THE FEMORAL ONTOGENY AND LONG BONE HISTOLOGY OF THE MIDDLE TRIASSIC (?LATE ANISIAN) DINOSAURIFORM ASILISAUROS KONGWE AND IMPLICATIONS FOR THE GROWTH OF EARLY DINOSAURS

C. T. GRIFFIN* and STERLING J. NESBITT
Department of Geosciences, Virginia Polytechnic and State University, 4044 Derring Hall, 1405 Perry Street, Blacksburg, Virginia 24061, U.S.A., ctgriff@vt.edu; sjn2104@vt.edu

ABSTRACT—The ontogeny of early-diverging dinosauromorphs is poorly understood because few ontogenetic series from the same species-level taxon are known and what is available has not been extensively documented. The large numbers of skeletal elements of the silesaurid Asilisaurus kongwe recently recovered from Tanzania provide an opportunity to examine the ontogenetic trajectory of the earliest known member of Ornithodira and one of the closest relatives to Dinosauria. We examined the ontogeny of the femur and the histology of a series of long bone elements. We observed bone scar variation in a series of femora (n = 27) of different lengths (73.8–177.2 mm). We hypothesize that most femora follow a similar developmental trajectory; however, we observed sequence polymorphism in the order of appearance and shape of bone scars, and we quantified this polymorphism using ontogenetic sequence analysis (OSA). Additionally, five femora, three tibiae, a fibula, and a humerus were thin-sectioned to examine osteological tissues. No lines of arrested growth (LAGs) are present in any specimen, and there is little histological information about the ontogenetic stage of femora, although none have slowed or ceased growth. The woven-fibred bone present in the cortex of elements sectioned is similar to that of the earliest dinosaurs. This sequence polymorphism provides an alternate hypothesis for the robust/gracile dichotomy found in early dinosaurs often interpreted as sexual dimorphism. The shared femoral features found in Asilisaurus and early dinosaurs suggest that this ontogenetic pattern is plesiomorphic for Dinosauria, and that size is a poor predictor of maturity in early dinosauromorphs.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Knowledge of ontogeny is often crucial to understanding the evolution and paleobiology of a clade (e.g., Sánchez-Villagra, 2012; Thewissen et al., 2012). Ontogenetic series of fossil organisms allow for the study of the development of phylogenetic characters, character polarity, heterochronic evolution, and especially the homology of characters (e.g., Sánchez-Villagra, 2012; Thewissen et al., 2012). Although hypotheses can be proposed about the evolution of development within a clade based on extant members of that clade, paleontology provides the sole source of information about phenotypic evolution in geological time, and as such the study of ontogeny in fossil organisms is vital to studying development in an evolutionary context.

Studies of dinosaur ontogeny are common (Chinsamy-Turan, 2005; Padian and Lamm, 2013) and have been utilized to understand various aspect of dinosaur paleobiology, including life history and the evolution of growth rates (e.g., Horner et al., 1999, 2000, 2001; Padian et al., 2001; Erickson et al., 2004; Horner and Padian, 2004), the synonymy of species (e.g., Carr, 1999; Horner and Goodwin, 2009; Scannella and Horner, 2010), ecology and extinction (Codron et al., 2012), sexual dimorphism (Raath, 1990; Klein and Sander, 2008), and even the evolution of feathers (Xu et al., 2009). Understanding the development of dinosaurs and their relatives is therefore a key factor in understanding the evolution and paleobiology of one of history’s most dominant group of animals.

Studies of Jurassic and Cretaceous dinosaur ontogeny are also common (e.g., Chinsamy, 1993; Varriocio, 1993; Rimblot-Baly et al., 1995; Curry, 1999; Horner et al., 1999, 2000; Erickson and Tumanova, 2000; Erickson et al., 2004; Horner and Padian, 2004). Yet, our understanding of dinosaurian growth decreases as we approach their origins in the Late Triassic (Langer, 2004; Langer and Benton, 2006), and although early dinosaur remains are represented in most Upper Triassic deposits, the absence of abundant well-preserved skeletal elements of the same species-level taxon limits our understanding of early dinosaurian paleobiology, especially ontogeny. Besides discussions of postcranial skeletal variation (Colbert, 1989, 1990; Genin, 1992) and allometry (Rinehart et al., 2009) of the early netheropod Coelophysis bauri, a study on the long bone histology of Plateosaurus engelhardtii (Sander and Klein, 2005), and a brief discussion of a specimen interpreted as a juvenile Thecodontosaurus antiquus (Benton et al., 2000; this specimen was later renamed T. caducus [Yates, 2003] before being placed in the genus Pantydraco [Galton et al., 2007]), Triassic dinosaur ontogeny is still relatively unexplored.

Most studies of early dinosaurian ontogeny focus on growth features through histological analyses (Massospondylus, Chinsamy,
1993; *Euskelosaurus*, Ricqlès, 1968; *Thecodontosaurus*, Sander et al., 2004; *Plateosaurus*, Sander et al., 2004; Sander and Klein, 2005; Klein and Sander, 2007; *Syntarsus*, Chinsamy, 1990; *Lesothosaurus*, Knoll et al., 2010; *Scutellosaurus*, Padian et al., 2004) or allometry (Rinehart et al., 2009), whereas others have focused on differences of ‘robustness’ within a sample of the same species of dinosaur (Raath, 1977, 1990; Colbert, 1990; Rinehart et al., 2009). For example, when variation has been reported in early dinosaurs, polymorphism is often interpreted as indicative of sexual dimorphism rather than individual variation or ontogenetic patterns. A study of *Thecodontosaurus antiquus* interpreted the presence of more robust individuals as indicative of sexual dimorphism (Benton et al., 2000). Variation between two individuals of the Late Triassic theropod *Coelophysis bauri* collected from Ghost Ranch, New Mexico (differences in skull, neck, limb length, and sacral fusion), was interpreted as the result of sexual dimorphism (Colbert, 1990). However, other workers studying Ghost Ranch *C. bauri* have found no evidence for dimorphism in either limb length or sacral fusion, but did report a “relatively small” degree of sexual dimorphism in the neck and skull lengths (Rinehart et al., 2009:117). Morphological variation in several bones, most importantly in six muscle features of the proximal portion of the femur, has been recognized in the Early Jurassic theropod *Syntarsus* (= *Coelophysis*, Bristowe and Raath, 2004) rhodesiensis (Raath, 1977, 1990). Raath (1977, 1990) concluded that the apparent bimodal variation of ‘robust’ and ‘gracile’ features indicated sexual dimorphism, rather than taxonomic diversity or individual variation, and that robust features developed at the onset of sexual maturity in only one sex.

Until recently, the features present in the ‘robust and ‘gracile’ morphological suites sensu Raath (1977, 1990), particularly of the femur, were only thought to be present in coelophysoyd theropod dinosaurs (Tykoski and Rowe, 2004). However, it is now clear that these features have a wider distribution among dinosaurs, because they are present in the noasaur theropod *Masiakasaurus knopfleri* (Carrano et al., 2002; Lee and O’Connor, 2013), the early sauropodomorph *Saturnalia tupiniquim* (S.J.N., pers. obs.), other early theropods (Tykoski, 2005), and even outside Dinosauria in close relatives (*Silesaurus opolensis*, Pachowski et al., 2014; *Asilisaurus kongwe*, see below). The possibility that differences between the two morphs represent changes in ontogeny has only been touched on (Raath, 1977, 1990; Lee and O’Connor, 2013), although several studies have suggested that bone scars of hind limb elements increase in prominence during ontogeny in both extant (*Alligator mississippiensis*, Brochu, 1992, 1996, Tumarkin-Deratzian et al., 2007; *Branta canadensis*, Tumarkin-Deratzian et al., 2006) and extinct archosaurs (*Dromomerongregorii*, Nesbitt et al., 2009).

Here, we use a close relative of dinosaurs, *Asilisaurus kongwe*—an early-diverging silesaurid from the early Middle Triassic of Tanzania (Nesbitt et al., 2010)—to understand the origin of the gracile-robust dichotomy present in dinosaurs. To this end, we critically examined the changes in femoral scars of *A. kongwe* across a series of different sizes and examined the long bone histology of *A. kongwe*.

*Asilisaurus kongwe* is an ideal taxon to examine the dichotomy of gracile and robust femoral morphs because (1) the femora of *A. kongwe* exhibit a combination of gracile and robust morphologies over different lengths; (2) the taxon is known from hundreds of long bones from two localities; and (3) it is one of the oldest known members of Ornithodira and is part of one of the proximal outgroups of Dinosauria (Nesbitt et al., 2010). In this study, we describe the ontogenetic trajectory of a series of *Asilisaurus kongwe* femora, as well as histological characteristics of the long bones, and hypothesize that the pattern of development and ontogenetic variation found in *Asilisaurus* may be plesiomorphic for Dinosauria. Therefore, this study has implications for understanding the growth, development, and skeletal variation of early dinosaurs.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, New York, U.S.A.; GR, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, New Mexico; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; QG, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; SAM, Iziko South African Museum, Cape Town, South Africa; TMM, Vertebrate Paleontology Laboratory, The University of Texas at Austin, Austin, Texas, U.S.A.

**MATERIALS AND METHODS**

**Provenance and Taxonomic Justification**

All of the femora assigned to a silesaurid and specifically *Asilisaurus kongwe* originate from a series of localities within the Anisian (Lucas, 1998; Hancox, 2000; Abdala et al., 2005; Rubidge, 2005; Hancox et al., 2013) Lufia Member of the Manda beds in two major areas sampled by our team within the Ruhuhu Basin: a western area and an eastern area. Within the Lufia Member in both areas, all of the remains come from a similar stratigraphic horizon (i.e., about ~2/3 the stratigraphic distance from the contact with the underlying Kingori Sandstone) in bands of small outcrops (~100–1000 m²) that follow along strike. Admittedly, the localities in which these remains are found are difficult to correlate to exact stratigraphic level because of patchy outcrops surrounded by dense vegetation, but the localities appear to be within tens of meters of each other stratigraphically. Most of the femora come from the western area localities, which include the holotype locality of *A. kongwe* (NMT Z34). The holotype was found among largely disarticulated elements of silesaurids (see below) that were collected from the surface after weathering out of mudstone. Most of the femora (17 of total) and two tibiae (NMT RB209, 214) in this study were from this near monotypic bonebed, and a large serrated tooth and a single maxilla of a cynodont were also found here. In the same geographic area, and similar estimated stratigraphic position, another bonebed with silesaurids was also recovered (NMT Z9) with a similar taphonomic signature (i.e., largely disarticulated, elements from throughout the skeleton). Only one femur, one humerus, and one tibia were sampled from this locality (NMT RB226). One of the complete femora (NMT RB171) was found at a nearby locality among partial remains of an archosaur referable to a silesaurid (NMT Z29).

In the eastern area, silesaurid remains are much more rare, but occur as isolated partial skeletal elements. The nearly complete skeleton of *Asilisaurus kongwe* (NMT RB159) was collected from a locality (NMT Z137) with the remains of our smallest individual (NMT RB169). The dentary of the nearly complete skeleton (NMT RB159) shares all the autapomorphies of the holotype from the western area. From these associations, a general similarity of stratigraphic level for all of the *A. kongwe* specimens, and the identification of each element assignable to Silesauridae (see below), we hypothesize that all of the femora and long bone elements originate from a single species-level taxon, *A. kongwe*.

**Femora**—NMT RB19, 102, 109, 112, 159, 169, 171–172, 179, 185, 211–223, 226, 228–229. All of the femora bear character states of silesaurids, but unfortunately, there are no autapomorphies present in the femora of *Asilisaurus kongwe*. The femora preserving the proximal portion of the femur bear the following two character states found in most silesaurids: notch ventral to proximal end of the femur (character state 304[1] of Nesbitt et al., 2010; for detailed explanation and illustration of this and other Nesbitt et al., 2010, character states, see Nesbitt, 2011); and straight medial articular facet of the proximal portion of the femur (character state 309[1] of Nesbitt, 2010). Additionally, the proximal portions of the femora bear a straight groove on the proximal surface (character state 314[1] of Nesbitt, 2010), three similarly sized proximal tubera (sensu Nesbitt, 2010), and
distinct fourth trochanter—character states consistent with, but not exclusive to, silesaurids and *Asilisaurus kongwe*. The midshaft of the femur does not bear any character state exclusive to silesaurids or even Archosauria. Yet, the midshaft does bear a fourth trochanter, a character state present in some archosauriforms and all archosaurs. The ridge-like fourth trochanter is similar to that of the smaller specimens of *Silesaurus opolensis*. All femora except NMT RB226 were found among the holotype and referred specimens of *Asilisaurus kongwe* at a locality (NMT Z34) consisting of similarly sized, disarticulated skeletons of *Asilisaurus* (Nesbitt et al., 2010). Specimen NMT RB226 was found in another bonebed of small silesaurids at the same stratigraphic horizon (NMT RB Z90). To date, *Asilisaurus kongwe* is the only species-level taxon of silesaurid known from the Manda beds, and all evidence available to us indicates that there is not more than one species-level taxon of silesaurid.

**Humerus**—NMT RB225. There are no character states that clearly place NMT RB225 within Silesauridae or within Archosauria. However, the distal condyles of NMT RB225 are reduced as in other silesaurids (e.g., *Silesaurus opolensis*, Dzik, 2003) and in a partial skeleton of *Asilisaurus kongwe* (NMT RB159). Specimen NMT RB225 is from a locality (NMT RB Z90) consisting of thousands of disarticulated remains of a small silesaurid. To date, it is not clear if all the remains belong to one species-level taxon of silesaurid and/or *Asilisaurus kongwe*, but here we refer to it as *Asilisaurus kongwe* based on similarity and proximity to other diagnostic skeletal elements.

**Tibiae**—NMT RB209, 214, 224. The proximal and distal ends of the tibiae do not possess any unique character states of *Asilisaurus kongwe* or any other silesaurid. They do possess character states placing them within Dinosauriformes. For example, the anterior portion of NMT RB209 bears a straight cnemial crest (character state 328[1] of Nesbitt, 2010), whereas the posterior portion of the proximal part bears two nearly equally sized condyles (character state 331[1] of Nesbitt, 2011). The distal ends of the tibiae bear a slot for a small ascending process of the astragalus (character state 356[1] of Nesbitt, 2010). Each of the tibiae is either from the type locality (NMT Z34) or from another locality that has produced thousands of disarticulated remains that likely pertain to *Asilisaurus kongwe* (NMT Z90).

**Fibula**—NMT RB209, articulated with a tibia (NMT RB209; see above). Currently, there are no fibula character states exclusive to silesaurids. The proximal end of the fibula is mediolaterally compressed, and the anterior end of the proximal edge is slightly curved and pointed as in other dinosauriforms (Nesbitt, 2010, 2011). This fibula was found in near articulation with a tibia, and the tibia clearly bears three character states with dinosauriforms. Additionally, NMT RB209 is from the holotype locality of *Asilisaurus kongwe* (see Femora above).

**Preparation**

All specimens for which preparation was necessary were washed with sulfamic acid (10% concentration) and scrubbed with a toothbrush before being cleaned of matrix with a Micro-Jack 1 airscribe (www.paleotools.com). All specimens that were histologically sampled were first molded with PolyTek PlatSil 71-10 RTV silicone rubber prior to thin sectioning. Casts using Smooth-Cast 300 casting polyurethane resin (www.reynoldsam.com) were made of each specimen in order to preserve morphological detail. Additionally, all specimens that underwent destructive sampling were first photographed using a Canon Rebel Xsi digital SLR camera.

**Femoral Ontogeny**

Twenty-six femora ranging from 73.8 to 177.2 mm in length were included in our series, in addition to a cast of one femoral element, SAM-PK-10598 (n = 27). We measured the maximum width of the proximal end of the femur and the maximum femoral length (both in mm) of the five complete femora (NMT RB169, 172, 171, 159 [left and right elements]) in our sample with a Cen-Tech 6 inch digital caliper. We used R (www.r-project.org) to construct a simple linear regression ($R^2 = 0.974$) of these five femora, with the width of the proximal femoral end as the dependent variable and the maximum femoral length as the independent variable. A simple, or least squares, linear regression was preferable because only one variable, maximum femoral length ($y$), was uncertain. We then used the linear model returned by the regression ($y = 4.69x + 9.19$; in which $x$ is width of the proximal femoral end and $y$ is the maximum femoral length) to estimate the maximum femoral length of incomplete femora by inputting the measured width of the proximal femoral ends into the linear formula as $x$, allowing a hypothesized ontogenetic sequence of femoral lengths (the returned $y$ values) to be estimated (Fig. 1; Table S1, Supplementary Data); 95% confidence intervals were calculated for each estimated femur length in R (Table S1).

Bone scars were identified based on morphology and location when compared with femoral muscle scars of extant crocodilians and avian dinosaurs (Rowe, 1986; Baumel and Witmer, 1996; Hutchinson, 2001), hypothesized muscle scars of non-avian dinosaurs (Sereno, 1991; Novas, 1993; Bonaparte et al., 1999; Hutchinson, 2001; Butler, 2010), and other silesaurids (Dzik, 2003; Ferigolo and Langer, 2006; Langer and Ferigolo, 2013). Eleven muscle features or states showing variation were used in this study: the fourth trochanter, which was present in all specimens in a blade-like, gracile morph or a rounded, robust morph; a protrusion on the distolateral side of the fourth trochanter; the attachment scar of the M. caudofemoralis brevis; the linea intermuscularis cranialis and linea intermuscularis caudalis; two portions of a scar on the lateral surface of the ‘greater trochanter’ that we hypothesize is homologous to the dorsolateral trochanter observed in several dinosaurs (Bonaparte et al., 1999; Langer, 2003; Butler, 2010) and silesaurids (Ferigolo and Langer, 2006; Nesbitt et al., 2007; Langer and Ferigolo, 2013; unnamed Otis...
Chalk silesaurid, TMM 31100-1309); the anterior trochanter and the trochanteric shelf, which were fused in some specimens but separate in others (and therefore treated as an independent character); and a large muscle scar on the anterolateral surface of the proximal end of the femur that does not seem to be homologous with any described archosaurian muscle scar, which we here name the anterolateral scar. The presence, absence, or morphological variant of each muscle scar was recorded for each specimen, and this allowed us to construct a hypothesized developmental trajectory followed by the majority of the individuals studied.

**Histological Sectioning**

We sampled bone tissue for study as close to the midshaft region as possible in all elements (femora, NMT RB211, 210, 212, 226, 213; all other non-femoral elements) with the exception of NMT RB213, which was serially sectioned along the entire length of the element. Histological signals can differ between elements, even between different elements in the same individual (e.g., Horner et al., 2000), and this has been reported in silesaurids as well (Silesaurus opolensis, Fostowicz-Frehlik and Sulej, 2010). Because of this, we sampled several elements, not just femora, in order to understand the long bone histology of *Asilisaurus kongwe* in a more comprehensive manner. Sections of the bone to be thin-sectioned were removed from the specimen by sawing with an Isomet 4000 diamond wafering blade at 5000 rpm, with the exception of NMT RB213, for which this was unnecessary. The removed bone was then embedded in Castolite AP, a clear polyester resin, and immediately vacuumed for 1.5 minutes to remove bubbles before allowing several days for the resin to cure. In the case of NMT RB213, the entire specimen was embedded in resin. Wafers of resin and embedded bone were cut with the Isomet 4000 diamond wafering blade at 200 rpm, and then ground with a 1200-grit grinding disc and polished with a microcloth polishing disc with 0.3-micron slurry. The entire sample was ground down with a 1200-grit grinding disc and polished with a 203-mm-thick plastic slide with Aron Alpha (Type 201) cyanoacrylate, which was recommended by Lamm (2013) for mounting smaller specimens, before removing excess material by first cutting then grinding the wafer down with a Hillquist thin-section machine. All slides were then ground down to appropriate thicknesses by hand, first with a 1200-grit grinding disc, then a 2400-grit disc and microcloth disc with 0.3-micron slurry to polish. Slides were examined with an Olympus BX60 microscope under both plane- and cross-polarized light (the latter with a quartz wedge), and images were captured with cellSens standard software. The exception to this is the histology slides of the femur (NMT RB225), which were examined with an Olympus BX51 research microscope under plane- and cross-polarized light, and images were captured with Lumenera Infiniity capture imaging software. High-resolution images of these histological slides were uploaded to Morphobank (www.morphobank.com, project 2188).

**Ontogenetic Sequence Analysis**

Ontogenetic sequence analysis (OSA) is a parsimony-based method of reconstructing ontogenetic sequences based on discrete ontogenetic events independent of size while accounting for developmental sequence polymorphism (Colbert, 1999; Colbert and Rowe, 2008), and is therefore an ideal method for reconstructing the developmental sequence(s) of bone scars in our hypothesized ontogenetic series of *Asilisaurus kongwe*. Although cladistic ontogeny is a common and powerful method for reconstructing developmental sequences with a small amount of sequence variation (e.g., Brochu, 1992, 1996; Tumarkin-Deratzian et al., 2006), this method is less useful for samples with a large amount of variation (e.g., Tumarkin-Deratzian et al., 2007) because variation is eliminated to form a consensus tree, resulting in a low-resolution reconstructed sequence. The OSA method predicts all equally parsimonious sequences, allowing all potential ontogenetic sequences (with all semaphoronts sensu Hennig [1966]) in the studied population to be determined, even when data are missing (as is often the case in fossil ontogenetic series, which are inherently incomplete). A relatively large sample size is necessary for this method to be most effective, because OSA has been shown to better detect sequence polymorphism with larger sample sizes (De Jong et al., 2009). We followed the procedure of Colbert and Rowe (2008; detailed by Z. Morris, unpubl.). In summary, after constructing a data set of irreversible developmental event characters in each specimen, a parsimony-based cladistics program is used to optimize these developmental events onto trees, which are in turn used to construct reticulating diagrams showing hypothesized developmental pathways. Because all pathways must connect the least mature semaphoront to the most mature, the procedure is first undertaken with all trees rooted to the least mature semaphoront (normal treatment), then again with all trees rooted to the most mature semaphoront (reverse treatment).

We constructed a table of developmental events (the 11 bone scars referenced above, scored as characters; Table 1) similar to cladistic analysis, with each individual specimen treated as an operational taxonomic unit (OTU). Because femoral scars increase in number and prominence during ontogeny in many archosaurs (e.g., Brochu, 1992, 1996; Tumarkin-Deratzian et al., 2006, 2007; Nesbitt et al., 2009), we hypothesize that the absence of a scar is the immature character state, and the presence of a scar is the mature state. Further, because the smaller, gracile morph of the fourth trochanter is present in almost all the smallest individuals, and the robust morph is present in the largest individuals, we hypothesize that the more prominent morph is the more mature of the two. Characters were either absent (scored as [0]) or present (scored as [1]), except in the case of the fourth trochanter, which was present in all specimens as either a gracile (scored as [0]) or robust (scored as [1]) morph. Missing information was scored as [?]. We then removed redundancies, or specimens that showed the identical suite of character states, because they represent the same semaphoront. In these cases, multiple specimens (NMT RB211 and 215; NMT RB223 and 213; NMT RB228 and 217; NMT RB218 and 112) were treated as the same OTU in the table. For the reverse treatment (with the mature semaphoront as the outgroup), the identical procedure was followed except that absent/immature characters were scored as [1] and present/mature characters were scored as [0]. Because specimens representing the least mature (NMT RB169; all characters scored as [0]) and most mature (NMT RB216; all characters scored as [1]) character suites possible were present in the data set, there was no need to include hypothetical least mature or most mature semaphoronts in the data set. Tables were constructed in Excel and converted to NEXUS files with Mesquite (v. 2.75; Maddison and Maddison, 2011; NEXUS files for the normal and reverse treatments are available in Supplementary Data).

Using PAUP* (v. 4.0b10; Swofford, 2002), two heuristic searches were run with the tree-bisection-reconnection algorithm, adding specimens randomly and running 20,000 replicates: one with the least mature semaphoront as the outgroup and one with the most mature as the outgroup. We then condensed trees that had any branches with minimum length of zero so that polytomies would be recovered. We recovered 1260 trees rooted to the juvenile semaphoront and 160 rooted to the mature semaphoront, and visualized character changes along all branches for each tree. Reticulating sequence diagrams were then constructed following the procedure of Colbert and Rowe (2008), resulting in a single sequence diagram with semaphoronts arranged by reconstructed maturity score (i.e., the number of reconstructed
| Specimen   | dltp (1) | cfb (2) | dlp (3) | als (4) | dlt (5) | ts (6) | at (7) | ts+at (8) | lia (9) | lip (10) | 4th (11) | Observed maturity score | Reconstructed maturity score | % of max. femoral length | Semaphoront(s) |
|------------|---------|---------|---------|---------|---------|--------|--------|-----------|--------|---------|----------|------------------------|-----------------------------|-----------------------------|----------------|
| NMT RB169  | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0         | 0      | 0       | 0        | 0                      | 0                           | 0                           | 41.66 | S1         |
| NMT RB221  | 1       | 1       | ?       | 1       | 1       | 1      | 1      | 1         | 1      | 1       | 1        | 0                      | 8                           | 9                           | 46.67 | S18        |
| NMT RB20   | 0       | ?       | ?       | 0       | 0       | 0      | 1      | 1         | ?      | ?       | ?        | 2                      | 2, 3, 4                   | 54.22                      | S2, S3, S4 |
| NMT RB172  | ?       | 0       | 0       | 1       | 1      | 1      | 1      | 0         | 1      | 0       | 0        | 6                      | 6, 7                       | 54.39                      | S6, S11   |
| NMT RB185  | 0       | 1       | ?       | 0       | 0      | 1      | 1      | 1         | 0      | ?       | ?        | 4                      | 4, 8                      | 54.8                       | S5, S15   |
| NMT RB109  | 0       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 8                      | 8                           | 56.37                      | S12         |
| NMT RB19   | 0       | 0       | 1       | 1      | 1      | 1      | 1      | 1         | 0      | 1       | 1        | 7                      | 7                           | 56.53                      | S16         |
| NMT RB229  | 0       | 1       | ?       | 0       | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 7                      | 7                           | 56.63                      | S13         |
| NMT RB223  | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 0        | 10                     | 10                         | 56.79                      | S19         |
| NMT RB219  | 1       | 1       | ?       | 1       | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 8                      | 9                           | 58.83                      | S16         |
| NMT RB228  | 1       | 1       | 1       | 0       | 1      | 1      | 1      | 1         | 0      | 1       | 1        | 9                      | 9                           | 60.77                      | S17         |
| NMT RB211* | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 0        | 9                      | 9                           | 61.32                      | S16         |
| NMT RB218  | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 10                     | 10                         | 61.9                       | S20         |
| NMT RB112  | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 10                     | 10                         | 63.26                      | S20         |
| NMT RB212* | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 9                      | 9                           | 64.21                      | S18         |
| NMT RB222  | 1       | 1       | 1       | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 8                      | 8                           | 65.19                      | S14         |
| NMT RB102  | 0       | 0       | 0       | 0      | 0      | 1      | 0      | 1         | 0      | 1       | 0        | 3                      | 3                           | 67.02                      | S3         |
| NMT RB217  | 1       | 1       | 1       | 0      | 1      | 1      | 1      | 0         | 1      | 1       | 1        | 9                      | 9                           | 68.05                      | S17         |
| NMT RB215  | 1       | 1       | 1      | 1      | 1      | 1      | 1      | 0         | 1      | 1       | 0        | 9                      | 9                           | 68.08                      | S16         |
| NMT RB216  | 1       | 1       | 1      | 1      | 1      | 1      | 1      | 1         | 1      | 1       | 1        | 11                     | 11                         | 68.13                      | S22         |
| NMT RB213* | 1       | 1       | 1      | 1      | 1      | 1      | 1      | 1         | 1      | 1       | 0        | 10                     | 10                         | 68.71                      | S19         |
| NMT RB179  | 1       | ?       | ?       | 0      | 1      | 1      | 1      | ?         | ?      | ?       | ?        | 3                      | 5, 6, 9, 10                | 74.09                      | S6, S7, S9, S17, S21 |
| NMT RB171  | 1       | 1       | 1      | 1      | 1      | 1      | 1      | 1         | 1      | 1       | 1        | 10                     | 10                         | 77.4                       | S19         |
| NMT RB159 [R]* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 10 | 10 | 81.27 | S20 |
| NMT RB159 [L] | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 10 | 10 | 81.48 | S30 |
| NMT RB226* | 1 | ? | ? | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | 6 | 9, 10, 11 | 88.4 | S18, S19, S22 |
| SAM-PK-10598 | 1 | ? | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 10 | 100 | S21 |

Asterisk (*) on specimen number indicates a thin-sectioned specimen. 0 = character absent, 1 = character present, ? = location of character absent or too damaged to determine absence or presence of character. The fourth trochanter is present in all specimens, and occurs as either a ridge-like (bladed) or rounded morph (0 = ridge-like, 1 = rounded). Observed maturity score is determined by summing all character transformations (0–1) that have occurred in the specimen, whereas reconstructed maturity score is given by optimization of missing data by ontogenetic sequence analysis (OSA). Number in parentheses next to character abbreviation is the OSA character number. The OSA semaphoront(s) represented by each specimen are listed. Abbreviations follow Figures 2 and 3.
developmental events that have occurred in that individual) and connected by developmental events to other semaphoronts, illustrating the number of potential developmental sequences leading from the least mature to the most mature state. The reconstructed maturity score for each specimen may differ from the observed maturity score because of different optimizations of missing data, and hereafter we refer to the reconstructed maturity score when referencing maturity scores. To determine the modal sequence (the sequence that appears to be most frequently utilized by the specimens representing the sample), we assigned each semaphoront a specimen frequency support weight based on the number of specimens represented by the semaphoront. Because of different optimizations of missing data, multiple semaphoronts sometimes represented the same specimen, and in these cases the weight of the specimen was divided evenly between all the semaphoronts representing it; for example, a semaphoront representing three specimens, one of which is also represented by another semaphoront, would be assigned a frequency support weight of 2.5. Additionally, OSA sometimes predicts semaphoronts that do not occur in the sample, and these are included in the analysis but given a frequency support of zero (0). We added the specimen frequency weights of all the semaphoronts in every sequence, and the modal sequence was that sequence with the greatest total frequency weight, representing the highest number of specimens in our sample. Additionally, we found the mean sequence position of each developmental character and used this to order a hypothetical mean OSA developmental sequence, although it is important to note that this sequence is not one that was returned by OSA, unlike the modal sequence.

**DESCRIPTION**

The femur of *Asilisaurus* is sigmoidal in lateral and anterior views, and the proximal portion (Fig. 2) is relatively simple, with no distinct neck between the femoral head and the femoral shaft. The femoral head is medially flattened and deflected, ventral and medial to the femoral head is the ‘notch’ apomorphic for Silesauridae (Nesbitt et al., 2010), and the femur also possesses a straight sulcus on the proximal surface. The proximal end of the femur also bears three tubera, anterolateral, anteromedial, and postero-medial. Well-preserved bone scars are present along the length of the femur, but most are restricted to the proximal half of the element (Fig. 3; see below). The distal condyles of the femur are poorly differentiated from the shaft and are simply rounded. The middle part of the distal surface bears a deep concavity that is roughly circular in distal view.

**Dorsolateral Trochanter**

We hypothesize that the thin scar located on the anterior distolateral surface of the ‘greater trochanter’ in *Asilisaurus kongwe* (Fig. 2) is homologous to the dorsolateral trochanter (Bonaparte et al., 1999), a flange-like extension of the ‘greater trochanter’ present in early ornithischians (e.g., *Laxicursor diagnosticus*, Sereno, 1991; *Eocursor parvus*, Butler, 2010), early saurischians (e.g., *Herrerasaurus ischiguastensis*, Novas, 1993:fig. 7; *Saturnalia tupiniquim*, Langer, 2003) including neotheropods (*Coelophysis bauri*, *Liliensternus liliensterni*, Nesbitt, 2011), and the
FIGURE 3. The proximal ends of femora of *Asilisaurus kongwe* showing variation in the presence, absence, and morphology of bone scars, in descending order of size. A, NMT RB159 in anterolateral and B, posteromedial views. Robust fourth trochanter is present. C, NMT RB216 in anterolateral and D, posteromedial views. Robust fourth trochanter is present. E, NMT RB102 in anterolateral and F, posteromedial views. Gracile fourth trochanter is present. The most proximal part of the femur is missing. G, NMT RB218 in anterolateral and H, posteromedial views (left femur). Robust fourth trochanter is present. I, NMT RB185 in anterolateral and J, posteromedial views. Fourth trochanter is too damaged to determine morph. K, NMT RB221 in anterolateral and L, posteromedial views (left femur). Gracile fourth trochanter is present. M, NMT RB169 in anterolateral and N, posteromedial views (left femur). Gracile fourth trochanter is present. Labeling of bone scars indicates presence in that specimen; absent scars are not labeled. Left femora have been horizontally mirrored for ease of visual comparison with right femora. Abbreviations: *at* + *ts*, fusion of the anterior trochanter and trochanteric shelf; all other abbreviations follow Figure 2. Scale bar equals 1 cm.
silesaurids *Sacisaurus agudoensis* (Ferigolo and Langer, 2006; Langer and Ferigolo, 2013), *Eucoelophysis baldwini* (Nesbitt et al., 2007), *Silesaurus opolensis* (Nesbitt, 2011; although it is absent in smaller *S. opolensis* specimens [Nesbitt et al., 2007; Piechowski et al., 2014]), and an unnamed silesaurid (TMM 31100-1303). Nesbitt (2011) considered the dorsolateral trochanter to be a synapomorphy of the clade Silesauridae + Dinosauria. The dorsolateral trochanter was hypothesized by Rowe (1986) to correspond to an attachment of a branch of the M. iliotrochanterici in Aves (hypothesized by Hutchinson [2001] to be homologous to M. pubo-ischi-femoralis internus 2 in Crocodylia). Given that a similar scar is absent in lagerpetids (e.g., *Dromomeror gregorii*, Nesbitt et al., 2009), it is clear from phylogenetic analyses (Langer and Benton, 2006; Irims et al., 2007; Nesbitt et al., 2010) that the presence of a dorsolateral trochanter is derived for dinosauromorphs. Although this scar is absent in most of the smaller femora (NMT RB169, 220, 185, 109, 19, 229; Fig. 3I–N), it becomes common with increasing size early in the series of *A. kongwe* femora (NMT RB223), initially only present on the anterior distolateral surface of the ‘greater trochanter’ (Fig. 2A). As size increases, the scar extends to the posterior distolateral face of the ‘greater trochanter’ (Fig. 2B), a feature that is not present in the dorsolateral trochanter of any other dinosauromorphs we have examined.

**Insertion Scar of the M. Caudofemoralis Brevis**

The insertion scar of the crocodilian M. caudofemoralis brevis (CFB; hypothesized by to be homologous to M. caudofemoralis pars pelvica in Aves [Hutchinson, 2001; Schachner et al., 2011]) is slightly proximal and lateral to the fourth trochanter in *A. kongwe*, bordered anterolaterally by the linea intermuscularis cranialis (Fig. 2B). The CFB (along with the M. caudofemoralis longus) is present in crown group saurians (e.g., *Varanus*, Hutchinson, 2001:fig. 1; *Iguana*, Schachner et al., 2011:fig. 2B), but in early archosauriforms it is shifted distally along with the M. caudofemoralis longus as the internal trochanter of non-archosauriform archosauromorphs transitioned into the fourth trochanter of archosauriforms. This attachment scar is present in the second-smallest femur of our sample (NMT RB221; Fig. 3L) and is present in femora of all sizes, absent in only three (NMT RB169, the smallest, in addition to NMT RB19 and 102; Fig. 3F, N). This scar is therefore one of the most common in our hypothesized ontogenetic series, and we consider it to be one of the first scars to form during ontogeny.

**Fourth Trochanter**

The fourth trochanter is the insertion of the M. caudofemoralis longus (CFL; hypothesized to be homologous to M. caudofemoralis pars caudalis in Aves [Hutchinson, 2001; Schachner et al., 2011]), along with an associated medial depression that is present in many taxa (e.g., Hutchinson, 2001; Langer, 2003). The fourth trochanter is an archosauromorph novelty, and some debate has surrounded its evolutionary history: Gregory and Camp (1918:524; cited in Hutchinson, 2001) hypothesized that the internal trochanter of basal Archosauromorpha is homologous with the fourth trochanter, whereas other studies have asserted that the fourth trochanter is a novel structure arising independently of the internal trochanter (Parrish, 1983, 1992). Although the latter hypothesis was ostensibly supported by the suggestion that *Erythrosuchus* possessed both an internal trochanter and fourth trochanter (Parrish, 1992), the hypothesized ‘fourth trochanter’ of Parrish was the attachment point for the M. iliofemoralis, not the M. caudofemoralis (Gower, 2003). The internal trochanter of lizards and the fourth trochanter of archosaurs are both the attachment point for the M. caudofemoralis (Nesbitt, 2011), and we follow Gregory and Camp (1918), Gower (2003), and Nesbitt (2011) in homologizing the two structures.

In *A. kongwe*, the fourth trochanter is a large crest elongated in a proximal to distal orientation on the postero-medial face of the proximal portion of the diaphysis (Fig. 2B). This scar is present in all specimens in our sample, and there is a medial rugose pit closely associated with the fourth trochanter in all specimens. A small protrusion on the distolateral face of the fourth trochanter is not present in the smallest specimens (NMT RB169, 172; Fig. 3F, N) but is present in the majority of the larger ones. In smaller specimens, the fourth trochanter is ridge-like, especially the most proximal portion of the ridge, whereas in many larger specimens (e.g., NMT RB159 [left and right elements], NMT RB226, SAM-PK-10598) it has a rounded, robust morphology (Figs. 2B, 3B, D, H). Therefore, although this feature is present in all specimens examined, its morphology is variable between specimens and appears to be roughly correlated with femoral size.

**Anterolateral Scar**

A large, raised, roughly disc-shaped feature, which we here name the anterolateral scar (= ‘dorsolateral ossification’ sensu Piechowski et al., 2014), is present in nearly all specimens on the anterolateral surface of the proximal end of the femur of *Asilisaurus kongwe*, anterior to the ‘greater trochanter’ and posterior to the femoral head (Fig. 2A). The external surface of this feature is covered in coarse bone fibers with no particular orientation, and the edges of the scar are poorly cemented to the rest of the femur. This scar also appears in other silesaurids (e.g., *Silesaurus opolensis*, Dzik, 2003:fig. 13; Piechowski et al., 2014; the unnamed Otis Chalk silesaurid TMM 31100-1309) and is likely a feature only present in silesaurids given that we have not recognized it in any other archosaur taxon. Although this ossification has been hypothesized to be an extension of the dorsolateral trochanter in *Silesaurus opolensis* (Piechowski et al., 2014), in which this scar is closely associated with the dorsolateral trochanter. In both *A. kongwe* and *S. opolensis*, these two scars are separate in most individuals (*Asilisaurus kongwe*, Fig. 2; *Silesaurus opolensis*, Piechowski et al., 2014:figs. 4, 10), and we hypothesize that these two closely associated bone scars are different structures. Given that this feature is not present in any extant reptile, the muscle(s), if any, associated with this scar are unknown. However, the iliofemoral ligament in extant crocodiles, hypothesized to be homologous with the pubofemoral ligament in Aves (Tsai and Holliday, 2015), inserts into the “lateral metaphyseal surface of the femur” (Tsai and Holliday, 2015:22), and this insertion in *Alligator mississippiensis* and the anterolateral scar of *A. kongwe* are broadly similar in location (compare Fig. 2A and Tsai and Holliday, 2015:fig. 6B). Therefore, the anterolateral scar may be the ossification of the iliofemoral ligament insertion. The anterolateral scar is occasionally absent in smaller *Asilisaurus* femora (NMT RB169, 220, 185, 109, 19, 229; Fig. 3E, I, M), but as size increases the scar becomes increasingly common: in femora of length greater than 70% of the largest femur, the scar is only absent in two (NMT RB179, SAM-PK-10598). This absence is especially conspicuous in SAM-PK-10598, which is the largest femur in the sample.

To investigate the morphology of the scar further, we sectioned through the feature in a serially sectioned proximal end of the femur of *Asilisaurus kongwe* (NMT RB213, sections A28 and 30; Fig. 4A, B). The scar consists of very dense bony tissues with little vascularization and is easily differentiated from the outer cortex of the main body of the femur. The vascularization that is preserved is concentrated in the inner portions of the thickest portion of the feature, and the long axis of the vascular canals are oriented parallel with the outer surface of the feature. Sharpey’s fibers are aligned perpendicular to the outer cortex of the femur and are arranged in clear bands that are more apparent near the contact with the rest of the femur relative to that of the outer portions of the scar.
FIGURE 4. Long bone histology of *Asilisaurus kongwe*. A, the anterolateral scar (NMT RB213, slide A30) under cross-polarized light (with quartz wedge) viewed at 40× magnification; B, close up of anterolateral scar showing Sharpey’s fibers, indicated by arrowheads, respectively; C, cortical bone of a femur (NMT RB210, slide C2) under cross-polarized light with quartz wedge; D, E, cortical bone of a femur (NMT RB210, slide C1) under D, cross-polarized light (with quartz wedge) and E, plane-polarized light; F, cortical bone of a humerus (NMT RB225, slide J2) under cross-polarized light; G, cortical bone of a tibia (NMT RB214, slide I2) under cross-polarized light with quartz wedge. Erosional line, not LAG, is visible; H, cortical bone of a fibula (NMT RB209, slide G2) under cross-polarized light with quartz wedge. Micrograph scale bars equal 200 μm (A), 500 μm (B), and 100 μm (C–H). *Asilisaurus kongwe* reconstruction scale bar equals 10 cm.
Trochanteric Shelf

The trochanteric shelf is thought to have originated in Dinosauria (Hutchinson, 2001) and was hypothesized to be homologous with the insertion of the M. iliofemoralis externus in Aves (Hutchinson, 2001; this muscle was hypothesized to be homologous to the M. iliofemoralis in Crocodylia [Hutchinson, 2001]). The trochanteric shelf is absent in two of the smaller specimens (NMT RB169, RB220), and is generally present with the anterior trochanter (e.g., Figs. 2A, 3), although in one specimen the anterior trochanter is present whereas the trochanteric shelf is absent (NMT RB220; Fig. 3E; see below for discussion).

Anterior Trochanter

The anterior, or ‘lesser,’ trochanter is an important feature in archosaur phylogenetics, hypothesized to have originated in Dinosauria (Hutchinson, 2001) as part of the anterior side of the trochanteric shelf (Novas, 1996; Hutchinson, 2001) and is the insertion scar of the M. iliofemoralis caudalis (hypothesized by Hutchinson [2001] to be homologous to the M. iliofemoralis in crocodilians). Anterior trochanter-like structures are present in some pseudosuchian archosaurs, generally in large adults (e.g., Ornithosuchidae [Walker, 1964], as well as Aetosauria and Crocodylomorpha [Hutchinson, 2001:table 2]), although these features do not appear to represent a synapomorphy for Archosauria (Gauthier, 1986). The insertion of the M. iliofemoralis was more distal in early-diverging archosaurs, including the extant Crocodylia, and moved to a more proximal position on the femur in Dinosauria, forming a true anterior trochanter (Hutchinson, 2001). The anterior trochanter was therefore hypothesized to be a synapomorphy for Dinosauria (Hutchinson, 2001); however, the presence of an anterior trochanter in the non-dinosauriform dinosauromorph *Dromomeron gregorii* (Nesbitt et al., 2009) indicates that an anterior trochanter was present in at least some non-dinosauriform dinosauromorphs. Whereas many dinosauromorphs possess both an anterior trochanter and trochanteric shelf in the femora (*Marasuchus lilloensis*, *Pseudolagosuchus major*, *Silesaurus opolensis*, *Herrerasaurus ischigualastensis*, and *Saturnalia tupiniquin* [Nesbitt, 2009]), many individuals, but not all, of early-diverging theropod dinosaurs possess an anterior trochanter but lack a trochanteric shelf (e.g., *Coelophysis bauri*; Colbert, 1990; the gracile morph of ‘Syntarsus’ rhodesiensis, Raath, 1977, 1990), and smaller femora of *Saturnalia tupiniquin* also lack a well-defined trochanteric shelf but possess an anterior trochanter (Nesbitt et al., 2009). The anterior trochanter, along with the trochanteric shelf, is absent in the non-dinosauriform dinosauromorphs *Lagerpeton chanarensis* and *Dromomeron romeri* and only appears in larger individuals of *Dromomeron gregorii* (Nesbitt et al., 2009).

The anterior trochanter is present in all *Asilisaurus* femora but the smallest (NMT RB169; Fig. 3M), and in one individual the anterior trochanter is present whereas the trochanteric shelf is absent (NMT RB220; Fig. 3E). Conversely, in some larger *Asilisaurus* femora, the two structures cannot be differentiated and

FIGURE 5. A, general order of appearance of the bone scars of the proximal end of the femur in the majority of *Asilisaurus kongwe* individuals, scaled by relative femoral length compared with the largest femur in the series (SAM-PK-10598, 177 mm in length). The shortest femur in the series (NMT RB169, 73.8 mm in length) is also indicated. Each muscle scar abbreviation indicates the appearance of that feature in development. There is a zone of developmental transition from the ridge-like to the rounded morph of the fourth trochanter in which both morphs are equally common; B, relative order of appearance of bone scar characters based on the OSA modal sequence; C, relative order of appearance of bone scar characters based on the mean OSA sequence. Abbreviations follow Figures 2 and 3. Scales in B and C are dimensionless and illustrate relative, not absolute, timing.
FIGURE 6. Ontogenetic sequence analysis (OSA) reticulating diagram of femoral bone scar development in *Asilisaurus kongwe* showing 33 unique parsimonious developmental sequences. Semaphoronts are represented by ellipses, with width proportional to frequency support. Semaphoronts are ranked by maturity score (0–11). Semaphoronts with a frequency support of less than 1 (those with multiple maturity scores because of different optimizations) have an ellipse width equal to those with frequency support of 1 for visual clarity. Character transitions are listed with the path on which they occur, and all character changes proceed in an irreversible direction from immature to mature (0–1). Characters are listed in Table 1.
femorotibialis lateralis and Mm. puboischiofibulares medialis and lateralis, respectively, in Aves [Hutchinson, 2001]; the M. adductor femoris 1 and 2 has been hypothesized to be homologous with the M. pubo-ischio-trochantericus in Sphenodon [Schachner et al., 2011]). Like the linea intermuscularis cranialis, it is a plesiomorphic archosaur character, normally connecting the base of the ‘greater trochanter’ with the proximal posterior end of the lateral condyle (Hutchison, 2001). In A. kongwe, it originates distal to the fourth trochanter and terminates at roughly the same level as the linea intermuscularis cranialis, although on the posterior end of the diaphysis (Fig. 2B). The linea intermuscularis caudalis of A. kongwe also intersects with a morphologically similar line that originates on the distal end of the fourth trochanter, similar to the ridge on the distal dorsolateral side of Sacsaurus agudoensis (Ferigolo and Langer, 2006). The linea intermuscularis caudalis is not present in smaller femora that possess the linea intermuscularis cranialis, appearing later in our qualitative ontogenetic series (first present in NMT RB109).

Asilisaurus Histological Specimens

Femora—All of the femora selected for histological sectioning were incompletely preserved, but their lengths were reconstructed based on complete elements (see Fig. 1; Table S1). All sections were taken as close to the midshaft as possible. We sampled a variety of sizes, but were unable to sample the larger specimens of Asilisaurus because of a lack of specimens. All of the femoral specimens have undergone partial recrystallization of the bone in the medullary cavity, compressive fracturing throughout the specimens, and the medullary cavity is infilled by calcite crystals.

Generally, all of the specimens have a similar morphology in section throughout the length of the femur. Each specimen is nearly circular, with a similarly shaped medullary cavity. The medullary cavity and the inner portion of the cortex lack trabecular bone at the midshaft as preserved, but as noted by Werning (2013), the large crystals within the medullary cavity may have destroyed these structures during fossilization. The cortex is thickest at midshaft (Fig. 4C–E) and thins proximally and distally. The most proximally sampled sections have a very thin cortex with trabecular bone nearly reaching the outer surface. The trabecular bone is formed by thin, parallel-fibered endosteal lamellae.

The microstructure of the cortex is nearly uniform throughout with no discontinuities (e.g., lines of arrested growth [LAGs]). The bone tissue is consistently woven-fibered throughout with circumferentially oriented fibers most common. The outermost cortex bears more circumferentially oriented fibers than the middle and inner cortex. The entire cortex is moderately to well vascularized by primary osteons. Throughout the cortex, the primary osteons are predominantly longitudinal, but they anastomose throughout the cortex, particularly in the outer cortex. The larger specimens bear a combination of longitudinal and radial primary osteons where some of the radial primary osteons stretch for at least half of the width of the cortex. The radius of primary osteons is consistent with a few exceptions of larger radii in the histological sections closer to the proximal end. Primary osteons are encircled by thin bands of parallel-fibered bone tissue and osteocyte lacunae, yet the osteocyte lacunae are not oriented radially around the primary osteons. A high density of osteocyte lacunae is present throughout the cortex, as in other dinosauromorphs (Werning, 2013), and the density of the osteocyte lacunae slightly decreases from the inner to outer cortex. The shape and distribution of the osteocyte lacunae show no apparent pattern. No secondary osteons were observed in any example. Compared with the histological features of the femur of Silesaurus opolensis (Fostowicz-Frel and Sulej, 2010), the
relative thickness of the cortex, the distribution of longitudinal primary osteons and osteocyte lacunae, and the woven-fibered bone tissues throughout the cortex are very similar. In *Asilisaurus kongwe*, the densities of both the primary osteons and osteocyte lacunae and the number of primary osteons that Anastomose are relatively higher than in *S. opolensis.*

**Humerus**—The histological sections from NMT RB225 were taken as close to the midshaft as possible, but because the element was not complete, it is not clear how close we sampled from the midshaft. Comparisons with a complete humerus of *Asilisaurus kongwe* (NMT RB159) suggest that we sampled between 5 and 10 mm of the midshaft.

The medullary cavity bears no trabeculae, and it appears that recrystallization did not postdepositionally remove trabeculae because the area that is recrystallized is restricted to the inner-most portion of the cavity. The cortex consists entirely of primary osteons of which most are longitudinal. Some of the primary osteons clearly Anastomose and form a reticulated pattern with no favored orientation (Fig. 4F). A weak band of fewer primary osteon Anastomoses are present in the mid cortex relative to the inner and outer cortex, and this band is visible throughout the section. Primary osteons reach the periosteum. As a result, the external surface of the humerus near the midshaft is decorated in proximodistally oriented grooves and ridges, creating a fibrous surface. A similar external morphology of long bones is a characteristic of fast-growing stages in tetrapods, including crocodilians (Tumarkin-Deratzian et al., 2007) and birds (Tumarkin-Deratzian et al., 2006; Erickson et al., 2009). Like in the femur, no secondary osteons are present. Additionally, like the femur, there is a high density of osteocyte lacunae without any clear orientation, whereas some of the osteocyte lacunae are clearly circumscribed around the primary osteons.

Comparisons between the humerus of *Asilisaurus kongwe* and other archosaurs are difficult given that humeri are relatively rarely preserved in the skeletons of early archosaurs and are particularly rare among dinosauromorphs. Overall, the tissues present in the humerus are very similar to those of the femur of *A. kongwe.*

**Tibiae**—Our histological sample originally consisted of three samples, two from the distal halves of tibiae (NMT RB214, 224) and one from the proximal third of a tibia (NMT RB209) in articulation with a fibula (also sampled; see below). Specimen NMT RB209 is highly fractured and is of little utility, whereas the section of NMT RB224 was taken too close to the distal end to have much use when reconstructing the growth of *A. kongwe.* The sample from the largest tibia (NMT RB214) is closest to the midshaft of the tibia and is within an estimated 20% of the midshaft; the following description relies on NMT RB214.

The medullary cavity is largely infilled by calcite crystals, but there is clear evidence from shattered bone shards in the medullary cavity that trabeculae were present prior to fossilization. The inner cortex consists of unremodeled compact coarse cancellous bone deposited during cortical drift. Here, the longitudinal primary osteons are surrounded by either parallel-fibered or woven-fibered bone with longitudinal osteons. The longitudinal osteons reach the external surface of the bone, but the external surface of the bone did not have a fibrous texture like that of the humerus. No LAGs are present, but one portion of the fibula is clearly banded in the outer cortex. These bands are short and do not circumscribe the section. There are relatively fewer osteocyte lacunae than in the femur and tibia, and these osteocyte lacunae are located in bands throughout the preserved cortex.

In comparison with other *A. kongwe* long bones sampled, the degree of banding present in the fibula is atypical. Moreover, the banding in the fibula is not typical of any other long bones of dinosauromorphs sampled thus far. Yet, no other fibulae have been sampled among dinosauromorphs.

**Femoral Ontogeny**

The large number of femora sampled, with femoral size being taken as a proxy for relative age, allows a general qualitative pattern of development of the bone scars of the proximal end of the femur to be hypothesized in *Asilisaurus kongwe.* This allows for the testing of this proxy (commonly assumed in paleontology) against size-independent methods of sequence reconstruction (i.e., OSA), as well as testing the utility of qualitatively reconstructing growth trajectories with size. These femoral scar features developed at different times in ontogeny, and there is a common ontogenetic trajectory that the majority of individuals seem to follow (Fig. 5A; Table 1). The smallest specimen examined, NMT RB169, lacks all muscle scars with the exception of a ridge-shaped gracile fourth trochanter, which we take to be the most immature femoral state in our sample (Fig. 3M, N). Based on our qualitative sequence, we hypothesize that next the attachment scar for the M. caudofemoralis brevis develops along with the linea intermuscularis cranialis and the anterior trochanter. The trochanteric shelf then develops, followed by the protrusion on the distolateral part of the fourth trochanter, the linea intermuscularis caudalis, and the anterior portion of the dorsolateral tendon scar. The anterolateral scar and the posterior side of the dorsolateral trochanter appear next in the sequence. The rounded, robust morph of the fourth trochanter commonly begins appearing at this point in the series, although it does not become the dominant morph until later. Fusion between the anterior trochanter and the trochanteric shelf becomes common next, and lastly the robust fourth trochanter becomes the dominant fourth trochanter morph.

Despite the existence of a common ontogenetic trajectory, there is a large amount of variability in the presence and morphology of bone scars between *Asilisaurus* specimens of roughly the same size in our sample. We interpret this variability as in part signaling a lack of strict relationship between size, age, and skeletal maturity, and in part indicating the presence of sequence polymorphism—variability in the timing and relative sequence of development between individuals within a population (Garn et al., 1966), which violates the traditional idea of distinct, ordered ontogenetic stages undergone by all individuals of a species during ontogeny. Developmental studies with large samples of extant taxa have revealed that sequence polymorphism is surprisingly common (Cubbage and Mabee, 1996; Mabee and Trendler, 1996; Sheil and Greenbaum, 2005; De Jong et al., 2009; Morris, 2013), and recent studies have utilized ontogenetic sequence analysis (OSA; see below) in an attempt to describe
and quantify sequence polymorphism in fossil organisms (Morris et al., 2013; Olori, 2013). Sequence polymorphism is not only present but also common in our sample of A. kongwe femora. As previously mentioned, the morphology of the fourth trochanter, although gracile in smaller specimens and robust in larger ones, is difficult to predict based either on femoral size or on the presence/absence of other bone scars in a large portion of the ontogenetic series. The first occurrence of the robust fourth trochanter is in NMT RB229 (ninth smallest in the series), and the last occurrence of the gracile morph is in NMT RB171 (23rd largest in the series). In this region, there appears to be no pattern to which of the two morphs will be present in a specimen, nor does either morph seem to be associated with the presence or absence of other muscle scars. Specimen NMT RB102 presents another example of polymorphism: although 17th by size in the ontogenetic series, this specimen has a gracile fourth trochanter and lacks all other muscle features but the anterior trochanter and the linea intermuscularis cranialis, appearing far less developed than femoral size alone would suggest (Fig. 3E, F). In contrast, NMT RB221 appears far more developed than would be expected (Fig. 3K, L): although the second smallest in the series, this specimen displays every mature muscle scar except a robust fourth trochanter and the linea intermuscularis caudalis, including fusion between the anterior trochanter and the trochanteric shelf, which does not appear unambiguously again in the series until NMT RB216, which is 20th by size in the series. Although NMT RB159 is one of the largest specimens in the series, containing every mature muscle feature, it lacks this trochanteric fusion (Figs. 2A, 3A). The anterolateral scar becomes common early in the ontogenetic series, but in two of the largest specimens (SAM-PK-10598 and NMT RB179) it is conspicuously absent.

Ontogenetic sequence analysis (OSA) returned a total of 33 unique (but often partially overlapping) equally parsimonious ontogenetic sequences, with sequences diverging early in ontogeny and multiple ontogenetic changes occurring between most semaphoronts (Fig. 6). A single modal sequence with a frequency weight of 11.67 was returned (Figs. 5B, 6; Table S2), 43.2% of the total weight of the sample (27). However, because the total frequency weight of all sequences was 225.96, the modal sequence only represented 5.16% of the total weight of all sequences, indicating a large amount of variation in the sample. Most sequences contained some characters that appear to develop simultaneously because these characters have an unresolved sequence order with respect to each other. This could indicate either that these characters do develop simultaneously in the given sequence, or that we simply lack enough ontogenetic sample to resolve the two. Distinguishing between the two possibilities for given characters in a sequence is impossible using OSA alone. In the modal sequence, the anterior trochanter develops first, followed by the linea intermuscularis cranialis, the linea intermuscularis caudalis, and the distolateral protrusion on the fourth trochanter. The anterior portion of the dorsolateral trochanter and the trochanteric shelf develop next, unresolved with respect to each other. Next, the anterolateral scar develops, followed by the insertion scar of the CFB and the posterior portion of the dorsolateral trochanter. Finally, the anterior trochanter and trochanteric shelf fuse into one continuous scar, and the fourth trochanter develops into the robust morph. Notably, the anterior trochanter develops first in all sequences (Fig. 6). Seven semaphoronts that were not observed in our sample were predicted by the analysis. The modal sequence returned by the OSA and the qualitative sequence described previously are remarkably similar (Fig. 5A, B), and even the exceptions to this agreement only differ by a single developmental step. The only notable difference between the two is the insertion scar of the CFB, which develops first in the OSA modal sequence and seventh in the qualitative analysis sequence, but this is probably a result of the low resolution inherent in the qualitative assessment, along with the fact that the modal sequence only represents roughly 5% of the total weight of all sequences. Additionally, the OSA mean sequence is very similar to the modal sequence (Fig. 5B, C), with only four characters differing by more than one position between the two sequences. Most characters had a wide range of sequence positions because of the prevalence of sequence polymorphism in the sample (Fig. 7; Table S3). The linear regression of femoral size versus observed maturity score showed an overall poor correlation between size and maturity (Fig. 5A; R² = 0.1306; P = 0.06406; linear formula returned was y = 0.046x + 2.26179, in which x is the length of the femur in mm and y is the observed maturity score). This insignificant correlation is partly because of missing data, which results in mature specimens being assigned anomalously low observed maturity scores. A strict reading of Figure 7A may suggest that there are two developmental sequences present in our sample: one in which the individuals are more mature at smaller sizes, and one in which the individuals are less mature at these same sizes. However, this is an artifact of missing data (which in the regression of observed maturity score is identical with character absence). Even if all characters scored as missing really were absent, the low-maturity individuals could still not be part of the same developmental sequence, because the specimens making up the hypothetical trajectory in Figure 5A (NMT RB102, 185, 220, 226, 179) have conflicting developmental characters. For example, NMT RB220 (length = 96.08 mm) only possesses the anterior trochanter and linea intermuscularis cranialis, whereas NMT RB179 (length = 131.3 mm) only possesses the anterior trochanter and both portions of the dorsolateral trochanter. Thus, although it appears that the two may share the same developmental trajectory in Figure 5A, for this to be true, this trajectory would have to lose character 9, then gain it back again to reach the most mature developmental state.

Reconstructed maturity score accounts for this missing data; however, the overall poor correlation between size and developmental maturity holds even in the regression of femoral size and reconstructed maturity score (R² = 0.2551; P = 0.001432; linear formula returned was y = 0.061x + 0.605, in which x is the length of the femur in mm and y is the reconstructed maturity score). Higher maturity scores tended to have larger size ranges and therefore more variability (Fig. 8C), but this may be an artifact of sample size, because more specimens with high rather than low maturity scores are present in the sample, and size range follows total specimen frequency support for each maturity score closely (Fig. 8C). With the possible exception of some of the smallest and largest individuals, overall size has little to do with developmental maturity in our sample, and femoral size is a poor predictor of maturity.

**Histology**

The character states of the bony tissues of the long bones (femur, tibia, fibula, humerus) of Asilisaurus kongwe are consistent across element sampled. All share a relatively large medullary cavity with no trabeculae, only primary osteons preserved, longitudinal canals predominate but anastomoses are present in the outer cortex, woven-fibered bone tissues throughout the cortex, and a high density of osteocyte lacunae. None of the specimens sampled show any indication of having slowed or stopped growth before death. These characteristics of the bony tissues of limb bones of A. kongwe are remarkably similar to those of the Late Triassic silesaurid Silesaurus opolensis (Fostowicz-Freliek and Sulej, 2010). In particular, the histological tissues of A. kongwe (NMT RB210; Fig. 4C–E) and S. opolensis (ZPAL Ab III/405; Fostowicz-Freliek and Sulej, 2010) femora are virtually identical. The bony tissues of A. kongwe are very similar to those of the coelophysid theropods Coelophysis bauri (AMNH...
unnumbered; tibia) and ‘Syntarsus’ rhodesiensis (OG 715, femur). The most obvious difference between *A. kongwe* and coelophysids is that the coelophysids have more anastomoses throughout the cortex. Furthermore, LAGs were recorded in the outer cortex of ‘Syntarsus’ rhodesiensis (Chinsamy, 1990; Chinsamy-Turan, 2005) and *Saturnalia tupiniquim* (Stein, 2010), whereas no LAGs were found in any long bone of *A. kongwe* sampled.

**DISCUSSION**

**Growth of Asilisaurus**

We hypothesize that our sample (n = 27) represents an ontogenetic series of femora of a single, species-level taxon because of the large size range of femora attributable to *Asilisaurus kongwe* or found in nearby bonebeds consisting almost exclusively of *A. kongwe* material. As *Asilisaurus* matured, different bone scars developed at different times. To understand the relative order of appearance of these bone scars, we utilized the common assumption that size is correlated with relative age; i.e., larger femora are at a later developmental stage than smaller femora. However, because the development of bone scars is indicative of skeletal maturity, this assumption is challenged by the abundant variation in bone scar presence and appearance between femora of roughly the same size (and therefore the same assumed developmental stage), showing that similarly sized individuals can represent several stages of skeletal maturity. Additionally, some smaller femora appear to be more skeletally mature than some larger femora when presence of bone scars is taken as indicative of skeletal maturity. This suggests that femoral size and relative skeletal maturity (as measured by degree of bone scar development) are somewhat disjunctive, although size gives a rough estimate for skeletal maturity in our sample in the largest and smallest individuals.

The use of size as a proxy for developmental maturity in paleontology has been challenged in other studies: overall long bone size is a poor indicator of skeletal maturity in the Late Triassic sauropodomorph *Plateosaurus engelhardti*, a common early dinosaur (Sander and Klein, 2005; Klein and Sander, 2007). Osteohistology was used to determine skeletal maturity and change in growth rate in this dinosaur, and skeletally mature individuals were found across the entire size range sampled. In addition, different stages of growth (termed ‘fast growth’ and ‘slow growth’) were variable across sizes. Rejecting sexual dimorphism, the authors hypothesized that strong developmental plasticity, found in extant ectothermic reptiles as a response to environmental factors, is the cause of the large variability in size at maturity in *Plateosaurus* (Sander and Klein, 2005; Klein and Sander, 2007). Brochu (1992) explored the relationship between size and overall skeletal maturity in *Alligator mississippiensis*, finding that although an approximate relationship exists between maturity and size, there is a considerable amount of variability in developmental timing, and larger individuals cannot be assumed to be more developmentally mature than smaller individuals. At the level of individual skeletal elements, the relationship between size and maturity becomes even less clear: although a general trend of *A. mississippiensis* individuals from early stages of ontogeny always being smaller than individuals from very late stages holds, size ranges of ontogenetic stages overlap significantly. Most strikingly, a 50-mm-length alligator femur was found to be several developmental stages more mature than a 100-mm-length femur, and femora of a single length may represent up to four different ontogenetic stages (Brochu, 1992). Similarly, a study of the developmental pattern of ossification of the humerus, ulna, and femur in relation to size in *Ophiacodon* and *Dimetrodon* found that size correlates poorly with developmental stage in these animals (Brinkman, 1988). Noting the similarities between the nature of early-diverging...
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synapsid and crocodylomorph archosaur ontogeny, Brochu (1992) suggested that the pattern of poor correlation between size and maturity may be plesiomorphic to amniotes. The poorly understood relationship between overall size and developmental maturity is not simple and adds a complication to studying the ontogeny of fossil organisms, especially if developmental variation is characteristic of a species or clade.

The closure of neurocentral sutures has been used as an indicator of ontogenetic stage in archosauriforms, including phytosaurs (Irmis, 2007) and extant crocodilians (Brochu, 1996), in both of which the neurocentral sutures of the axial skeleton fuse in a posterior-anterior pattern during ontogeny. Notably, in nearly all A. kongwe vertebral specimens, the neurocentral sutures are open; however, in the largest specimen with femora and vertebral elements (NMT RB159, which possesses all mature character states but trochanteric fusion), the neurocentral sutures of the cervical, sacral, and caudal vertebrae are closed, suggesting that this individual is near skeletal maturity. If this specimen does represent a skeletally mature individual in which lateral growth has almost completely ceased, this provides a rough size at skeletal maturity for the A. kongwe femora. In our sample of A. kongwe femora, size seems to be somewhat correlated with relative age and developmental maturity, but there are enough exceptions to this trend to suggest that sequence polymorphism plays a large role in determining individual variation.

The OSA method allows for the visualization and quantitative analysis of sequence polymorphism, and the large number of equally parsimonious developmental sequences predicted by OSA, differing in major ways from the both the modal sequence and the qualitative sequence, indicates that sequence polymorphism is prevalent in our sample, resulting in a number of anomalously mature and immature specimens (Figs. 6, 7). The high level of agreement between our qualitative sequence (determined utilizing the assumption that size is a reasonable proxy for age) and the OSA modal sequence indicates that size correlates somewhat with developmental maturity in our sample. However, the large amount of polymorphism indicated by the OSA, as well as the poor correlation between femoral size and maturity score (R² = 0.1386; Fig. 5A), shows that this assumption of size as a proxy for developmental maturity is tenuous for much of our sample and cannot be relied on with any degree of certainty.

The lack of LAGs in the femora of Asilisaurus kongwe prevents a direct comparison between absolute ontogenetic age (based on annual LAGs) and development of bone scars on the external surface of the femur (maturity scores; see below), although the histology does not indicate a slowing or stoppage of growth in the individuals sampled. Because of this lack of data, we cannot test for any relationship between size and age or skeletal maturity and age. We histologically sampled femora with reconstructed lengths (Fig. 1; Table S1) that spanned much of the larger sizes and higher maturity scores observed across our total sample, and it was clear that no LAGs were present even in specimens with the highest maturity score or presumably from older individuals. Comparisons between the histology of the femora sampled (reconstructed sizes; Table S1), femur lengths, and maturity scores reveal a relationship that implies that (1) A. kongwe did not deposit annual LAGs during ontogeny and reached larger sizes recorded in our sample over years; or (2) A. kongwe grew rapidly and reached the large sizes and highest maturity scores in our sample in less than a year.

We reject the latter hypothesis for the following reasons. For all the femora in our sample (femoral lengths: 73.8–177.2 mm) to come from individuals less than 1 year in age, an extremely high rate of growth would be necessary, because the largest, most mature femur thin-sectioned (NMT RB226) is over twice the length of the smallest, least mature femur in the series (NMT RB169; Fig. 6; Table S1). The similarity between the bone tissues of Asilisaurus kongwe and the early theropod ‘Syntarsus’ rhodesiensis suggests that these two taxa had similar growth rates, and the femur of ‘Syntarsus’ rhodesiensis has been shown to require multiple years of growth to reach a size comparable to the largest femora of A. kongwe (Chinsamy, 1990), indicating that A. kongwe would require several years of growth at a similar rate to reach full size. Further, the absence of LAGs may be common for silesaurids: a femur from an unnamed silesaurid recently recovered from the Middle Triassic Ntawere Formation of Zambia also lacks LAGs, despite its exceptionally large size (~350 mm in length; Peecook et al., 2013).

The bone tissue present in A. kongwe provides evidence against the presence of growth rates high enough to achieve adult body size in 1 year. Although the sustained fibrolamellar tissue complex present in A. kongwe indicates a relatively more rapid rate of growth than that of extant crocodilians (Padian et al., 2004; Huttenlocker et al., 2013), collagen fibers are more organized and arranged circumferentially in a large portion of the cortices of the elements thin-sectioned (Fig. 4C, D, G), indicating a slower rate of growth for much of the latter part of life in the individuals sampled (Huttenlocker et al., 2015). The vascular size and level of vascularization in A. kongwe are much less than in extant birds (Castanet et al., 1996; Horner et al., 2001; Padian et al., 2001; Starck and Chinsamy, 2002), which commonly attain adult body size in under a year (Padian et al., 2004; Stark and Chinsamy, 2004). Thus, similarly vascularized tissue would be expected in A. kongwe if the taxon reached adult size in the same time. Longitudinal vascular canals dominate the cortices of all elements (Fig. 4), with only some slightly anastomosing canals, and this vascular style is characteristic of slower growth rates relative to strongly anastomosing, radial, and lami-nar vascular styles (Castanet et al., 1996, 2000; Padian et al., 2001). However, growth had not completely ceased in the individuals sampled, as evidenced by anastomosing, vascularized perosteal surfaces (Fig. 4) and lack of external fundamental system (EFS) in all elements, indicating that no element thin-sectioned belonged to a fully skeletally mature individual in which lateral growth had ceased. We therefore hypothesize that A. kongwe did not deposit annual LAGs but that continuous, multi-year growth was typical of this species, and that the majority if not all of the elements thin-sectioned were from individuals at least 1 year old. This hypothesis may be falsified with the discovery of annual LAGs in larger A. kongwe femora; however, based on observations of neurocentral suture fusion, one of the largest specimens included in our sample is probably near skeletal maturity (NMT RB159), and this would preclude the discovery of femora much larger than those present in our current sample.

**Implications for Growth and Evolution of Non-Dinosaurian Dinosauromorphs**

The similarity between the femoral ontogeny of Asilisaurus kongwe and the ontogenetic changes in the bone scars of the proximal portion of the femur in the Late Triassic non-dinosaurian dinosauriform Dromomeron gregorii (Nesbitt et al., 2009) suggests that certain ontogenetically controlled features may be common throughout Dinosauromorpha. Smaller specimens of D. gregorii (TMM 31100-764, 1234, and 1308) do not possess either an anterior trochanter or a trochanteric shelf, and because of the appearance of both at the same ontogenetic stage (appearing in the two largest specimens, TMM 3100-464 and 1306), Nesbitt et al. (2009) suggested a coupling of the anterior trochanter and trochanteric shelf in development, similar to what is present in A. kongwe. Both anterior trochanter and trochanteric shelf are absent in all specimens of the non-dinosauriform dinosauromorphs Lagerpeton chanarensis and Dromomeron romeri, and because absence of these features in some specimens of D. gregorii was thought by Nesbitt et al. (2009) to be ontogenetically controlled, this indicates that the
described specimens of both *L. chanarensis* and *D. romeri* may represent a developmental stage too immature to display the anterior trochanter and trochanteric shelf. This variability in the presence or absence of the anterior trochanter introduces a complication in the methodological evolution of archosaur systematics, in which it has been considered a crucial character. Many archosaur phylogenies (Gauthier, 1986; Novas, 1992; Langer and Benton, 2006) have followed Bakker and Galton (1974) in using the presence of an anterior (= ‘less’) trochanter to separate early dinosaurs from other archosaurs. Similarly, the trochanteric shelf, along with the anterior trochanter, have been hypothesized to be synapomorphies of Dinosauriformes (Novas, 1996).

The trochanteric shelf and anterior trochanter are hypothesized to have evolved as a single unit, as opposed to the trochanteric shelf appearing earlier in ornithodiran evolution than the anterior trochanter (Nesbitt et al., 2009), following Hutchinson’s (2001) hypothesis of the M. iliobicipitalis splitting into the M. ilipectoralis externus and the M. iliobicipitalis in the evolution of bird-line archosaurs. The fact that both *Lagerpeton chanarensis* and *Dromomeron romeri* lack these muscle characters introduces a complication to this hypothesis, because this absence could indicate that the anterior trochanter and trochanteric shelf of dinosauriforms have a different evolutionary history than that of *D. gregorii*, and the shared character is the result of convergent evolution, not homology. However, the anterior trochanter and trochanteric shelf could be plesiomorphic in Dinosauria, and simply secondarily absent in *L. chanarensis* and *D. romeri*, or the individuals known from these species are too developmentally immature to possess these characters. The close ontogenetic variability of these features in the early-diverging ornithodirans *D. gregorii* and *A. kongwe* indicates that care should be taken in using the presence or absence of these features as an important indicator in archosaur systematics, especially with the consideration that archosaurian muscle scars increase in prominence as the individual grows (Brochu, 1992).

The fourth trochanter of *D. gregorii* displays ontogenetic change in morphology similar to that described in *A. kongwe*. The morphology of the fourth trochanter is mound-like with a central rounded ridge (TMM 31100-1234), whereas larger specimens of *D. gregorii* (TMM 31100-464 and 1306) show a bulbous, ridgeless distal end of the fourth trochanter, although the proximal portion of the trochanter retains the morphology of smaller specimens (Nesbitt et al., 2009). This development is similar to the progression we described in *A. kongwe* (see above), because the fourth trochanter changes from a gracile, ridged fourth trochanter in smaller specimens to a robust, rounded shape in larger specimens. Also notable is the development of an anterior-posterior expansion of the distal end of the fourth trochanter in the two larger specimens of *D. gregorii* (Nesbitt et al., 2009), which may be compared with the development of the protrusion on the distolateral face of the fourth trochanter that is present in most larger specimens of *A. kongwe* (NMT RB217, RB215, RB216, RB213, RB171, RB159, RB226; SAM-PK-10598). In both *A. kongwe* and *D. gregorii*, the fourth trochanter is present in all specimens, and as such its presence is far less variable than the anterior trochanter and trochanteric shelf. This is unsurprising, because even hatching *Alligator* individuals possess a fourth trochanter (Brochu, 1992), and the muscle scar seems to be a widespread archosaurian character.

The similarity between the most common ontogenetic sequence of *A. kongwe* (both qualitative and the size-independent modal sequence) and the sequence described for *D. gregorii* (Nesbitt et al., 2009; based on length), along with the close phylogenetic relationship of the two taxa and the evidence for widespread sequence polymorphism in early dinosaurs (see below), suggests that sequence polymorphism may be present in *D. gregorii* development. However, because the series of *D. gregorii* femora lacks evidence of sequence polymorphism, sequence polymorphism may be a synapomorphy of Dinosauriformes and may be absent in *D. gregorii* and other non-dinosauriform sauropodomorphs. Alternatively, this lack of evidence may be the result of the small sample size of *D. gregorii* femora (n = 5) studied by Nesbitt et al. (2009). As more specimens are recovered, the increase in sample size will allow the presence or absence of sequence polymorphism in the ontogeny of this clade to be more rigorously tested, in addition to allowing better resolution in the relative developmental timing of different bone scars.

Although both the line of intermusculi caudalis and the line of intermusculi caudalis are present in *D. gregorii*, the order of development described by Nesbitt et al. (2009) is the opposite of that which we have qualitatively described in *A. kongwe*. The line of intermusculi caudalis is only present in the largest specimen of *D. gregorii* (TMM 31100-1306), and the line of intermusculi caudalis appears early in ontogeny, and is present in all but the smallest femur of *D. gregorii*. In *A. kongwe*, we observed the reverse: the line of intermusculi caudalis is present in all but the smallest specimen (NMT RB169) with one exception (NMT RB185), whereas the line of intermusculi caudalis develops slightly later, first appearing in the sixth femur in the series (NMT RB109); this same order holds in the OSA modal sequence. The presence of both muscle scars in *D. gregorii* and *A. kongwe* support Hutchinson’s (2001) hypothesis that these intermuscular lines are archosaur synapomorphies, but this hypothesis may require revision in the future, because the presence of these characters seems to be at least partly tied to developmental timing. Because the presence of many phylogenetically important characters appears to be at least partially ontogenetically controlled for these early-diverging dinosauromorphs, care should be taken in their utilization as important characters in systematics.

A series of 14 nearly complete femora ranging from roughly 90 to 110 mm in length are known from the silesaurid *Sacisaurus agudoensis* (Langer and Ferigolo, 2013); however, these femora lack variation similar to that reported for *Dromomeron gregorii* (Nesbitt et al., 2009) or that we have reported in *Asilisaurus kongwe*. All described femora of this taxon possess the same bone scars as the most skeletally mature individuals of *Asilisaurus* except for the trochanteric shelf, the line of intermusculi caudalis, as well as a developed linea intermusculi caudalis—although a ridge extends distally from the fourth trochanter along the posteralateral surface of the femur, similar to *Asilisaurus*, it does not extend to the proximal half of the femur (Langer and Ferigolo, 2013). All *S. agudoensis* femora also possess a flange-like dorsolateral trochanter similar in morphology to that of *Silesaurus opolensis* (Piecchowski et al., 2014) and an unnamed Otis Chalk silesaurid (TMM 31100-1309; Nesbitt et al., 2010), as well as *Tawa hallae* (GR 241; Nesbitt et al., 2009). Lack of these three bone scars in *S. agudoensis* could indicate that all described femora of this taxon belong to skeletally immature individuals or that this taxon does not possess the same ontogenetic trajectory. Potentially, recovery of more *S. agudoensis* femora across a larger size range or histological sampling could resolve this dilemma.

A recent study of a hypothesized growth series (n = 33) of *Silesaurus opolensis* femora reported a large amount of variation in bone scars of the proximal end of the femur, quantified by measurements of distances between several femoral landmarks (Piecchowski et al., 2014). This study reported a smaller number of variable femoral ossifications than we have reported for *Asilisaurus*, probably because of the smaller size range of femora (roughly 140–200 mm in length) available for study; however, the authors acknowledge that the study only compares femora of later ontogenetic stages, and they use previously published
histology (Fostowicz-Frelík and Sulej, 2010) and degree of neurocentral suture fusion (Brochu, 1996; Irmis, 2007) to estimate that at least most of the S. opolensis femora in the sample are close to skeletal maturity.

Piechowski et al. (2014) reported that four ossifications show variation in the sample, with these features present in five of the longest individuals: the anterolateral scar (= ‘dorsolateral ossification’ of Piechowski et al., 2014), the distal protrusion on the fourth trochanter (= ‘fourth trochanter ossification’ of Piechowski et al., 2014), the trochanteric shelf, and an ‘overhang structure’ on the distolateral end of the femoral head (also present in A. kongwe; Fig. 2) interpreted as a calcification of articular cartilage. The authors report two classes of Silesaurus femora, those lacking these ossifications and those possessing them, and propose that the four ossifications developed simultaneously in ontogeny. Additionally, the lack of a postomedial tuber (= ‘tuber’ of Ezcurra, 2006) is reported as being associated with presence of the ossified structures. The anterior, dorsolateral, and fourth trochanters are not variable, but present in all femora figured (Piechowski et al., 2014:figs. 2, 4, 10). How closely associated the anterior trochanter and trochanteric shelf are in those individuals that possess both is unreported, as is the presence/absence of the linea intermusculares and insertion of the M. caudofemoralis brevis.

We report that the presence/absence of all bone scars but the fourth trochanter is variable in our sample of A. kongwe femora, and that the scars appear to develop at different times during ontogeny, rather than simultaneously. Because of the similarity between the bone scars and the close relation of these taxa, we hypothesize that the femoral bone scars of Silesaurus opolensis also follow this pattern of sequential rather than simultaneous development. Because only five of the S. opolensis femora were reported to possess the variable femoral features, the sample size over the given length range may be too small to determine the relative timing of development of these features. The postomedial tuber, which is reported to be absent in those S. opolensis femora possessing the four variable femoral ossifications, is present in Asilisaurus femora possessing these same ossifications (e.g., NMT RB156; Fig. 2). Additionally, we report variation in femoral features not reported to be variable in the S. opolensis sample, such as the presence of the anterior trochanter, and this is probably because of the lack of smaller femora of S. opolensis.

We predict that as more S. opolensis femora are recovered, variation more in line with what we have reported in Asilisaurus will be observed, and that smaller femora will show variation in these features not thought of as constant in Silesaurus (e.g., the anterior trochanter).

In the absence of absolute ontogenetic age data, femoral size was taken as an approximation of ontogenetic age in Silesaurus opolensis, although the lack of strict correspondence between size and age was acknowledged (Piechowski et al., 2014). Although the five femora with the most bone scars and ossifications are some of the largest, Piechowski et al. state that “size ranges of Silesaurus opolensis femora with and without [the four additional] ossifications overlap strongly … [and] the range of variability … seems to be largest among specimens close to the mean of the sample” (2014:1391). They do not interpret this variation as intraspecific variation but as sexual dimorphism, drawing on the apparently bimodal split between those similarly sized individuals that lack extra ossifications and possess the postomedial tuber and those that lack the postomedial tuber but possess extra ossifications. Piechowski et al. (2014) follow Raath (1990) in hypothesizing that the more robust femora in the population represent females.

Following our interpretation of variation in femoral scars in Asilisaurus individuals of similar size, we interpret similar variation in Silesaurus opolensis femora as intraspecific variation in growth trajectories, and not sexual dimorphism. Although Piechowski et al. used 33 femora in a principal component analysis (PCA), only 12 femora (plus one very incomplete femur) were used to chart the bimodal ossification patterns that were used to hypothesize sexual dimorphism (2014:fig. 10), limiting the opportunity to observe any intrapopulation variation in bone scars. Because only five ossification structures were variable, and were always present together, there is currently no evidence of sequence polymorphism in this species; however, the reported variability is consistent with (1) size as a poor correlate for age in this size range, or (2) size as a poor correlate for skeletal maturity as measured by bone scar development in this size range, or (3) a combination of both of these factors. As in A. kongwe, variation in bone scar development between similarly sized individuals could indicate that similarly sized individuals are of different ages, that bone scars develop at different ages in different individuals, or that both of these factors are complicating the ontogenetic signal, even if sequence polymorphism in relative timing of bone scars is completely absent in S. opolensis. We hypothesize that the recovery of more S. opolensis specimens will eliminate the bimodal distribution of presence/absence of the four variable bone scars. Further histological investigation could provide a control on ontogenetic age in this population, because LAGs have been reported in the tissues of S. opolensis long bone elements (Fostowicz-Frelík and Sulej, 2010).

**Implications for Growth in Early Dinosaurs**

Asilisaurus, being both one of the earliest known bird-line archosaurs and an early-diverging non-dinosaurian dinosauriform (Nesbitt et al., 2010), is in an excellent temporal and phylogenetic position to guide understanding of developmental traits plesiomorphic for dinosaurs. Whereas differences in bone fusion and appearance and morphology of bone scars have been used as evidence for sexual dimorphism in some early dinosaurs (‘Syntarsus’ rhodesiensis, Raath, 1977, 1990; Coelophysis bauri, Colbert, 1990; Thecodontosaurus antiquus, Benton et al., 2000), our data from Asilisaurus kongwe suggest that this variability can also be explained by understanding the differences in the developmental sequences between individuals in a population, especially sequence polymorphism. The existence of a common developmental trajectory taken by most individuals of A. kongwe, with variation resulting from a deviation from this trajectory, indicates that sequence polymorphism is the major cause of variation observed in the bone scars of the proximal portion of the femur. Depending on the feature in question, size alone may be a poor indicator of maturity or musculoskeletal development in A. kongwe, with some individuals maturing at both different rates and in different sequences than the majority. The relatively large sample size (n = 27) across a wide size range (73.8–177.2 mm) of femora utilized in this study, as well as the large number of muscle features analyzed (n = 11, including the fusion observed between the anterior trochanter and the trochanteric shelf), allows a clearer picture of early ornithodiran ontogeny than previously available, especially of patterns that may be plesiomorphic for dinosaurs or more inclusive clades (e.g., Dinosauriformes, Dinosaururomorpha). Because ontogenetic series of early dinosaurs and other bird-line archosaurs are rare, the ontogeny of A. kongwe can serve to help interpret developmental patterns and variation found in closely related animals, especially early dinosaurs.

Morphological variation similar to that which we described for Asilisaurus kongwe has been described in various elements of the postcranium of the Early Jurassic coelophysoid theropod ‘Syntarsus’ (= Megagnosaurus) rhodesiensis (Raath, 1977, 1990). These studies also focused on variation in femoral muscle scars, and although most variation is interpreted as a function of age, Raath found “unequivocal evidence of bimodal variation” (1990:96) in the muscle scars and trochanters of the femur, with
robust morphs possessing a more highly developed musculature than the gracile morphs. Features of the robust morph described by Raath (1977, 1990) include a bulbous and rugose ‘greater trochanter,’ a broad lesser trochanter, the presence of an obturator ridge sensu Raath (1977, 1990), a posterior femoralis region outlined by heavy scarring, a rugose and sharply rimmed insertion pit for the CFB, and a rugose distal patellar ridge. In contrast, the gracile morph is described with a flat and smooth ‘greater trochanter,’ a narrow lesser trochanter, the absence of an ‘obturator ridge,’ lack of scarring in the posterior femoralis region, the insertion pit for the CFB smooth and not sharply rimmed, and a smooth distal patellar ridge.

In ‘Syntarsus’ rhodesiensis, robust femoral features are only found in specimens of a certain size (quantified by maximum width of femur head), and all specimens below this ostensible ontogenetic stage, as well as some above it, exhibit gracile features (Raath, 1977, 1990). The apparent bimodal distribution found in these muscle features, along with the presence of both morphs in individuals of similar size, led the author to conclude that the variation found in ‘Syntarsus’ rhodesiensis is the result of sexual dimorphism, with the point where robust features first appear in ontogeny as the hypothesized age of sexual maturity. All 10 of the robust femora are at or above this hypothesized stage of development, and of the eight gracile morphs four are above this size.

A robust/gracile dichotomy has also been reported in the femur of the Triassic coelophysoid Coelophysis bauri, with the robust morph differentiated from the gracile by an enlarged trochanteric shelf, and this along with proportional differences has been suggested to be indicative of sexual dimorphism in this species (Gauthier, 1984), although the Coelophysis material was not actually examined for Gauthier’s (1984) study. Ostensible bimodal variation in proportional differences in C. bauri individuals, also termed ‘robust’ and ‘gracile,’ has been described between two individuals of roughly the same size (Colbert, 1990), although these terms referred to differences in postcranial element proportions and sacral fusion patterns, not femoral morphs as in ‘Syntarsus’ rhodesiensis (Raath, 1977, 1990). These proportional differences were also interpreted as sexual dimorphism and not intraspecific variation (Colbert, 1990), and others have followed this interpretation for variation in cranial and postcranial proportions in the Ghost Ranch population of C. bauri (Gay, 2005; Smith and Merrel, 2006; Rhinehart et al., 2009). However, the claim that bimodal variation is present in this population has been disputed (Genin, 1992).

The noasaurid theropod Masiakasaurus knopfleri has also been reported to possess a robust/gracile dichotomy in the bone scars of the femur, as well as in bone scars of the tibia and fusion of the tibia and astragalocalcaneum, that was poorly correlated with size (Carrano et al., 2002; Lee and O’Connor, 2013). In the sample of 13 femora described, robust individuals possessed prominent bone scars, whereas gracile individuals either completely lacked scars or had very poorly developed scars; in the 12 tibiae described, the same pattern holds, with gracile individuals also lacking fusion of the tibia and astragalocalcaneum (Carrano et al., 2002). This variation is described as bimodal, although a detailed description of what scars are absent or present in each individual was not presented in this study. A recent study of the osteohistory of M. knopfleri found that individuals grew differently, with variation in the ages and sizes at which maturity was reached in this taxon (Lee and O’Connor, 2013). The authors interpret this variation as developmental plasticity, similar to interpretations of Plateosaurus (Sander and Klein, 2005; Klein and Sander, 2007), except Lee and O’Connor (2013) argue that this plasticity in response to environmental factors only occurred in the earliest stages of ontogeny, after which the growth trajectory was set. The two robust M. knopfleri individuals thin-sectioned in this study (one femur and one tibia) did not have the largest asymptotic size or fastest growth rate, and there was no clear ontogenetic trend in either morph, although the robust morphs are both at or very close to complete cessation of linear growth. Because of this, Lee and O’Connor (2013) interpret these two morphs as two different states of maturity, with the robust morphs as the mature state, similar to our interpretation of Asilisaurus kongwe variation.

Based on our observations of the ontogeny of A. kongwe, we suggest that the similar variation present in the femur of ‘Syntarsus’ rhodesiensis individuals of similar size is not the result of sexual dimorphism but is another example of variation caused by sequence polymorphism. The lack of robust morphs in smaller specimens indicates that the development of robust musculature is at least partially tied to developmental timing, and we hypothesize that the four larger gracile specimens are simply less developmentally mature than their more robust counterparts. It should be noted that all Raath’s (1990) gracile specimens above the hypothesized age of sexual maturity are still smaller than the mean robust morph; whereas individuals at a late stage of ontogeny are clearly large and robust, and those at an early stage are smaller and gracile, there is an area of overlap between the two extremes, with developmental maturity being mostly unrelated to size during a significant portion of development. Because Coelophysis bauri is both closely related and morphologically similar to ‘Syntarsus’ rhodesiensis, this explanation of the variation in the postcranial skeleton of ‘Syntarsus’ should be considered when interpreting variation in C. bauri. Variation in bone fusion and bone scars in C. bauri has been reported (Colbert, 1989, 1990) but not in detail, and the majority of these characters are not available for study in A. kongwe, limiting our ability to compare these taxa.

Whereas polymorphism is more pronounced in A. kongwe, possibly as a result of the larger sample size and number of features studied, bimodal variation is absent. Although we have described the presence of less-developed, gracile morphs of larger size and more-developed robust morphs, most muscle features tend to be variable on a continuum and the presence or absence of certain muscle features does not necessarily correlate with the presence or absence of others in the same individual. We suggest that this ontogenetic pattern of individual variability in the timing of muscular development is plesiomorphic for Dinosauria and should be considered when interpreting variation observed between individuals within a dinosaurian species, especially early-diverging dinosaur taxa. A thorough understanding of individual and developmental variation is a vital part of properly understanding the phylogeny of early dinosaurs, particularly coelophysoids (Tykoski, 2005). A phylogenetic study that assumes all taxa are known from adult individuals may place those taxa only known from immature individuals in artificially basal positions relative to other taxa in the analysis, and simply removing data by ignoring ontogenetically variable characters does little to rectify this problem (Tykoski, 2005). Treating characters known to be ontogenetically variable as missing data instead of absent in specimens thought to be developmentally immature may present a better method for dealing with this difficulty (Tykoski, 2005), but more work on ontogenetic variability in phylogenetically important characters is necessary to resolve this difficulty.

CONCLUSION

The close relative of dinosaurs Asilisaurus kongwe is a fast-growing dinosauriform that has similar bony tissues throughout the long bones. Our sample of different sizes of long bones of A. kongwe represents an ontogenetic series, but with the exception of the smallest and largest femora, the relative ages of the specimens sampled are poorly constrained because of a large amount of intraspecific variation in bone scar development. Absolute
age is unknown because no LAGs are present within long bones. The femur provides the best record of ontogeny in *A. kongwe*. The 11 scars of the proximal end of the femur of *Asilisaurus kongwe* do not appear simultaneously in ontogeny, but have a developmental order that is fairly consistent in most individuals. However, sequence polymorphism is common, and size is a poor indicator of skeletal maturity in many specimens: some smaller individuals appear anomalously mature and some larger individuals appear underdeveloped, whereas some femora appear more robust than others of the same size. This variability in development is well known in extant vertebrates, and similar variability has been observed in early dinosaurs and non-dinosaurian dinosauromorphs; however, in dinosaurs, it has often been interpreted as sexual dimorphism. This ontogenetically controlled variability in the presence and appearance of femoral scars must be accounted for when undertaking phylogenetic studies, and although some solutions to this difficulty have been proposed, more work on the impact of ontogenetically variable characters on phylogenetic studies is necessary. Because sequence polymorphism is common in many extant animals, and the similarities between *A. kongwe* development and the development of early dinosaurs indicate that this pattern may be plesiomorphic to dinosaurs, developmental sequence variation should be investigated when studying intraspecific variation and growth in dinosaurs and close dinosaur relatives.

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