations on the latter's surface. On the medial and capital metaphyseal surfaces, the fibrocartilage sleeve attaches to a continuous, striated shelf of cortical bone. The expanded metaphyseal attachment of fibrocartilage has also been noted by Haines (1969) on the crocodylian distal humerus. The attachment sites of fibrocartilage and hyaline cartilage can be distinguished by a prominent metaphyseal line. The hyaline cartilage leaves the smooth, calcified cartilage-covered growth plate, underneath which lies the subchondral trabecular bone (Fig. 2-10d, e). Unlike fibrocartilage, hyaline cartilage does not attach to cortical bone and is restricted to the growth plate surface (Fig. 2-10g, h). The distinction between fibrocartilage and periosteum attachments is more ambiguous, reflecting the gradual transition between these tissues.

A patch of loose connective tissue on the craniomedial metaphysis separates the fibrocartilage sheath proximally and the perichondrium distally (Fig. 2-10a, e, f). Kuznetsov and Sennikov (2000) hypothesized this tissue as a synovial bursa, as it lies external to the hip joint capsule and facilitates craniocaudal sliding contact between the medial metaphysis and the ventral acetabular rim during hindlimb-adducted locomotion (the "high walk"). On skeletal specimens, the putative bursal tissue presents as an exposed patch trabecular bone, bordered by cortical bone both proximally and distally (Fig. 2-10h). In contrast to juvenile individuals, adult crocodylians possess fewer and more robust exposed trabeculae at this location, but the morphology of other

cartilaginous osteological correlates exhibit no distinguishable ontogenetic variation between juveniles and adults. The crocodylian femoral growth plate surface remains smooth across the ontogenetic series sampled, in contrast to the increase in rugosity in the pelvic peduncular growth plates (Fig. 2-10b, g, 2-12c).

In birds, the fibrocartilage sleeve encapsulates the hyaline cartilage superficially and forms the entire proximal femoral articular surface (Graf et al., 1993). The fibrocartilage layer exhibits little medial attachment to the cortical bone, thickens along the superficial surface of the femoral neck (*facies articularis antitrochanterica*, Baumel and Witmer, 1993), and attaches to the hyaline cartilage layer on the medial side of the greater trochanter (Fig. 2-11b). Osteological correlates of the hyaline cartilage attachment are the same as those seen in crocodylians, but reduction of the metaphyseal fibrocartilage attachment is reflected by the lack of distinct, striated cortical shelves on the bony metaphyseal collar, distal to the calcified cartilage layer (Fig. 2-11e, f, g). A narrow patch of exposed trabecular bone is present at the metaphyseal boundary ventral to the joint capsule of the femoral head, and is covered by loose, fibrous perichondrium in freshly dissected animals. The presence of exposed trabecular bone distal to the fibrocartilage collar is similar to the putative bursa morphology in crocodylians. In juvenile birds, the thick, vascularized hyaline cartilage layer occupies large portions of the femoral chondroepiphysis and can be distinguished from the superficial fibrocartilage layer, whereas in skeletally mature birds, the hyaline cartilage is reduced to a thin layer and gradually transitions into the superficial fibrocartilage layer. Nevertheless, the topological relationship of fibro- and hyaline cartilage remains similar across ontogeny.

Summary:

The highly specialized hip joint morphology of extant sauropsids complicates homology inferences. Turtles possess the simplest form of hip joint, in which the femoral and the acetabular articular surfaces consist of thin layers of hyaline cartilage at adulthood, lacking an extensive fibrocartilage sleeve and intrinsic joint ligaments. Diapsid hip joints share topologically consistent soft tissue attachments, allowing putative inferences of homology. In lizards, crocodylians, and birds, the dorsal portion of the acetabulum consists of fibrocartilaginous articular pads, which can be further distinguished into a cranial acetabular labrum and a caudal antitrochanter. In contrast, the ventral portion possesses hyaline cartilage articular surfaces. The ligamentum capitis femoris originates from the ventral acetabular rim and inserts onto the fovea capitis on the proximal femur. The chondroepiphysis of the proximal femur consists of a periphery of fibrocartilage encapsulating a hyaline cartilage core. Osteological correlates of joint soft tissue discussed are summarized in Table 2-4.

DISCUSSION

Homology of the supraacetabulum

Hypotheses of hip joint soft tissue homology are summarized in Fig. 2-3. Diapsids possess distinct supraacetabular soft tissues. The acetabular labrum attaches to the cranial rim of the acetabulum and extends into the dorsal acetabular cavity in crocodylians, lepidosaurs, and some palaeognaths (Firbas and Zweymüller, 1971). Though osteological correlates of the labrum are topologically consistent on the dorsal acetabular rim, its attachment surface texture differs between lepidosaurs, crocodylians, and birds. Neornithes in particular lack distinct surface textures between labral- and hyaline cartilage attachments on the supraacetabulum, which hampers inferences on the medial

extent of the acetabular labrum. Nevertheless, labral tissues within the acetabulum in lepidosaurs, crocodylians, and basal birds are homologous among diapsids.

Functions of the supraacetabulum in non-avian diapsids

The acetabular labrum maintains joint congruence during the wide range of hip adduction angles achieved by crocodylians and lizards during terrestrial locomotion (Reilly and Elias, 1998; Clemente et al., 2013). The acetabular labrum functions as an important weight-bearing structure in dysplastic human hip joints models, in which the femoral head is smaller than the acetabulum (Henak et al., 2011). Under such loading environment, the femoral articular surface rests primarily on the labrum during the support phase, rather than the hyaline cartilage-covered lunate surface of the acetabulum. In non-avian diapsids, the proximal femur articulates primarily with the labrum during adducted hip postures. The labrum may therefore mitigate hip joint loading during more vertical femoral postures.

Functions of the supraacetabulum in birds

In neornithines, the labrum does not occupy a large volume of the adult avian acetabulum and only forms a small slip of fibrous tissue extending laterally from the ilial acetabular rim. Reduction of the acetabular labrum in birds may be associated with the evolution of a more protracted femoral posture in contrast to non-avian theropods (Gatesy, 1991; Gatesy and Middleton, 1997; Allen et al., 2013), such that much of the proximal femur articulates with the antitrochanter on the caudodorsal acetabulum instead of the craniodorsal labrum. Furthermore, avian hindlimb abduction-adduction is facilitated by femoral axial rotation (Stolpe, 1932; Hutchinson and Gatesy, 2009; Kambic et al., 2014). The relatively small amount of femoral head movement within the

acetabulum suggests that the avian hip would not experience the drastic changes in bony joint congruence and loading direction as those of lepidosaurs and crocodylians, thus deemphasizing the role of the acetabular labrum. However, the habitually-protracted position and axial rotation of the femur affect the antitrochanter region of the acetabulum.

Homology of the antitrochanter

The diapsid antitrochanter is a single meniscus in *Sphenodon*, an elastic cartilage pad of lizards, two overlapping menisci of crocodylians, and a bony, fibrocartilage-covered buttress in birds. The antitrochanter is marked by a grooved border in lepidosaurs and by the laterally extended ilial and ischial peduncular growth plate surfaces in archosaurs. The single meniscus of *Sphenodon* and the deep meniscus crocodylians possess a ligamentous attachment to the ilial acetabulum, which leaves a distinctive notch on the bony surface. Topological similarity among diapsid antitrochanters suggests independent modifications of a homologous fibrous structure in the caudal acetabulum. This inference supports the assessment by Farlow et al. (2000) that the avian antitrochanter is homologous with those of non-avian theropods (contra Hertel and Campbell, 2007). Moreover, presence of the antitrochanter has been noted in basal dinosauromorphs (Langer et al., 2010), suggesting that modification of this fibrocartilaginous articular surface at the caudal acetabulum is intimately linked with the acquisition of avian locomotor posture within the theropod lineage (Hutchinson and Allen, 2009).

Meniscus-like structures have also been observed in the caudal acetabulum of amphibians and juvenile mammals (Canillas et al., 2011). Given this wide phylogenetic distribution of fibrous articular pads on the caudal acetabulum, the antitrochanter may be

a plesiomorphic tetrapod feature, with subsequent losses in turtles and mammals. However, whether the menisci-like antitrochanter observed in crocodylian, *Sphenodon*, and amphibians are convergences or representative of the plesiomorphic tetrapod condition remains unclear. Further knowledge on the polarity of this character in the sauropsid fossil record will offer unique insights in the evolution of tetrapod hip joint function.

Function of the lepidosaurian antitrochanter

The antitrochanter of lepidosaurs differs from the putatively homologous structures in archosaurs in both gross topology and microstructure. In the lizards studied, the antitrochanter is located exclusively on the caudodorsal ilial acetabulum, with no inclusion of the ischial surface. Moreover, the antitrochanter of lizards resembles elastic cartilage like that found in mammalian pinnae (Fig. 2-4b; Cox and Peacock, 1977) and processes of arytenoid cartilages (Sato et al., 1990) in microstructure. Lizards abduct the hip during locomotion, such that the femur not only medially compresses the acetabulum during the stance phase but also experiences substantial gliding and axial rotation within the acetabulum during protraction and retraction (Irschick and Jayne, 1999). The presence of an elastic articular structure within the acetabulum may function to maintain joint contact during the wide range of hip articulation experienced during locomotion.

Function of the crocodylian antitrochanter

The crocodylian hip joint is highly mobile and permits a wide range of femoral postures during locomotion, including substantial femoral axial rotation and hyper-retraction (Reilly and Elias, 1998; Blob and Biewener, 2001; Tsai et al., 2012). The ligamentous connections between the antitrochanter menisci, the acetabulum, and the

femur allow these structures to maintain dynamic contact with each other during joint excursion, similar to posture-related movement between the meniscus, the distal femur, and the tibial plateau of the human knee joint (Pena et al., 2006; Vedi et al., 1999). Knee joint menisci are ubiquitous among tetrapods (Haines, 1942) and are thought to maintain joint congruence (Barnett, 1954), facilitate load bearing (MacConaill, 1932; Messner and Gao, 1998), and provide mechanoreception (O'Connor and McConnaughey, 1978; Zimney, 1988). In particular, Barnett (1954) observed that menisci pads are present in joints that undergo both uniaxial movements (e.g. long-axis rotation, flexion and extension) and gliding movements with dynamic rotation centers.

The evolutionary history of Crocodylia may explain why crocodylians use a complex set of ligaments and meniscus structures to satisfy a functional demand achievable by a simple cartilaginous pad in lizards. Whereas lepidosaurs inherited the sprawling locomotor posture plesiomorphic to tetrapods (Romer, 1956; Rewcastle, 1983; Russell and Bauer, 2008), basal pseudosuchian archosaurs are inferred to possess adducted hindlimb posture and parasagittal locomotor behavior, with subsequent reversion to the abducted hindlimb posture in crocodylomorphs (Parrish, 1987; Kubo and Benton, 2007). The intrinsic joint ligaments might have first functioned as joint stabilizers in parasagittal pseudosuchian archosaurs, and were subsequently modified into the meniscal complex in crocodyliformes to allow greater degree of femoral abduction and rotation during sprawling locomotion. Interestingly, the antitrochanter of *Sphenodon* also possesses a meniscus-like morphology, despite their abducted hindlimb posture plesiomorphic for tetrapods. In light of the deep evolutionary history and wide morphological disparity of fossil rhynchocephalians (Evans and Jones, 2010), the

functional significance of the antitrochanter meniscus in *Sphenodon*, remains an avenue for future studies on lepidosaurian locomotor evolution.

Functions of the avian antitrochanter

The avian antitrochanter's role in compressive load bearing is poorly understood. Hutchinson and Gatesy (2009) noted the antitrochanter's function as a physical limit to femoral abduction during stance and locomotion and is thus likely loaded in both compression and translational shear. In contrast, Hertel and Campbell (2007) and Troy et al. (2009) suggested the antitrochanter functions as a sliding surface against the femoral neck, and experiences little compression during stance and locomotion. Prior to skeletal maturity, the avian antitrochanter attaches to the laterally oriented growth plate surfaces on the ilial-ischial junction, and is comprised of a hyaline cartilage core and a fibrocartilaginous articular surface. The subsequent ossification of the hyaline cartilage core reduces the thickness of the hyaline cartilage, such that skeletally mature adults possess only the thin, superficial composite layer of fibro-hyaline cartilage (Wess et al., 1997). Since a bone is more resilient to compressive stress than hyaline cartilage, the ossification sequence of the antitrochanter during ontogeny suggest that it indeed experiences compressive load. On the other hand, the parallel-fibered fibrocartilaginous morphology of the avian antitrochanter is consistent with its function as a sliding articular surface. The collagen fibers in the avian antitrochanter is oriented largely parallel to the loading direction of the femoral neck during femoral long axis rotation (Main and Biewener, 2007; Hutchinson and Gatesy, 2009; Kambic et al., 2014). These results suggest that the avian antitrochanter is suited for resisting both compressive and shear stresses (Freemont and Hoyland, 2006) when the femoral head acts as a pivot within the

acetabulum (articulationis coxocapitalis, Baumel and Raikow, 1993) and the femoral neck (the trochanteric region) compresses and glides against the antitrochanter (articulationis coxotrochanterica, Baumel and Raikow, 1993).

My dissections found only a single articular surface on the antitrochanter of neognaths, Firbas and Zweymuller (1971) described an atitrochanter meniscus in large palaeognaths and suggested it as an adaptation for large body size. However, the antitrochanter meniscus is not described in small bodied palaeognaths (e.g., *Apteryx*, Berge, 1982), thus its role in load bearing in large, terrestrial birds remains uncertain.

Homology and function of the inner acetabular membrane

My results suggest that the membranous inner acetabular wall is correlated with the presence of intrinsic ligaments. In archosaurs, the inner acetabular membrane is a thick, ligamentous structure. Its fibrous composition and inter-osseous attachment topology is consistent with that of a ligament (Skahen et al., 1997). A membranous (perforated) inner acetabular wall evolved independently in the crocodylian and avian lineage, as stem archosaurs (e.g., phytosaurs), ornithodirans (e.g., lagerpetids, silesaurs), and pseudosuchians (e.g., poposauroids, aetosaurs) lack perforated acetabulae (Nesbitt, 2011). An unossified (“perforated”) inner acetabular wall has been associated with the evolution of vertically oriented femoral postures (Serenó, 1991; Brusatte et al., 2010), because the unossified inner wall is thought to correlate with more vertically directed compressive loads from the femur (Kuznetsov and Sennikov, 2000; Kubo and Benton, 2007). However, extant crocodylians possess an unossified inner wall despite their habitually abducted hindlimb postures, whereas basal ornithodirans and pseudosuchians possess inner acetabular walls enclosed by bone, despite inferences of vertically oriented

femoral postures (Parrish, 1987; Nesbitt, 2011). In both birds and crocodylians, the membranous inner wall prevents compression of the ligamentum capitis and accommodates its movement within the synovial cavity, similar to the role of the pulvinar-filled acetabular notch in mammals (Bardakos and Villar, 2009). Therefore, an unossified inner acetabular wall is an osteological correlate for the presence of intrinsic ligaments in the hip joint.

Homology of the capsular and intrinsic ligaments

The iliofemoral ligament of lepidosaurs and crocodylians is topologically similar and homologous to the avian pubofemoral ligament (*sensu* Baumel and Raikow, 1993). In all three clades, this robust ligament originates on the craniodorsal acetabular rim, but whereas in non-avian diapsids the iliofemoral ligament inserts to the lateral metaphyseal surface of the femur, the avian pubofemoral ligament inserts on the cranial metaphyseal surface. Hutchinson (2001b) inferred the avian proximal femur underwent medial deflection during theropod evolution, such that the anatomical femoral head transitioned from a craniocaudal to mediolateral orientation. Accordingly, the ancestrally lateral metaphyseal surface of non-avian diapsid is homologous to the cranial metaphyseal surface of birds. The avian “pubofemoral ligament” (Baumel and Raikow, 1993) is homologous with the iliofemoral ligaments of crocodylians and lizards as they share homologous attachments and structure. In contrast, the avian “iliofemoral” ligament (*sensu* Baumel and Raikow, 1993) is a neomorphic structure.

Based on morphological similarity, attachment homology, and the lack of other candidate structures, the ligamenta capitis of diapsids are here inferred to be homologues. In crocodylians and lepidosaurs, the ventral acetabulum possesses two ligamentous

connections to the proximal femur. In lizards, the pubofemoral and ischiofemoral ligaments form part of the ventral joint capsule and converge to form the ligamentum capitis, whereas in crocodylians the cranial and caudal crura of the ligamentum capitis are within the synovial cavity and distinct from the joint capsule. The decoupling of crocodylian ventral joint ligaments from the synovial capsule is similar to the ligamentum capitis morphology observed in birds. Though I identified only a single ligamentum capitis in wet specimens of neornithes, the flat, band-like morphology of this ligament suggests that it may consist of both the ligamentum teres and posterior acetabular ligaments as observed in *Struthio* and by Cracraft in the pigeon (1971). This identification is corroborated by the observation of distinct osteological correlates for the two ligaments on the proximal femur of recent palaeognaths, indicative of the separate nature of the teres and posterior acetabular ligaments (Fig. 2-11f, g). If the lepidosaur condition is the plesiomorphic diapsid condition, then the archosaur ligamentum capitis evolved from fusion of the ancestral pubofemoral and ischiofemoral ligaments. Under this hypothesis, the two synonymous avian ligaments described by Baumel and Raikow (1993) are non-homologous neomorphs, secondarily derived from the synovial capsule. Interestingly, the mammalian ligamentum capitis originates on the transverse acetabular ligament (Fuss and Bacher, 1991), a condition similar to that of lizards, wherein the ligamentum capitis also arises from the convergence of iliofemoral and ischiofemoral ligaments at the ventral acetabular rim. This suggests the mammalian ligamentum capitis is also derived from the junction of the two ventral capsular ligaments, and is convergent with the sauropsid morphology.

Function of the capsular and intrinsic ligaments

Joint ligaments physically limit excursion (Girgis et al., 1975; Kivlan et al., 2013). The incorporation of fibrocartilage in the mammalian transverse acetabular ligament (Milz et al., 2001) and a muscle (*m. ischiotrochantericus*) in the hip joint capsule of lizards and crocodylians suggest that joint ligaments are intimately associated with the loading environment. The range of motion of the mammalian hip joint is thought to be partially influenced by the ligamentum capitis, such that the joint cannot assume positions where the ligament is impinged between the femoral and acetabular surfaces (Jenkins and Camazine, 1971; Hammond, 2013). The identification of intracapsular ligaments and their osteological correlates in archosaur hip joints sets the stage for further investigation on the roles of these structures in constraining hip joint range of motion. Moreover, joint ligaments provide proprioceptive feedback (Johansson et al., 1991; Knoop et al., 2011) against excessive joint excursion, serving to prevent muscle tear and articular cartilage damage. In particular, the cranial crus and acetabular labrum of crocodylians may provide sensory feedback on hip adduction angles used during terrestrial locomotion (Reilly and Elias, 1998). Though this study did not assess the presence of mechanoreceptors, the tensile behavior of ligaments may be informative regarding the roles of ligaments in joint range of motion.

Homology and functions of the chondroepiphysis

The presence of a distinct femoral head has been noted as an important functional character during the locomotor evolution of pseudosuchians (Nesbitt, 2007) and ornithomirans (Nesbitt et al., 2010). The femoral head has been used as a proxy for the center of hip joint rotation in archosaurs from which to infer joint range of motion, even in taxa with markedly smaller femoral heads than the acetabula (Hutchinson et al., 2005;

Bates et al., 2010; Bates and Schachner, 2011; Maidment et al., 2013). However, the difficulty in resolving femoral head regional homologies and the effects of intracapsular ligaments impact inferences of archosaur hip joint range of motion and kinematics. Overall, the attachment homology of joint ligaments, acetabular soft tissues, and femoral cartilages support previous assessments of archosaur femoral surface homology by Hutchinson (2001b), as well as his inference of medial femoral deflection during avian evolution. However, data on intracapsular ligament homology question traditional paleontological definition of the archosaur femoral head. The femoral head is commonly defined as the craniomedial extension of the proximal femur, which forms an “overhang” from the proximal metaphysis (e.g., Hutchinson, 2011b; Nesbitt, 2011). However, whereas the avian fovea capitis is located on the sub-spherical femoral head, it is located between the femoral head (*sensu* Hutchinson, 2011b; “anteromedial tuber” *sensu* Nesbitt, 2011) and the medial protuberance (the “posteromedial tuber” *sensu* Nesbitt, 2011) of crocodylians and lepidosaurs. If the non-avian diapsid condition is the ancestral character state, then the avian condition can be achieved in two ways: by changing the attachment site of the ligamentum capitis or by expanding the medial protuberance. Under the first hypothesis, the fovea capitis is shifted craniad in crown-lineage theropods, whereas the medial protuberance is lost. Under the second hypothesis, the location of the fovea capitis remains unchanged during theropod evolution, but the medial protuberance is enlarged and became part of the anatomical femoral head. These two hypotheses can be tested using osteological correlates of fibrocartilage, hyaline cartilage, as well as the fovea capitis in fossil archosaurs leading to the crown groups.

The sauropsid proximal femoral epiphysis consists of a hyaline cartilage core surrounded by a peripheral sleeve of fibrocartilage. The mineralizing secondary centers within the lepidosaurian chondroepiphysis fuses to the metaphyseal growth plates at skeletal maturity. Because of epiphyseal fusion, only skeletally immature lepidosaurs possess subchondral surfaces homologous to those in archosaurs. Carter et al. (1998) characterized lepidosaurs as possessing long bone ossification patterns similar to that of mammals, such that endochondral and perichondral ossification proceeds largely synchronously. This contrasts the condition in archosaurs, in which endochondral ossification is delayed relative to perichondral ossification, resulting in a cartilage cone extending deep into the metaphysis (Carter et al., 1998). However, results of this study showed that in juvenile lizards, the concave, irregularly-rugose metaphyseal growth plate articulates with the convex ventral surface of the secondary center via a trough-cone articulation. This morphology is consistent with the definition of a cartilage cone according to Carter et al. (1998). The trough-cone articulation and rugose metaphyseal growth plate likely provides mechanical support to the chondroepiphysis against tensile and shear strain by increasing its contact surface area with the metaphyseal growth plate.

Irregular rugosity on the growth plate surface is an osteological correlate for thick hyaline cartilage. The crocodylian cranial acetabular cartilage (*cartilago acetabularis*, Cong et al., 1998) remains a considerable portion of the cranioventral acetabulum and excavates visible irregular rugosities on the ilial- and ischial peduncles of large adults. A similar topological relationship between thick hyaline cartilage and growth plate rugosity has also been observed on the unossified antitrochanter of juvenile ostriches, and on the acetabulum and glenohumeral joints of *Dermochelys* (Gervais 1872; personal

observation). The crocodylian proximal femur possesses a thinner chondroepiphysis than that of the lizard, and the relative thickness of the crocodylian chondroepiphysis decreases as the animal matures (Holliday et al., 2010). This may explain the lack of rugosity on the proximal femoral growth plate in the ontogenetic sample studied—the chondroepiphysis simply never reaches the absolute thickness at which rugosity develop. These observations suggest that growth plate rugosity is an osteological correlate for thick hyaline cartilage.

Crocodylians stabilize the chondroepiphysis using an expanded fibrocartilage sleeve. The hyaline cartilage core on the crocodylian proximal femur does not insert into the metaphysis via a trough-cone articulation as in lizards. Instead, the metaphyseal fibrocartilaginous sleeve expands onto both the hyaline core and the metaphyseal cortical bone. Crocodylians may compensate for the lack of trough-cone metaphyseal articulation by strengthening the chondroepiphysis peripherally using fibrocartilage, which is more resilient against tensile and shear stress than hyaline cartilage (Freemont and Hoyland, 2006). Thus, the fibrocartilaginous sleeve may prevent avulsion of the hyaline core from the metaphyseal growth plate during femoral excursion. The fibrocartilage sleeves also serve as the attachment sites of the iliofemoral ligament and the ligamentum capitis on the metaphyseal junction and may function as an enthesis organ to reduce tensile and shear stress experienced by the growth plate during joint excursion (Benjamin et al., 2002). The metaphyseal bursa ventral to the joint capsule was described by Kuzenetsov and Sennikov (2000) as a “synovial cushion” between the femoral metaphyseal surface and the ventral acetabular rim during hip adduction, allowing craniocaudal sliding motion between the concave medial metaphysis and the convex ventral acetabular rim. The bursa

thus functions as an accessory articular surface in the crocodylian hip joint, as it is subjected to translational shears loads only during hip adduction.

Neornithes retain a thinner layer of chondroepiphysis at adulthood (Holliday et al., 2010), and lack either the trough-cone metaphyseal articulation or the expanded metaphyseal fibrocartilage sleeve found in lizards or crocodylians. The fibrocartilage sleeve expands apically and envelops the hyaline cartilage core, such that the articular surface is fibrocartilage. However, in contrast to crocodylians and non-avian theropods (Tsai et al., 2013), the avian fibrocartilage sleeve attaches narrowly on the femoral neck and the capital metaphyseal junction. I propose two non-mutually exclusive mechanical hypotheses to explain the reduction of the fibrocartilage sheath. The small metaphyseal attachment of the fibrocartilage sleeve may be associated with the reduction of proximal femoral hyaline cartilage thickness, as thinner hyaline cartilage presumably requires less peripheral fibrocartilage sleeve for mechanical support. Additionally, reduction of the metaphyseal fibrocartilage reflects decreased femoral movement during avian terrestrial locomotion, in contrast to the more mobile hip joint kinematics observed in crocodylians (Reilly and Elias, 1998) and hypothesized for non-avian theropods (Hutchinson et al., 2005; Hutchinson, 2006).

The avian femoral head retains a visible layer of hyaline cartilage in histological sections, whereas the femoral neck region is entirely fibrous. This difference in soft tissue composition may be associated with localized loading regimes. The fibrocartilaginous articular surface on the femoral neck may alleviate shear strain during its sliding articulation with the antitrochanter (Kambic et al., 2014), whereas the hyaline cartilage on the femoral head would be better suited for compressive loading against the

supraacetabulum. Attachment topologies of fibro- and hyaline cartilage support the inference that the femoral head and trochanteric regions are homologous across archosaurs (Hutchinson, 2001b) and provide support for the use of these regions as anatomical landmarks.

Cartilage cones, endochondral bone, and the evolution of secondary mineralizing centers

My results agree with the morphological assessment of Haines (1969) and Horner et al. (2001). A cartilage cone is present in the pre-hatchling *Alligator* (MUVC-AL 114), and remnants of the cartilage cone are present in the juvenile *Chelydra*. The cartilage cone is absent in the current samples of post-hatching juvenile *Alligator* and *Gallus*, likely because the specimens were mature enough such that the cartilage cones were already obliterated by endochondral ossification. Using 2D finite element models, Carter et al. (1998) suggested that retention of the cartilage cone within the archosaur metaphysis results in structurally weaker endochondral bone, thus inhibiting the formation of secondary centers. However, I show that lizards develop secondary centers despite retention of the cartilage cone, suggesting that the two structures are not mutually exclusive. The relationship between the cartilage cone, endochondral ossification, and secondary center of ossification may be more complex than suggested by Carter et al. (1998), and that further studies are needed to understand the role of joint loading on the evolution long bone ossification patterns in tetrapods.

Evolutionary transformations of archosaur hip joint soft tissue characters

This study identified osteological correlates of hip joint articular soft tissues in Sauropsida, and proposed their evolutionary transformations leading to each crown lineages (Summarized in Fig. 2-13). Since hip joint soft tissue characters leave consistent

osteological correlates, results of this study allow investigation on how joint soft tissues may be associated with evolutionary transition in body size and locomotor behavior in fossil taxa. For example, independent transitions between quadrupedality and bipedality have been inferred in both ornithomimid (Carrano, 2010; Langer et al., 2010; Nesbitt et al., 2010) and pseudosuchian (Walker, 1964; Nesbitt, 2007; Bates and Schachner, 2012) lineages. Interestingly, the metaphyseal cartilage cone is independently lost in crocodylians, theropods, and sauropods (Tsai et al., 2013), suggesting a link between chondroepiphyseal attachment morphology and locomotor postural transitions. A test of such association is beyond the scope of this study, but remains an avenue for further investigations. Results of this study also suggest that presence of pubofemoral and ischiofemoral ligaments within the joint capsule may be associated with the perforated inner acetabular wall, allowing the latter to be used as a proxy for the presence of intracapsular ligaments in fossil taxa. Inclusion of intracapsular ligaments in studies of fossil archosaur hip joint kinematics would help constrain joint range of motion, thus improve reconstruction of locomotor behavior. Lastly, irregularly rugose growth plate surfaces are associated with thick layers of hyaline cartilage across extant sauropsids, thus the presence of such morphology in fossil taxa allow identification of the sequence of gain and loss of thick hyaline cartilage in the fossil record. Thick hyaline cartilage is reconstructed here as plesiomorphic of Diapsida, and is retained by lepidosaurs, stem suchians (e.g., poposauroids), and sauropods. Lepidosaurs further modified this morphology by calcifying the hyaline cartilage core, whereas stem suchians and sauropods maintained thick, uncalcified core of hyaline cartilage on the proximal femur. In particular, stem suchians likely possessed even thicker layers of epiphyseal cartilage

than crocodylians, and sauropods would have possessed the absolutely thickest layer of epiphyseal cartilage on the limb bones of any tetrapod. The mechanical properties and function of these joints remain poorly understood, and remain areas of future studies. Overall, the archosaur hip joint exhibits high degree of homoplasy and thus emphasizes the importance of archosaurs in future studies on the functional adaptation of the locomotor apparatus.

CONCLUSION

Despite gross differences in bony hip joint morphology, the hip joint soft tissues of archosaurs and outgroups show remarkably conserved topology and function. The archosaur hip joint exhibits regionally distinct articular soft tissues, in which hyaline cartilage facilitate compressive loading, whereas fibrocartilage facilitate sliding articulation and mechanical support for the hyaline cartilage. Homology and functional associations between joint ligaments and articular tissues inform joint range of motion and constraints to hip kinematics. Finally, both femoral and acetabular soft tissues differentially contribute to hip joint articulation and load bearing among different lineages. Specifically, the presence of thick hyaline cartilage, an acetabular labrum, and mobile meniscus-like structures in the diapsid hip joint facilitates further research on the mechanical role of these tissues in vertebrate joint loading, articulation and growth. Results of this study thus offer novel directions for research in connective tissue biology.

Thus far, hindlimb function of fossil archosaurs has been reconstructed based on musculoskeletal anatomy and quantitative modeling techniques (Hutchinson et al., 2005; Hutchinson and Allen 2009; Bates et al., 2010; Bates and Schachner, 2011; Maidment et al. 2013). This study illuminates the complexities among articular surface composition,

ligamentous constraints, joint articulation, and load bearing in the archosaur hip joint.

Moreover, this study provides osteological correlates from which to infer the presence of articular soft tissues in osteological specimens, including fossil taxa. These new data will allow the use of anatomically informed hip joint reconstruction for quantitative modeling studies in both extant and fossil archosaurs and expands our knowledge on the transitions in hindlimb posture, kinematics, loading mechanics, and locomotor behavior during archosaur evolution.

Table 2-1. Synonyms of anatomical structures the epiphyseal region used in this study and selected literature. Quotation marks are included as used by the authors.

This study	Chondroepiphysis	Articular surface	Secondary center	Metaphyseal collar	Metaphyseal growth plate
Parson 1905	Cartilage	Articular cartilage	Epiphysis	Diaphysis	Epiphyseal line
Haines, (1969; 1975)	Cartilaginous epiphysis, growth cartilage	-	Epiphyseal bone, secondary center of ossification	Diaphysis	Diaphyseal plate
Barreto et al., 1993	Articular end of growth plate	-	-	Metaphyseal bone	metaphyseal ends of growth plates
Carter et al, 1998	Chondroepiphysis	Articular surface	Secondary ossific nucleus	Diaphyseal sleeve	Growth plate
Leunig et al., 2000	Articular cartilage	Articular cartilage	Epiphysis	Metaphysis	Growth plate
Horner et al., 2001;	Cartilaginous epiphysis	Articular cartilage	Secondary center of ossification	Metaphysis	“Epiphysis”
de Ricqlès et al., 2003a, b	-	-	-	Metaphyseal region, Metaphysis	Epiphyseal/ “Articular” surface
Cardoso, 2009	-	-	Epiphysis	-	Metaphyseal surface
Holliday et al., 2010	Cartilaginous epiphysis, articular cartilage	Articular cartilage	Secondary center of ossification, bony epiphysis	Bony metaphysis	Epiphyseal growth plate
Bonnan et al., 2010	Chondroepiphysis	Articular surface	Secondary ossification center	-	Calcified cartilage, Articular surface
Bonnan et al., 2013	Articular cartilage	Articular hyaline cartilage	Secondary ossification center	Metaphysis	Sub-articular surface

Table 2-2. Anatomical Abbreviations.

2 nd . ctr	secondary center	pb	pubis
att	antitrochanter	ppi	pubic peduncle of ilium
brs	bursa	lab	acetabular labrum
cc	calcified cartilage	L. cdcf	caudal ligamentum capitis femoris
cr	cartilaginous (nodular) region	L. cf	ligamentum capitis femoris
cn	cartilage cone	L. ilf	iliofemoral ligament
dm	deep meniscus	L. isf	ischiofemoral ligament
ec	Elastic cartilage	L. pf	pubofemoral ligament
gp	growth plate	L. pac	posterior acetabular ligament
fbm	fibrous matrix	L. crcf	cranial ligamentum capitis femoris
fc	fibrocartilage	L. t	ligamentum teres
fm	femur	lcc	loose connective tissue core
fov	fovea capitis	lr	ligamentous region
fov. lt	fovea capitis of ligamentum teres	m. istr	<i>m. ischiotrochantericus</i>
fov. pac	fovea capitis of posterior acetabular ligament	pcf	peripheral collagen fiber
hc	hyaline cartilage	ppi	pubic peduncle of the ischium
icf	internal collagen fiber	R. cp	capital region
il	ilium	R. tr	trochanteric region
int. tr	internal trochanter	sm	superficial meniscus
is	ischium	T. istr	tendon of <i>m. ischiotrochantericus</i>

Table 2-3. Sauropsid specimens and techniques used to investigate hip joint anatomy.

Specimen number	Taxon	Clade	Ontogenetic stage	Specimen	Histology	Imaging
FMNH 31011	<i>Alligator mississippiensis</i>	Crocodylia	Adult	Skeletal	N/A	N/A
MUVC-AL 76	<i>Alligator mississippiensis</i>	Crocodylia	Juvenile	Wet	Femur and acetabulum	N/A
MUVC-AL 100	<i>Alligator mississippiensis</i>	Crocodylia	Juvenile	Wet	N/A	μ CT in I2KI
MUVC-AL 102	<i>Alligator mississippiensis</i>	Crocodylia	Subadult	Wet	N/A	CT μ CT in I2KI
MUVC-AL 105	<i>Alligator mississippiensis</i>	Crocodylia	Juvenile	Wet	Femur and acetabulum	N/A
MUVC-AL 106	<i>Alligator mississippiensis</i>	Crocodylia	Embryo	Wet	N/A	N/A
MUVC-AL 112	<i>Alligator mississippiensis</i>	Crocodylia	Juvenile	Wet	N/A	N/A
MUVC-AL 113	<i>Alligator mississippiensis</i>	Crocodylia	Subadult	Wet	Acetabulum	Photogrammetry
MUVC-AL 114	<i>Alligator mississippiensis</i>	Crocodylia	Embryo	Wet	Femur and acetabulum	N/A
MUVC-AL 602	<i>Alligator mississippiensis</i>	Crocodylia	Adult	Wet	N/A	Photogrammetry
MUVC-AL 703	<i>Alligator mississippiensis</i>	Crocodylia	Adult	Wet	N/A	N/A
MUVC-AL 711	<i>Alligator mississippiensis</i>	Crocodylia	Adult	Wet	N/A	N/A
FMNH 9150	<i>Caiman crocodilus</i>	Crocodylia	Subadult	Skeletal	N/A	N/A
FMNH 218507	<i>Melanosuchus niger</i>	Crocodylia	Subadult	Skeletal	N/A	N/A
FMNH 22030	<i>Crocodylus acutus</i>	Crocodylia	Adult	Skeletal	N/A	N/A
FMNH 213394	<i>Crocodylus acutus</i>	Crocodylia	Adult	Skeletal	N/A	N/A

FMNH 51691	<i>Crocodylus plaustris</i>	Crocodylia	Adult	Skeletal	N/A	Photogrammetry
FMNH 22026	<i>Crocodylus porosus</i>	Crocodylia	Adult	Skeletal	N/A	Photogrammetry
NMNS004834~ F003968	<i>Crocodylus porosus</i>	Crocodylia	Adult	Skeletal	N/A	N/A
FMNH 82681	<i>Gavialis gangeticus</i>	Crocodylia	Adult	Skeletal	N/A	Photogrammetry
NMNS005529- F042904	<i>Tomistoma schlegelii</i>	Crocodylia	Adult	Skeletal	N/A	N/A
FMNH 206755	<i>Tomistoma schlegelii</i>	Crocodylia	Subadult	Skeletal+Ligament	N/A	N/A
FMNH 11113	<i>Sphenodon punctatus</i>	Lepidosauria	Adult	Skeletal	N/A	N/A
FMNH 197942	<i>Sphenodon punctatus</i>	Lepidosauria	Adult	Skeletal+Ligament	N/A	N/A
FMNH 211217- 18	<i>Sphenodon punctatus</i>	Lepidosauria	Adult	Wet	N/A	N/A
FMNH 22041	<i>Iguana iguana</i>	Lepidosauria	Adult	Skeletal	N/A	N/A
FMNH 22201	<i>Iguana iguana</i>	Lepidosauria	Adult	Skeletal	N/A	N/A
MUVC-LI 039	<i>Iguana iguana</i>	Lepidosauria	Juvenile	Wet	N/A	N/A
MUVC-LI 032	<i>Ctenosaura similis</i>	Lepidosauria	Juvenile	Wet	Femur and acetabulum	N/A
FMNH 250611	<i>Heloderma horridum</i>	Lepidosauria	Adult	Skeletal	N/A	N/A
MUVC-VNI 006	<i>Varanus exanthematicus</i>	Lepidosauria	Juvenile	Wet	N/A	N/A
FMNH 31338	<i>Varanus gouldi</i>	Lepidosauria	Adult	Skeletal	N/A	N/A
FMNH 22191	<i>Varanus komodoensis</i>	Lepidosauria	Adult	Skeletal	N/A	Photogrammetry
FMNH 22198	<i>Varanus komodoensis</i>	Lepidosauria	Subadult	Skeletal	N/A	Photogrammetry
FMNH 22199	<i>Varanus</i>	Lepidosauria	Subadult	Skeletal	N/A	N/A

	<i>komodoensis</i>						
FMNH 22200	<i>Varanus komodoensis</i>	Lepidosauria	Subadult	Skeletal	N/A	N/A	N/A
FMNH 221856	<i>Varanus nebulosus</i>	Lepidosauria	Adult	Skeletal	N/A	N/A	N/A
MUVC-VNI 001	<i>Varanus niloticus</i>	Lepidosauria	Adult	Skeletal	N/A	N/A	N/A
MUVC-VNI 005	<i>Varanus niloticus</i>	Lepidosauria	Adult	Wet	N/A	N/A	N/A
FMNH 22204	<i>Varanus salvator</i>	Lepidosauria	Adult	Skeletal	N/A	N/A	N/A
MUVC-LI 044	<i>Gekko gecko</i>	Lepidosauria	Adult	Wet	N/A	N/A	N/A
MUVC-AV 013A	<i>Gallus gallus</i>	Aves	Subadult	Wet	Femur and acetabulum	N/A	N/A
MUVC-AV 014	<i>Gallus gallus</i>	Aves	Adult	Wet	Femur and acetabulum	N/A	N/A
MUVC-AV 017	<i>Meleagris gallopavo</i>	Aves	Subadult	Wet	N/A	N/A	N/A
MUVC-AV 015	<i>Buteo jamaicensis</i>	Aves	Adult	Wet	N/A	N/A	N/A
MUVC-AV 005	<i>Cathartes aura</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
MUVC-AV 012A	<i>Corvus brachyrhynchos</i>	Aves	Adult	Wet	N/A	N/A	N/A
MB-Av 539	<i>Emeus crassus</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
MB-Av 682	<i>Dinornis novaezealandiae</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM unnumbered	<i>Struthio camelus</i>	Aves	Subadult	Skeletal	N/A	N/A	N/A
LACM 1014SN	<i>Struthio camelus</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM 1136SN	<i>Struthio camelus</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM 112605	<i>Struthio camelus</i>	Aves	Subadult	Skeletal	N/A	N/A	N/A
LACM 102342	<i>Apteryx mantelli</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM 102334	<i>Apteryx australis</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM 101689	<i>Tinamus solitarius</i>	Aves	Adult	Skeletal	N/A	N/A	N/A
LACM CSULB	<i>Rhea pennata</i>	Aves	Adult	Skeletal	N/A	N/A	N/A

6335						
LACM 63164	<i>Geochelone pardalis</i>	Chelonia	Adult	Skeletal+Ligament	N/A	N/A
LACM 163620	<i>Geochelone niger</i>	Chelonia	Adult	Skeletal	N/A	N/A
LACM 163620	<i>Geochelone niger</i>	Chelonia	Adult	Skeletal	N/A	N/A
NMNS003619~ F003772	<i>Dermochelys coriacea</i>	Chelonia	Adult	Skeletal+Ligament	N/A	N/A
LACM 171756	<i>Dermochelys coriacea</i>	Chelonia	Adult	Skeletal+Ligament	N/A	N/A
MUVC-CH 002	<i>Chelydra serpentina</i>	Chelonia	Juvenile	Wet	N/A	N/A
MUVC-CH 001	<i>Chelydra serpentina</i>	Chelonia	Juvenile	Wet	N/A	N/A

Table 2-4. 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	Lateral metaphyseal collar of the proximal femur (cranial metaphyseal collar in aves)
Acetabular labrum	Ventral side of supraacetabular rim (cranial portion of acetabular roof).
Antitrochanter fibrocartilage	Caudodorsal portion of acetabular roof (lepidosaur); Laterally oriented growth plate surface of the ilio- and ischial peduncles (archosaur).
Superficial meniscus: Origin	Caudal edge of the ilial acetabular rim
Superficial meniscus: Insertion	Ischial acetabular surface
Deep meniscus: Origin	Indentation on the ischial peduncle of ilium
Deep meniscus: Insertion	Synovial membrane on the caudodorsal acetabular rim.
Ligamentum capitis: Origin	Cranioventral and caudoventral rim of acetabulum in lepidosaurs. Cranioventral and caudoventral rim of inner acetabular foramen in archosaur.
Ligamentum capitis: Insertion	Apical surface of the convex fovea capitis (lepidosaur); Cranial surface of the convex fovea capitis (crocodylia); one or two concave surfaces of the fovea capitis (Aves).
Expanded metaphyseal attachment for fibrocartilage sheath	Striated cortical bone surface
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.
Tendon of <i>m. ischiotrochantericus</i> : Insertion	Lateral metaphysis of the proximal femur, caudal to the iliofemoral ligament insertion. Merges with the joint capsule.

Table 2-5. Prescribed homologies among hip joint ligaments illustrated in figure 3.

Lepidosauria	Crocodylia	Aves
Pubofemoral ligament	Cranial ligamentum capitis	Ligamentum teres (Cracraft, 1971)
Ischiofemoral ligament	Caudal ligamentum capitis	Posterior acetabular ligament (Cracraft, 1971)
Iliofemoral ligament	Iliofemoral ligament	Pubofemoral ligament
N.A.	N.A.	Ischiofemoral ligament
N.A.	N.A.	Iliofemoral ligament

A. Phylogeny of epiphyseal morphology

B. Neontological nomenclature

C. Paleontological nomenclature

D. Nomenclature employed in this study

Figure 2-1. Evolutionary relationships of the tetrapod epiphyseal region and their anatomical nomenclature. All epiphyses are shown in cross sectional view. **A.** Secondary centers of mineralization are independently acquired by mammals and lepidosaurs. **B.** Nomenclature commonly used by neontological, soft tissue-based studies. **C.** Nomenclature commonly used in the paleontological literature and studies focused mainly on osteology. **D.** Nomenclature of the epiphyseal region adopted by the current study.

Figure 2-2. A. Photogrammetric model of an alligator left femur (MUVC-AL 113) in cranial, lateral, and proximal views. **B.** Photogrammetric model of a rhea left femur (LACM CSULB 6335) in the same views. Relative orientation between the femoral head-greater trochanter axis (green labels) and the mediolateral axis of the distal condyles (green 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 is represented in green, mediolateral plane in red, craniocaudal plane in blue.

Figure 2-3. Schematic representation of hip joint tissues homology in Diapsida. Tissues are labeled according to nomenclature seen in literature, but the color schemes are based on inferred homology in this study (Table 1-1). Cut ends of excised ligaments are signified by hatch marks. **A.** Disarticulated left hip joint of a generalized lepidosaur, femur in medial view. **B.** Disarticulated left hip joint of a generalized crocodylian, femur in medial view. **C.** Disarticulated left hip joint of a generalized bird, femur in caudal view.

Figure 2-4. Gross morphology of lepidosaur acetabular soft tissues. Soft tissue attachments are preceded by an asterisk (*). All scale bars represent 1cm. **A.** Schematic drawing of a lepidosaur pelvis showing the area of magnification (black dotted inset). **B.** Extrinsic ligaments of *Iguana iguana* (UMNH-LI 039) left hip joint in lateral view. **C.** Intrinsic structures of the same hip joint in lateral view after reflection of the iliofemoral ligament. **D.** Osteological correlates of joint soft tissues of a skeletonized left hip joint of *Varanus komodoensis* (FMNH 22199) in lateral view. **E.** Dissected left hip joint of *Sphenodon punctatus* (FMNH 211217-18) in lateral view. **F.** Skeletonized left hip joint of *Sphenodon punctatus* (FMNH 11113) in lateral view.

Figure 2-5. Microstructure of lizard supraacetabular tissues. **A.** Schematic drawing showing the histological sectional plane of 1-5B. **B.** Horizontal (dorsoventral) section of a *Ctenosaura similis* acetabulum (MUVCL-032) along the dotted line in 1-5B, showing craniocaudally distinct labral and antitrochanteric tissues. Scale is 2 mm. **C.** The antitrochanter (red dotted inset in B) consists of an elastic cartilage core interspersed by internal collagen fiber bundles, and surrounded by a peripheral layer of collagen fiber. Scale is 240 μm .

Figure 2-6. Gross morphology of the crocodylian acetabulum and microstructure of the acetabular labrum. Soft tissue attachments are preceded by an asterisk (*). All scale bars represent 2mm. **A.** Schematic drawing of the intrinsic ligaments of an *Alligator mississippiensis* acetabulum in lateral view. Black inset shows the area of magnification in 1-6C and D, dotted line represents the histological sectional plane in 1-6F. **B.** Extrinsic ligaments of the alligator left hip joint capsule (MUV-AL 703) in lateral view. **C.** The hip joint (MUV-AL 112) in dorsal view after excision of the iliofemoral ligament, showing the dual ligamentum capitis insertions onto the fovea capitis. **D.** Intrinsic structures of the alligator acetabulum (MUV-AL 602) in lateral view after removal of the femur. **E.** Osteological correlates of joint soft tissues of a skeletonized *Crocodylus plaustri* pelvis (FMNH 51691); pubis not shown. **F.** Axial (transverse) section of an *Alligator* acetabular labrum with associated iliofemoral ligament (MUV-AL 113). The labrum consists of a loose, fibrous matrix surrounded both superficially and intrinsically by internal collagen fibers.

Figure 2-7. Morphology of the *Alligator* antitrochanter region (MUV-AL 113). Soft tissue attachments are preceded by an asterisk (*). **A.** Schematic representation of distinct soft tissue structures within the joint capsule. **B.** The superficial meniscus shows fibrous attachment to the acetabular labrum, as well as ligamentous attachment to the hyaline cartilage surfaces of the ilial and ischial antitrochanter. Scale is 1 mm. **C.** The deep meniscus shows distinct cartilaginous and ligamentous regions, as well as fibrous attachment to the *m. ischiotrochantericus* ligament and the caudal ligamentum capitis. Scale is 2 mm. **D.** Magnified view of the transition between the deep meniscus' cartilaginous and ligamentous regions (white dotted inset in 1-6C), showing thick bundles of parallel collagen fiber bundles oriented along the ligamentous region. Scale is 250 μ m.

Figure 2-8. Gross morphology and microstructure of avian acetabular soft tissues. Soft tissue attachments are preceded by an asterisk (*). **A.** Schematic drawing of an avian pelvis showing the area of magnification (black dotted inset). **B.** The hip joint of an adult *Struthio camelus* (LACM 1014SN) in ventral view after excision of the ischiofemoral ligament, showing the dual ligamentous insertions onto the fovea capitis. Scale is 1 cm. **C.** The acetabulum of *Corvus brachyrhynchos* (MUV-012A) in lateral view. Scale is 5 mm. **D.** Osteological correlates of joint soft tissues of a skeletonized subadult *Struthio camelus* (LACM uncatalogued) in lateral view. Scale is 2 cm. **E.** Axial (transverse) section of a *Gallus* acetabular labrum with associated iliofemoral ligament (MUV-013A). Scale is 500 μ m. **F.** Magnified view of the intermediate region between the

hyaline acetabular cartilage and the fibrocartilaginous acetabular labrum (black dotted inset in 1-8D). Scale is 10 μm . **G.** Axial (transverse) section of a *Gallus* antitrochanter (MUVC-AV 014) at the site of ilial-ischial fusion, showing the fibrocartilage layer superficial to the hyaline cartilage. Scale is 500 μm .

Figure 2-9. Gross morphology and microstructure of the lizard proximal femoral epiphyseal region. Soft tissue attachments are preceded by an asterisk (*). **A.** Ventral view of an *Iguana* right hip joint (MUVCL-039), showing ventral ligament attachments. The abducted femur is in medial view. Scale is 5 mm. **B.** Osteological correlates of joint soft tissues on a subadult *Varanus komodoensis* right femur (FMNH 22199) in medial view. Scale is 1 cm. **C.** Growth plate surface of a subadult *Varanus niloticus* right femur (MUVCL-VNI 001) in proximal view. Osteological correlate of the secondary center presents as a longitudinal groove. Scale is 1 cm. **D.** Parasagittal section of a juvenile *Ctenosaura* femur (MUVCL-032). Scale is 5 mm. **E.** Fibrocartilage is present on the capital metaphyseal junction (red inset in 1-9D). Scale is 500 μ m. **F.** Fibrocartilage is present on the trochanteric metaphyseal junction (green inset in 9D), Scale is 500 μ m. **G.**

Transverse section of contralateral *Ctenosaura* femur. Scale is 5 mm. **H.** Fibrocartilage is present on the lateral metaphyseal junction (red inset in 9G). Scale is 500 μm . **I.** Fibrocartilage is present on the medial metaphyseal junction (green inset in 1-9G). Scale is 500 μm .

Figure 2-10. Gross morphology and microstructure of the crocodylian proximal femoral epiphyseal region. Soft tissue attachments are preceded by an asterisk (*). **A.** Medial view of the right femur of a subadult alligator (MUV-AL102), showing excised ligamentum capitis attaching to the cranial surface of the convex fovea capitis. Scale is 1 cm. **B.** IKI-enhanced μ CT of the contralateral, articulated hip joint, showing a distinct fibrocartilage sleeve surrounding a hyaline core on the proximal femur. Scale is 1 cm. **C.** Reconstructed 3D surface model of a juvenile alligator proximal femur (MUV-AL 100) in medial view, based on IKI-enhanced μ CT scan of the articulated hip joint. Fibrocartilage is colored in red, hyaline cartilage in blue. Scale is 2 mm. **D.** Parasagittal section of a juvenile alligator (MUV-AL 105) proximal femur. Scale is 2 mm. **E.**

Transverse section of the contralateral proximal femur. Fibrocartilage forms a metaphyseal collar around the hyaline cartilage core. Scale is 500 μm . **F.** Transverse section of a pre-hatchling alligator hip joint (MUV-AL 106). The chondroepiphysis extends deep into the metaphysis as a cartilage cone. Scale is 2 mm. **G.** Osteological correlates of soft tissues on an adult *Crocodylus plaustis* (FMNH 51691) proximal femur in proximomedial view. Scale is 5 cm. **H.** Magnified view of the metaphyseal surface near the fovea capitis on an alligator (MUV-AL 112) corresponding to the black dotted inset in 1-10G. Fibro- and hyaline cartilage attachment can be distinguished by a prominent metaphyseal line. Fibrocartilage attachment is indicated by a raised shelf of cortical bone. The fovea capitis is indistinct from the rest of the hyaline cartilage attachment surface. Scale is 1mm.

Figure 2-11. Gross morphology and microstructure of the avian proximal femoral epiphyseal region. Soft tissue attachments are preceded by an asterisk (*). **A.** Cranial view of a *Corvus brachyrhynchos* right femur (MUVc-AV 012A), showing excised ligamentum capitis attaching to the fovea capitis on the capital surface of the femoral head. Scale is 2 mm. **B.** Parasagittal section of a *Gallus gallus* proximal femur (MUVc-AV 014). The chondroepiphysis on the femoral neck and metaphyseal junction consists only of fibrocartilage, whereas the capital surface of the femoral head is covered by a dual layer of fibro- and hyaline cartilage. Scale is 2 mm. **C.** Parasagittal section of the

same proximal femur at its ligamentous insertions. The ligamentum capitis femoris attaches to the medial pubic acetabular rim with the inner acetabular membrane. Scale is 2 mm. **D.** Magnified view of the fovea capitis (black dotted inset in 1-10C). The ligamentum capitis femoris inserts on the proximal femur via a series of intermediate tissues. Scale is 200 μ m. **E.** Osteological correlates of soft tissues on a *Struthio* proximal femur (LACM 1014SN) in caudal view. Scale is 2 cm. **F.** Osteological correlates of soft tissues on an *Emeus* proximal femur (MB-av 539) in proximocaudal view, showing distinct insertions for the ligamentum teres (fov. lt) and posterior acetabular ligament (fov. pac). Scale is 2 cm. **G.** Osteological correlates of soft tissues on a *Rhea* (LACM CSULB 6335) proximal femur in medial view, showing distinct insertions for the ligamentum teres and posterior acetabular ligament. Scale is 2 cm.

Figure 2-12. Irregular rugosities on the growth plate surface (green arrow) are the osteological correlates of thick hyaline cartilage. **A.** Humeral head of an adult *Dermochelys* (FMNH 171756). Scale is 2 cm. **B.** Proximal femur of a juvenile *Varanus* (LACM 163943). **C.** Pubic peduncle of an adult *Crocodylus* ischium (FMNH 22030). Scale is 1 cm. **D.** Ischial peduncle of a juvenile *Struthio* ilium (LACM 112605). Scale is 1 cm.

Figure 2-13. Evolutionary history of the hip joint characters in sauropsids, with emphasis on archosaurs. Turtles are used as outgroup to Diapsida (Carroll, 2013). Presence of character states are represented by (+) and are highlighted in green. Absence of character states are represented by (-) and are highlighted in red. Ambiguous character states are represented by (?), and are highlighted in gray. Silhouettes of taxa (phylogics) depicted here are provided by S. Hartman, T. M. Keesey, N. Kelley, A. A. Farke, B. McFeeters, S. Werning, G. E. Lodge, and Benchill (Wikipedia user).

CHAPTER 3

Homology, homoplasy, and evolution of saurischian hip joint articular soft tissues

INTRODUCTION

The evolutionary origin of Saurischia is characterized by a suite of anatomical features that arose sequentially within the theropod and sauropodomorph lineages, culminating in the drastically divergent *bauplans* of birds and sauropods (Allen et al., 2009; Hutchinson and Allen, 2009; Sanders et al., 2011). In particular, numerous musculoskeletal transitions in the sauropodomorph and theropod hindlimb distinguish their morphologies from that of crocodylians, the only surviving clade of archosaurs aside from birds (Gatesy and Middleton, 1997; Wilson and Carrano, 1999; Hutchinson, 2001a, b; Benson and Choiniere, 2012). Numerous studies have been dedicated to the functional significance of hindlimb characters during the evolution of archosaur locomotion, including cursorial bipedality (dinosauromorphs, Nesbitt et al., 2009; herrerasaurids, Grillo and Azevedo, 2011), cursorial quadrupedality (silesaurids, Nesbitt et al., 2010), graviportal bipedality (large theropods, Hutchinson et al., 2005; Bates et al., 2012; basal sauropodomorphs, Mallison, 2010a, b), graviportal quadrupedality (sauropods, Wilson and Carrano, 1999; Yates and Kitching, 2003), knee-driven bipedality (avialans, Gatesy and Middleton, 1997; Carrano, 1998), flight (Gatesy and Dial, 1996; Clarke et al., 2006; Heers and Dial, 2007; Chatterjee and Templin, 2007) and perching (Serenio and Rao, 1992; Backus et al., 2005). Moreover, the rich evolutionary history of Saurischia features multiple, independent transitions in body size, including gigantism (sauropods, Sander et al., 2011; Theropods, Christiansen and Fariña, 2004; Lee et al., 2014a) and miniaturization (sauropods, Stein, et al., 2010; non-avian theropods,

Turner et al., 2007; avialans, Hainsworth and Wolf, 1972). Throughout these transitions, the hip joint functions as an important load-bearing structure in both bipedal and quadrupedal saurischians of all body sizes. Therefore, new anatomical data on hip joint soft tissues should elucidate patterns in hindlimb functional morphology and evolution of the avian lineage.

However, our understanding of saurischian, 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 2013; Tsai and Holliday 2014). 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, 1942a) 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; Fierbas and Zweymüller, 1971; Fujiwara et al., 2010; Tsai and Holliday, 2014). Thick layers of epiphyseal cartilage have also been inferred for extinct saurischians (sauropods, Cope, 1878; Marsh, 1896; Hay, 1908; theropods, Hutchinson et al., 2005; Gatesy et al., 2009; Holliday et al., 2010), suggesting that articular soft tissues played crucial mechanical and physiological roles in the evolution of saurischian hindlimbs, and likely influenced the terminal morphologies seen in clades as disparate as sauropods and birds.

Extant birds walk using a habitually flexed femoral posture relative to the vertebral column (Gatesy and Dial, 1996) and a locomotor cycle largely driven by knee flexion and femoral axial rotation (Kambic et al., 2014). Numerous musculoskeletal studies have been dedicated to the evolutionary origin of this unique locomotor repertoire within non-avian theropods (Gatesy, 1995; Hutchinson, 2001a, b; Gatesy et al., 2009; Bates et al., 2012). In contrast, there has been little concerted effort to investigate the evolution of archosaur hip joints thus far (but see Kuznetsov and Sennikov, 2000; Tsai and Holliday, 2014). 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, 2010a) and desiccated epiphyseal cartilage (Schwarz et al., 2007) are very occasionally observed on the end of fossil long bones. However, the preserved cartilage conforms to the subchondral shape when present in fossils, and thus offers little information on articular surface morphology. Moreover, although the anatomy of extant archosaur hip joints have received some attention in the comparative literature (but see Stolpe, 1932; Haines, 1938; 1942a; 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). The physical absence of articular soft tissues in the fossil record and gaps in our anatomical knowledge impacts studies of saurischian hip joint character evolution and functional shifts in locomotor behavior, ecology, and evolution leading to each terminal clade.

Here, I investigate the sequence of evolutionary transitions in the hip joint of saurischian-line dinosauromorphs. I infer the presence and topology of joint soft tissues in fossil saurischians and their outgroup archosauromorphs using phylogenetically informed osteological correlates (Tsai and Holliday, 2014), 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 dinosaur lineages leading to sauropods and birds, 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 3-1 and illustrated in Fig. 3-1. In order to characterize the shift of ligamentous attachments within the saurischian lineage, nomenclature for osteological correlates of joint ligaments follows the prescribed homology in Tsai and Holliday (2014). Although crocodylians and birds form the Extant Phylogenetic Bracket (EPB; Witmer, 1995) for Archosauria, 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, 2014).

I used reference axes (Tsai and Holliday, 2014; Fig. 3-1c) to account for the evolutionary shift in femoral condylar orientation among saurischians, such as the independent evolution of medially deflected femoral heads in theropods (Hutchinson, 2001b) and sauropodomorphs: (Martinez and Alcober, 2009; Yates et al., 2010), and the dorsal inclination of the femoral heads in theropods: (Bates et al., 2012; Wilson and Carrano, 1999). The mediolateral plane (red) passes through the distal condyles and intersects the femoral midshaft long axis. The craniocaudal plane (blue) is perpendicular to the mediolateral plane and intersects the latter at the femoral midshaft long axis. Additionally, an 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, are used to describe the orientation of acetabular soft tissue structures. Lastly, throughout this study the proximal attachments of ligaments are noted as the origins, whereas the distal attachments are noted as the insertions.

Data collection

I studied a broad phylogenetic range of archosauromorphs along the saurischian lineage (N= 108 taxa; Table 3-2), including 51 theropods and 31 sauropodomorphs, and scored discrete osteological characters on the proximal femur and the acetabulum. Fossil specimens were studied by observation and digital photography (Sony DSC-F828). 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, I sampled only taxa represented by adult

or subadult individuals, and excluded young juvenile and neonates from the comparative analysis. Nevertheless, young juvenile and neonate individuals are noted for potential ontogenetic transitions in hip joint character states. For taxa represented by multiple individuals (e.g., *Allosaurus*), I 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 noted as a young juvenile or neonate individual in literature. Institutional abbreviations are summarized in Table 3-3.

Ancestral state reconstruction of hip joint soft tissues

Hip joints were examined for discrete osteological correlates of hip joint cartilages, ligaments, and articular pads (Tsai and Holliday, 2014). Osteological correlates of hip joint articular soft tissues are detailed in Table 3-4. I identified 14 characters based on osteological correlates of putatively homologous soft tissues in extant diapsids (Tsai and Holliday, 2014). These osteological characters serve as proxies for the presence, orientation, thickness, and shapes of articular soft tissues.

I 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 (Fig. 3-2) were constructed using Mesquite (V2.73) based on published studies, with branch lengths based on hypothesized divergence date between sister clades and sister taxa (Archosauromorpha, Ezcurra et al., 2014; Archosauriformes, Brusatte et al., 2010; Nesbitt, 2011; Dinosauromorpha, Langer et al., 2013; Sauropodomorpha, Wilson, 2005; Martinez 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; Ericson et al., 2006; Brown et al., 2008; Phillips et al., 2010). I constructed a “default” phylogenetic tree (Fig. 3-2a), in which Silesauridae is considered as non-dinosaurian dinosauriformes (Brusatte, 2010; Nesbitt, 2011), Herrerasauridae as basal theropods (Sues et al., 2011), *Eoraptor* as the basal-most sauropodomorph (Martinez and Alcober, 2009), and *Archaeopteryx* as the basal-most avialan (Turner et al., 2012). Additionally, I analyzed alternative tree topologies to account for ambiguous phylogenetic placement of Silesauridae as stem-ornithischians (Langer and Ferigolo, 2013), Herrerasauridae as the basal-most saurischians (Novas et al., 2010), *Eoraptor* as a basal theropod (Sues et al., 2011) and *Archaeopteryx* as a stem-deinonychosaur (Xu et al., 2011; Godefroit et al., 2013). Four additional trees were modified from the “default” tree based on alternative placements of each contentious taxon (Fig. 3-2b-e).

Discrete characters were analyzed using the Trace Character History function of Mesquite (V2.73; Maddison and Maddison, 2015) using the Likelihood reconstruction method (Schluter et al., 1997; Pagel, 1999). Relative likelihood of character states at each node was reconstructed on the composite phylogeny of Saurischia (n= 108 taxa) using a marginal probability reconstruction of Markov k-state 1 (Mk1) parameter model (Lewis, 2001). This method assumes 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). Since hip joint osteological characters of basal archosaurs are highly variable (Nesbitt, 2011), character gains and losses in basal Dinosauria likely occurred with little directional bias.

Ancestral state at each given node is reconstructed 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 (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 (*). I focused on the results from the “default” phylogenetic tree (Fig. 3-2a), and reported results from the four alternative trees only if they returned significantly different character state estimations from the “default” tree. I 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 (Fig. 3-8, 3-9, 3-10). Lastly, I used cartilage correction factors derived from extant archosaurs (Holliday et al., 2010) to develop thickness estimates for proximal femoral epiphyseal cartilages of 9 exemplary extinct dinosauromorphs along the saurischian lineage.

RESULTS

Overview of hip joint osteological correlates

Saurischians exhibit a wide range of osteological characters in the hip joint, many of which are not present in extant birds and crocodylians. Outgroup comparisons potentially allow robust inferences of soft tissue transitions leading to each terminal saurischian taxon. Most theropods and sauropodomorphs possess an unossified inner acetabular wall, resulting in a ring-shaped bony acetabulum (Fig. 3-3c-i). This “perforated acetabular” (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. 3-4). 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. 3-5). 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. If the thin layer of calcified cartilage is weathered away, 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. I reconstruct the antitrochanter of saurischian-line archosaurs as a simple articular pad as in extant birds and lepidosaurs, rather than the complex meniscus structure in crocodylians (Tsai and Holliday, 2014), due to the early phylogenetic split between ornithomirans and pseudosuchians (Nesbitt, 2011) and because the crocodylian meniscus possess few unambiguous osteological correlates.

The hip joint of basal dinosaurs 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. 3-6). The femoral attachment of the iliofemoral ligament presents as a shallow depression in silesaurids (Fig. 3-6b, 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, 2014). 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 inferred to associate with the internal shift of the pubofemoral and ischiofemoral ligaments, I infer the origins of these two ligaments on the inner pubic and ischial acetabular rims in dinosauiromorphs with a perforated acetabulum. In contrast, dinosauiromorphs 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 capitis 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, 2001), which includes both the femoral head (capital) and trochanteric regions (Fig. 3-7). 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 fibrohyaline cartilage structure in these regions (Fig. 3-6a-h, 3-7b-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. 2-10h). 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.

An unperforated acetabulum indicates that the inner acetabular wall is lined by hyaline cartilage, a condition best exemplified by extant lepidosaurs and turtles (Tsai and Holliday, 2014). In contrast, a perforated acetabulum indicates that a ligamentous acetabular membrane forms the inner acetabular wall. Although it is not known whether the membrane physically restricts the femoral head medial insertion in dinosaurs, the femoral head of extant archosaurs never inserts medially beyond the inner acetabular rim and into the pelvic cavity (Stolpe, 1932; Kuznetsov and Sennikov, 2000). Therefore I 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, I used the acetabular membrane as the indicator of functional acetabular depth.

Among extant sauropsids, presence of the acetabular membrane is associated with an intracapsular origin of the pubofemoral and ischiofemoral ligaments. Tsai and Holliday (2014) 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 I 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, I scored the acetabulum as “fully perforated” only if the ilial portion of the inner acetabular wall is emarginated (ilium: ventral acetabular flange absent, *sensu* Martinez 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, 2014). Although Sereno and Arcucci (1994a) 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 has been noted by Dzik (2003) and Nesbitt et al. (2010) as possessing an unperforated acetabulum, and the “perforated” morphology on the puboischial margin of *Asilisaurus* (Fig. 3-3a) was noted as due to breakage (Nesbitt, personal communication). The acetabulum remains incompletely perforated at Dinosauria (RL= 0.90*), and the fully perforated character state evolved independently in Ornithischia (represented by *Lesothosaurus*) and Saurischia. It is unclear if sauropodomorphs and theropods independently evolved a fully perforated acetabulum, because ancestral character state for Saurischia (RL= 0.21) is ambiguous.

Basal sauropodomorphs retained an incompletely perforated acetabulum (RL~0.99*), with a single transition to a fully perforated condition in the common

ancestor of *Efraasia* and more derived sauropodomorphs. Basal sauropodomorphs such as *Panphagia* possess incompletely perforated inner acetabular walls, in which ventral rim of the ilium forms a distinct indentation (Fig. 3-3b). This indentation receives of the ventral acetabular ligaments during femoral adduction, and corresponds to the acetabular membrane in taxa with perforated acetabulae. Basal theropods possess a fully perforated acetabulum (RL= 0.99*), with one reversion to the unperforated morphology in *Eodromaeus*. Alternative placement of Silesauridae as basal ornithischians (Fig. 3-2b) resolves the ancestral state for Saurischia with the presence of an incompletely perforated acetabulum (RL= 0.04*). These results indicate as much as three convergent evolutionary acquisition of a perforated acetabulum within ornithischians, theropods, and sauropodomorphs. Since the perforated acetabulum is the osteological correlate for internalized pubofemoral and ischiofemoral ligaments, these results suggest as much as three convergent evolutions of the ligamentum captis femoris within Dinosauria.

2. Pelvis, lateral expansion of the supraacetabular rim. (0) expanded, (1) reduced.

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. 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.

Basal dinosauromorphs possess a laterally expanded supraacetabular rim (RL~0.01*, Fig. 3-3a) but sauropods and theropods independently reduced the rim.

Among basal sauropodomorphs, plateosaurids (*Ruehleia* + *Plateosaurus*, RL~0.99*, Fig. 3-3c) and the common ancestor of *Saraksaurus* and more derived sauropodomorphs (RL~0.99*, Fig. 3-3d, 3-4a, b) possess reduced supraacetabular rims, but it is unclear if the two lineages independently reduced the supraacetabular rim (RL= 0.84). Basal theropods maintained a laterally expanded supraacetabular rim in the stem lineage, but the most derived taxa in each clade independently reduced the rim. The supraacetabular rim is reduced in *Carnotaurus* among Ceratosauria, *Torvosaurus* among Megalosauroida, and Tyrannosauridae among Tyrannosauroida (RL~0.99*, Fig. 3-4e). Among basal Maniraptoriformes, *Ornithomimus* and *Falcarius* possess expanded supraacetabular rims whereas most other Maniraptoriformes possess reduced rims. The ancestral state of the rim is ambiguous at Maniraptoriformes (RL= 0.25), Maniraptora (RL= 0.43), and Therizinosauria (RL= 0.35). However, among the two therizinosaurs studied, the basal *Falcarius* possess a laterally expanded supraacetabular rim, whereas the derived *Nothronychus* possesses a reduced rim, similar to the trend observed in more basal theropod clades. Oviraptorosauria (RL= 0.99*, Fig. 3-3h) and Paraves (RL= 0.93*, Fig. 3-3i, 3-4f) possess reduced the supraacetabular rim, but the current data are insufficient to determine the two clades are convergent (RL= 0.83).

Among Paraves, only *Unenlagia* possesses an expanded supraacetabular rim and is inferred to have undergone a reversion. However, close inspection of the specimen indicates that the rim only appeared to be expanded due to the deep medial excavation of the muscular attachments on the preacetabular ilium. Therefore, *Unenlagia* technically possesses an unexpanded supraacetabular rim, similar to other deinonychosaurs. All alternative tree topologies yielded similar patterns in character state transitions as the

“default” phylogenetic tree. Overall, sauropodomorphs and multiple lineages of theropods independently reduced the supraacetabular rim.

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

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, since 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. 3-3a), and this morphology is retained in Saurischia (RL~0.03*) and Sauropodomorpha (RL~0.01*, Fig. 3-3b-d). The ancestral state of Theropoda is ambiguous (RL~0.51). Both Herrerasauridae (RL~0.99*, Fig. 3-3e) and Neotheropoda (*Tawa* + more derived theropods, Fig. 3-4c) possess ventrolaterally oriented supraacetabular rims, but *Eodromaeus* possess a laterally oriented rim. The ventrolaterally oriented supraacetabular rim is retained among the basal theropod lineage, and underwent two unambiguous transitions to the laterally oriented state in *Carnotaurus* and Avetheropoda (Allosauroidae + Coelurosauria, RL= 0.99*, Fig. 3-4d). It is unclear whether the ventrolaterally oriented supraacetabular rim in Megalosauroidae (RL~0.01*)

signifies a retention of the basal Neotheropoda morphology or a secondary reversion, because the ancestral state of Orionides (Megalosauroidae + Avetheropoda) is equivocal (RL= 0.74). Alternative placement of Herrerasauridae (Fig. 3-2c; RL= 0.94*) and *Eoraptor* (Fig. 3-2d; RL= 0.89*) resolves the ancestral state reconstructed for Theropoda as retaining a laterally oriented supraacetabular rim. I 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, Size of the bony antitrochanter. (0) unexpanded, (1) expanded.

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. Skeletally mature birds (Stolpe, 1932; Baumel and Witmer, 1993), maniraptorans (Allen et al., 2007; Maryańska, 2002; Turner et al., 2012), and some ornithischians (Romer, 1927; Maidment and Barrett, 2012) possess expanded bony antitrochanters. In contrast, basal dinosaurs (Thulborn, 1972; Novas, 1994; Butler, 2010), and sauropodomorphs (Wilson, 2002; Langer, 2003) possess unexpanded antitrochanters. 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*, Fig. 3-3a-g), and this morphology is maintained throughout sauropodomorphs. Basal theropods also retain an unexpanded antitrochanter, and this character state is maintained in more derived theropods until Maniraptora (RL= 0.06*). Maniraptorans underwent several

independent transitions in antitrochanter morphology, such that the ancestral state at each node within Maniraptora is unresolved. Among the two therizinosaurs studied, only *Nothronychus* possesses an expanded antitrochanter. Similarly, among the two oviraptorosaurs studied, only *Khaan* possesses an expanded antitrochanter (Fig. 3-3h). The common ancestor of Pennaraptora (Oviraptorosauria + Paraves, Foth et al., 2014) possess an unresolved character state (RL= 0.13).

All deinonychosaurs included in this study except for *Utahraptor* (Fig. 3-3i) possess an expanded antitrochanter. Among Deinonychosauria, only Velociraptorinae (*Velociraptor* + *Deinonychus*), can be unambiguously reconstructed as possessing an expanded antitrochanter (RL= 0.99*), whereas all other nodes in Deinonychosauria remain unresolved. *Archaeopteryx* possess an unexpanded antitrochanter, whereas all other avialans possess expanded antitrochanters (RL= 0.95*). The ancestral avialan antitrochanter morphology is unresolved. Alternative placement of *Archaeopteryx* as a stem-deinonychosaur resolves the character transition at each node within Maniraptora considerably. Under the alternate topology, the ancestral Paraves (RL= 0.11*) and Pennaraptora (RL= 0.11*) possess unexpanded antitrochanters, whereas the ancestral Avialan possesses an expanded antitrochanter (RL= 0.96*). These results suggest that an expanded antitrochanter evolved multiple times within the maniraptoran radiation, likely correlated with independent convergences in 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 large sauropods, the ischial peduncle is cranially concave and forms a cranially oriented “U” shape in ventral view (Fig. 3-4b, dotted outline). This morphology first

appeared in Anchisauria (RL= 0.99*) and is retained throughout Sauropoda. In contrast, basal dinosauromorphs and theropods never evolved a cranially concave ischial peduncle (RL= 0.01*).

In sauropods, the lateral surface of the ischial peduncle is markedly less rugose than the medial surface (Fig. 3-4b). Because growth plate rugosities are associated with hyaline cartilage thickness, the lateral surface of the ischial peduncle is inferred to possess only a thin layer of hyaline cartilage core underneath its fibrocartilage surface. Correspondingly, the ilial peduncle of the sauropod ischium is also bipartite, possessing a rugose medial surface and a smooth lateral surface. These osteological correlates indicate that in sauropods, articulation between the ilium and the ischium consists of a hyaline cartilage synchondrosis medially, as well as a fibrocartilaginous antitrochanter laterally. Since the cranially oriented concavity of the ischial peduncle is continuous with the acetabular “ceiling”, the acetabular labrum is inferred to extend into the ischial peduncle, terminating medial to the antitrochanter. Sauropods possess a craniocaudally expansive attachment surface for the acetabular labrum and a small, cranially oriented antitrochanter (Fig. 3-5a).

In well-preserved theropod ilia (e.g., *Allosaurus*, Fig. 3-4d; *Tyrannosaurus*, Fig. 3-4e), the dorsal edge of the ischial peduncle is slightly indented. This morphology is not homologous with the deeply concave, U-shaped ischial peduncle of sauropods, because the antitrochanter retains a craniolateral orientation and does not show mediolateral distinction in rugosities. Overall, results indicate that dinosauromorphs and theropods possess craniolaterally oriented antitrochanters that consisted only of hyaline and fibrocartilage, whereas anchisaurian sauropodomorphs, including all sauropods, possess

cranially oriented antitrochanters that incorporated the acetabular labrum as part of the articular surface. All alternative tree topologies yielded similar patterns in character state transitions as the “default” tree.

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

The bony antitrochanter of archosauromorphs exhibits a diverse range of ossification patterns, likely associated with ontogeny, phylogeny, and load bearing function. Among extant archosaurs, crocodylians maintain an open synchondrosis between the ischial and ilial peduncles throughout ontogeny, even as large adults (Tsai and Holliday, 2014). 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. Firstly, most taxa are represented by small numbers of individuals, for which ontogenetic status cannot be consistently inferred. Secondly, in contrast to birds, non-avian dinosaurs achieve sexual maturity prior to skeletal maturity (Erickson et al., 2007; Lee et al., 2008), such that many “adult” specimens represent animals still undergoing active bone growth. The current analysis addresses these caveats by only considering specimens inferred to be adults or subadults. I 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, I 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. 3-3a). The bony antitrochanters of all sauropodomorphs studied retained the open synchondrosis (Fig. 3-3b-d, 3-5a). 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 “default” phylogenetic tree (Fig. 3-2a). The bony antitrochanter is co-ossified in *Herrerasaurus*, *Coelophysis*, Ceratosauria (RL~0.99*, Fig. 3-3e, 3-5b), and avialans (RL~0.99*). In *Herrerasaurus* only the largest individual studied (MCZ 4381, Fig. 3-3e) possesses a co-ossified bony antitrochanter; whereas all *Coelophysis* specimens 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. Similar convex-concave articulation between the ilium and ischium is present in *Siats*, Tyrannosauroidae, and *Falcarius* (Fig. 3-5d). Among

Tyrannosaurus, the largest individual (FMNH PR 2081) possesses incipient fusion of at the bony antitrochanter (Fig. 3-5c), but the peduncles are not co-ossified. The convex-concave articulation is absent in Megalosauroidea and Deinonychosauria. Finally, the bony antitrochanter is co-ossified in all avialans, including both *Archaeopteryx* and one specimen of *Patagopteryx* (MACN N-11) included in this analysis. 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. 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 most saurischians possess an open synchondrosis at the bony antitrochanter during much of their lifespan, supporting a hyaline cartilage antitrochanter similar to that observed in juvenile birds. However, evolutionary inference of a co-ossified antitrochanter remains elusive due the multiple instances of its gain among phylogenetically disparate theropod taxa (see Discussion). Additional data on the ontogenetic data on basal theropods and Paraves will provide further insights on the evolution of antitrochanter ossification.

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

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 $\sim 45^\circ$, whereas a medially deflected femoral head possesses a proximodistal angle close to 0° (Fig. 3-1c). 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 “default” 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.

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, 2014). 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) have noted the similarity between rugose

subchondral surfaces of dinosaurs with the ossifying growth plates of juvenile mammals and birds, this study do not employ growth plate rugosities as an ontogenetic indicator because extinct saurischians that possess growth plate rugosities retain them throughout ontogeny, even as large-bodied adults (Brochu, 2003; Tidwell et al., 2005).

Basal dinosauromorphs possess smooth subchondral growth plates on the proximal femur (RL~0.01*, Fig. 3-6a, 3-7a, j), but this morphology is independently lost in silesaurids (Fig. 3-7k), 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= 0.98*) possess highly rugose growth plate surfaces. It is unclear whether the plateosaurid morphology (Fig. 3-6j, 3-7l) and that of the more derived sauropodomorphs (Fig. 3-6k, 3-7m) resulted from a single or two independent acquisition (RL= 0.82), because *Adeopapposaurus* possesses a smooth growth plate similar to *Eoraptor* and basal dinosauromorphs. Nevertheless, growth plate rugosities are maintained throughout Sauropodomorpha.

Theropods retained the smooth proximal femoral growth plate in basal dinosauromorphs (Fig. 3-6e, l, m, 3-7e) 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. 3-7o), *Allosaurus*, but not in smaller, presumably juvenile individuals. Rugose growth plates are present in tyrannosaurids (RL= 0.98*, Fig. 3-7f) but absent in basal tyrannosauroids (RL~0.01*). Thus the ancestral state of Tyrannosauroidea is ambiguous

(RL= 0.87). Lastly, although the stem Maniraptoriformes lineage maintained smooth growth plates, *Ornithomimus*, *Anzu* (Fig. 3-7q), and *Deinonychus* independently evolved rugose growth plates on the proximal femur. All alternative tree topologies yielded similar patterns in character state transitions as the “default” phylogenetic tree. I conclude 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 in contrast to the smoother trochanteric regions (Fig. 3-6d, k, 3-7d, l, m). 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 a bare minimum of 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= 0.89*), indicating that both lineages possess thick hyaline cartilage on the femoral head. The

absence of femoral head rugosities in *Adeopapposaurus* (Martinez, 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. In well preserved femora of *Apatosaurus* (FMNH 25112) and *Camarasaurus* (DNM 4514, Fig 2-7d), the capital growth plate surface is covered by patches of elevated, shelf-like bony structures, immediately bordering the metaphyseal collar. I suspect that these elevated bony structures are calcified, preserved hyaline cartilage. The proximal femoral growth plate of theropods possess less pronounced rugosities overall, with a more even distribution across the entire growth plate surface. All alternative tree topologies yielded similar patterns in character state transitions as the “default” tree.

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

In sauropods and some theropods, 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. 3-7f, 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. Basal dinosauromorphs lack transphyseal striations (RL~0.01*) but underwent multiple transitions to the derived morphology during 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 absent throughout the crownward stem lineage, but are present in *Ceratosaurus* (Fig. 3-7o), Allosauroidea (RL= 0.91*), Tyrannosauridae (RL= 0.98*, Fig. 3-7f), *Ornithomimus*, and *Anzu*. These results indicate that sauropodomorphs and multiple lineages of theropods independently gained transphyseal striations.

The absence of transphyseal striations in extant archosaurs makes inferring soft tissues in extinct dinosaurs difficult. Nevertheless, I suspect 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 non-avian dinosaurs, the fovea capitis ranges from indistinct in sauropodomorphs (Fig. 3-7d, m), planar in tyrannosaurids (Fig. 3-7f), and deeply convex in *Bambiraptor*. These observations indicate that the insertion depth of the ligamentum capitis, as well as the thickness of the epiphyseal hyaline cartilage, varies across extinct theropods. 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 along the stem lineage. Basal tyrannosauroids possess an indistinct fovea, but tyrannosaurids evolved a distinct, planar fovea (RL~0.99*, Fig. 3-7f). Maniraptoriformes basally retain an indistinct fovea capitis (RL~0.99*) but underwent numerous independent transitions to the distinct planar or concave morphology within the clade. The fovea capitis is indistinct in *Ornithomimus*,

Falcarius, *Deinonychus* (Fig. 3-6p) and *Utahraptor*, but presents as a patch of planar surface on the femoral heads of *Nothronychus* and *Velociraptor*, a shallow concavity in *Anzu* (Fig. 3-6o, 3-7q), and a deep concavity in *Bambiraptor*, *Sinornithoides*, and avialans. The available data are unable to resolve the ancestral state of Paraves (RL= 0.12). Nevertheless, all alternative tree topologies indicate that multiple lineages of Maniraptoriformes independently gained a distinct fovea capitis.

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), sauropodomorphs (Novas, 1996; Müller et al., 2015), and birds (Tsai and Holliday, 2014) 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.

Basal dinosauromorphs possess a shallow but distinct ischiofemoral ligament sulcus (RL~0.01*, Fig. 3-7a, j). Basal sauropodomorphs such as *Plateosaurus* (SMNS F 14-91294, Fig. 3-7l) and basal sauropods such as *Patagosaurus* (MACN CH 1986)

retained the dinosauromorph morphology, whereas derived sauropods such as *Diplodocus* (DMNH 462, Fig. 3-6k) and *Camarasaurus* (YPM 4625, DNM 4514, Fig. 3-7d, 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. Basal Maniraptoriformes such as *Ornithomimus* possessed a deep sulcus (RL= 0.93*, Fig. 3-7g), and this morphology is retained by Deinonychosaurs (Fig. 3-6p, 3-7i). In contrast, reversions to a shallow, indistinct sulcus independently occurred in *Nothronychus* among therizinosaurs, *Anzu* among oviraptorosaurs (Fig. 3-7q), as well as Euornithes (*Patagopteryx* + more derived avialans, RL= 0.01*). All alternative tree topologies yielded similar patterns in character state transitions as the “default” phylogenetic tree.

In most theropods that possess a deep ischiofemoral ligament sulcus, the ischiofemoral ligament sulcus extends caudoventral to the femoral neck, resulting in a hook-shaped overhang at the synovial bursa attachment ventral to the femoral head (Fig. 3-f, h, n, o). This morphology indicates that the ischiofemoral ligament wraps around the caudoventral portion of the femoral neck, and is distinct from the pubofemoral ligament throughout most of its passage. In contrast, reduction of the sulcus in derived maniraptorans indicates that the passage of the ischiofemoral ligament shifted onto the articular surface of the femoral head, and has merged with the pubofemoral ligament proximally. This indicates that derived maniraptorans possess a longer ligamentum capitis femoris than basal theropods, similar to those of extant birds. Lastly, although 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 theropods.

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, 2014). 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 post- neonatal juvenile crocodylians and birds (Tsai and Holliday, 2014).

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= 0.03*, Fig. 3-7j), but Dinosauriformes evolved a cartilage cone (RL= 0.98*). In particular, silesaurids possess a deep, highly distinct trough on the growth plate surface (Fig. 3-6i, 3-7j); whereas dinosaurs possess a shallow, indistinct trough that gradually fades into the convex contours of the proximal femur (Fig. 3-7n, o). 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. 3-7n), but the cone is absent in *Herrerasaurus* (Fig. 3-7e). Basal neotheropods retain very shallow cartilage cones (RL~0.99*, Fig. 3-6l, 2-7n), but the cone is absent in Orionides (RL~0.99*). All alternative tree topologies yielded similar patterns in character state transitions as the “default” 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. 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, 2014). 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. In contrast, 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. 3-6a). Dinosauriformes possess expanded metaphyseal collars ($RL \sim 0.99^*$). In particular, Silesaurids expand the collar on the capital and entire medial periphery of the proximal femoral growth plate (Fig. 3-6b, 3-7b), whereas basal saurischians expand the collar only on the capital periphery of the growth plate (*Plateosaurus*, Fig. 3-6c; *Coelophysis*, Fig. 3-6e). Among dinosaurs, sauropodomorphs expand the collar both laterally and -medially, surrounding the femoral head in a C-shaped “cuff” in proximal view (Fig. 3-6d, k, 3-7d). 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. 3-7d), 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. 3-6f, m). Among maniraptorans, the shelf-like metaphyseal collar remains expanded on the lateral part of the femoral head in *Falcarius*, the most basal taxon in this study. *Falcarius* only possesses an expanded metaphyseal collar on the lateral surface of the femoral head, but not on its capital extent. This indicates that *Falcarius* possesses distinct bony attachment for the fibrocartilage sleeve only on the lateral portion of the femoral head, whereas the remainder of the proximal femur possess cartilage morphology more similar to derived maniraptorans.

In Pennaraptora, the metaphyseal collar is unexpanded and indistinguishable from the growth plate surface (RL~0.01*, Fig. 3-6h, o, p). This indicates that the fibrocartilage sleeve possesses little bony attachment onto the bony metaphysis in oviraptorosaurs, dromaeosaurs, and avialans. Moreover, in extant birds, the fibrocartilage sleeve expands proximally and integrates with the hyaline cartilage core, forming a composite cartilage layer on the articular surface (Wess et al., 1997). I therefore infer that the common ancestor of oviraptorosaurs and Paraves possesses bird-like epiphyseal cartilage on its

proximal femur, in which the articular surface is formed by a composite of fibro- and hyaline cartilage. All alternative tree topologies yielded similar patterns in character state transitions as the “default” tree.

Estimates of hip joint cartilage thickness

I used cartilage correction factors (CCFs) described by Holliday et al. (2010) for *Alligator*, juvenile *Struthio*, and adult *Struthio* to estimate the thickness of femoral epiphyseal cartilage in 9 fossil dinosauromorphs, and based the inference on similarity in growth plate morphology. Reconstructed taxa were given maximum and minimum estimates of cartilage thickness where applicable. Thickness of the acetabular labrum and antitrochanter cartilage were not estimated due to the lack of quantitative data in extant archosaurs. Instead, discrete osteological correlates are used to infer their acetabular soft tissue morphology.

Reconstructed epiphyseal cartilage thicknesses are summarized in Table 3-5. In alligators and adult ostriches, the smooth growth plate surfaces support cartilage caps that contribute up to 6.3% and 4.7% of the total femur length, respectively (Holliday et al., 2010). Juvenile ostriches possess a rugose femoral growth plate that supports a cartilage cap that contributes up to 6.4% of the total femur length. Assuming similar distribution of cartilage thickness on either end of the femur, I estimated the minimal thickness of the proximal cartilage cap to be 2.4% femur length for a smooth growth plate, based on the adult ostrich morphology. Additionally, I estimated the maximal thickness of the cartilage cap to be 3.2% femur length for a smooth growth plate, based on adult alligators. Cartilage cap thickness estimates are more equivocal for the rugose growth plate morphology, because among extant tetrapods, growth plate rugosities tend to only

be present in skeletally immature specimens undergoing active ossification of the epiphyseal cartilage. Nevertheless, I estimated the thickness for the proximal cartilage cap to be 3.2% of femur length for a rugose growth plate, based on data from juvenile ostriches.

The femoral head morphology of sauropods complicates estimates of femoral cartilage thickness, because the highly convoluted subchondral growth plates in this clade are not seen in any other archosaurs. Among tetrapods, only the leatherback turtle *Dermochelys* possesses a similarly rugose growth plate on the proximal humerus (Gervais, 1872; Snover and Rhoudin, 2008; Tsai and Holliday, 2014), but the lack of cartilage correction factors for this taxon prevents quantitative comparisons with sauropods. Moreover, individual rugosities on the sauropod proximal femoral growth plate reach amplitudes up to 20 mm, greater than the articular cartilage thickness in any extant tetrapod. Because femur length measurements in this study were based on the “peaks” of the rugosities, rather than the “valleys”, cartilage thickness estimates were accordingly based on the “peaks”. The minimal thickness estimate of the sauropod proximal femoral epiphysis is based on the juvenile *Struthio*, which adds a cartilage cap 3.2% of the length of the bony femur. The maximal estimate is based on the geometric congruence between the bony acetabulum and the femoral head. The sauropod acetabulum is sub-circular in outline, whereas the bony femoral head is largely ellipsoid in medial view, with the long axis of the ellipse oriented craniocaudally. Due to the reduction of the supraacetabular rim and the lack of growth plate surface on the acetabular “ceiling”, the acetabular labrum probably contributed very little to the thickness of the acetabular articular surface. Assuming minimal thickness for the labrum

and synovial fluid layers, the epiphyseal cartilage on the proximal femur would need to occupy virtually the entire circular outline in the acetabular rim in order to maintain congruent hip articulation. Therefore, I estimate the maximal thickness of sauropod proximal femoral cartilage as the dorsoventral height of the bony acetabulum minus the proximodistal height of the bony femoral head.

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 (e.g., 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 attachment 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

Saurischians underwent multiple, iterative convergences and divergences in hip joint anatomy, suggesting a spectrum of locomotor and physiological 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, I used osteological correlates of articular soft tissues to provide the first anatomical reconstructions of saurischian hip joints. Moreover, I used maximum

likelihood ancestral state reconstruction to optimize the transition of hip joint character during the evolution of sauropods and theropods. The following sections examine the evolutionary transitions of several key anatomical features in the saurischian hip joint. First, I describe the evolutionary gain of cartilage cone among basal dinosauromorphs and its implications on the origin of dinosaur locomotor posture. Second, I describe the characteristics of the sauropod hip joint and their significance during the evolution of graviportal locomotion in this clade. Lastly, I investigated the transition in theropod hip joint leading to the extant condition, and inferred the role of supraacetabular ossification, intrinsic joint ligaments, and composite fibro-hyaline cartilage layers in hip joint range of motion during the evolution of the characteristic avian locomotor posture.

Evolution of the cartilage cone in non-dinosaurian Dinosauromorpha

The basal dinosauromorph hip joint is exemplified by lagerpetids and *Marasuchus*. The inner acetabular walls of lagerpetids and *Marasuchus* are unperforated, indicating that the ventral joint ligaments remain as capsular in their origin. The height of the acetabulum is relatively tall compared to the dorsoventral and mediolateral diameter 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*. Estimates of femoral cartilage thickness are used to infer the thickness of acetabular cartilages. 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 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* is not preferred over the reconstruction based on *Alligator*. Instead, 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. Since 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, my results suggest that basal dinosauromorphs were able to adopt a more abducted femoral posture than dinosaurs during locomotion.

Silesaurids retain the basal dinosauromorphs morphology in their acetabulum, but possess several features on their proximal femoral epiphysis not seen in other dinosauromorphs. The subchondral surface of silesaurid proximal femora is terminally planar, and possesses an angled junction with the femoral head (Fig. 3-6b, 3-7b). 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., 2014). These observations indicate that silesaurids retain the cartilage cone in postnatal juveniles and adults. The silesaurid epiphyseal morphology is unlike either extant crocodylians or birds, as 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, thus allowing congruent articulation with the acetabulum. Since silesaurids possess similar subchondral morphology to those of lepidosaurs, I hypothesize that silesaurids also possess a convex epiphyseal cartilage cap that inserts into the metaphysis via a cartilage cone.

Although silesaurids possess osteological correlates for a lepidosaur-like cartilage cap on the proximal femur, it is not known if silesaurids calcify 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 equally likely that silesaurids retain uncalcified epiphyseal cartilage caps throughout life, as in other archosaurs. 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. 3-8a). 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, 2014). 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.

The prominent cartilage cone complicates epiphyseal cartilage thickness reconstructions in silesaurids, as neither birds nor crocodylians possess a cartilage cone in post-neonatal individuals. The epiphyseal cartilage shape of silesaurids is here reconstructed based on extant lepidosaurs based on similarity in growth plate morphology. Although cartilage correction factors have never been developed for lepidosaurs, I hypothesized a semi-ellipsoid, convex hyaline cartilage cap with a metaphyseal cartilage cone extension, surrounded on the periphery by a well-developed fibrocartilage sleeve. 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. The cartilage cap's apex is inferred to be capital relative to the midpoint of the proximal femur in lateral view, because the well-developed metaphyseal shelf on the capital region indicates prominent fibrocartilage sleeve around the femoral head (Fig. 3-6b, 3-7b).

Silesaurids retain a laterally expanded supraacetabular rim, suggesting that the epiphyseal cartilage articulates with the supraacetabular labrum dorsally in parasagittal locomotor posture (Fig. 3-8a). However, an abducted femoral posture remains mechanically possible because the pubofemoral and ischiofemoral ligaments are capsular in their origins. Overall, results of this study support previous inferences that basal

dinosauromorphs were able to assume adducted hindlimb postures (Dzik, 2003; Nesbitt et al., 2009; 2010) but also suggest that the hip joints of lagerpetids, *Marasuchus*, and silesaurids may also be capable of a greater range of mediolateral and axial rotation than traditionally reconstructed. 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, Schachner and Bates, 2011).

Evolution of the graviportal hip joint in 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. 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 appear in close temporal and phylogenetic association early on during the evolution of sauropodomorphs.

Sauropods possess extremely thick layers of epiphyseal hyaline cartilage on the highly convoluted, irregularly rugose growth plates on their femoral heads. In an *Apatosaurus* with an 1801 mm long femur, a 224 mm tall bony femoral head, and a 660 mm tall acetabulum, the minimal cartilage thickness is inferred to be 57.6 (± 20.2) mm based on the cartilage correction factor of the juvenile *Struthio*. Even with this minimal thickness reconstruction, the femoral head remains ellipsoid in medial view and must articulate with a largely circular bony acetabulum. The acetabular “ceiling” of sauropods supported a fibrous acetabular labrum, as it lacks osteological correlates of thick hyaline cartilage. In order to maintain hip articulation, the labrum needs to be 378 mm thick. In

contrast, the maximal thickness reconstruction assumes negligible thickness for the acetabular labrum (Fig. 3-9a), and estimate 436 mm of epiphyseal cartilage on the proximal femur based on height congruence between the bony femoral head and the acetabulum.

Although the loading conditions of sauropod articular cartilage and acetabular labrum are unknown, the minimal- and maximal estimates of articular cartilage thickness suggest profound mechanical differences between the two reconstructions. Under the minimal estimate, the ellipsoid femoral head remains incongruent with the sub-circular bony acetabulum, such that the acetabular labrum must occupy the remainder of the joint space. During femoral protraction and retraction, the femoral head is inferred to compress against the labrum unequally, resulting in substantial deformation in the labrum. In contrast, the maximal estimate reconstructs the femoral head as a largely spherical articular surface, in which the dorsal hemisphere is formed by hyaline cartilage (Fig. 3-9a). Among non-mineralized skeletal tissues, hyaline cartilage is more resistant to compression compared to fibrous tissues (Schanagl et al., 1997; Freemont and Hoyland, 2006), thus would serve as a better load-bearing structure than the fibrous acetabular labrum. Moreover, the hyaline cartilage core of sauropods is surrounded on three sides by the fibrocartilage sleeve. The fibrocartilage sleeve has been hypothesized to provide additional mechanical support against avulsion and excessive deformation of the hyaline cartilage core (Tsai and Holliday, 2014). These lines of evidence indicate that the maximal cartilage thickness estimate provided a hip joint more suitable for compressive load bearing, and are associated with the evolution of graviportal locomotor behavior.

Therefore, the maximal cartilage thickness estimate is preferred over the minimal reconstruction scheme based on the cartilage correction factor of juvenile *Struthio*.

A medially deflected femoral head evolved near the base of Sauropodomorpha, whereas thick femoral head cartilage layers are present in plateosaurids (Fig. 3-8b) and the common ancestor of *Mussaurus* and sauropods. Both lineages are characterized by relatively larger estimated body size compared to other sauropodomorphs (Sanders et al., 2011), and Yates (2004) and Sander et al. (2011) suggested that sauropodomorphs underwent rapid evolution of large body size independently among multiple lineages during the Late Triassic. The available data on the morphology of femoral growth plates in small basal sauropodomorphs are limited, therefore it is not possible to determine if plateosaurids and more derived sauropodomorphs retained thick hyaline cartilage from a common ancestor, or underwent convergent graviportal adaptations in the hip joint. In particular, the small-bodied sauropodomorph *Adeopapposaurus* is phylogenetically bracketed by plateosaurids and *Mussaurus* but possesses smooth subchondral growth plates without rugosities. Additional data on the basal sauropodomorphs will provide further insight on the potential of convergent “experiment” graviportal hip joints within the stem 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. 3-7l), 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. 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 sauropodomorph is expected to experience much greater absolute magnitudes of compressive and shears 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.

The supraacetabular rim is reduced in all but the most basal sauropodomorphs (Fig. 3-3b, 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.

Sauropods possess a craniocaudally expanded acetabular labrum and a small, cranially oriented antitrochanter. The expanded labrum indicates that the femoral head maintains articulation with the labrum during femoral protraction and retraction. In

contrast, the greatly reduced fibrocartilaginous surface of the antitrochanter can only contact the femoral neck during extreme femoral protraction and lateral rotation. Early reconstructions of sauropods by Hayes (1908) and Tornier (1909) indeed insisted on articulation between the femoral neck and the antitrochanter, resulting in an abducted, lizard-like femoral posture. This “sprawling” reconstruction has since been discarded in favor of an adducted hindlimb posture based on ribcage shape, muscle attachments, and preserved trackways (Holland, 1910; Wilson and Carrano, 1999; Wilhite, 2003). The presence of extremely thick epiphyseal hyaline cartilage on the femoral head region further supports the adducted hindlimb posture, such that only the femoral head and supraacetabular labrum function as the load-bearing articular surfaces. These lines of evidence indicate that in sauropods, the antitrochanter and the femoral neck experience little articulation with each other during stance and locomotion. Instead, the fibrocartilaginous surface of the antitrochanter forms the caudolateral limit of the hip joint capsule, and constrains femoral head inside the acetabulum. Retention of epiphyseal cartilage on the femoral neck likely served an ontogenetic rather than articular function, as the fast, sustained growth of the femur necessitates continuous ossification of the epiphyseal cartilage at either ends.

Basal sauropodomorphs possess an incompletely perforated acetabulum (Fig. 3-3b), indicative of capsular ventral joint ligaments (Fig. 3-8b). 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. 3-7c).

The passage taken by the intrinsic joint ligaments and the length of the ligamentum capitis become increasingly difficult to infer in Sauropoda due to reduction of the posteromedial tuber. Nevertheless, if the pubofemoral and ischiofemoral ligaments still attach to the femoral head, the ligaments would run parallel to each other and as flat, sheet-like structures between the acetabular membrane and the femoral fibrocartilage sheath (Fig. 3-9a). Although fusion between the pubofemoral and ischiofemoral ligaments cannot be determined, the two ligaments' parallel passage suggests that they constrained femoral protraction and retraction during sauropod locomotion.

Evolution of the hyper-parasagittal hip joint in basal Theropoda

The hip joint evolution of theropods is best exemplified by characterized by differential combinations of character state transitions, which suggest unique locomotor adaptations in each clade. The basal theropod hip joint morphology is exemplified by *Coelophysis* (Fig. 3-9b). In contrast to basal dinosauriformes, in basal theropods the supraacetabular rim is oriented ventrolaterally, whereas the cartilage cone excavates a shallower trough on the femoral growth plate. Moreover, basal theropods acquired a fully perforated inner acetabular wall, as well as a distinct ischiofemoral ligament sulcus on the caudomedial femoral neck. These transitions indicate a strong evolutionary shift towards a highly constrained locomotor posture, in which femoral axial rotation and abduction is severely limited. The basal theropod morphology is termed the “hyper-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 in theropods compared to silesaurids, indicating a reduction of the extent of its metaphyseal insertion. 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 correction factor of adult *Struthio*, a 240 mm *Coelophysis* femur would possess a cartilage cap $5.6 (\pm 2.0)$ mm in thickness on its proximal end. In contrast, the cartilage correction factor of *Alligator* reconstructs a $7.6 (\pm 2.0)$ mm cartilage cap. The articular surface on the proximal femur is reconstructed here as a convex surface, in which the reconstructed thickness of epiphyseal cartilage fills in the cartilage cone trough, because the proximal femur of taxa bracketing basal

theropods (basal dinosauiromorphs and tetanurans) possess convex subchondral and articular surfaces. The two alternative reconstruction schemes are presented here as the maximal- and minimal estimates of proximal femoral articular cartilage thickness in *Coelophysis*.

In basal theropods, the femoral head inserts into the acetabulum craniomedially and is confined laterally by the ventrolaterally oriented supraacetabular rim (Fig. 3-9b). The orientation of the rim indicates that the iliofemoral ligament no longer functions to constrain femoral lateral rotation, instead is restricted to lateral stabilization of the femur. The entire proximal femoral growth plate is covered by hyaline cartilage and articulates with the labrum on the acetabular “ceiling”. In contrast, the antitrochanter is unexpanded, faces craniolaterally, and articulates with the metaphyseal fibrocartilage sheath at the trochanteric region of the proximal femur. Since the femoral head is craniomedially deflected, the condyles remain perpendicular to the craniocaudal axis of the animal during femoral protraction and retraction. The proximal femur of basal theropods possesses a distinct fibrocartilage shelf, which forms the ventral half of the capital and lateral portion of the femoral head. This morphology indicates that fibrocartilage sleeve attaches extensively to the metaphysis, and that the entire ventral half of the femoral head consisted of a fibrocartilage articular surface.

Under this configuration, the femur cannot undergo axial rotation but is instead “locked” into protraction and retraction. In particular, the femoral head region is inferred to undergo dorsoventral translation within the cranial acetabulum during femoral movement. The fully perforated inner acetabular wall indicates that the two ventral joint ligaments are located inside the hip joint capsule. The amount of femoral head

displacement is inferred to be constrained by the intrinsic joint ligaments. In particular, the ischiofemoral ligament provides a robust connection between the ischial inner acetabular rim and the femoral head at the fovea capitis. During femoral retraction, the fovea capitis is displaced craniad relative to the ischium, suggesting that the ischiofemoral ligament is stretched during this posture. This indicates that the ischiofemoral ligament functions as an internal constraint to femoral head displacement during femoral protraction and retraction.

The hyper- parasagittal hip joint morphology is largely retained in basal ceratosaurs but underwent minor modifications in *Carnotaurus* (MACN CH 894) and Megalosauroida. Basal ceratosaurs such as *Eoabelisaurus* (MPEF 3990), *Elaphrosaurus* (MB.R. 4960), and *Ceratosaurus* (UMNH VP 5278, BYU VP 881-12893, BYU VP 465-4970) possess hip joints largely similar to those of more basal theropods (Fig. 3-7o; Gilmore, 1920), despite the evolution of large body size in *Ceratosaurus*. However, ceratosaurs possess mediolaterally wider femoral heads and more distinct ischiofemoral ligament sulcus (Fig. 3-7o), giving the proximal femur a more spherical appearance than those of more basal theropods. These transitions suggest that ceratosaurs evolved a more constrained articulation between the femoral head and the acetabulum, such that the femoral head functioned as the center of hip rotation, in contrast to the extensive dorsoventral femoral head excursion inferred in basal theropods. However, the fibrocartilage sleeve remains highly prominent in the femoral head region in ceratosaurs, suggesting that the capital extent of the proximal femur remains under substantial translational movement during locomotion.

In the derived ceratosaur *Carnotaurus* and in megalosauroids, the supraacetabular rim maintains its basal ventrolateral orientation, but the mediolateral width of the rim is reduced. This indicates that the craniolateral portion of the hip joint capsule reverts to a more ligamentous morphology. The reduction of lateral bony constraint allowed these taxa to undergo greater amount of femoral abduction than basal theropods. However, mediolateral rotation remains unlikely due to the need to maintain articulation between the antitrochanter and the fibrocartilaginous trochanteric regions.

Lastly, ceratosaurs maintain extensive fusion of the antitrochanter, a trait shared with *Coelophysis* (Fig. 3-5b) but not with any other basal theropods (e.g., *Dilophosaurus*, Fig. 3-4c). In contrast, megalosauroids retain an unfused antitrochanter as in basal dinosauromorphs (e.g., *Piatnitzkysaurus*, Fig. 3-3f). The theropod pelvis remains unfused in more derived taxa along the stem lineage and underwent another transition to the fused state at Euornithes. The mechanical and ontogenetic significance of pelvic fusion is poorly understood and warrants further study. However, because antitrochanter fusion results from ossification of the hyaline cartilage synchondrosis, a fused antitrochanter indicates a largely fibrocartilaginous articular surface, with little remnants of the hyaline cartilage core underneath. If the hyaline cartilage core of the antitrochanter functioned to dissipate compressive force, as hypothesized in Chapter 1, the fully co-ossified antitrochanter of *Coelophysis* and ceratosaurs may have functioned to resist shear forces against the metaphyseal fibrocartilage sheath, rather than compressive forces against the femoral neck.

Evolution of coupled hip protraction-abduction in Avetheropoda

The hip joints of avetheropods (Allosauroidea + Coelurosauria) underwent several major transitions from the basal theropod condition. The most apparent of these transitions is the reversion to a laterally oriented supraacetabular rim (e.g., *Allosaurus*, Fig. 3-3g) and a fully medially deflected femoral head. These morphologies have led to numerous skeletal reconstructions of avetheropods with a hinge-like hip joint articulation, in which the femoral head inserts into the acetabulum medially, perpendicular to the craniocaudal axis of sacrum (Gatesy et al., 2009). Under this orientation, the lack of dimensional congruence is apparent between the femoral head and the acetabular fossa. However, present inference of hip joint soft tissue anatomy questions the traditional reconstruction and argues that avetheropods retain a craniomedially oriented femoral head articulation. This reconstruction reduces the craniocaudal incongruence between the femur and the acetabulum and has profound implications on the evolution of hip joint range of motion in theropods.

The avetheropod femoral morphology is best exemplified by allosauroids, tyrannosauroids (*Tyrannosaurus*, Fig. 3-10a), and basal coelurosaurians. The metaphyseal collar is expanded on the capital and craniomedial periphery of the growth plate, indicative of a well-developed bony attachment for the fibrocartilage collar. In particular, the metaphyseal collar on the craniolateral metaphysis forms a raised shelf, bordered by a right-angled outline. Since the ventral outline of the metaphyseal collar signifies the ventral extent of the femoral head, the entire ventral half of the avetheropod femoral head is inferred to be fibrocartilaginous, with the hyaline cartilage core covering only the terminal growth plate surface (e.g., *Allosaurus*, Fig. 3-6f).

The subchondral growth plate surface of the avetheropod proximal femur lacks a cartilage cone trough but possesses a dichotomy in growth plate texture. Small avetheropods generally possess a smooth growth plate (Ostrom, 1969; Padian, 1986), whereas the growth plate is rugose in tyrannosauroids, *Allosaurus*, *Ornithomimus* and *Anzu*. Similarly a rugose growth plate surface is also present in a large individual of *Ceratosaurus* (Fig. 3-7o) but is absent in all other basal theropods. The level of growth plate rugosities in theropods never achieves the same level of convoluted texture as in the femoral heads of sauropods. Moreover, unlike sauropods, the rugosities on theropod growth plates are more evenly distributed across the growth plate surface and largely take the form of transphyseal striations oriented perpendicular to the capital-trochanteric axis. These observations suggest that the thickness of theropod epiphyseal cartilage are thinner than the maximal estimate for sauropod femoral head cartilage, and that theropods possess a more evenly distributed cartilage thickness across femoral head and trochanteric region.

Epiphyseal cartilage reconstructions for avetheropods with smooth epiphyseal surface are based on cartilage correction factors of adult *Struthio* and *Alligator*. For a 329 mm *Tanycolagreus* femur, the minimal estimate of epiphyseal cartilage thickness is 7.7 (± 2.7) mm of hyaline cartilage on the proximal femur; whereas maximal estimate is 10.4 (± 2.7) mm. In contrast, epiphyseal cartilage reconstruction for avetheropods with rugose growth plate surface is based on the cartilage correction factors of *Alligator* and juvenile *Struthio*. For a 1280 mm *Tyrannosaurus* femur, the minimal estimate is 40.3 (± 10.6) mm of hyaline cartilage on the proximal femur; whereas maximal estimate is 40.1 (± 4.1) mm. Admittedly, neither *Alligator* nor juvenile *Struthio* is a perfect candidate for cartilage

reconstruction in large theropods, because neither extant model possess the combination of rugose femoral growth plates with expanded metaphyseal collar as present in avetheropods. Nevertheless, cartilage thickness estimates here represent the most phylogenetic constrained attempt to date at non-avian theropod epiphyseal anatomy.

Avetheropod hip joints were able to undergo greater range of abduction than those of basal theropods. Unlike in basal theropods, the supraacetabular rim of avetheropods reverted to a lateral orientation, thus eliminating the bony lateral constraint of the acetabulum. However, femoral abduction and axial rotation would have been limited by the need for the femoral neck (trochanteric region) of the proximal femur to remain in close association with the bony antitrochanter. Although avetheropods possess distinct hyaline cartilage cores on the growth plate surface of the femoral neck and the bony antitrochanter, both articular surfaces are formed by a superficial layer of fibrocartilage, as in extant archosaurs (Tsai and Holliday, 2014). The craniolateral orientation of the bony antitrochanter in avetheropods indicates that in order for the antitrochanter to remain in contact with the femoral neck, the femur must undergo coupled abduction and protraction.

Moreover, the articulation between the femoral neck and the antitrochanter in avetheropods permits femoral axial rotation, during which the femoral head acts as the fulcrum within the craniomedial acetabular fossa. In extant birds, the femur undergoes substantial axial rotation during terrestrial locomotion (Kambic et al., 2014). In contrast to Coombs (1978) and Hertel and Campbell (2007), the antitrochanter does not limit femoral axial rotation in birds. Instead, the presence of fibrocartilage on the avian femoral neck and antitrochanter articular surfaces, as well as a stout ligamentum capitis

on the proximal femur, strongly suggest that the femoral head acts as a fulcrum during femoral axial rotation, and that the femoral neck and antitrochanter undergo axial compression and dorsoventral translation motion against the antitrochanter during femoral axial rotation (Tsai and Holliday, 2014). In avetheropods, the femoral neck possesses highly integrated attachment of fibrocartilage, hyaline cartilage, and subchondral growth plate. Correspondingly, antitrochanters also maintain an open synchondrosis, suggesting the retention of a hyaline cartilage core at the ilioischial joint in addition to the superficial fibrocartilage surface. The highly integrated relationship between hyaline cartilage, fibrocartilage, and subchondral bone in the caudal acetabulum indicates that the avetheropod femoral neck and antitrochanter were able to withstand substantial amount of compression and translation during locomotion.

The femoral head of avetheropods is tightly constrained by extrinsic and intrinsic joint ligaments, allowing its function as a fulcrum against the sliding articulation between the fibrocartilaginous surfaces of the femoral neck and the antitrochanter. Craniodorsally, the iliofemoral ligament originates on the supraacetabular rim and inserts into the fibrocartilage on the craniolateral metaphyseal collar. The iliofemoral ligament can only contribute to the joint capsule when the femoral head is oriented craniomedially relative the craniocaudal axis sacrum. Ventrally, the pubofemoral and ischiofemoral ligaments are located intrinsic to the hip joint capsule. The pubofemoral ligament originated cranioventrally on the pubic inner acetabular rim, traversed between the femoral head and the acetabular membrane, and attached onto the fovea capitis. In contrast, the ischiofemoral ligament traversed within its sulcus caudomedial to the femoral head. The topological relationship between the ventral ligaments indicates that the pubofemoral

ligament functioned to stabilize the femoral head as a fulcrum against the femoral neck-antitrochanter articulation, whereas the ischiofemoral ligament functioned to limit femoral retraction (Fig. 3-10a).

Overall, my results conclusively show that the avetheropod femur inserts into the acetabulum craniomedially, in contrast to the fully medial articulation seen in traditional reconstructions in physical skeletal mounts (Carpenter et al., 1994; Lindsay et al., 1996) and in digital biomechanical models (Gatesy et al., 2009; Hutchinson et al., 2005). A fully medial articulation is not supported because it denies the femoral neck-antitrochanter articulation, compresses the iliofemoral ligament at the craniodorsal joint capsule, and interferes with the passage of the ischiofemoral ligament. Lastly, a craniomedial hip joint articulation for avetheropods is supported phylogenetically, because both basal theropods and extant birds possess a cranially associated femoral head-labrum articulation and a caudally associated femoral neck-antitrochanter articulation. Under the new reconstruction, the avetheropod hip joint is able to undergo substantial abduction and axial rotation during femoral protraction, associated with the evolution of a more avian like, “crouched” femoral posture (Allen et al., 2013), and the separation of the hindlimb and the tail musculatures as distinct locomotor modules in theropods (Gatesy and Thomason, 1995; Gatesy and Dial, 1996).

Evolution of the avian-like hip joint in Maniraptora

The evolutionary transitions in the maniraptoran hip joint are characterized by the apparent segregation of the proximal femur and the acetabulum as distinct evolutionary modules. The most basal maniraptoran included in this analysis, *Falcarius*, exhibits transitional hip joint morphology between basal avetheropods and other maniraptorans.

The proximal femur of *Falcarius* possesses an expanded metaphyseal shelf on the lateral surface of the femoral head, but a reduced metaphyseal shelf on the capital extent of the femoral head (Fig. 3-6g). This morphology indicates that in *Falcarius*, the fibrocartilage sleeve has been integrated with the hyaline cartilage in the capital extent of the femoral head but retains a distinct bony attachment on the lateral metaphyseal surface. In more derived maniraptorans, total reduction of the metaphyseal collar on the proximal femur indicates that fibro- and hyaline cartilage has been integrated into the composite articular structures, as seen in birds. The current available data indicates that evolution of integrated fibro-hyaline cartilage within the hip joint evolved only once in Pennaraptora. However, given the limited number of therizinosaurs and oviraptorosaurs in this study sample, additional data may revise the current evolutionary reconstruction.

The overall avian-like subchondral morphology of derived maniraptorans indicates that adult and juvenile *Struthio* provide better estimate for epiphyseal cartilage thickness than *Alligator*. Nevertheless, cartilage correction factors from both taxa are used here for comparison. For a 185 mm *Velociraptor* femur with a smooth subchondral surface, minimal estimate based on *Alligator* is 4.4 (± 1.5) mm of hyaline cartilage on the proximal femur; whereas maximal estimate based on adult *Struthio* is 5.8 (± 1.5) mm. Most maniraptorans possess smooth subchondral surfaces similar to adult *Struthio*, but *Anzu* and *Deinonychus* possess rugose growth plates indicative of thick hyaline cartilage layers (Fig. 3-6p, 3-7p). The rugose growth plate morphology indicates that *Anzu* and *Deinonychus* possess relatively thicker epiphyseal cartilage compared to other maniraptorans. However, the rugose proximal femoral growth plates of *Anzu* and *Deinonychus* are not surrounded by an expanded metaphyseal collar as in more basal

theropods. The combination of these osteological correlates indicate that these two maniraptoran taxa possess a thick hyaline cartilage layer that is completely encapsulated by fibrocartilage on its articular surface, similar to the morphology in skeletally immature birds. Therefore, the maximal cartilage thickness for these taxa is inferred using juvenile *Struthio*, which possesses a similarly rugose growth plate texture. For a 490 mm *Anzu* femur, the minimal estimate based on *Alligator* is 15.4 (± 4.1) mm of hyaline cartilage, whereas the maximal estimate based on juvenile *Struthio* is 15.7 (± 5.5) mm. Although it is possible that the thick hyaline cartilage layers on *Anzu* and *Deinonychus* indicate ontogenetically immature status in these particular specimens, the relationship between thick cartilage, body size, and ontogenetic status in maniraptorans remain difficult to infer due to the current limited sample of maniraptorans with well-preserved femoral growth plates.

In contrast to basal avetheropods and *Falcarius*, derived maniraptorans possess more distinct foveae capitis and shallower ischiofemoral ligament sulci. These morphologies indicate a decrease in epiphyseal cartilage thickness, an increase in pubofemoral ligament insertion depth, as well as a shift in the ischiofemoral ligament's passage onto the femoral articular surface. In extant birds, the ischiofemoral ligament does not excavate a distinct sulcus on the femoral head (Baumel and Raikow, 1993; Tsai and Holliday, 2014). Instead, the avian ischiofemoral ligament travels across the femoral articular surface, largely parallel to the pubofemoral ligament. The two ligaments are often fused throughout their lengths as the ligamentum capitis femoris (Cracraft, 1971; Martin et al., 1994). Reduction of the ischiofemoral ligament sulcus in maniraptorans indicates the incipient fusion of the two intrinsic joint ligaments, as well as a transition in

the function of the ischiofemoral ligament. In basal avetheropods, the ischiofemoral ligament wraps around the caudomedial femoral head and functioned as an internal constraint against femoral retraction. In contrast, maniraptorans moved the ischiofemoral ligament onto the capital extent of the femoral head, such that the ischiofemoral ligament is able to aid pubofemoral ligament in constraining femoral head movement during femoral axial rotation. The shifting role of the ischiofemoral ligament is therefore correlated with the evolution of avian-like femoral motion within Maniraptora.

The most unusual evolutionary transition in the maniraptoran hip joint is the multiple, independent acquisition of bird-like antitrochanter in each sub-clade. Maniraptorans basally retain the relatively unexpanded antitrochanter morphology in outgroup avetheropods. This basal character state is best exemplified by the basal therizinosaur *Falcarius* (UMNH VP 12368, 14658) but also evident in *Anzu* (CM 78001), *Utahraptor* (BYU VP 7510-1007), and *Archaeopteryx* (HMN 1880, BSP S6). In contrast, derived members of each clade appear to have independently acquired an expanded antitrochanter. This morphology is particularly evident in Dromaeosauridae, as the most derived taxa (*Deinonychus* and *Velociraptor*) possess laterally expanded, bird-like antitrochanters (Fig. 3-10b). The available data is not able to resolve the ancestral state at each ancestral node within Maniraptora, due to the inclusion of only two taxa each for Therizinosauria and Oviraptorosauria. However, other studies on maniraptoran pelvic morphology generally support the current inference of independent antitrochanter expansions in each clade. The basal therizinosaur *Jianchangosaurus* possess unexpanded antitrochanters similar to *Falcarius* (Pu et al., 2013), whereas derived therizinosaurs such as *Nothronychus*, *Enigmosaurus*, and *Segnosaurus* possess bird-like, expanded

antitrochanters that often approach the remainder of the acetabulum in size (Zanno, 2010). Basal oviraptorosaurs such as *Avimimus* (Kurzanov, 1981) and *Caudipteryx* (Hertel and Campbell, 2007, contrasting interpretation) possess expanded antitrochanters, suggesting an early transition to the bird-like morphology and subsequent reversion in *Anzu*. The early divergence of Maniraptora during the Jurassic (Xu et al., 2001b; Hu et al., 2009; Godefroit et al., 2013) complicates evolutionary inferences of antitrochanter morphology among derived taxa. The poor fossil record of Jurassic maniraptorans results in long ghost lineages, obscuring much of the early character transitions that could have taken place preceding the Cretaceous taxa in the current analysis. Nevertheless, the independent acquisition of an avian-like acetabular morphology among each maniraptoran lineage indicate multiple convergences in locomotor behavior, likely associated with independent evolutionary enlargement of forelimbs, cranial shifted center of mass, and habitually flexed femoral postures (Allen et al., 2013).

CONCLUSION

The evolutionary history of Saurischia is characterized by multiple, iterative convergences and divergences in hip joint anatomy. Both theropods and sauropodomorphs evolved intrinsic hip joint ligaments, which constrained femoral head movement during hip excursion. Moreover, theropods and sauropodomorphs independently modified the fibrocartilage collar to provide mechanical support for thick layers 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, the theropod lineage underwent several major transitions in hip joint morphology along the stem lineage, with clade-specific combination of character transitions within basal theropods, avetheropods, and Maniraptora. 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. In particular, maniraptorans evolved a composite fibro-hyaline cartilage on the proximal femur, and independently evolved bird-like antitrochanters within Therizinosauria, Oviraptorosauria, Deinonychosauria, and Avialae. These data indicate highly divergent locomotor adaptations within Saurischia worthy of additional phylogenetic and functional analyses.

Table 3-1. 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	<i>m. ischiotrochantericus</i>
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 3-2. Archosauriform taxa studied and imaging techniques used to investigate hip joint anatomy. All photogrammatized specimens were also photographed.

Taxon	Specimen identification	Imaging technique
Outgroup archosauriforms		
<i>Gracilisuchus</i>	MCZ 4116, MCZ 4118	Photogrammetry
Phytosaur indet.	TMM 43685	Photogrammetry
<i>Chanaresuchus</i>	MCZ 4035, 4036, 4037, PVL 6244	Photogrammetry
<i>Vancleavea</i>	PEFO 2427, 34035, 14269	Photography
<i>Trilophosaurus</i>	TMM 31025.77, 31025.79B, 31025.140, 31025.190, 31025.781, 31025.1000, 31025.1050, 31025. 1073	Photogrammetry
<i>Hyperodapedon</i>	MCZ 2643, 3640, 3641, 4608, 4610, 4611, 4637	Photogrammetry
Outgroup dinosauriforms		
<i>Asilisaurus</i>	NMT RB159	Laser scan
<i>Silesaurus</i>	GR 261, PEFO 34347	Photogrammetry
<i>Eucoelophysis</i>	GR 195, 225	Photogrammetry
<i>Lagosuchus</i>	MCZ 4137, MCZ 4346 (Cast of PVL 4619)	Photogrammetry
<i>Lagerpeton</i>	MCZ 4121	Photogrammetry
<i>Dromomeron</i>	GR 218, 219, 234, TTUP 12539X, 18331, UMNH VP H4-712-100626	Photogrammetry
Ornithischians		
<i>Lesothosaurus</i>	NHMUK RUB 17	Laser scan
Sauropodomorphs		
<i>Adeopapposaurus</i>	PVSJ 610	Photogrammetry
<i>Alamosaurus</i>	TMM 41541, 40597, 45889, 45891	Photogrammetry
<i>Amargasaurus</i>	MACN N-15	Photogrammetry
<i>Ammosaurus</i>	YPM 208	Photogrammetry
<i>Anchisaurus</i>	YPM 1883	Photogrammetry
<i>Argyrosaurus</i>	FMNH P13019	Photogrammetry
<i>Apatosaurus</i>	CM 3018, 83, 35, 21752, YPM 1940, 1960, 1980, 1981, FMNH 25112, LACM 52844, UMNH VP 21125, FMAC 403, BYU 681-4499, 681-12914, 681-16964	Photogrammetry
<i>Barosaurus</i>	NAMAL 106, YPM 429	Photogrammetry
Diplodocid indet.	UMNH VP 7558	Photogrammetry
<i>Brachiosaurus</i>	FMNH P 25107	Photogrammetry
<i>Brachytrachelopan</i>	MPEF-PV 1716	Photogrammetry
<i>Camarasaurus</i>	BYU 661-9047, CM 11338, 11393, DNM 2401, 4514, TMM 42423, UMNH VP 5285,	Photogrammetry

	YPM 1901, 1910, 4625, 5851, 5857	
<i>Cedarosaurus</i>	DMNH 37045	Photography
<i>Chubut giant titanosaur</i>	MEF unnumbered	Photogrammetry
<i>Dicraeosaurus</i>	MB. R 4886	Photogrammetry
<i>Efraasia</i>	SMNS 12216	Photogrammetry
<i>Haplocanthosaurus</i>	CM 572, FHPR 1106	Photogrammetry
<i>Leonerasaurus</i>	MPEF-PV 1663	Photogrammetry
<i>Mussaurus</i>	MLP unnumbered	Photogrammetry
<i>Panphagia</i>	PVSJ 874	Photography
<i>Diplodocus</i>	DMNH 1494, 462, DINO 2921, CM 84, 94, 21710, 21788, 21745, BYU 681-17014, BMNH unnumbered	Photogrammetry
<i>Giraffatitan</i>	HMN SII	Photogrammetry
<i>Patagosaurus</i>	MACN CH 233, 239, 240, 933, 1299, 1986	Photogrammetry
<i>Plateosaurus</i>	MB. R 4430, SMNS 58958, F14 91294, F29 91302, F61 91309, F65 91310, GPIT 1	Photogrammetry
<i>Rapetosaurus</i>	FMNH PR 2209	Photogrammetry
<i>Ruehleia</i>	MB. R 4179	Photogrammetry
<i>Sarhsaurus</i>	TMM 43646-282	Photogrammetry
<i>Sauroposeidon</i>	YPM 5449	Photogrammetry
<i>Supersaurus</i>	BYU 725-13018	Photogrammetry
<i>Tehuelchesaurus</i>	MPEF PV 1125	Photogrammetry
<i>Tornieria</i>	MB. R 2637, 2649, 2666, 2671, 2700, 2713, 2716, 2722, 2733	Photogrammetry
<i>Eoraptor</i>	PVSJ 512	Photography
Theropods		
<i>Chindesaurus</i>	GR155, PEFO 33982	Photography
<i>Herrerasaurus</i>	MACN 18060, MCZ 4381, MLP 61-VIII-2-3, PVSJ 373	Photogrammetry
<i>Staurikosaurus</i>	MCZ 1669	Photogrammetry
<i>Eodromaeus</i>	PVSJ 560	Photography
<i>Tawa</i>	GR 155, 235, H2-054-100606, H3-267-070526, H3-474, H3- 485-120817, H4 -469-11818	Photogrammetry
<i>Coelophysis</i>	CM 76863, 81179, DMNH 14729, 22702, GR 245, MNA V3118, TTUP 15041, UCMP 129618, UMNH VP H2-388- 110816, YPM 41197	Photogrammetry, laser scan
<i>Liliensternus</i>	MB. R 2175 (two individuals)	Photogrammetry
<i>Dilophosaurus</i>	TMM 43246-126, UCMP 37302, 77270	Photogrammetry, laser scan
<i>Cryolophosaurus</i>	FMNH PR 1821	Photogrammetry
<i>Elaphrosaurus</i>	MB. R 4960	Photogrammetry

<i>Ceratosaurus</i>	BYU VP 881- 12893, 765-4970, TPI 1010, UMNH VP 5278	Photogrammetry
<i>Ligabueino</i>	MACN PV N42	Photography
<i>Carnotaurus</i>	MACN CH 894	Photogrammetry
<i>Eoabelisaurus</i>	MPEF-PV 3990	Photogrammetry
<i>Torvosaurus</i>	BYU 725-2014, 725-2015, 725-4977	Photogrammetry
<i>Megalosaurus</i>	BMNH (UK) 31811	Computed tomography
<i>Condorraptor</i>	MPEF-PV 1686, 1687, 1688, 1689, 1690, 1691, 1692, 1693, 1696, 1704	Photogrammetry
<i>Piatnitzkysaurus</i>	MACN CH 895	Photogrammetry
<i>Marshosaurus</i>	UMNH VP 6372, 6373, 6374, 6378, 6379, 6380, 6384, 6386, 6387	Photogrammetry
<i>Siats</i>	FMNH PR 2716	Photogrammetry
<i>Tyrannotitan</i>	MPEF PV 1156, 1157	Photogrammetry
<i>Allosaurus</i>	BYU 671-8901, 725-4842, 725-5163, 725-17281, DINO 11541, DMNH 2149, 44397, DNM 2974, FMNH P 25114, MCZ 4397, UMNH VP 6317, 7149, 7892, 7894, 7896, 7899, 8114, 8118, 8119, 8121, 8122, 8124, 8232, 22267, 20726, UMNH VP-DNM 2540	Photogrammetry, laser scan
<i>Stokesosaurus</i>	UMNH VP 2383, 2938, 6051, 6052	Photogrammetry
<i>Teratophoneus</i>	RAM 9132, UMNH VP 16690	Photogrammetry
<i>Tyrannosaurus</i>	BMNH (US) 2001.4.1, CM 9380, FMNH PR 2081, LACM 150164, MOR 555, TMM 40811	Photogrammetry, laser scan
<i>Gorgosaurus</i>	FMNH PR 2211	Photography
<i>Coelurus</i>	YPM 2010	Photogrammetry
<i>Tanycolagreus</i>	TPI 1011	Photogrammetry
<i>Ornitholestes</i>	YPM 56681 (Cast of AMNH 619)	
<i>Compsognathus</i>	BSP AS I-563	Photography
<i>Ornithomimus</i>	RAM 6794, RAM 14182	Photogrammetry
<i>Falcarius</i>	UMNH VP 12361, 12368, 12375, 14535, 14540, 14541, 14658, 14665	Photogrammetry
<i>Nothronychus</i>	UMNH VP 16420	Photography
<i>Khaan</i>	IGM 100-1002	Laser scan
<i>Anzu</i>	CM 78000, 78001	Photogrammetry
<i>Unenlagia</i>	MACN cast of MCF PVPH 78	Photogrammetry
<i>Bambiraptor</i>	FIP 001	Laser scan
<i>Deinonychus</i>	MCZ 4371, RAM 1856 (cast of	Photogrammetry

	AMNH 3015), YPM 5235	
<i>Velociraptor</i>	IGM 100-985, 100-986	Laser scan
<i>Utahraptor</i>	BYU 2586, 7510-10073, 7510-14567, 7510-18078, 1833	Photogrammetry
<i>Sinornithoides</i>	IVPP V9612	Computed tomography
<i>Archaeopteryx</i>	HMN 1880, BSP S6	Photography
<i>Patagopteryx</i>	MACN N-03, N-11	Photogrammetry
<i>Dinornis</i>	BSP Ag68-I-2A7a	Photography
<i>Tinamus</i>	LACM 101689 SN	Photography
<i>Apteryx</i>	LACM 102342	Photogrammetry
<i>Rhea</i>	LACM CSULB 6335	Photogrammetry
<i>Struthio</i>	LACM 1014 SN, 1136 SN, LACM 112605	Photogrammetry
<i>Gallus</i>	MUVC-AV 014	Photography
<i>Meleagris</i>	MUVC-AV 017	Photography, computed tomography
<i>Aythya</i>	BSP unnumbered	Photography

Table 3-3. Institutional abbreviations

BMNH (US)	Burpee Museum of Natural History
BSP	Paläontologisches Museum München
BYU	Brigham Young University Museum of Paleontology
CM	Carnegie Museum of Natural History
DINO	Dinosaur National Monument
DMNH	Denver Museum of Natural History
DNM	Dinosaur National Monument
FHPR	Utah Field House of Natural History
FIP	Florida Institute of Paleontology
FMNH	Field Museum of Natural History
GPIT	Institute for Geosciences, Eberhard-Karls-Universität Tübingen
GR	Ruth Hall Museum of Paleontology
HMN	Museum für Naturkunde Berlin
IGM	Mongolian Geological Institute
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology
LACM	Natural History Museum of Los Angeles County
MACN	Museo Argentino de Ciencias Naturales
MB.R	Museum für Naturkunde Berlin
MCZ	Museum of Comparative Zoology
MDM	Mesalands Dinosaur Museum
MLP	Museo de La Plata
MNA	Museum of Northern Arizona
MOR	Museum of the Rockies
MPEF	Museo Paleontológico Egidio Feruglio
MUVC	University of Missouri Vertebrate Collection
NAMAL	North American Museum of Ancient Life
NHMUK = BMNH (UK)	Natural History Museum, London
NMT	National Museum of Tanzania
PEFO	Petrified Forest National Park
PVL	Instituto Miguel Lillo
PVPH	Museo Carmen Funes
PVSJ	Instituto y Museo de Ciencias Naturales, San Juan
RAM	Raymond M. Alf Museum of Paleontology
SMNS	Staatliches Museum für Naturkunde Stuttgart
TMM	Texas Memorial Museum
TPI	North American Museum of Ancient Life
TTUP	Museum of Texas Tech University
UCMP	University of California Museum of Paleontology
UMNH	Utah Museum of Natural History
YPM	Yale Peabody Museum of Natural History

Table 3-4. 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 sheath	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.

Table 3-5. Reconstructed thicknesses of the proximal femoral epiphyseal cartilage among Dinosauromorpha based on cartilage correction factors proposed by Holliday et al. (2010). Cartilage thickness is estimated based on similarities in subchondral growth plate surface textures.

Taxon	Femur length (mm)	Estimated cartilage thickness based on <i>Alligator</i> (mm)	Estimated cartilage thickness based on juvenile <i>Struthio</i> (mm)	Estimated cartilage thickness based on adult <i>Struthio</i> (mm)	Estimated cartilage thickness based on other criteria (mm)
<i>Dromomeron</i>	135	4.3±1.1	NA	3.2±1.1	NA
<i>Asilisaurus</i>	137	NA	NA	NA	13.6*
<i>Plateosaurus</i>	590	18.6±4.9	18.9±6.6	NA	NA
<i>Apatosaurus</i>	1801	NA	57.6±20.2	NA	436**
<i>Coelophysis</i>	240	7.6±2.0	NA	5.6±2.0	NA
<i>Tanycolagreus</i>	329	10.4±2.7	NA	7.7±2.7	NA
<i>Tyrannosaurus</i>	1280	40.3±10.6	41.0±14.3	NA	NA
<i>Velociraptor</i>	185	5.8±1.5	NA	4.4±1.5	NA
<i>Anzu</i>	490	15.4±4.1	15.7±5.5	NA	NA

*Silesaurids possess growth plate morphologies that preclude the use of cartilage correction factors derived from extant archosaurs. See text for estimation methods.

**Maximal estimate of sauropod cartilage thickness is derived from the difference in dorsoventral height between the femoral head and the acetabulum.

Figure 3-1. **A.** 3D surface model of a *Tyrannosaurus* left pelvis (FMNH PR 2081) 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 *Tyrannosaurus* left femur 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 is 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. Tissues nomenclature and color schemes are labeled according to homology inferences in Table 2-1, Figure 2-3.

Figure 3-2. Simplified topologies of phylogenetic trees used in this study. **A.** The “default” phylogenetic tree based on published studies. **B.** Alternate placement of Silesauridae as stem ornithischians. **C.** Alternate placement of Herrerasauridae as the sister taxon to Theropoda + Sauropodomorpha. **D.** Alternate placement of *Eoraptor* as a basal theropod, rather than as a basal sauropodomorph. **E.** Alternate placement of *Archaeopteryx* as a stem-deinonychosaur, rather than as the basal-most avialan.

Figure 3-3. 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 3-4. Osteological correlates of the acetabular labrum and antitrochanter. All pelves shown in left ventral view. **A.** *Sarhsaurus* (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 3-5. 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.** *Coelophysis* (UCMP 129618, mirrored). 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 3-6. 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 not shown due to the thick hyaline cartilage attachment in these taxa.

Figure 3-7. 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 3-8. 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 (2014). Cut surfaces of bones and ligaments are marked by daggers (†) 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.

Figure 3-9. Hip joint soft tissue reconstructions of dinosaurs. 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 (2014). Cut surfaces of bones and ligaments are marked by daggers (†) before the labels. **A.** *Apatosaurus*. Cranial section is shown in caudal view. **B.** *Coelophysis*. 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 3-10. Hip joint soft tissue reconstructions of dinosaurs. 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 (2014). Cut surfaces of bones and ligaments are marked by daggers (†) before the labels. **A.** *Tyrannosaurus*. 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. **B.** *Deinonychus*. Cranial oblique section is shown in caudal oblique view.

CHAPTER 4

Convergence and disparity in saurischian dinosaur hip joints associated with gigantism

INTRODUCTION

Saurischian dinosaurs, which include birds, non-avian theropods, sauropodomorphs, and a number of stem taxa, range over 7 orders of magnitude in body size (Benson et al., 2014) and evolved multiple, independent occurrences of gigantism (Sander et al., 2004; Lee et al., 2014) and miniaturization (Stein, et al., 2010; Turner et al., 2007). Therefore, saurischians are an invaluable tool for exploring patterns of evolutionary transition between appendicular anatomy and body size.

Saurischians evolved a great diversity of limb bone morphologies, suggesting an equally diverse range of locomotor behaviors (Carrano 2001; Hutchinson 2006). Although theropods maintained facultative bipedality throughout their evolutionary history (Carrano 1999), sauropodomorphs underwent a secondary reversion to quadrupedality (Yates and Kitching, 2003). In both clades, the hindlimbs function as important load bearing structures, and numerous studies have explored hindlimb mechanics and locomotor postures of saurischians using limb bone dimensional scaling (Carrano, 2001; Bonnan, 2007) and computationally intensive modeling techniques (Hutchinson et al., 2005; Gatesy et al., 2009; Mallison 2010b; Bates et al., 2012; Maidment et al., 2013). However, due to the lack of articular soft tissues in the fossil record, inferences of joint loading, range of motion, and kinematics remain challenging (Holliday et al., 2010; Bonnan et al., 2013). In many archosaurs, the terminal, subchondral surfaces of limb bones differ in shape and size, such that substantial

assumptions are needed to physically articulate adjacent bony elements (Hutchinson et al., 2005; Gatesy et al., 2009). Moreover, many dinosaurs possess rugose subchondral surfaces, similar to the ossifying growth plates of juvenile birds, mammals, and lepidosaurs (Owen, 1842; 1875; Marsh, 1896). These lines of evidence indicate that gigantic saurischians constructed their articular surfaces using enormous volumes of soft tissue to cope with increased loading (Cope, 1878; Hay, 1908; Holliday et al., 2010; Chapter 3).

Insights on the anatomy and function of appendicular joints are critical to understanding the locomotor behavior, ecology, and evolution of vertebrates. In particular, interactions between 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, 1942a) of limb elements. These necessary functions are relevant to the construction of appendicular joints in vertebrates across the entire spectrum of body size. Gigantic terrestrial vertebrates experience an exponentially greater magnitude of limb joint loading compared to those of small-bodied taxa, because whereas joint surfaces scale to the surface area of the organism, body mass scales to the organism's overall volume (Schmidt-Nielsen, 1984). Therefore, evolutionary transitions in body size are expected to exert selective pressures on appendicular joint anatomy of terrestrial vertebrates. Substantial work has been devoted to the relationship between body size and bony appendicular joint morphology (e.g. mammals: Biewener, 1991; Godfrey et al., 1991; dinosaurs: Wilson and Carrano, 1999; Carrano, 2000; Hutchinson et al., 2005). However, despite the highly disparate joint soft tissue morphologies present

among amniotes (e.g., independent evolution of epiphyseal centers: Haines, 1942a; presence of fibrocartilage in sliding joints: Barnett, 1954; vascularized hyaline cartilage: Snover and Rhoudin, 2008), few studies have linked articular soft tissue adaptations to body size (Malda et al., 2013), because the evolutionary history of sauropsid joints leading to the extant condition is poorly understood (Haines, 1938; 1942; Tsai and Holliday, 2014).

Among extant amniotes, mammals and lepidosaurs possess secondary mineralizing centers, which divide the epiphyseal cartilage into the superficial articular cartilage and the metaphyseal growth cartilage (Moodie, 1908; Haines, 1942b; Enlow, 1969). At skeletal maturity, the articular cartilage is reduced to a thin layer, whereas the growth cartilage is generally obliterated following the secondary center's fusion to the metaphysis (Haines, 1941; 1975; Buffrénil et al., 2004). In contrast, archosaurs (crocodylans, birds, and their extinct relatives) retain the basal tetrapod condition, 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). Moreover, the epiphyseal cartilage of archosaurs contains both hyaline cartilage and fibrocartilage (Tsai and Holliday, 2014). The contribution of each tissue, as well as the overall thickness of the epiphyseal cartilage, differs among extant groups. In Neoaves, the epiphyseal cartilage is reduced to a thin layer at adulthood (Cracraft, 1971; Fierbas and Zweymüller, 1971); whereas in large palaeognaths and crocodylans, thick layers of epiphyseal cartilage contribute significantly to the size and shape of the articular surface even at skeletal maturity (Fujiwara et al., 2010; Holliday et al., 2010). These derived morphologies among extant archosaurs complicate inferences of

the ancestral condition and body size adaptations, thus present major hurdles in studies of sauropsid locomotor evolution and joint functional biology.

Here I show that giant saurischian-line dinosaurs build their hip joints in two fundamentally different ways. I identified transitions in both discrete and continuous hip joint characters using a comprehensive sample of fossil saurischians and outgroup archosaurs. Discrete characters or osteological correlates of articular soft tissues were combined with continuous characters, which included both linear and area measurements of the subchondral surfaces. I used dimensional incongruence between the femoral and acetabular subchondral surfaces as proxies for the amount of soft tissues once present in the hip joint. I then tested whether gigantic saurischians evolved highly cartilaginous hip joints using phylogenetic comparative methods. Results of this study inform the first reconstruction of dinosaur hip joint anatomy, as well as its mechanical (e.g., articulation, load bearing) and physiological (e.g., bone growth, joint maintenance) adaptations.

MATERIALS AND METHODS

Osteological correlates and anatomical reference axes:

Anatomical abbreviations used in this study are summarized in Table 3-1, and the osteological correlates of articular soft tissues are illustrated in Fig. 4-1. In order to characterize the suite of morphological transitions within the saurischian crown lineage, nomenclature for osteological correlates of joint ligaments follows Tsai and Holliday (2014) and inferences made in Chapter 3. In all extant archosaurs, an unossified inner acetabular wall is the osteological correlate for presence of an acetabular membrane. Therefore, acetabular membranes are inferred to be present in extinct saurischians that also possess unossified inner acetabular walls. Since the inner acetabular wall is not

osseous in many archosaurs, I define the tube-shaped bony surface of the acetabulum as the *bony acetabulum*. In contrast, the socket-shaped surface formed by the bony acetabulum and the membranous inner acetabular wall is termed the *acetabular fossa*. The cranial, osseous portion of the supraacetabulum consists of the acetabular labrum, the attachment of which can be distinguished by the absence of growth plate surfaces (Chapter 1). The caudal portion of the supraacetabulum consists of the ischial peduncle of the ilium, and the ilial peduncle of the ischium. Lateral expansions of the two peduncular growth plate surfaces form the bony antitrochanter, which supported a cartilaginous articular surface distinct from acetabular labrum during life. The surface area of the bony antitrochanter is used as the proxy for the size of the cartilaginous antitrochanter (Fig. 4-1).

On the proximal femur, the cartilaginous cap consists of a hyaline cartilage core and a peripheral fibrocartilage sleeve. The hyaline core attaches to the calcified cartilage-covered growth plate surface and is confluent between the femoral head (capital) and trochanteric regions. If the thin layer of calcified cartilage is weathered away, the growth plate surface can be identified by the exposed trabecular bone immediately deep to the calcified cartilage layer. Surface area of the growth plate is used as the proxy for the extent of the epiphyseal hyaline cartilage attachment. 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. The metaphyseal collar can be distinguished from growth plate surface by a prominent metaphyseal line and from the bony diaphysis by a prominent ridge. Surface area of the

metaphyseal collar is used as the proxy for the extent of the fibrocartilage sleeve (Fig. 4-1).

To account for the evolutionary shifts in femoral condylar orientation among saurischians, such as the independent evolution of a medially deflected femoral head among lineages (theropods: Hutchinson, 2001b; sauropodomorphs: Martinez and Alcober, 2009; Yates et al., 2010), I use reference axes (Tsai and Holliday, 2014) to navigate the evolutionary changes in femoral head position and morphology (Fig. 3-1-c).

Data collection:

I studied a broad phylogenetic range of sauropsids (N= 108 taxa; Table 3-2), including 51 theropods and 31 sauropodomorphs, for continuous and discrete osteological characters on the proximal femur and the acetabulum. For taxa represented by multiple individuals (e.g., *Allosaurus*), I 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 noted as a young juvenile or neonate individual in literature.

Fossil specimens were studied by observation, linear measurements, and digital photography (Sony DSC-F828). Many specimens (N= 68 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/~snave/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). Prior to each photography session, removable markers were arbitrarily placed on the specimens as landmarks. Additionally, scale bars were included within each frame for proper scaling of the resultant point cloud. For a typical photogrammetry project, the fossil specimen was photographed between 50 and 80 times at incremental angles. The specimen is rotated to another side and additional set of photographs are taken until the specimen is documented adequately.

For a typical disarticulated specimen, the two photo sets were analyzed separately using the Bundler and PMVS program packages. Bundler automatically reconstructs a sparse point cloud from each photo set, whereas PMVS further refines it as a dense point cloud (.ply file output). The dense point cloud undergoes further processing in Geomagic Studio (V11), such as scaling, background removal, and deletion of extraneous “artifact” pointclouds. Point clouds reconstructed from different views of the same specimen were combined in Geomagic based on overlaps of arbitrary landmarks. The use of arbitrary markers maintains independence of the reconstruction from the actual morphology of the specimens. Lastly, the “wrap surface” function is used to generate a 3D polygonal surface using the combined point cloud. The output surface model depends heavily on the photography input (Mallison and Wings, 2014). Using high resolution photographs, the 3D models can capture sufficient amount of surface details, such as color and surface rugosities. The photogrammetric models acquired for this study are sufficient for the level of character analysis presented here.

Additionally, the 3D dataset is supplemented by surface models acquired from laser and CT scans. The CT and laser scan data were acquired from published literature (Allen et al., 2013; Hutchinson et al., 2007; Mallison, 2010a; Bates et al., 2012). Laser

scans were acquired using a NextEngine 3D Laser Scanner HD (Platt et al., 2010). All 3D models were converted into .ply and .stl file formats and imported into Geomagic (V11) for analyses. The use of 3D models allows quantitative assessment of continuous, three-dimensional osteological characters on the subchondral surfaces.

Discrete character coding:

The hip joints of saurischian-line archosaurs were examined for discrete characters, including osteological correlates of hip joint articular soft tissues. Hip joint articular soft tissues of diapsids and their osteological correlates are detailed in Table 3-4. I identified 14 osteological characters based on osteological correlates of putatively homologous articular soft tissues among extant diapsids (Tsai and Holliday, 2014). These osteological characters serve as proxies for the presence, orientation, thickness, and shapes of articular soft tissues. The evolutionary transition of hip joint osteological correlates is explored in Chapter 3 using maximum likelihood ancestral state reconstruction. Results from the ancestral state reconstruction are used to establish the basal versus derived states for each of the discrete characters presented here:

Continuous measurements:

In order to maintain the broad phylogenetic scope of the current study, I selected one representative individual from each taxon for continuous character analysis. Criteria for choosing the representative individual includes an adequate quality of subchondral preservation, completeness of hip joint elements, and inferred ontogenetic status as an adult or subadult. Linear dimensions were measured using a SPI 31-518-4 dial caliper and a tape measure, as well as from reconstructed 3D surface models of hip joints using

the *measure distance* function of Geomagic (V11). Linear dimensions of the femora include total femur length, femoral head height, femoral head width, and femoral head circumference, as well as the capital-trochanteric length of the growth plate surface (*facies articularis antitrochanterica*, hereby abbreviated as FAA length). Linear dimensions of the acetabulae include craniocaudal length, dorsoventral height, mediolateral depth, and overall circumference. I used femur length as a proxy for body mass following Turner and Nesbitt (2013) and Lee et al. (2014). Femur length has been shown to predict both maximum and minimum body mass estimates of sauropsids included in this study regardless of the methodological differences in obtaining individual mass estimates (e.g., Anderson et al., 1985; Gunga et al, 1999; 2007; Seebacher, 2001; Therrien and Henderson, 2007; Allen et al., 2009).

Surface area dimensions were measured from reconstructed 3D surface models of hip joints by highlighting relevant osteological correlates and using the *select area* function of Geomagic (V11). In most taxa examined, associated hip joint material from a single individual is used for surface area analyses. In taxa lacking associated hip joints, composite hip joints metrics used when the comprising individuals are deemed similar in both body size and ontogenetic stage based on other osteological indicators (e.g., skeletal proportions, sutural fusion). Surface measurements of the proximal femur include the overall subchondral bony surface, as well as the attachment areas of fibrocartilage (the metaphyseal collar) and hyaline cartilage (the growth plate). Surface measurements of the acetabulum include the overall area of the acetabular fossa, the area of the bony acetabulum, the attachment area of the acetabular labrum, and the attachment area of the antitrochanter. The femoral and antitrochanteric growth plates of many saurischians

possess substantial rugosities. Because the current goal is to distinguish the overall congruence of the bony hip joint, growth plate rugosities could potentially inflate the surface area of the bony femoral and acetabular surfaces. Moreover, it is difficult to quantitatively compare the amount of growth plate rugosity among fossil materials at various states of preservation, erosion and preparation. In order to ensure comparable measurements of bony joint congruence across the samples, the femoral growth plates were uniformly smoothed in Geomagic. The smoothing process eliminated rugosities by reducing the height difference between the “peaks” and “valleys” of the growth plate. I then independently addressed the significance of growth plate rugosities on soft tissue attachment by scoring its presence and morphology as discrete characters 8, 9, 10, and 13.

All continuous data were log-transformed prior to phylogenetic comparative analysis. Taxa for which a quantitative character is zero were excluded from the allometric analyses concerning that character. For example, the proximal femora of basal archosauromorphs such as *Chanerasuchus*, *Hyperodapedon*, and the phytosaur TMM 43685 lack a distinct separation between the metaphyseal collar and the subchondral growth plate therefore these taxa are excluded from the analysis for metaphyseal collar surface area.

Phylogenetic Comparative Analysis

Phylogenetic tree construction:

I used phylogenetic comparative methods to investigate the association between body size and hip joint anatomical characters. Osteological correlates were used as

proxies for articular soft tissues. Composite phylogenetic trees (Fig. 3-2) were constructed using Mesquite (V2.73) based on published studies, with branch lengths based on hypothesized divergence date between sister clades and sister taxa (Archosauromorpha, Ezcurra et al., 2014; Archosauriformes, Brusatte et al., 2010; Nesbitt, 2011; Dinosauromorpha, Langer et al., 2013; Sauropodomorpha, Wilson, 2005; Martinez 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; Ericson et al., 2006; Brown et al., 2008; Phillips et al., 2010). Pterosaurs were excluded from this analysis due to the already highly derived appendicular morphology in the basal-most taxon. I constructed a “default” phylogenetic tree (Fig. 3-2a), in which Silesauridae is considered as non-dinosaurian dinosauriformes (Brusatte, 2010; Nesbitt, 2011), Herrerasauridae as basal theropods (Sues et al., 2011), *Eoraptor* as the basal-most sauropodomorph (Martinez and Alcober, 2009), and *Archaeopteryx* as the basal-most avialan (Turner et al., 2012). Additionally, I analyzed alternative tree topologies to account for ambiguous phylogenetic placement of Silesauridae as stem-ornithischians (Langer and Ferigolo, 2013), Herrerasauridae as the basal-most saurischians (Novas et al., 2010), *Eoraptor* as a basal theropod (Sues et al., 2011) and *Archaeopteryx* as a stem-deinonychosaur (Xu et al., 2011; Godefroit et al., 2013). Four additional trees were modified from the “default” tree based on alternative placements of each contentious taxon (Fig. 3-2b-e).

Phylogenetic trees were exported as .phy files for subsequent analysis in R using RStudio (V3.1.1.). Since all theropod other than *Coelophysis* and *Herrerasaurus* are trimmed from the tree in sauropodomorph-specific analysis, alternative placement of *Archaeopteryx* (Fig. 3-2e) is only used in theropod-specific and pan-saurischian analyses.

Are osteological characters predicted by body size?

Phylogenetic logistic regression (PLR) was used to test the association between body size and discrete hip joint characters while accounting for phylogenetic relationships (Ives and Garland, 2010). Data were analyzed in R (Version 3.1.1) using the packages *ape* (Paradis et al., 2004) and *phylolm* (Ho et al., 2014), with femur length as the independent variable. Each discrete character was tested for its association with log femur length using the Comparative Analysis with Generalized Estimating Equations function (*compar.gee*; Paradis and Claude, 2002). I tested the association between discrete characters and body size in the sauropod and theropod lineages. A number of osteological characters are acknowledged to be non-independent with each other. For example, a taxon with concentrated rugosities on the femoral head growth plate region needs to possess a rugose subchondral growth plate. A test of association between pairs of discrete characters is beyond the scope of the current study. Therefore, I analyzed the relationship between each discrete character and body size independently of other discrete characters.

Are hip joint dimensions predicted by body size?

Phylogenetic reduced major axis regression (PRMA) was used to test the relationship between body size and continuous hip joint characters while accounting for phylogenetic relationships (Butler and King, 2004; Revell, 2012). Data were analyzed in R (Version 3.1.1) the statistical packages *ape* (Paradis et al., 2004), *caper* (Orme, 2013), *pgls* (Mao and Ryan, 2012), and *phytools* (Revell, 2012). I used femur length as the independent variable. Pairs of characters were tested for association via *compar.gee*, and for scaling relationship via *phyl.RMA*.

Allometric changes in femoral shape were assessed by the scaling relationships between the width and height of the femoral head, as well as the FAA length. Allometric changes in acetabular shape were assessed by the scaling relationships between the depth, height, and length of the acetabulum. I identified allometric changes in the linear congruence of the bony hip joint by comparing each femoral linear metric with its corresponding acetabular metrics. Additionally, I assessed allometric changes in the composition of articular soft tissue using attachments surface areas. Allometric changes in hip joint bony congruence were assessed by scaling relationships between total femoral subchondral surface and the acetabular fossa. Allometric changes in femoral fibro- and hyaline cartilage attachments were assessed by scaling relationships between the metaphyseal collar and the growth plate. Allometric changes in acetabular tissue attachment surfaces were assessed by scaling relationships between the acetabular fossa, the bony acetabulum, and the supraacetabulum. Additionally, I measured the surface area of the ilial antitrochanter in order to incorporate taxa in which the ilium is the only preserved acetabular element. I identified allometric changes in surface area congruence of the bony hip joint by comparing each femoral surface area metrics with its corresponding acetabular metrics. For linear dimensions, I infer isometric scaling if the regression slope does not differ significantly from 1. For surface area metrics, I infer isometric scaling if the regression slope does not differ significantly from 2. Positive and negative allometry is inferred respectively if the regression slopes is significantly greater or less than the isometric value.

RESULTS

Few osteological characters track with body size

Results of the phylogenetic logistic regression are summarized in Table 4-1 to 4-4 and Figure 4-6. Among saurischians, only a few osteological correlates for hip joint articular soft tissues are predicted by body size. Within the sauropod lineage, rugosities on the proximal femoral growth plate (8) are positively associated with body size. However, phylogenetic logistic regression is unable to determine the association of acetabular perforation (1), capital concentration of irregular growth plate rugosities (9), transphyseal striations (10), and metaphyseal collar expansion (14) with body size. These characters underwent only one transition to the derived state within the sauropod lineage, and the derived state is maintained throughout the Sauropodomorpha (Chapter 3). Moreover, the sauropodomorph taxa in the current study include only for two instances of evolutionary trend towards large body size in Plateosaurids and Anchisauridae. Therefore, the number of iterative transitions in the state of these characters is insufficient to determine their association with body size using phylogenetic logistic regression. In sauropodomorphs, the evolution of concentrated irregular rugosities on the femoral head (9), transphyseal striations (10), and metaphyseal collar expansion (14) preceded evolutionary increase in body size, because these characters were present in small, basal taxa and were retained in gigantic, terminal taxa. Overall, the hip joint morphology of sauropods was highly conserved throughout their evolutionary history. All alternative tree topologies returned statistically identical results as the “default” phylogenetic tree.

Within the theropod lineage, no hip joint osteological characters showed significant correlation with body size (Table 4-2). Phylogenetic logistic regression was unable to determine the association of proximal femoral growth plate rugosities (8) with body size. Rugosities are absent on the growth plate of theropods along the stem lineage

leading to birds but are present in all large-bodied theropods (e.g., *Tyrannosaurus*, *Allosaurus*, *Ceratosaurus*), as well as several smaller forms (e.g., *Ornithomimus*, *Anzu*, *Deinonychus*). Within Maniraptoriformes, taxa with rugose growth plates are bracketed by those possessing smooth growth plates. The sporadic occurrence of growth plate rugosities within theropods indicates that multiple lineages independently evolved thick epiphyseal cartilages (Chapter 3). Although sauropods and multiple lineages of gigantic theropods possessed thick layers of hyaline cartilage, evolutionary transitions in hip joint soft tissues were unassociated with body size transitions in either lineage. All alternative tree topologies returned statistically identical results as the “default” tree.

Large saurischians possess absolutely greater hip joint soft tissue

Results of the phylogenetic logistic regression are summarized in Tables 4-5 to 4-13 and Figures 4-2 to 4-5. Within the saurischian lineage, hip joint dimensions scale to overall positive allometry relative to femur length, suggesting that large saurischians possess relatively larger bony hip joints than would be predicted by femur length (Fig. 4-2, 4-3a-c, f, g). However, substantial overlaps in confidence intervals between corresponding metrics indicate that the regression slopes do not differ significantly from each other (Tables 4-5 to 4-13). Since the relative dimensions of the subchondral (bony) femoral and acetabular surfaces remain consistent across the body size spectrum, large saurischians are inferred to possess proportionally similar, but absolutely greater, volumes of soft tissues in their hip joints.

Gigantic sauropods use a relatively small amount of acetabular labrum and antitrochanter cartilage for maintaining hip joint articulation (Fig. 4-3d, e, h). Within the sauropod lineage, most hip joint metrics scale to positive allometry relative to femur

length. However, the regression slopes for labral attachment area, total bony antitrochanter surface area, and ilial bony antitrochanter surface area do not differ significantly from isometry. These results indicate that during the evolution of sauropod gigantism, attachment surface for the acetabular labrum and the antitrochanter cartilage increases at a lesser rate than other hip joint dimensions relative to femur length. Overall, results of this study indicate a trend of reducing supraacetabular soft tissue attachment during the evolution of sauropod gigantism.

In contrast, gigantic theropods possess absolutely greater amount of acetabular labrum and antitrochanter fibrocartilage in the hip joint than their smaller relatives (Fig. 4-4, 4-5). Attachment surface areas of the acetabular labrum and the antitrochanter scale to positive allometry relative to femur length, but the regression slopes do not differ from each other (Fig. 4-5d, h). These results indicate that the acetabular labrum and antitrochanter cartilage contribute significantly to hip joint articulation across the theropod body size spectrum and that both supraacetabular structures contribute significantly to hip joint articulation during theropod evolution.

The largest sauropods and theropods used absolutely greater amount of fibrocartilage to construct their proximal femoral articular surfaces than their smaller relatives. With the exception of pennaraptorans (Oviraptorosauria + Paraves, Foth et al., 2014), all saurischians retained the basal dinosauriform morphology in possessing a distinct metaphyseal collar surrounding the subchondral growth plate surface on the proximal femur. The metaphyseal collar serves as the bony attachment surface for the fibrocartilage sleeve peripheral to the hyaline cartilage core. The lack of a distinct metaphyseal collar necessitated the exclusion of pennaraptorans from the analyses of

metaphyseal collar surface area. Nevertheless, in both theropods and sauropods, the metaphyseal collar surface scales to positive allometry relative to femur length. The scaling pattern of the metaphyseal collar surface area does not differ significantly from that of the subchondral growth plate, suggesting that gigantic saurischians used similar proportions, but greater absolute amounts of fibro- and hyaline cartilage to build their hip joint as their smaller relatives. Nevertheless, this morphology indicates that the entire ventral half of the femoral head articular surface of gigantic theropods and sauropods consisted of a robust sleeve of fibrocartilage. Most alternative tree topologies returned statistically identical results as the “default” phylogenetic tree.

DISCUSSION

Overall, my results show that large theropods and sauropods independently evolved highly incongruent bony hip joints, in which congruence would have been maintained by thick layers of soft tissues (Fig. 4-6). However, difference in the patterns of character state transitions between the two lineages indicate that large sauropods and theropods build their hip joints in fundamentally different ways. Numerous character state transitions indicate that large theropods and sauropods convergently evolved highly incongruent bony hip joints compared to their smaller relatives.

Saurischian dinosaurs evolved a wide diversity of hip joint morphology and locomotor postures, as well as seven orders of magnitude in body size (Sander et al., 2004; Stein, et al., 2010; Turner et al., 2007; Lee et al., 2014). The very largest saurischians possess incongruent bony hip joints and rugose subchondral surfaces, leading to numerous inferences of thick articular cartilage layers (Cope, 1878; Hay, 1908). This study used phylogenetic comparative methods to test the relationship

between body size, articular soft tissue composition, and hip joint dimensions of saurischians. Only a few hip joint characters in the analysis showed correlated evolution with body size transitions in saurischians. Moreover, most bony hip joint metrics of saurischians scale to positive allometry, but the allometric relationships scale similarly to each other. This indicates that although large saurischians possess relatively larger bony hip joints than their smaller relatives, the relative proportion of soft tissue contribution in the hip joint remain largely consistent across the body size spectrum.

The highly cartilaginous sauropod femoral head in the evolution towards graviportality

Sauropods used enormous amount of hyaline cartilage on the femoral head to maintain articulation with a highly reduced acetabular labrum (Fig. 4-7a). Gigantic sauropods possess hyaline cartilage cores that reached up to 436 mm in thickness as in an 1801 mm *Apatosaurus* femur (Chapter 3). Sauropodomorphs evolved medially deflected, highly cartilaginous femoral head regions early on in their evolutionary history, prior to the evolutionary increase in body size. In contrast, the isometric scaling patterns of the attachment surfaces of the labrum and the antitrochanter indicate that these soft tissues were reduced during evolutionary increase of body size. In particular, reduction of the antitrochanter results in a largely circular outline for the acetabulum, which articulates with the spherical outline of the cartilaginous femoral head (Chapter 3). In contrast, sauropodomorphs reduced the ancestral femoral neck-antitrochanter articulation during the evolutionary increase in body size. Instead, the cranially oriented antitrochanter forms the caudal limit of the hip joint capsule, and constrains the femoral head inside the acetabulum.

Femur length is a significant predictor for the presence of thick hyaline cartilage in dinosauromorphs leading to sauropods. Evolutionary increase in body size occurred multiple times in the sauropod lineage: once within basal dinosauromorphs and twice among sauropodomorphs. Among basal dinosauromorphs, silesaurids evolved larger body size compared to lagerpetids and *Marasuchus* (Turner and Nesbitt, 2013), whereas sauropodomorphs underwent multiple increase in body size along the stem-lineage leading to sauropods (Yates, 2004; Sander et al., 2011). The small-bodied *Adeopapposaurus* possessed smooth subchondral growth plates, and smooth subchondral growth plates have also been reported for the small-bodied *Pampadromaeus* (Müller et al., 2015) and *Saturnalia* (Lager, 2003). In contrast, thick hyaline cartilage is present in plateosaurids and common ancestor of *Mussaurus* and sauropods. Thick hyaline cartilage has been hypothesized to function as a reservoir for growth plate cartilage in dinosaurs by Holliday et al (2010). Thus the independent gains of thick cartilage in silesaurids and sauropodomorphs may indicate hypertrophied growth rate or growth period.

The epiphyseal hyaline cartilage layer of silesaurids and sauropodomorphs differ in absolutely thickness and attachment morphology on the subchondral growth plate, likely associated with the absolute magnitude of body size. The largest silesaurids reach up 345 mm (NHMUK R16303, Barrett et al., 2014) in femur length and is estimated to possess up to 28.5 mm of epiphyseal hyaline cartilage at the proximal femur based on methods described in Chapter 3. Among silesaurids, the epiphyseal hyaline cartilage attaches to the subchondral growth plate via a cartilage cone surrounded by shallow (<1 mm), irregular rugosities. Although the cartilage cone is variably present in basal sauropodomorphs, it is absent in sauropods. Instead, the sauropod hyaline cartilage core

attaches to the subchondral growth plate via highly convoluted rugosities up to 20 mm in amplitude. The evolutionary transition of the metaphyseal growth plate from a cartilage cone-dominated articulation to a rugosities-dominated articulation is may be associated with need for the extremely thick layer of hyaline cartilage to resist shear forces during femoral protraction and retraction. Compared to the cartilage cone-trough articulation, the highly convoluted rugosities in sauropods provides a highly interdigitated junction between the hyaline and calcified cartilage layers at the growth plate, thus may function to increase the amount of traction between the two tissues under locomotion-induced translational shear loads.

Sauropodomorphs retain the basal dinosauriform morphology of an expanded metaphyseal collar, indicative of a well-developed bony attachment for the fibrocartilage sleeve. Fibrocartilage is more resistant to tensile and translational shear loads than hyaline cartilage (Schanagl et al., 1997; Freemont and Hoyland, 2006), thus the presence of fibrocartilage on the periphery of the femoral head provided additional mechanical support against avulsion of the thick epiphyseal hyaline cartilage layer during femoral excursion. Additionally, the fibrocartilage may also increase the axial compressive resistance of the femoral head hyaline cartilage. Since hyaline cartilage is weaker in its compressive resistance compared to bone, a purely hyaline epiphyseal cartilage would undergo axial deformation under compressive loads, decreasing in dorsoventral height and overfilling the periphery of the subchondral growth plate. The fibrocartilage sleeve may serve to limit the extent of such deformation by acting as an inextensible sleeve around the hyaline cartilage core, analogous to the function of the annulus fibrosus in the intervertebral discs in mammals (Markolf and Morris, 1974). Therefore, although the

evolutionary gain of an extensive fibrocartilage sleeve precedes gigantism in sauropodomorphs, retention of this basal Dinosauriformes character facilitated the increase in hyaline cartilage thickness. Therefore, the fibrocartilage sleeve is a key innovation during the evolution of sauropod gigantism.

Theropod hip joints underwent clade-specific transitions during body size evolution

Gigantic theropods build their hip joints using extensive amounts of supraacetabular articular pads, as well as contact between the femoral neck and the antitrochanter (Fig. 4-7b). Evolution of the theropod hip joint is characterized by high level of phylogenetic signal, which complicate inferences of character transitions associated with gigantism. Among theropods, the osteological correlates of articular soft tissues cannot be reliably predicted by femur length; whereas all hip joint dimensions scale to overall positive allometry relative to femur length. These results indicate gigantic theropods possess overall similar types, distribution, and proportions of hip joint soft tissues as their smaller relatives. However, as in the sauropod lineage, dimensional similarity in the bony hip joint across the theropod body size spectrum indicates absolutely thicker layers of articular soft tissue in gigantic taxa. This inference is consistent with the presence of rugose subchondral growth plates on the proximal femur of the largest theropods. Although the rugosities on the theropod proximal femur never approaches the same level of convoluted texture as in sauropods, reconstructed cartilage thickness using cartilage correction factors (Holliday et al., 2010) nevertheless indicate that large theropods possessed epiphyseal cartilage layers thicker than those of mammals and most extant birds. A 1280 mm *Tyrannosaurus* femur would have had as much as 41 mm of epiphyseal cartilage on the proximal end (Chapter 3).

In theropods, the surface areas of the acetabular labrum and antitrochanter scale to positive allometry relative to body size, contributing to the overall bony overlap between the femur and the acetabulum. Since these two surface areas provide attachment for the acetabular labrum and antitrochanter cartilage, respectively, large theropods are inferred to use large amounts supraacetabular soft tissues in addition to thick layers of femoral epiphyseal cartilage in maintaining hip joint congruence. Unlike sauropods, theropods maintain the basal diapsid hip joint articulation (Tsai and Holliday, 2014), in which the femoral head (capital region) articulates with the acetabular labrum and the fibrocartilaginous surface femoral neck (trochanteric region) articulates with the antitrochanter at the caudal acetabulum. Moreover, theropods show distinct osteological correlates for intracapsular ligaments at the femoral head region, suggesting that the femoral head is constrained within the cranial acetabular fossa and acted as a fulcrum during femoral protraction, retraction, and axial rotation. In contrast, the fibrocartilaginous surfaces of the femoral neck and antitrochanter likely resisted translational shear loading during femoral axial rotation, as in extant birds (Kambic et al., 2014). The antitrochanters of non-avian theropods tend to maintain an open synchondrosis, rather than being ossified as in extant birds. The open synchondrosis morphology allows substantial volume of hyaline cartilage core, deep to the superficial layer of fibrocartilage spanning the ilial and ischial peduncles. Although this morphology is present in non-avian theropods across the body size spectrum, the presence of an extensive hyaline cartilage core in the antitrochanter may have provided additional load bearing abilities in large theropods, serving as a pliant yet incompressible articular pad against the femoral neck.

The theropod hip joint underwent transitions in the orientation of the supraacetabular rim and the femoral head, but neither of these characters is predicted by body size. Basal theropods possessed a ventrolaterally oriented supraacetabular rim, but the rim shifted to a fully lateral orientation in Orionides, and maintained this position throughout the avian stem lineage (Chapter 3). Similarly, theropods basally possess a craniomedially deflected femoral head, whereas Avetheropods shifted to a fully medially deflected femoral head. These characters do not differ between gigantic theropods and their small relatives; For example, the large megalosauroid *Torvosaurus* retains a ventrolaterally oriented supraacetabular rim, similar to smaller basal theropods such as *Coelophysis* and *Dilophosaurus*. In contrast, the supraacetabular rim and femoral head orientation of *Tyrannosaurus* did not differ from the small basal coelurosaur *Compsognathus*, suggesting similar hip joint articulation among the closely related taxa. Overall, the thickness of theropod hip joint articular soft tissue thickness is heavily influenced by body size. In contrast, the lack of correlation between body size and other hip joint characters indicates that the theropod hip joint underwent clade-specific transitions, and is more influenced by factors such as the step-wise acquisition of avian-like body shape (Allen et al., 2013) and locomotor posture (Hutchinson and Allen, 2009) at each node along the stem lineage.

Dorsally inclined proximal femora and their implications for epiphyseal morphology

In many saurischians, the proximal femur is dorsally inclined, such that the femoral head is elevated relative to the femoral midshaft. This morphology is by far most prevalent in large bodied sauropods (Bonnar 2010, 2013; Carrano, 2005) and theropods (Hutchinson, 2001b). Femoral head inclination has also been hypothesized to be an

adaptation for gigantism in sauropods (Wilson and Carrano, 1999) and theropods (Bates, 2012). However, dorsally inclined proximal femora are also present in smaller saurischians, such as oviraptorosaurs (*Khaan*, Balanoff and Norell, 2014; *Anzu*, Lamanna et al., 2014), small-bodied sauropods (*Magyarosaurus*, Stein et al., 2010), and some extant birds (e.g., *Struthio* and *Rhea*, Tsai and Holliday, 2014). Whereas previous work (Stovall and Langston, 1950; Wilson and Sereno, 1995) tends to address this morphology as a bivariate character, this study shows that proximal femoral elevation can be achieved in multiple ways among saurischians. Among theropods, oviraptorosaurs and extant birds, the femoral head is markedly convex relative to the metaphyseal line, such that the dorsal inclination of the proximal femur is largely attributed to the sub-spherical growth plate surface on the femoral head. In contrast, the proximal femur of *Nothronychus* (UMNH VP 16420) is inclined dorsally by both femoral head convexity as well as the dorsal tilting of the femoral neck. Moreover, the growth plate surfaces of *Allosaurus* (UMNH VP 2560; DMNH 44397; FMNH P 25114) tyrannosaurids and *Ornithomimus* (RAM 6794) are only slightly convex relative to the metaphyseal line, instead achieved dorsal inclination due to the dorsal tilting of the femoral neck, as well as the expanded metaphyseal collar. I therefore suggest that the dorsal inclination of the theropod femoral head may be associated with differences in the distribution of fibro- and hyaline cartilage attachments on the femoral head, as well as extent of ossification of the subchondral surface.

Sauropods evolved dorsally inclined proximal femoral in multiple ways. Among sauropods, macronarians possessed a wide range of femoral head morphologies. *Camarasaurus* (DNM 4514), *Sauroposeidon* (YPM 5449), and *Cedarosaurus* (DMNH

37045) achieved dorsal inclinations of the proximal femur via highly convex subchondral surfaces on the femoral head. The convex femoral heads of *Camarasaurus* and most other macronarians likely supported thinner layers of epiphyseal hyaline cartilage compared those of diplodocoids and titanosaurs. In contrast, *Brachiosaurus* (FMNH P25107), *Giraffatitan* (MB.R. 2694, 2181.83, 5016), and *Argyrosaurus* (FMNH P13019) possessed less convex growth plates on the femoral head, similar to the basal sauropod *Patagosaurus* (MACN 1986) and the sauropodomorph *Mussaurus* (MLP unnumbered). Dorsal inclinations of the femoral head in these taxa are achieved by increased femoral neck angle relative to the midshaft long axis. Moreover, *Alamosaurus* (TMM 41541) and *Rapetosaurus* (FMNH PR 2209) possessed similar femoral head morphology as *Argyrosaurus* but possessed laterally deflected femoral midshaft and beveled distal condyles (Wilson and Carrano, 1999). Finally, diplodocoids such as *Barosaurus* (NAMAL 106), *Diplodocus* (CM 84; DMNH 462), and *Apatosaurus* (CM 85, 3018; FMNH 25112) possess largely planar subchondral growth plates on the femoral head, but the rugosities in this region appears to be greater than those of macronarians in amplitude and surface area. *Dicraeosaurus* (MB.R. 2692, 2695), *Barosaurus* (NAMAL 106) and *Tornieria* (MB.R. 2671) in possess dorsally elevated, but not inclined, femoral heads compared to the trochanteric region, similar to *Brachiosaurus*, *Giraffatitan*, and *Argyrosaurus*. However, unlike macronarians, the subchondral surfaces of these diplodocoids remain largely planar and replete with highly convoluted rugosities, even among sauropods. The combination of these osteological correlates indicates that diplodocoids too possessed a dorsally inclined femoral head, albeit one comprised largely of hyaline cartilage. Results of this study show that the dorsal inclination of the bony

femoral head in sauropods is influenced by multiple morphologies, including differential level of cartilage thickness, growth plate ossification, and femoral neck-to-midshaft angles. The dorsally inclined proximal femur of titanosaurs has been associated with wide-gauge sauropod trackways, and is inferred to be an adaptation for increase graviportal locomotor behaviors (Wilson and Carrano, 1999). Nevertheless, interaction between femoral neck-to-midshaft angles, articular cartilage thickness, and ligamentous constraints remain unknown in sauropods. Overall, the variation in femoral head dorsal inclination suggests a wide range of femoral articular morphology among sauropods. Despite the early, concerted evolutionary transition towards graviportal locomotion, the morphological diversity of sauropod hip joints potentially indicates a spectrum of epiphyseal cartilage thickness, load bearing mechanics, joint dynamics, and growth strategies within this clade of gigantic archosaurs.

Evolution of epiphyseal cartilage in bird-like theropods

The evolution of cartilage thickness, type, and distribution in Maniraptoriformes is of potential interest due to the wide spectrum of body size in this clade. Gigantic body size (>2 tons) independently evolved in ornithomimosaur (*Deinocheirus*, Lee et al., 2014a), therizinosaurs (*Therizinosaurus*, Barsbold, 1976), and oviraptorosaurs (*Gigantoraptor*, Xu et al., 2007). Although paravians never evolved similar magnitudes of gigantic body size, deinonychosaurs (*Utahraptor*, Kirkland et al., 1993; *Achillobator*, Perle et al., 1999), and Neornithes (Dinornithidae, Bunce et al., 2003) nevertheless produced moderately large taxa (>200 kg). The relationship between hip joint morphology and body size within Maniraptoriformes, in particular pennaraptorans, is difficult to interpret due to the lack of well-preserved hip joints of gigantic taxa in this

study. Among well-preserved Maniraptoriformes included in this analysis, *Ornithomimus* (RAM 14182), *Anzu* (CM 78000) and *Deinonychus* (MCZ 4371) possess rugose femoral growth indicative of thick hyaline cartilage but are bracketed by taxa possessing smooth femoral growth plates. Although these three taxa are moderately large for their respective clades, they are within the lower end of the body size spectrum among non-avian theropods (Turner et al., 2007). Therefore, the association between hyaline cartilage thickness and body size remains difficult to infer without additional sample of large bodied Maniraptoriformes.

Moreover, Pennaraptorans possess a continuous subchondral growth plate surface without a distinct metaphyseal collar. This morphology is the osteological correlate for a bird-like distribution of femoral epiphyseal cartilages, in which the fibrocartilage sleeve possess little bony attachment on the metaphysis, and forms the articular surface of the proximal femur by completely encapsulating the hyaline cartilage core (Chapter 3). The evolution of the composite fibro-hyaline cartilage core within Pennaraptora, as well as its mechanical and ontogenetic role during the evolutionary decrease within the stem avian lineage (Turner et al., 2007), as well as the evolution of determinate growth among extant birds (Erickson, 2005), remains poorly understood. The evolution of maniraptoriform hip joint anatomy thus remains an open avenue for future studies in locomotor and growth adaptations associated with independent gain of gigantism and sustained miniaturization along the avian stem lineage (Lee et al., 2014b).

Ontogenetic significance of hip joint cartilages thickness in saurischians

Most saurischians retain significant proportions of femoral epiphyseal cartilage and incompletely fused acetabulae. In extant birds, mammals, and lepidosaurs, thick

epiphyseal cartilages (Haines, 1938) and unfused acetabulae (Cracraft 1986; Bolter and Zihlman, 2003; Conrad, 2006) occur in skeletally immature individuals. However, I refrained from using these characters as ontogenetic indicators because extinct saurischians retain these “unfinished” morphologies throughout ontogeny, even as large-bodied adults (Brochu, 2003; Tidwell et al., 2005). Moreover, some extant sauropsids do retain of thick hyaline cartilage layers and unfused pelvic elements at adulthood (e.g., the proximal humerus of *Dermochelys*, Gervais, 1872; the anterior acetabular cartilage in crocodylians, Tsai and Holliday, 2014). In Chapter 3 I showed that basal dinosauromorphs possessed smooth subchondral growth plate surfaces, and unfused antitrochanters, with independent transitions to the derived state in multiple saurischian lineages.

I hypothesize that the transitions from smooth to rugose growth plates are due paedomorphosis. Studies in dinosaur growth dynamics have shown that non-avian dinosaurs maintain active skeletal growth after achieving sexual maturity (Padian et al., 2001; Erickson et al., 2007). Therefore, retention of the juvenile characteristics, such as a thick femoral epiphyseal cartilage and an unfused antitrochanter likely facilitated the evolution of gigantism in sauropods and multiple lineages of theropods. In contrast, I hypothesize that the evolution of a fused antitrochanter is due to peramorphosis, in which a co-ossified antitrochanter indicates cessation of acetabular growth. The antitrochanter remains an open synchondrosis in the sauropod and theropod stem lineage, but underwent transitions to the co-ossified state in *Herrerasaurus*, *Coelophysis*, Ceratosauria (except *Ceratosaurus*), and Avialae. Antitrochanter co-ossification show no significant relationship with body size, but appears to co-occur with smooth subchondral growth

plates on the proximal femur, suggesting a possible relationship of overall cartilage thinning in these taxa. The independent evolution of acetabular co-ossification in theropods may be influenced by specific transitions in growth dynamics, as well as load-bearing modalities at the caudal acetabulum.

CONCLUSION

The evolutionary history of Saurischia is characterized by multiple, independent evolutionary transitions in body size, as well as a wide diversity of hip joint morphology and locomotor postures. In both sauropods and theropods, the largest taxa maintained hip joint congruence using extremely thick layers of articular soft tissues. In particular, gigantic sauropods possessed thicker layers of epiphyseal hyaline cartilage on the femoral head region than gigantic theropods and maintained hip joint congruence primarily using the largely cartilaginous femoral head. In contrast, gigantic theropods maintained hip joint articulation using substantial contributions from the acetabular labrum and the antitrochanter cartilage. Nevertheless, the size of the hyaline cartilage core of gigantic theropod hips exceeded those of most extant vertebrates. Both theropods and sauropodomorphs used an extensive fibrocartilage collar as mechanical support for thick layers of hyaline cartilage core. These findings indicate that the femoral articular cartilages of giant sauropods were built to sustain heavy compressive loads whereas those of giant theropods experienced compression and translational shear forces. These data indicate that saurischian hips underwent divergent transformations in soft tissue morphology reflective of body size, locomotor posture, and joint loading.

Table 4-1. Results of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the sauropod lineage using the “default” phylogenetic tree. Significant associations between body size and the derived character state are noted by an asterisk (*). Lack of significant correlation is denoted as “NS”. Characters which transitions cannot be predicted by femur length using phylogenetic logistic regression are indicated by “N/A”. Invariable characters are not analyzed.

Character#	Character name	Character states	P-value	Direction of relationship
1	Perforated acetabulum	(0) absent (1) present	N/A	
2	Lateral expansion of the supraacetabular rim	(0) expanded (1) reduced	0.587	NS
3	Orientation of the supraacetabular rim	(0) laterally oriented (1) ventrolaterally oriented	0.607	NS
4	Expansion of the bony antitrochanter	(0) unexpanded (1) expanded	Not analyzed	
5	Shape of the ischial peduncle of the ilium	(0) flat (1) cranially concave	0.591	NS
6	Co-ossification of the bony antitrochanter	(0) open synchondrosis (1) co-ossified	Not analyzed	
7	Femoral head deflection	(0) cranio-medially deflected (1) medially deflected	0.577	NS
8	Surface texture of the proximal femoral growth plate	(0) smooth (1) rugose	0.004*	Positively correlated
9	Capital concentration of irregular rugosities on the femoral head	(0) absent (1) present	N/A	
10	Transphyseal striations	(0) absent (1) present	N/A	
11	Fovea capitis	(0) indistinct (1) distinct (planar or concave)	Not analyzed	
12	Ischiofemoral ligament sulcus	(0) shallow (1) deep	Not analyzed	
13	Cartilage cone trough	(0) absent (1) distinct	0.116	NS
14	Expanded metaphyseal Collar	(0) Unexpanded (1) Expanded	N/A	

Table 4-2. Results of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the theropod lineage using the “default” phylogenetic tree. Significant associations between body size and the derived character state are noted by an asterisk (*). Lack of significant correlation is denoted as “NS”. Characters which transitions cannot be predicted by femur length using phylogenetic logistic regression are indicated by “N/A”. Invariable characters are not analyzed.

Character#	Character name	Character states	P-value	Probability of derived character state
1	Perforated acetabulum	(0) absent (1) present	0.705	NS
2	Lateral expansion of the supraacetabular rim	(0) expanded (1) reduced	0.594	NS
3	Orientation of the supraacetabular rim	(0) laterally oriented (1) ventrolaterally oriented	0.120	NS
4	Expansion of the bony antitrochanter	(0) unexpanded (1) expanded	0.720	NS
5	Shape of the ischial peduncle of the ilium	(0) flat (1) cranially concave	Not analyzed	NS
6	Co-ossification of the bony antitrochanter	(0) open synchondrosis (1) co-ossified		
7	Femoral head deflection	(0) craniomedially deflected (1) medially deflected	0.546	NS
8	Surface texture of the proximal femoral growth plate	(0) smooth (1) rugose	N/A	
9	Concentration of irregular rugosities on the femoral head	(0) absent (1) present	Not analyzed	
10	Transphyseal striations	(0) absent (1) present	0.205	NS
11	Fovea capitis	(0) indistinct (1) distinct (planar or concave)	0.272	NS
12	Ischiofemoral ligament sulcus	(0) shallow (1) deep	0.879	NS
13	Cartilage cone trough	(0) absent (1) distinct	0.997	NS
14	Expanded metaphyseal Collar	(0) Unexpanded (1) Expanded	0.319	NS

Table 4-3. P-values of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the sauropod lineage using alternative tree topologies. Significant associations between body size and the derived character state are noted by an asterisk (*). Characters which transitions cannot be predicted by femur length using phylogenetic logistic regression are indicated by ‘N/A’. Invariable characters are not analyzed.

Character#	Silesauridae as stem ornithischians	Herrerasauridae as stem saurischians	<i>Eoraptor</i> as stem theropod	<i>Archaeopteryx</i> as stem deinonychosaur
1	N/A	N/A	N/A	N/A
2	0.587	0.596	0.594	0.587
3	0.605	0.638	0.576	0.607
4	Not analyzed			
5	0.591	0.592	0.592	0.591
6	Not analyzed			
7	0.577	0.589	0.708	0.577
8	0.003*	0.004*	0.007*	0.004*
9	N/A	N/A	N/A	N/A
10	N/A	N/A	N/A	N/A
11	Not analyzed			
12	Not analyzed			
13	0.119	0.118	0.116	0.116
14	N/A	N/A	N/A	N/A

Table 4-4. P-values of phylogenetic logistic regressions between body size (femur length) and hip joint osteological characters in the theropod lineage using alternative tree topologies. Significant patterns in correlations are noted by an asterisk (*). Characters which transitions cannot be predicted by femur length using phylogenetic logistic regression are indicated by “N/A”. Invariable characters are not analyzed.

Character#	Silesauridae as stem ornithischians	Herrerasauridae as stem saurischians	<i>Eoraptor</i> as stem theropod	<i>Archaeopteryx</i> as stem deinonychosaur
1	0.710	0.689	0.758	0.715
2	0.594	0.590	0.529	0.564
3	0.119	0.131	0.120	0.124
4	0.720	0.715	0.718	0.886
5	N/A	N/A	N/A	N/A
6	0.515	0.525	0.516	0.220
7	0.546	0.545	0.496	0.568
8	N/A	N/A	N/A	N/A
9	0.703	0.698	0.796	0.707
10	0.205	0.202	0.205	0.215
11	0.272	0.268	0.272	0.272
12	0.880	0.880	0.880	0.879
13	0.999	0.994	0.997	0.992
14	0.319	0.316	0.319	0.370

Table 4-5. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using the “default” tree (Fig. 3-2a).

Character	Allometry	Null slope	RMA slope	R-squared	P-value (diff. from isometry)	95% conf. Interval
Femoral head circumference	Positive	1	1.39	0.951	<0.001	1.247 1.533
Femoral head height	Positive	1	1.306	0.556	0.041	0.972 1.639
<i>facies articularis antitrochanterica</i> length	Positive	1	1.212	0.915	<.001	1.095 1.330
Femoral head width	Positive	1	1.339	0.819	<0.001	1.135 1.543
Acetabular length	Positive	1	1.228	0.749	0.029	1.004 1.453
Acetabular depth	Positive	1	1.038	0.682	0.014	1.038 1.718
Acetabular height	Positive	1	1.296	0.902	0.004	1.090 2.502
Acetabular circumference	Positive	1	1.242	0.913	0.030	1.005 1.478
Femoral subchondral surface area	Positive	2	2.467	0.923	0.002	2.167 2.768
Femoral growth plate surface area	Positive	2	2.453	0.919	0.003	2.146 2.761
Femoral metaphyseal collar surface area	Positive	2	2.810	0.793	0.004	2.203 3.417
Acetabular labrum attachment surface area	Isometry	2	2.186	0.839	0.282	1.819 2.553
Iliac bony antitrochanter area	Isometry	2	2.272	0.553	0.373	1.609 2.934
Bony acetabulum	Positive	2	2.420	0.902	0.0239	2.030 2.829
Acetabular fossa	Positive	2	2.481	0.919	0.008	2.110 2.851
Bony antitrochanter surface area	Isometry	2	2.229	0.880	0.266	1.774 2.684

Table 4-6. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of Silesauridae (Fig. 3-2b).

Character	Allometry	Null slope	RMA Slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.391	0.951	<0.001	1.248 1.535
Femoral head height	Positive	1	1.306	0.555	0.041	0.972 1.641
<i>facies articularis antitrochanterica</i> length	Positive	1	1.212	0.915	<0.001	1.095 1.33
Femoral head width	Positive	1	1.337	0.818	<0.001	1.133 1.542
Acetabular length	Positive	1	1.227	0.750	0.030	1.003 1.451
Acetabular depth	Positive	1	1.378	0.682	0.014	1.038 1.718
Acetabular height	Positive	1	1.3	0.902	0.003	1.093 1.506
Acetabular circumference	Positive	1	1.24	0.911	0.032	1.001 1.48
Femoral subchondral surface area	Positive	2	2.469	0.925	0.002	2.172 2.767
Femoral growth plate surface area	Positive	2	2.455	0.918	0.003	2.147 2.767
Femoral metaphyseal collar surface area	Positive	2	2.805	0.799	0.004	2.208 3.402
Acetabular labrum attachment surface area	Isometry	2	2.185	0.839	0.283	1.818 2.552
Iliac bony antitrochanter area	Isometry	2	2.269	0.552	0.377	1.606 2.932
Bony acetabulum	Positive	2	2.441	0.903	0.0205	2.042 2.840
Acetabular fossa	Positive	2	2.49	0.919	0.007	2.119 2.861
Bony antitrochanter surface area	Isometry	2	2.234	0.879	0.259	1.777 2.692

Table 4-7. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of Herrerasauridae (Fig. 3-2c).

Character	Allometry	Null slope	RMA slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.39	0.951	<0.001	1.248 1.532
Femoral head height	Positive	1	1.306	0.560	0.041	0.974 1.638
<i>facies articularis antitrochanterica</i> length	Positive	1	1.211	0.914	<0.001	1.093 1.329
Femoral head width	Positive	1	1.339	0.820	<0.001	1.135 1.543
Acetabular length	Positive	1	1.223	0.748	0.032	0.999 1.447
Acetabular depth	Positive	1	1.377	0.684	0.013	1.039 1.716
Acetabular height	Positive	1	1.292	0.915	0.004	1.087 1.498
Acetabular circumference	Positive	1	1.247	0.916	0.026	1.012 1.481
Femoral subchondral surface area	Positive	2	2.461	0.924	0.002	2.162 2.761
Femoral growth plate surface area	Positive	2	2.448	0.919	0.003	2.142 2.755
Femoral metaphyseal collar surface area	Positive	2	2.805	0.781	0.005	2.182 3.428
Acetabular labrum attachment surface area	Isometry	2	2.185	0.841	0.281	1.820 2.550
Iliac bony antitrochanter area	Isometry	2	2.275	0.555	0.365	1.613 2.938
Bony acetabulum	Positive	2	2.424	0.902	0.025	2.026 2.822
Acetabular fossa	Positive	2	2.479	0.920	0.008	2.111 2.848
Bony antitrochanter surface area	Isometry	2	2.23	0.882	0.261	1.779 2.682

Table 4-8. Reduced major axis regressions between body size (femur length) and hip joint measurements in the sauropod lineage using alternative placement of *Eoraptor* (Fig. 3-2d).

Character	Allometry	Null slope	RMA Slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.39	0.951	<0.001	1.247 1.533
Femoral head height	Positive	1	1.306	0.556	0.041	0.972 1.639
<i>facies articularis antitrochanterica</i> length	Positive	1	1.18	0.917	0.001	1.067 1.293
Femoral head width	Positive	1	1.339	0.819	<0.001	1.135 1.543
Acetabular length	Positive	1	0.9986	0.832	0.036	1.174 1.349
Acetabular depth	Positive	1	1.378	0.682	0.014	1.038 1.718
Acetabular height	Positive	1	1.296	0.902	0.004	1.09 1.502
Acetabular circumference	Positive	1	1.242	0.913	0.030	1.005 1.478
Femoral subchondral surface area	Positive	2	2.467	0.923	0.002	2.167 2.768
Femoral growth plate surface area	Positive	2	2.453	0.919	0.003	2.146 2.761
Femoral metaphyseal collar surface area	Positive	2	2.816	0.782	0.005	2.191 3.44
Acetabular labrum attachment surface area	Isometry	2	2.186	0.839	0.282	1.819 2.553
Iliac bony antitrochanter area	Isometry	2	2.272	0.553	0.373	1.609 2.934
Bony acetabulum	Positive	2	2.429	0.902	0.024	2.030 2.829
Acetabular fossa	Positive	2	2.481	0.919	0.008	2.110 2.851
Bony antitrochanter surface area	Isometry	2	2.229	0.880	0.266	1.774 2.684

Table 4-9. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using the “default” tree (Fig. 3-2a).

Character	Allometry	Null slope	RMA slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.293	0.961	<0.001	1.208 1.378
Femoral head height	Positive	1	1.144	0.878	0.018	1.019 1.27
<i>facies articularis antitrochanterica</i> length	Positive	1	1.161	0.949	<0.001	1.086 1.236
Femoral head width	Positive	1	1.358	0.953	<0.001	1.272 1.444
Acetabular length	Positive	1	1.269	0.920	<0.001	1.167 1.371
Acetabular depth	Positive	1	1.332	0.779	<0.001	1.13 1.535
Acetabular height	Positive	1	1.277	0.933	<0.001	1.171 1.382
Acetabular circumference	Positive	1	1.26	0.953	<0.001	1.158 1.362
Femoral subchondral surface area	Positive	2	2.513	0.959	<0.001	2.335 2.691
Femoral growth plate surface area	Positive	2	2.489	0.958	<0.001	2.311 2.667
Femoral metaphyseal collar surface area	Positive	2	2.702	0.920	<0.001	2.357 3.047
Acetabular labrum attachment surface area	Positive	2	2.528	0.911	<0.001	2.274 2.783
Iliac bony antitrochanter area	Positive	2	2.428	0.839	0.005	2.128 2.829
Bony acetabulum	Positive	2	2.509	0.917	<0.001	2.249 2.769
Acetabular fossa	Positive	2	2.547	0.929	<0.001	2.303 2.791
Bony antitrochanter surface area	Positive	2	2.463	0.900	0.002	2.168 2.757

Table 4-10. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of Silesauridae (Fig. 3-2b).

Character	Allometry	Null slope	RMA Slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.293	0.961	<0.001	1.208 1.378
Femoral head height	Positive	1	1.145	0.878	0.018	1.019 1.271
<i>facies articularis antitrochanterica</i> length	Positive	1	1.161	0.949	<0.001	1.087 1.236
Femoral head width	Positive	1	1.358	0.952	<0.001	1.272 1.444
Acetabular length	Positive	1	1.269	0.921	<0.001	1.168 1.37
Acetabular depth	Positive	1	1.333	0.778	<0.001	1.130 1.533
Acetabular height	Positive	1	1.280	0.934	<0.001	1.174 1.385
Acetabular circumference	Positive	1	1.260	0.952	<0.001	1.157 1.363
Femoral subchondral surface area	Positive	2	2.516	0.960	<0.001	2.34 2.692
Femoral growth plate surface area	Positive	2	2.490	0.958	<0.001	2.313 2.668
Femoral metaphyseal collar surface area	Positive	2	2.702	0.9239	<0.001	2.366 3.038
Acetabular labrum attachment surface area	Positive	2	2.535	0.913	<0.001	2.283 2.786
Iliac bony antitrochanter area	Positive	2	2.482	0.841	0.004	2.133 2.831
Bony acetabulum	Positive	2	2.510	0.918	<0.001	2.261 2.78
Acetabular fossa	Positive	2	2.557	0.939	<0.001	2.313 2.801
Bony antitrochanter surface area	Positive	2	2.470	0.900	0.001	2.175 2.765

Table 4-11. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of Herrerasauridae (Fig. 3-2c).

Character	Allometry	Null slope	RMA Slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.293	0.961	<0.001	1.209 1.378
Femoral head height	Positive	1	1.145	0.879	0.018	1.020 1.270
<i>facies articularis antitrochanterica</i> length	Positive	1	1.160	0.9486	<0.001	1.082 1.234
Femoral head width	Positive	1	1.358	0.953	<0.001	1.273 1.444
Acetabular length	Positive	1	1.266	0.920	<0.001	1.164 1.368
Acetabular depth	Positive	1	1.336	0.786	<0.001	1.137 1.536
Acetabular height	Positive	1	1.274	0.933	<0.001	1.169 1.380
Acetabular circumference	Positive	1	1.261	0.953	<0.001	1.160 1.362
Femoral subchondral surface area	Positive	2	2.509	0.958	<0.001	2.331 2.688
Femoral growth plate surface area	Positive	2	2.460	0.967	<0.001	2.259 2.661
Femoral metaphyseal collar surface area	Positive	2	2.695	0.918	<0.001	2.348 3.041
Acetabular labrum attachment surface area	Positive	2	2.523	0.910	<0.001	2.268 2.777
Iliac bony antitrochanter area	Positive	2	2.483	0.843	0.004	2.135 2.831
Bony acetabulum	Positive	2	2.505	0.916	<0.001	2.245 2.765
Acetabular fossa	Positive	2	2.546	0.929	<0.001	2.303 2.790
Bony antitrochanter surface area	Positive	2	2.464	0.902	0.001	2.171 2.756

Table 4-12. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of *Eoraptor* (Fig. 3-2d).

Character	Allometry	Null slope	RMA slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.293	0.961	<0.001	1.208 1.378
Femoral head height	Positive	1	1.144	0.878	0.018	1.019 1.270
<i>facies articularis antitrochanterica</i> length	Positive	1	1.152	0.949	<0.001	1.078 1.226
Femoral head width	Positive	1	1.358	0.953	<0.001	1.272 1.444
Acetabular length	Positive	1	1.259	0.919	<0.001	1.157 1.36
Acetabular depth	Positive	1	1.332	0.779	<0.001	1.13 1.535
Acetabular height	Positive	1	1.277	0.933	<0.001	1.171 1.382
Acetabular circumference	Positive	1	1.26	0.953	<0.001	1.158 1.362
Femoral subchondral surface area	Positive	2	2.513	0.959	<0.001	2.335 2.691
Femoral growth plate surface area	Positive	2	2.489	0.958	<0.001	2.311 2.667
Femoral metaphyseal collar surface area	Positive	2	2.702	0.920	<0.001	2.357 3.047
Acetabular labrum attachment surface area	Positive	2	2.528	0.911	<0.001	2.274 2.783
Iliac bony antitrochanter area	Positive	2	2.478	0.839	0.005	2.128 2.829
Bony acetabulum	Positive	2	2.509	0.917	<0.001	2.249 2.769
Acetabular fossa	Positive	2	2.541	0.929	<0.001	2.303 2.791
Bony antitrochanter surface area	Positive	2	2.463	0.900	0.002	2.168 2.757

Table 4-13. Reduced major axis regressions between body size (femur length) and hip joint measurements in the theropod lineage using alternative placement of *Archaeopteryx* (Fig. 3-2e).

Character	Allometry	Null slope	RMA slope	R-squared	P-value (diff. from isometry)	95% Conf. Interval
Femoral head circumference	Positive	1	1.293	0.961	<0.001	1.208 1.378
Femoral head height	Positive	1	1.144	0.878	0.018	1.019 1.270
<i>facies articularis antitrochanterica</i> length	Positive	1	1.161	0.949	<0.001	1.086 1.236
Femoral head width	Positive	1	1.345	0.952	<0.001	1.26 1.43
Acetabular length	Positive	1	1.264	0.923	<0.001	1.164 1.364
Acetabular depth	Positive	1	1.332	0.779	<0.001	1.13 1.535
Acetabular height	Positive	1	1.267	0.935	<0.001	1.164 1.371
Acetabular circumference	Positive	1	1.251	0.954	<0.001	1.152 1.351
Femoral subchondral surface area	Positive	2	2.513	0.959	<0.001	2.335 2.691
Femoral growth plate surface area	Positive	2	2.489	0.958	<0.001	2.311 2.667
Femoral metaphyseal collar surface area	Positive	2	2.702	0.920	<0.001	2.357 3.047
Acetabular labrum attachment surface area	Positive	2	2.528	0.911	<0.001	2.274 2.783
Iliac bony antitrochanter area	Positive	2	2.478	0.839	0.05	2.128 2.829
Bony acetabulum	Positive	2	2.509	0.917	<0.001	2.249 2.769
Acetabular fossa	Positive	2	2.547	0.929	<0.001	2.303 2.791
Bony antitrochanter surface area	Positive	2	2.463	0.900	0.002	2.168 2.757

Figure 4-1. Discrete osteological correlates and continuous hip joint metrics were taken from the hip joints of saurischians. **A.** Femoral and pelvic elements of *Apatosaurus*. **B.** femoral and pelvic elements of *Allosaurus*. Surface areas of soft tissue attachments (red) were measured from 3D models.

Figure 4-2. Phylogenetic generalized reduced major axis regressions of hip joint linear dimensions vs. log femur length in the sauropod lineage using the “default” tree. Null hypothesized slopes ($= 1$) is signified by the black dotted line. **A.** femoral head circumference. **B.** femoral head height. **C.** *facies articularis antitrochanterica* length. **D.** femoral head width. **E.** acetabular length. **F.** acetabular depth. **G.** acetabular height. **H.** acetabular circumference. All hip joint linear dimensions scale to positive allometry relative to femur length.

Figure 4-3. Phylogenetic generalized reduced major axis regressions of hip joint surface area dimensions vs. log femur length in the sauropod lineage using the “default” tree. Null hypothesized slopes ($= 2$) is signified by the black dotted line. **A.** femoral subchondral surface area. **B.** femoral growth plate area. **C.** Femoral metaphyseal collar area. **D.** acetabular labrum attachment surface area. **E.** ilial bony antitrochanter area. **F.** bony acetabulum area. **G.** acetabular fossa area. **H.** bony antitrochanter area. Most hip joint surface area dimensions scale to positive allometry relative to femur length. Attachment areas for acetabular labrum, the ilial portion of the antitrochanter, and the whole antitrochanter scale to isometry relative to femur length.

Figure 4-4. Phylogenetic generalized reduced major axis regressions of hip joint linear dimensions vs. log femur length in the theropod lineage using the “default” tree. Null hypothesized slopes ($= 1$) is signified by the black dotted line. **A.** femoral head circumference. **B.** femoral head height. **C.** *facies articularis antitrochanterica* length. **D.** femoral head width. **E.** acetabular length. **F.** acetabular depth. **G.** acetabular height. **H.** acetabular circumference. All hip joint linear dimensions scale to positive allometry relative to femur length.

Figure 4-5. Phylogenetic generalized reduced major axis regressions of hip joint surface area dimensions vs. log femur length in the theropod lineage using the “default” tree. Null hypothesized slopes ($= 2$) is signified by the black dotted line. **A.** femoral subchondral surface area. **B.** femoral growth plate area. **C.** Femoral metaphyseal collar area. **D.** acetabular labrum attachment surface area. **E.** ilial bony antitrochanter area. **F.** bony acetabulum area. **G.** acetabular fossa area. **H.** bony antitrochanter area. All hip joint surface area dimensions scale to positive allometry relative to femur length.

Figure 4-6. Simplified phylogenetic tree showing major evolutionary transitions in body size and hip joint anatomy. Ancestral character state is estimated using maximum likelihood. Branches are color coded in reference to body size, with colored branches denoting larger body size. Character gains are marked by numerical designations summarized in Table 4-5. Character gains are indicated by ones; secondary losses are indicated by zeros. Silhouettes of taxa (phylopics) depicted here are provided by S. Hartman, T. M. Keesey, N. Kelley, A. A. Farke, B. McFeeters, S. Werning, E. Willoughby, and E. Östman (Wikipedia user).

Figure 4-7. Hip joint soft tissue reconstructions of representative gigantic saurischians. Joint ligaments are excluded. Tissues are labeled and color-coded based on inferred homology described in Tsai and Holliday (2014). **A.** Hip joint articulation in *Apatosaurus* is achieved using thick layers of femoral epiphyseal cartilage, with limited contribution of supraacetabular soft tissues. Minimal estimate of femoral hyaline cartilage thickness (based on CCF of juvenile *Struthio*) is shown as the dotted line. **B.** Hip joint articulation in *Tyrannosaurus* is achieved using extensive amounts of supraacetabular articular pads, as well as contact between the femoral neck and the antitrochanter.

CHAPTER 5

Conclusion

Archosaurs, the sauropsid clade which includes crocodylians, birds, and extinct forms such as nonavian dinosaurs, underwent numerous evolutionary transitions in appendicular anatomy and body size. This dissertation research explored the hip joint anatomy of extant sauropsids, provided the soft tissue basis for osteological characters in the archosaur hip joint, inferred the homology and evolutionary transformations of hip joint soft tissues leading to the sauropod and avian morphology, and presented the morphological adaptations during independent, repeated evolution of gigantism in Saurischia.

In chapter one, I showed that the archosaur hip joint exhibits regionally distinct articular soft tissues. Based on known material properties of hyaline and fibrocartilage, I inferred that hyaline cartilage regions facilitate compressive loading, whereas fibrocartilage regions facilitate sliding articulation and provides mechanical support for the hyaline cartilage. Inferred homology and topological associations between femoral and acetabular articular surfaces, as well as the attachments of capsular and intrinsic joint ligaments, are used to infer their functional significance in hip range of motion.

In chapter two, I showed that the evolutionary history of Saurischia is characterized by multiple, iterative convergences and divergences in hip joint anatomy. Sauropodomorphs underwent swift, concerted transitions in hip joint anatomy, culminating in the highly cartilaginous femoral heads of Sauropoda. In contrast,

theropods maintained thinner layers of hyaline cartilage on the femoral head, but underwent several clade-specific combinations of character transitions. In particular, pennaraptorans (Oviraptorosauria + Paraves) evolved a composite fibro-hyaline cartilage on the proximal femur, whereas multiple lineages of maniraptorans preceding Avialae independently evolved bird-like acetabulae.

In chapter three, I showed that saurischian hips underwent divergent transformations in soft tissue morphology among the sauropod and theropod lineages reflective of body size, which impacts inferences on joint loading and locomotor posture. Gigantic saurischians maintained hip joint congruence using extremely thick layers of articular soft tissues. Both theropods and sauropodomorphs used an extensive fibrocartilage collar as mechanical support for thick layers of hyaline cartilage core. Gigantic sauropods maintained hip joint congruence using an extremely thick layer of epiphyseal hyaline cartilage on the femoral head region, up to 436 mm on an 1801mm *Apatosaurus* femur. In contrast, theropods maintained hip congruence using extensive amount of acetabular labrum and antitrochanter-femoral neck articulation. Gigantic theropods possessed relatively thinner femoral hyaline cartilage compared to of sauropods. Yet with cartilage thickness up to 41 mm on a 1280 mm *Tyrannosaurus* femur, gigantic theropods nevertheless possess absolutely greater amount of hyaline cartilage in the hip joint than any extant tetrapods. These findings indicate that the femoral heads of gigantic sauropods were built to primarily sustain heavy compressive loads, whereas those of gigantic theropods experienced both compression and substantial amount of shear forces.

Overall, these studies provide the first anatomically-informed evolutionary reconstructions of appendicular joints in one of the most diverse radiations of vertebrates. Using phylogenetically-informed anatomical reconstructions, results from this study contribute significantly to archosaur evolution, comparative joint biology, locomotor mechanics, and connective tissue physiology. For example, new anatomical data on ligament attachments, cartilage composition, and cartilage thickness allow biologically meaningful articulation of archosaur hip joints, instead of assumption of joint articulation using bony proximal femora and acetabulae. Increased precision in joint articulation will inform future quantitative modeling analyses of archosaur hindlimbs (e.g., Hutchinson and Allen 2009; Maidment et al. 2013). Moreover, the presence of highly cartilaginous joints in crocodylians and extinct saurischians suggest that these animals loaded their joints in fundamentally different ways from mammals and extant birds. The loading mechanics of these cartilaginous joints remain poorly understood, and welcomes future investigations. Finally, the ontogenetic relationship between thick cartilage and the evolution of gigantism remain poorly understood. Osteological correlates of joint soft tissues presented here will inform future ontogenetic studies on the physiological mechanisms involved in archosaur body size evolution. By integrating data from in-vivo joint kinematics, connective tissue biology, loading mechanics, and paleontology, future studies on archosaur joints will enhance our understanding in the function, growth, and maintenance of the vertebrate locomotor apparatus. Ultimately, this dissertation research provides a major contribution to studies on the macroevolutionary transitions in the vertebrate locomotion.

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VITA

I was born in Taipei, Taiwan, as part of the generation which interest in natural sciences was amplified by the film "Jurassic Park". The film's portrayals of dinosaurs as active, dynamic organisms gave rise to my ceaseless wonders on the rise and fall of dinosaurs, their roles in the shifting terrestrial ecosystem, as well as the continued success of their avian descendants as rulers of the skies. Many of the questions we ask about the biology of extinct animals reflect how little we know about the biology of living animals.

Conversely, knowledge on living animals will allow us to understand the biology of their extinct relatives, and how the diversity of living organism came to be. I completed my B.S. in Ecology & Evolutionary Biology at University of California, Irvine. During my undergraduate career, I studied adaptive response of crocodilian bones to locomotion, results of which would ultimately shed light on reptilian bone biology, as well as improve interpretations of fossil skeletal forms and function. During my tenure as a PhD student in the Integrative Anatomy at the University of Missouri (MU) School of Medicine, I remain convicted in the importance of studies on structure-function relationships in vertebrates, as well as the field's applicability in paleontology, comparative vertebrate biology, and health sciences. Aside from my research aims on archosaur locomotion and joint biology, I have been actively involved in a number of teaching and public outreach events, including human gross anatomy, comparative vertebrate anatomy, scientific illustration, as well as mentoring other students. These experiences ultimately strengthen my skills as an educator, allowing me to not only fulfill my passion for anatomy and paleontology, but also allowing me to share that passion with both academics and the public at large.