

# Differential Limb Scaling in the American Alligator (*Alligator mississippiensis*) and Its Implications for Archosaur Locomotor Evolution

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## ABSTRACT

Bipedalism evolved multiple times within archosaurs, and relatively shorter forelimbs characterize both crocodyliforms and nonavian dinosaurs. Analysis of a comprehensive ontogenetic sequence of specimens (embryo to adult) of the sauropodomorph *Massospondylus* has shown that bipedal limb proportions result from negative forelimb allometry. We ask, is negative forelimb allometry a pattern basal to archosaurs, amplified in certain taxa to produce bipedalism? Given the phylogenetic position of extant crocodylians and their relatively shorter forelimb, we tested the hypothesis that prevalent negative forelimb allometry is present in *Alligator mississippiensis* from a sample of wild specimens from embryonic to adult sizes. Long bone lengths (humerus, radius, ulna, femur, tibia, fibula, third metapodials) were measured with their epiphyseal cartilage intact at all sizes. Our results show an overall isometric pattern for most elements regressed on femur length, humerus length, or total limb length. However, negative allometry was prevalent for the ulna, and the third metapodials scale with positive allometry embryonically. These data suggest that the general forelimb proportions in relation to the hindlimb do not change significantly with increasing size in *A. mississippiensis*. The negative allometry of the ulna and embryonically positive allometry of the third metapodials appears to be related to maintaining the functional integrity of the limbs. We show that this pattern is different from that of the sauropodomorph *Massospondylus*, and we suggest that if bipedalism in archosaurs is tied, in part, to negative forearm allometry, it was either secondarily lost through isometric scaling, or never developed in the ancestor of *A. mississippiensis*. Anat Rec, 292:787–797, 2009. © 2009 Wiley-Liss, Inc.

**Key words:** crocodylia; *Alligator mississippiensis*; morphometrics; allometry; bipedalism

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The Archosauria is a diverse vertebrate clade that includes the extant Crocodylia and Aves, as well as numerous extinct lineages such as nonavian dinosaurs and pterosaurs (see Brochu, 2001 for an overview). The evolution of bipedal posture is a recurring theme among the Archosauria (Hutchinson, 2006). Although the common ancestor of all archosaurs was probably quadrupedal (Brochu, 2001; Hutchinson, 2006), bipedalism associated with an erect posture characterizes the earliest dinosaurs (Carrano, 2000; Benton, 2004) and may have been present in some early crocodylomorphs (e.g., *Terrestrisuchus*; Sereno and Wild, 1992; Dodson, 2003). Certainly, the origin of bipedalism among various clades of archosaurs probably resulted from a complex mosaic of postural, locomotor, developmental, and heterochrony adaptations (e.g., Long and McNamara, 1995; Livezey, 1995; Carrano, 2000; Benton, 2004; Hutchinson, 2006).

Bipedalism in both fossil crocodyliform and dinosaur taxa has been diagnosed, in part, on the relative length of the forelimb compared with the hindlimb (Middleton and Gatesy 2000; Dodson 2003; Benton 2004). In most nonavian and avian theropod dinosaurs, for example, forelimb length is significantly shorter than the hindlimb (e.g., Middleton and Gatesy 2000) and this pattern is even retained in several extant avian taxa (e.g., Livezey, 1995; Dyke et al., 2006). Recently, Reisz et al. (2005) reported a heterochronic allometric pattern between the forelimb and hindlimb in the sauropodomorph *Massospondylus* over an ontogenetic series. Their data suggest that the forelimbs of this dinosaur became relatively shorter compared with the femur throughout ontogeny, resulting in bipedal limb proportions in the adult. Thus, Reisz et al. (2005) inferred that hatchling *Massospondylus* initially retained quadrupedal limb proportions, and further suggested that quadrupedal posture might be plesiomorphic for sauropodomorphs. In other words, the posture of quadrupedal sauropodomorphs was a paedomorphic retention of the juvenile pattern. Intriguingly, such a pattern may extend into other sauropodomorph dinosaurs (see Bonnan and Senter, 2007).

The *Massospondylus* (Reisz et al., 2005) data suggest more broadly that the prevalence of archosaur bipedalism may arise, in part, because of a deeply embedded developmental pattern of differential limb allometry. Could such a pattern persist in the most basal extant archosaurs, the crocodylians? Is it possible that the relatively longer hindlimbs in crocodylians arise due to negative allometric scaling of the forelimbs in relation to the hindlimbs throughout ontogeny? Does archosaur bipedalism arise due to an "amplification" of negative forelimb allometry with increasing size?

Here, we tested the hypothesis that the forelimb scales with negative allometry against femur size in the American alligator, *Alligator mississippiensis*. A sample from a single population of wild individuals from embryonic to adult stages provided us with an excellent opportunity to adequately test our hypothesis. Moreover, among crocodylians, the relatively generalized ecology and behavior of *A. mississippiensis* makes it an excellent model for general crocodylian limb anatomy (Meers, 2003). We predicted that our results should resemble in some form those of Reisz et al. (2005) for *Massospondylus*: prevalent negative forelimb allometry should account for the differences in the relative lengths between the forelimb and hindlimb in *A. mississippiensis* with increasing size.

## MATERIALS AND METHODS

### Specimens

All embryonic and postnatal specimens in this study were wild and were collected and euthanized by Louisiana Department of Wildlife and Fisheries biology staff under general scientific collection permits on the state-owned Rockefeller Wildlife Refuge (Chenier, LA) as part of an annual harvest. Postnatal specimens used in this study were donated to MFB as salvage from other studies. A total of 85 embryonic to adult specimens were measured for this study. Given that deviations in temperature not only influence sex determination in crocodylians (Pough et al., 1998) but may also effect average long bone lengths as they do in other reptiles and birds (e.g., Braña and Ji, 2000; Hammond et al., 2007), 49 embryonic specimens were collected randomly from six clutches starting approximately eight days after oviposition. Embryos were incubated at moderate temperatures (~31–32° C) (Allsteadt and Lang, 1995). Our procedure thus ensured that long bone growth was typical, because it is higher temperatures that lead to exaggerated long bone length in other sauropsid embryos (see Braña and Ji, 2000; Hammond et al., 2007). The embryos were collected by one of us (RME) biweekly and fixed in a 10% buffered formalin solution. Embryos were subsequently cleared and stained for cartilage, bone, or both following standard procedures (Dingerkus and Uhler, 1977; Hildebrand and Goslow, 2001). A total of 36 juvenile, sub-adult, and adult specimens were also collected at RWR from which limb measurements were taken.

Ideally, a sample of several crocodylians including *A. mississippiensis* would be measured to generate a larger, comparative dataset. Indeed, previous studies have compared the ossification patterns of various crocodylians simultaneously (e.g., Knüsel, 1944). However, we focused on *A. mississippiensis* both for practical and functional reasons. Many species of crocodylians are threatened or endangered, and it would be impractical to obtain large ontogenetic series from these animals. Moreover, the availability of numerous salvage specimens and embryos from *A. mississippiensis* made this study possible. Finally, the generalized ecology and functional morphology of *A. mississippiensis* (Meers, 2003) makes this species an ideal anatomical "intermediate" among the more specialized crocodylian taxa.

### Measurements and Data Collection

The length of the major forelimb (humerus, radius, ulna, metacarpal III) and hindlimb (femur, tibia, fibula, metatarsal III) long bones were measured in all specimens. In addition, distance measures of the deltopectoral crest (humerus) and fourth trochanter (femur) from the proximal ends of their respective elements were obtained. Following other morphometric studies of long bone heterochrony in dinosaurs and other archosaurs (e.g., Long and McNamara, 1995; Carrano, 2000; Middleton and Gatesy, 2000), total forelimb and hindlimb lengths were calculated as (humerus + radius + metacarpal III) and (femur + tibia + metatarsal III), respectively. It should be noted that the radiale and ulnare carpal bones of *A. mississippiensis* are elongate elements that may augment the relative length of the forelimb. Although these elements were not measured as part of

the overall forelimb length, their contribution was considered in the evaluation of our data (see Discussion).

For cleared and stained embryonic specimens, measurements were taken from standardized digital images collected from a digital camera or digital microscope imager (Celestron 22240). Image J software (NIH) was used to measure each of the embryonic limb elements, whereas juvenile and adult long bone measurements were captured using digital calipers. For consistency, all elements were measured with their articular (epiphyseal) cartilage intact. This posed no problems for the embryonic specimens whose cartilage was preserved and highlighted in the clearing and staining process. For juvenile, sub-adult, and adult limbs, lengths of all long bones except the metapodials were measured immediately upon dissection of the limbs to ensure that cartilage shrinkage due to dessication would not affect our results. Subsequent re-measuring of these elements immersed in a warm water bath (60°C) up to 24 hr after dissection revealed no significant changes in long bone dimensions (Sandrik, unpublished thesis; see Wright et al., 2005 for similar results with nasal septal cartilage).

Accurate *in situ* measurement of the metapodials posed a problem because these elements are deeply embedded in the manus or pes and bound by ligaments, making immediate measurement problematic. One of us (JLS) found that across juveniles and adults, ~6% of long bone length is composed of the epiphyseal cartilage (Sandrik, unpublished thesis). Therefore, after maceration and disarticulation of the manus and pes, metacarpal III and metatarsal III were measured, and an additional 6% of their total length was added to these measurements to account for the lost cartilage. Regression of metapodial measurements with and without cartilage adjustment yielded nearly identical results. Therefore, only the cartilage-adjusted results are reported here.

Femur length was used as a proxy for overall body size and mass for several reasons. First, femur length has been shown to be strongly correlated with body size and mass in numerous tetrapods including *A. mississippiensis* (see Farlow et al., 2005; Bonnan et al., 2008). Second, for the embryos, femur length was more easily standardized and measured. Direct measurement of total body size, in contrast, presents difficulties in embryos because of the dorsoventral curvature of the embryonic torso, and because head-rump length, while a good proxy for age, is not easily comparable with total body size. Finally, the femur is the main weight-support and propulsive element in archosaurian locomotion (Hutchinson, 2006) and provides an indirect means of comparing locomotor performance with size (see e.g., Bonnan et al., 2008).

SPSS software (v. 16) was used for normality tests, log10 transformation, and graphing of the results. Before performing any statistical analysis, all data were log10 transformed to normalize their distribution (Zar, 1999). Log10 transformation was preferred over the natural log because the results are more intuitive and for comparative purposes to recent studies on *A. mississippiensis* that also utilized this transformation (Farlow et al. 2005; Bonnan et al. 2008). Shapiro-Wilk tests were then used to determine if these data were normally distributed. Reduced major axis (RMA) regression of the log10 transformed variables was performed using 1,000 bootstrap replicates in a separate program, RMA Slope (Bohonak, 2004). In a “typical” or ordinary least squares

**TABLE 1. Shapiro-Wilk tests of normality on log10 transformed length measurements of *Alligator mississippiensis* limbs**

Measurement	Shapiro-Wilk Statistic	df	P
Femur	0.964	33	0.330
Humerus	0.956	33	0.202
Radius	0.961	33	0.267
Ulna	0.965	33	0.361
Metacarpal III	0.955	33	0.188
Tibia	0.960	33	0.266
Fibula	0.959	33	0.245
Metatarsal III	0.959	33	0.242
Deltopectoral Crest	0.954	33	0.175
Fourth Trochanter	0.964	33	0.344

Note that all measurements are normally distributed.

(OLS) regression, one variable is independent and assumed to have been measured without error (Zar, 1999). For biological samples, such criteria are difficult to meet because both variables in a given regression are continuous, sampled with error, and dependent (e.g., the humerus and femur are part of the same animal). RMA regression assumes that both variables are measured with error and are not independent, and this method is therefore preferred over OLS regression. RMA slopes were identified as allometric if the 95% confidence intervals did not include 1.0 (Leduc, 1987).

Slopes were compared between the embryonic and postnatal subsamples to test for significant differences in the limb proportions using a Student's *t*-test equation adapted from Zar (1999):

$$t = |b_1 - b_2| / s_{\text{error}}$$

where  $b_1$  is the postnatal slope,  $b_2$  is the embryonic slope, and  $s_{\text{error}}$  is the square root of the standard error of  $(b_1)^2$  plus  $(b_2)^2$ . Student's *t* values computed from this method were then compared against appropriate tables to determine if the slopes were significantly different from one another ( $\alpha = 0.05$ ).

## RESULTS

Shapiro-Wilk tests of the log10 transformed data reveal that all the variables are normally distributed (Table 1). Moreover, all RMA regressions reported here were robust and well-correlated ( $r^2 > 0.953$  for all parameters measured) (Table 2). RMA regression of log10 transformed long bone lengths on femur length yielded an almost universally isometric pattern (Fig. 1A,B, Table 2). That is, whatever the initial proportions of the elements were in relation to femur length did not change significantly with increasing size. The ulna was the only element to show negative allometry with increasing femur size, and only the distance measure of the fourth trochanter showed positive allometry (Fig. 1A,B, Table 2), which agrees with previous data from Dodson (1975). When forelimb elements are regressed on humerus length, an isometric pattern appears for the radius and metacarpal III, but once again the ulna shows negative allometry (Fig. 2, Table 2). As with the femur, positive allometry is reported for the relationship between deltopectoral crest distance and humerus length

**TABLE 2. RMA regression of linear measurements of *Alligator mississippiensis* long bone elements against total limb length**

Comparison	n	RMA Slope	r <sup>2</sup>	95% CI
Forelimb vs. Hindlimb	68	0.9829	0.991	0.956–1.024
Humerus vs. Femur	85	1.003	0.991	0.973–1.031
Radius vs. Femur	76	0.9634	0.987	0.920–1.006
Ulna vs. Femur <sup>a</sup>	75	0.9487	0.992	0.9248–0.9766
Metacarpal III vs. Femur	69	1.029	0.962	0.930–1.094
Tibia vs. Femur	76	0.9766	0.990	0.944–1.012
Fibula vs. Femur	77	0.9945	0.993	0.964–1.029
Metatarsal III vs. Femur	72	1.104	0.960	0.985–1.216
4th Trochanter <sup>b</sup>	62	1.121	0.971	1.047–1.206
Radius vs. Humerus	75	0.9871	0.993	0.958–1.016
Ulna vs. Humerus <sup>a</sup>	74	0.972	0.997	0.9596–0.9866
Metacarpal III vs. Humerus	68	1.057	0.953	0.923–1.140
Deltpectoral Crest <sup>b</sup>	64	1.192	0.976	1.135–1.258

<sup>a</sup>Negative allometry.

<sup>b</sup>Positive allometry.

(Fig. 2, Table 2), a result which differs from the isometric slope reported by Dodson (1975) for this measurement. Total forelimb and hindlimb lengths were also compared with one another as well as to separate elements within a given limb. For all comparisons except the ulna in the forelimb and the tibia in the hindlimb, isometry was reported (Fig. 3A,B, Table 3). Negative allometry was the result for both the ulna regressed on total forelimb length and the tibia regressed on total hindlimb length (Fig. 3A,B, Table 3).

The large difference in size between the smallest and largest individuals in the total sample was great enough that size alone could be swamping the effect of other signals in the data (Somers, 1989). In other words, the overall isometric pattern reported here could simply be due to the large size differences in the sample. Therefore, the total sample was divided into an embryonic and postnatal group. When regressed against the femur, all postnatal elements showed a pattern of isometry, but the embryonic sample showed negative allometry for the ulna and positive allometry for metacarpal III and metatarsal III (Table 4). The Student's *t*-test of the embryonic and postnatal slopes reflects these findings: there is a significant difference in slope for the ulna, metacarpal III, and metatarsal III between the subsamples (Table 4). When forelimb elements are regressed on the humerus in both sub-samples, there is a significant difference in the slope for metacarpal III: the embryonic specimens plot with positive allometry, whereas the postnatal subsample is isometric (Table 4). Against total forelimb length, there is a significant difference in the slopes reflected in the embryonic sample for the humerus (negative allometry), ulna (negative allometry), and metacarpal III (positive allometry) (Table 4). For total hindlimb length, only the slope of metatarsal III in the embryonic subsample (positive allometry) is significantly different from the isometric postnatal subsample (Table 4).

Finally, the relative proportions of the limb elements to one another were calculated (Table 5) and the trends

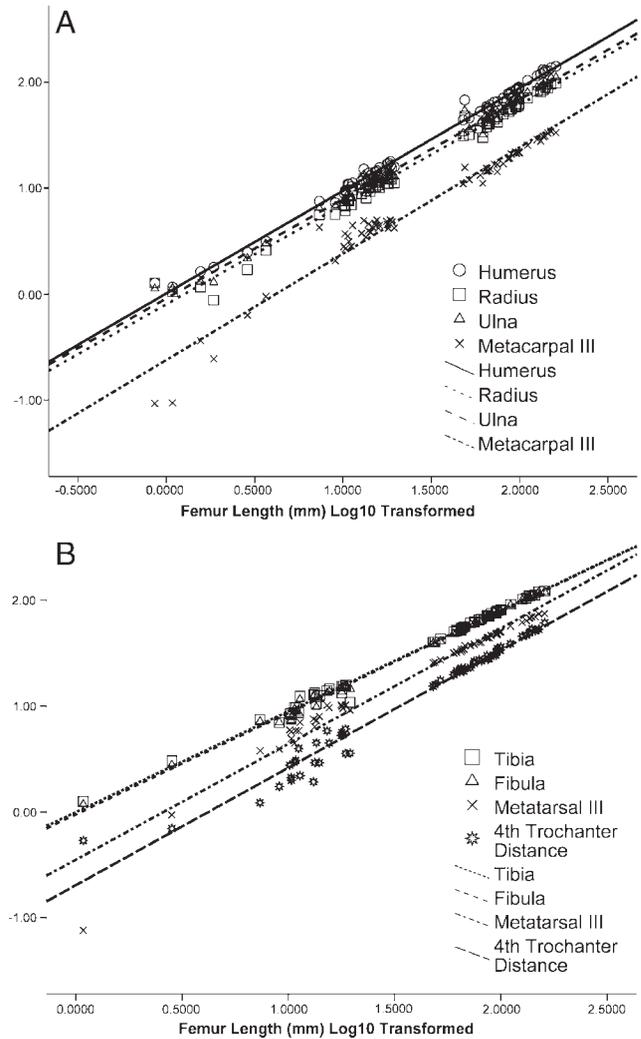


Fig. 1. Bivariate plots of long bone elements against femur length. All variables are Log10 transformed. Plot of **A**, forelimb long bones against femur length, and **B**, hindlimb long bones and fourth trochanter distance against femur length.

reported for the embryonic and postnatal subsamples are depicted in Fig. 4. In general, the proportions of the limb elements to one another were consistent with trends reported for archosaurs generally: the forelimbs were relatively shorter than the hindlimbs. On an average, the forelimb was ~22% shorter than the hindlimb, being 25% shorter in the postnatal subsample (Table 5). When compared with femur length, all elements except one show a decrease in their relative proportions within the postnatal subsample (Table 5). Only metatarsal III remains at ~51% the length of the femur regardless of size or subsample (Table 5). In the forelimb, the radius and ulna comprise ~80% of the humerus length, becoming slightly relatively shorter in the postnatal subsample (Table 5). Metacarpal III is a relatively small element and is on average only 27% the length of the humerus (Table 5).

Proportional contributions among the forelimb bones to total forelimb length show that approximately half of the total forelimb length is comprised of the humerus,

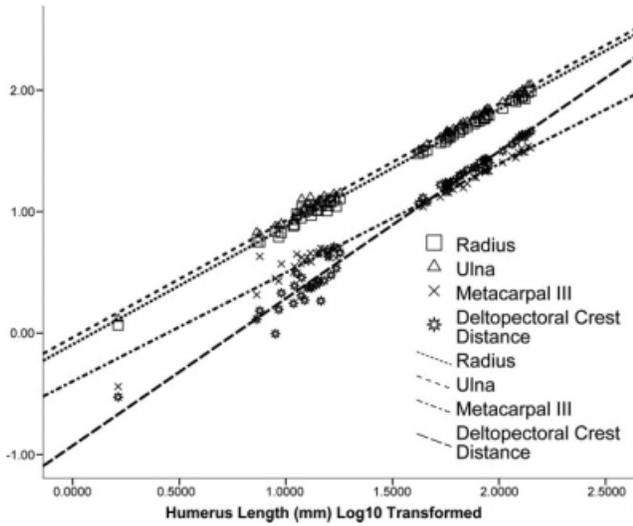


Fig. 2. Bivariate plot of forelimb long bone elements and deltopectoral crest distance against humerus length. All variable are Log10 transformed.

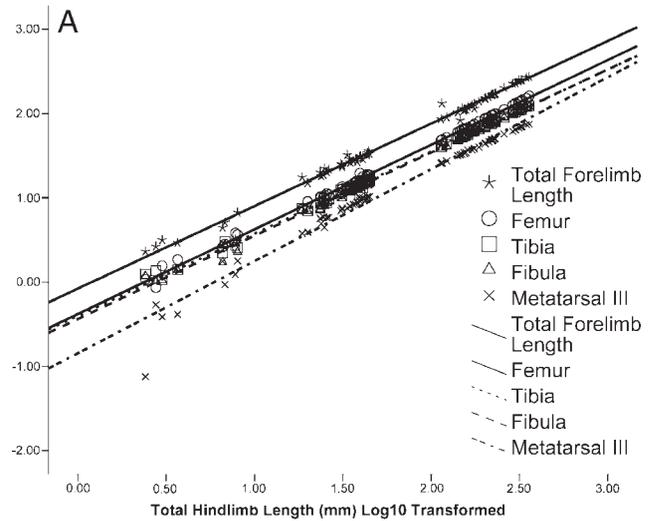
followed by that of the ulna (40%) and radius (36%) (Table 5). Given its small relative size, it is not surprising that metacarpal III contributes only ~14% to the total forelimb length (Table 5). In the hindlimb, the average contribution of the femur (43%), tibia (36%), and fibula (35%) to total hindlimb length were remarkably close (Table 5). Unlike the forelimb, metatarsal III contributes to ~21% of the total hindlimb length (Table 5). Overall, there is little to no variation in the relative contribution of the forelimb and hindlimb elements to their respective limbs between the embryonic and postnatal subsamples.

DISCUSSION

Scaling Trends and Functional Implications

We tested the hypothesis that the relatively shorter forelimbs in *A. mississippiensis* were a result of prevalent negative allometric scaling relative to the hindlimbs. Our results falsify our hypothesis: the combined results of the RMA regression on the total sample, the embryonic and postnatal slopes, and the proportional trends in the total and subsamples reveal relatively static limb scaling trends. For several elements, their initial relative proportions remain virtually unchanged relative to the femur, humerus, or total limb length during development. Almost without exception, the humerus, radius, femur, tibia, and fibula show no relative change in their overall proportions with increasing size or limb length.

In relation to total forelimb length, the embryonic subsample of the humerus shows a negative allometric trend, whereas an isometric trend is apparent postnatally. This result suggests that an initial lag in humerus growth relative to overall forelimb length is eventually surpassed during postnatal development. Against total hindlimb length, the tibia shows negative allometry across the embryonic and postnatal subsamples, but shows an isometric trend against femur length. This discrepancy suggests that whereas the tibia keeps pace with the femur during ontogeny, its relative contribution



B

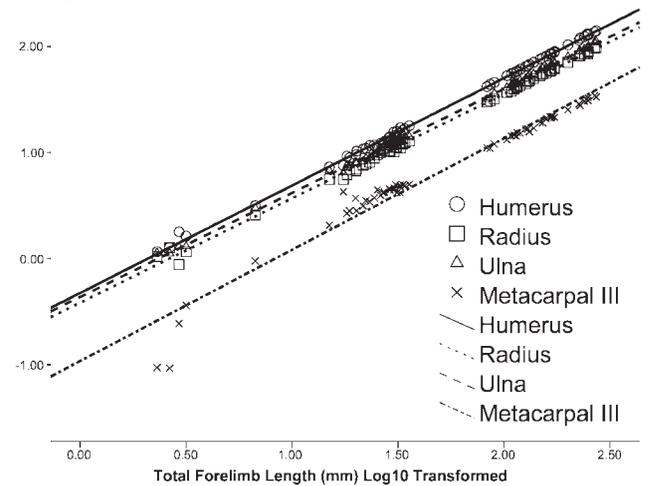


Fig. 3. Bivariate plots of long bone elements against total limb length. All variables are Log10 transformed. Plot of **A**, hindlimb long bones against total hindlimb length and **B**, forelimb long bones against total forelimb length.

TABLE 3. RMA regression of linear measurements of *Alligator mississippiensis* long bone elements against total limb length

Comparison	n	RMA Slope	r <sup>2</sup>	95% CI
Humerus/Forelimb	67	1.004	0.998	0.989–1.023
Radius/Forelimb	68	0.9766	0.992	0.942–1.011
Ulna/Forelimb <sup>a</sup>	67	0.9616	0.993	0.9266–0.9874
Metacarpal III/Forelimb	67	1.053	0.957	0.926–1.148
Femur/Hindlimb	71	1.005	0.997	0.986–1.029
Tibia/Hindlimb <sup>a</sup>	71	0.9740	0.996	0.9528–0.9964
Fibula/Hindlimb	71	0.9873	0.997	0.967–1.013
Metatarsal III/Hindlimb <sup>b</sup>	71	1.110	0.969	1.010–1.208

<sup>a</sup>Negative allometry.

<sup>b</sup>Positive allometry.

**TABLE 4. Comparison of slopes between the embryonic and postnatal sub-samples using Student's *t*-test**

Comparison	RMA Slope <sup>e</sup>	r <sup>2e</sup>	Std. error <sup>e</sup>	RMA Slope <sup>pn</sup>	r <sup>2pn</sup>	Std. error <sup>pn</sup>	t	p
Forelimb/Hindlimb	0.9798	0.97	0.04667	1.048	0.918	0.06642	0.840139	>0.05
Humerus/Femur	1.015	0.972	0.03749	1.02	0.917	0.06207	0.068953	>0.05
Radius/Femur	0.9613	0.951	0.06784	0.9943	0.917	0.05951	1.013192	>0.05
Ulna/Femur	0.9303	0.975	0.04384	1.016	0.908	0.06457	1.807784	<0.05
Metacarpal III/Femur	1.295	0.949	0.07229	0.980	0.934	0.05651	6.987135	<0.05
Tibia/Femur	0.9684	0.956	0.05847	0.9507	0.997	0.01019	0.307424	>0.05
Fibula/Femur	1.015	0.969	0.05232	0.9652	0.997	0.01153	0.975825	>0.05
Metatarsal III/Femur	1.357	0.902	0.182	0.9213	0.996	0.00979	2.39743	<0.05
Radius/Humerus	1.02	0.972	0.04877	0.9743	0.997	0.01191	0.966308	>0.05
Ulna/Humerus	0.9892	0.989	0.02109	0.9955	0.995	0.01533	0.43497	>0.05
Metacarpal III/Humerus	1.394	0.937	0.11	0.9534	0.992	0.01676	4.052773	<0.05
Humerus/Forelimb	0.9577	0.993	0.02146	1.016	0.999	0.00551	2.810987	<0.05
Radius/Forelimb	0.9527	0.967	0.05035	0.991	0.999	0.00738	0.768978	>0.05
Ulna/Forelimb	0.9179	0.973	0.04379	1.013	0.997	0.01265	2.268442	<0.05
Metacarpal III/Forelimb	1.311	0.916	0.1336	0.9684	0.993	0.01424	2.579063	<0.05
Femur/Hindlimb	0.9865	0.988	0.03864	1.036	0.999	0.00553	1.294371	>0.05
Tibia/Hindlimb	0.9384	0.985	0.0327	0.9851	0.999	0.00580	1.451135	>0.05
Fibula/Hindlimb	0.9745	0.987	0.03289	1.000	0.998	0.00773	0.797649	>0.05
Metatarsal III/Hindlimb	1.344	0.929	0.155	0.9546	0.998	0.00636	2.514378	<0.05

Note that, except for the comparison of humerus length versus forelimb length, it is only the ulna and third metapodials that show a significant difference in slope between the sub-samples.

**TABLE 5. Average contribution of long bones to total limb length**

Element/Total Length	n	Average percentage (%)	Embryonic subsample (%)	Postnatal subsample (%)
Humerus/Femur Length	85	91	91	90
Radius/Femur Length	76	66	70	63
Ulna/Femur Length <sup>a</sup>	76	74	79	70
Metacarpal III/Femur Length <sup>a</sup>	69	25	27	22
Tibia/Femur Length	76	84	87	82
Fibula/Femur Length	77	81	83	79
Metatarsal III/Femur Length <sup>a</sup>	72	51	51	51
Radius/Humerus Length	75	72	74	70
Ulna/Humerus Length	75	81	83	78
Metacarpal III/Humerus Length <sup>a</sup>	68	27	30	25
Total Forelimb Length/Total Hindlimb Length	66	78	81	75
Humerus/Total Forelimb Length <sup>a</sup>	68	50	49	51
Radius/Total Forelimb Length	68	36	36	36
Ulna/Total Forelimb Length <sup>a</sup>	68	40	41	40
Metacarpal III/Total Forelimb Length <sup>a</sup>	68	14	14	13
Femur/Total Hindlimb Length	72	43	42	43
Tibia/Total Hindlimb Length	72	36	37	35
Fibula/Total Hindlimb Length	72	35	35	34
Metatarsal III/Total Hindlimb Length <sup>a</sup>	72	21	22	21

<sup>a</sup>A significant difference in slope between the embryonic and postnatal subsamples as reported in Table 4. Note that between the embryonic and postnatal sub-samples there is generally little difference in the overall proportions of the limb elements.

to total hindlimb length lags in relation to the positive allometric growth reported for metatarsal III.

The ulna and metapodials show varying trajectories. The ulna consistently shows a negatively allometric trend, especially when compared with femur length and total forelimb length. In the embryonic subsample, negative allometry is quite stark, whereas the negative allometry is less pronounced in the postnatal growth of the ulna. For example, in comparison with femur length, the ulna appears initially to "lag" behind femoral growth during embryonic development, but eventually its growth almost parallels that of the femur postnatally (Table 4). This trend is also reflected in the proportions

of the ulna in the embryonic and postnatal samples: it is initially 79% of femur length, but its "lag" in growth results in it only measuring 70% of femur length postnatally (Table 5). Both metapodials (metacarpal III, metatarsal III) show positively allometric trends in the embryonic subsample, followed by isometric trends postnatally (Table 4). Relative to femur, humerus, or total limb length, the metapodials appear to have accelerated growth embryonically, followed by an isometric trend in the postnatal subsample (Table 4).

Our results suggest that, for *A. mississippiensis*, the relative proportions of the forelimb and hindlimb elements remain virtually unchanged throughout ontogeny.

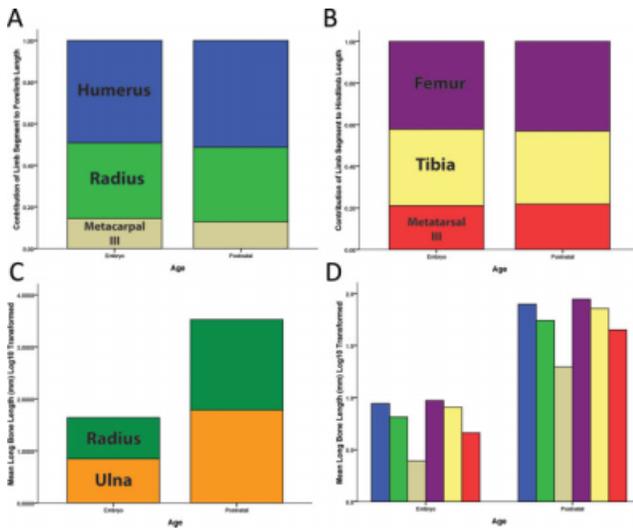


Fig. 4. Bar graphs showing the proportional contribution of various limb elements to total limb length in the embryonic and postnatal subsamples. Comparison of proportional contribution of mean relative element size in **A**, the forelimb and **B**, the hindlimb of the embryonic and postnatal subsamples. **C**, comparison of relative radius and ulna proportions in embryos and postnatal specimens. **D**, comparison of relative long bone proportions in embryos and postnatal specimens. For **D**, the color codes are the same as for **A–C**.

Conversely, the ulna and metapodials show more variability in their growth trajectories. Why should these elements be the exceptions to the overall isometric growth trends? For the ulna, there are several possible explanations for its relatively negative allometry. First, the length of the ulna includes the olecranon process, the insertion point for *M. triceps brachii* (Meers, 2003) which is the prime mover associated with extension of the antebrachium. As this region acts as the in-lever in a second order lever system (Hildebrand and Goslow, 2001; Liem et al., 2001), changes in the relative size of the olecranon process compared with the ulnar shaft would have significant effects on the mechanical advantage of the *M. triceps brachii*. The negative allometric scaling of the ulna may thus reflect either an increase in the relative contribution of the olecranon process to ulna size (with a subsequent reduction in shaft length), or a decrease in olecranon process size with no relative change in the length of the ulnar shaft. In the former case, the relative mechanical advantage of *M. triceps brachii* would increase in larger alligators, whereas a decrease in relative mechanical advantage would be predicted in the latter case. Unfortunately, the olecranon process is only subtly distinguishable from the shaft in adults, and it is extremely difficult to distinguish in embryos. Therefore, it cannot presently be determined which, if either, of the scenarios described above have an effect on the negative allometry of the ulna.

Another possibility is that the relative lengths of the radius and ulna during ontogeny are influenced by carpus morphology. Although the ulna shows negative allometry, it should be noted that this element is always absolutely longer than the radius. In *A. mississippiensis* and other crocodylians, the carpal series is typically more well-ossified and elongate along the lateral radius

axis (Mook, 1921; Romer, 1956; Meers, 2003). For example, the radiale is the largest and longest carpal bone, and is intimately associated with the radius. In contrast, the medial carpal series is shorter and often less well-ossified, especially in juveniles (Mook, 1921; Romer, 1956). Overall, this gives the crocodylian carpus an asymmetrical appearance, being longer laterally than medially. As Mook (1921) observed, the radiale appears to extend the length of the radius such that, when compared with the longer ulna plus its shorter, associated carpal (ulnare), both antebrachial bones are of approximately equal size. Could the asymmetrical carpus morphology influence antebrachial allometry in *A. mississippiensis*?

Carpus asymmetry has two possible implications for the negative allometry associated with the ulna. First, were the ulna to grow isometrically or with positive allometry, its length in combination with the ulnare might exceed the combined length of the radius and radiale. This in turn could affect manus use and orientation during locomotion by causing exaggerated radial deviation or other locomotor abnormalities. Second, *A. mississippiensis* has a natural space between the ulna and its associated carpals proximally, as well as between carpals and the medial metacarpals distally (see Meers, 2003: Fig. 18). In general, *A. mississippiensis* has natural ulnar deviation of the manus.

Moreover, manipulation of freshly dissected alligator specimens by two of us (MFB, DRW) shows that a small but noticeable piston-like, reciprocating action of the radius against the ulna is present. Collateral ligaments surrounding the radius and ulna proximally and distally allow the radius to slide distally, stretching the ligaments and soft tissues. When the radius is released, elastic energy stored in the ligaments and soft tissues allows passive rebounding of this element to its initial position. As the radius is slid distally in dissected specimens, its pressure on the radiale and lateral side of the metacarpus causes ulnar deviation of the manus, which is apparently facilitated by the naturally more open medial portion of the carpus. Thus, it is possible that the negative allometric scaling of the ulna may act in part to retain ulnar deviation of the manus, an action which may facilitate pronation and other movements during locomotion. Such movements might be critical during the transition from a sprawling gait to the so-called "high walk" observed in many crocodylians (e.g., Pough et al., 1998). A radius motion similar to this is known to be critical for automating flight movements in birds (see Vazquez, 1994). We note that such a movement between the radius and ulna may be condition basal to most or all archosaurs.

Certainly, the functional morphology of the antebrachium, carpus, and manus of *A. mississippiensis* cannot simply be reconstructed based on morphological observation and morphometric trends. However, it appears that the negative allometric scaling of the ulna in relation to femur, humerus, and forelimb size is not directly associated with relative limb segment lengths. If this were the case, one would also predict the radius to show negative allometric scaling rather than isometry. It seems likely that functional and phylogenetic constraints embedded within the crocodylian body plan have a stronger influence on ulnar morphology.

The strong positive allometry associated with the metapodials during embryonic growth may reflect one of two trends, or a combination thereof. First, the

allometric signal may indicate that the metacarpals and metatarsals grow relatively rapidly compared with the other limb elements embryonically, but that their growth slows significantly postnatally. However, second, we would be remiss if we did not also consider the possibility that the long bones of the forelimb and hindlimb may have accelerated growth relative to the metapodials postnatally. In other words, the metapodial growth rate may actually not change at all, but the ossification and growth of the humerus, femur, and other long bones may. The isometric growth of most major long bones (except the ulna, as detailed above) suggest our data best fit a trend of early, rapid growth of the metapodials followed by slowed growth postnatally. In either case, the relative contribution of the metacarpus and metatarsus to total forelimb and hindlimb length remains virtually unchanged throughout development, and the allometric pattern reported here may reflect how such a pattern is “maintained.”

The positive allometry reported for the deltopectoral crest and fourth trochanter distances on the humerus and femur, respectively, follows basic predictions of lever mechanics. For the humerus, the deltopectoral crest is the insertion region for the major protractors and adductors of the humerus (Mm. pectorals, deltoids, supracoracoideus) (Meers, 2003). The general pull of these muscles on the deltopectoral crest should act in a fashion similar to a second-order lever system (see Bonnan, 2004, 2007). An increased distance of the deltopectoral crest from the humeral head would therefore act to increase the relative mechanical advantage of forelimb protraction and adduction with a concomitant relative decrease in overall length of stride. A similar mechanical situation is predicted for the femur. The fourth trochanter is the insertion point for the Mm. caudofemorales, muscles shown to be the major femoral retractors in archosaurs (Gatesy, 1991, 1997). With increasing distance of the fourth trochanter from the femoral head, the greater the relative mechanical advantage of these muscles will be in retracting the hindlimb. Thus, as *A. mississippiensis* grows larger, the relative mechanical advantage of some of its major limb muscles should increase, a result that follows basic predictions from standard lever mechanics (Vogel, 1988; Hildebrand and Goslow, 2001; Liem et al., 2001).

### Implications for Alligator Mississippiensis

Our data collectively suggest that the scaling patterns we observe in *A. mississippiensis* limb proportions originate embryonically and are maintained throughout ontogeny. The patterns of negative (ulna) and positive (metapodials) allometry that we detected appear to be related to maintaining the functional integrity of limb posture during ontogeny. In particular, the negative allometry of the ulna may be associated with functional aspects of an asymmetrical carpus. The positive allometry associated with the deltopectoral crest and fourth trochanter appears to reflect biomechanical adaptations for locomotion in alligators with increasing size and mass.

Wiley et al. (2004) showed that the hindlimbs of *A. mississippiensis* supported more body mass than the forelimbs, and that the tail “dragged” the center of body mass toward the pelvis. They argued that the drag and mass of a heavy tail requires the hindlimbs of alligators

to be the major propulsive organs. However, they also indicated that the forelimbs are involved to a significant degree in propulsion to assist the hindlimbs in counteracting the drag of the tail (Wiley et al., 2004). These data fit our results: the relative proportions of the forelimbs would not be very likely to change given their role in propulsion and resistance against tail drag. In other words, negative forelimb allometry would act to decrease propulsive effectiveness.

We also find our data significant in light of a previous ossification study of *Alligator mississippiensis* by Rieppel (1993). It was found that much of the appendicular skeleton ossifies synchronously, with an initial lag in ossification between the forelimb and hindlimb until stage 23, and between the humerus and that of the radius and ulna until stage 28d (Rieppel, 1993). In the hindlimb, a similar temporary lag in ossification was noted between the femur and the crus elements (Rieppel, 1993). Moreover, digit III (metacarpal/metatarsal III) was the first element of the metapodials to ossify (Rieppel, 1993).

The lag in ossification between the stylopodial elements (humerus/femur) and those of the zeugopodium (antebrachium/crus) might help explain why the initial relative lengths of the radius, ulna, tibia, and fibula are longer embryonically than postnatally (Table 5). But why would this relationship begin to change later in development, with a noticeable decrease in antebrachial and crural element lengths in the postnatal sub-sample? As Rieppel (1993) notes, there is often compartmentalization and development along different trajectories among the stylopodial, zeugopodial, and autopodial (manus/pes) elements in lizards and *Alligator mississippiensis*. He noted that compartments which ossify later do so at a faster rate.

We posit that if the rate of ossification is related grossly to growth rate in a particular element, this would suggest that later ossifying elements not only ossify faster but have accelerated growth relative to other compartments. Thus, the initial difference in relative length between embryonic and postnatal zeugopodial elements might be tied to the later ossification of the stylopodium: the humerus and femur, lagging slightly behind their zeugopodial elements (and hence ossifying slightly later), eventually ossify faster than the antebrachium or crus. If ossification rate is related to growth rate, the humerus and femur eventually “outgrow” their zeugopodial elements. As the radius and ulna or tibia and fibula are being compared to the length of the humerus or femur, respectively, the antebrachial and crural bones will be relatively shorter in the postnatal sub-sample. This might also explain the strong positive allometry of the metapodials which ossify after the stylopodial and zeugopodial elements: having a much more rapid ossification and growth embryonically would explain this signal. Certainly, these posits require a more empirical approach to confirm whether or not the ossification and scaling patterns are indeed integrated, and we anticipate this as an area of fruitful future research.

### Implications for Archosaur Locomotion and Summary

Our data suggest broader trends for archosaur locomotor evolution, but a number of caveats must be stressed. Certainly, we recognize that our sample is from a single

population of a single species of extant crocodylian, and our data cannot provide a definitive “answer” to ancestral limb allometry in archosaurs. Moreover, we do not know whether our data for *Alligator mississippiensis* reflects those of other crocodylians generally, only applies to alligatoroids, or simply is restricted to this species. We would be remiss if we did not also acknowledge the long and complex locomotor history of extant crocodylians. Given that many crocodyliforms and basal crocodylians had a parasagittal gait, that some may have been bipedal (e.g., *Terrestrisuchus*), and that the sprawling gait of extant crocodylians may have arisen secondarily from a parasagittal one (Parrish, 1986; Brochu, 2001; Dodson, 2003), it would be simplistic to treat their development as an historical blueprint for all archosaurs. One could argue, for example, that prevalent negative forelimb allometry was present ancestrally in crocodyliforms and in basal archosaurs, only later to become “fixed” isometrically in extant crocodylians. Finally, even if we could show that the pattern we report for *A. mississippiensis* was characteristic of crocodylians generally, we cannot ascertain currently whether the pattern we report here was ancestral for all archosaurs.

Despite these caveats, the highly conservative limb morphology of extant crocodylians, and the generalized ecology and behavior of *Alligator mississippiensis* in particular (Meers, 2002, 2003), suggest our data and results may at least be broadly applicable to most extant crocodylians. We follow Meers (2003) in regarding *A. mississippiensis* limb anatomy as generally representative of crocodylians broadly. Furthermore, given the basal phylogenetic position of crocodylians (Brochu, 2001) and their relatively plesiomorphic quadrupedal gait (whether or not secondarily derived), the implications drawn from the limb growth of *A. mississippiensis* are arguably less problematic and more universal to archosaurs than those of extant birds. We emphasize that our purpose here is to postulate what our data may suggest broadly for crocodylians and other archosaurs, and to highlight possible future avenues of research related to differential limb development in extant and fossil archosaurs.

If our data on *Alligator mississippiensis* applies to extant crocodylians generally, this would suggest that the relative proportions of most limb segments in these archosaurs remains consistent throughout growth. If correct, we predict that future studies of other extant crocodylians should show a similar limb development and growth pattern to that reported here for *A. mississippiensis*. Moreover, estimates of total limb length could be generated for partial specimens in museum collections, or for partial datasets of crocodylian metrics. Certainly, for *A. mississippiensis*, our data suggest that, at least for this species, missing limb length data could be estimated with confidence. Future studies on other extant crocodylian taxa are necessary to verify this technique for crocodylians more broadly. We would be especially concerned about using our data to predict missing element sizes in highly specialized crocodylians, such as gharials, whose primarily aquatic locomotion has affected estimated body size calculations from the appendicular skeleton in other studies (Meers, 2002; Farlow et al., 2005). Regarding fossil crocodylians, our results, if applicable, may also be helpful in predicting the size and contribution of missing elements. As Farlow et al. (2005) have shown for fossil Mesoeucrocodylian crocodyliforms, femur size and body size

are tightly correlated and have been used successfully to predict the latter in most cases (except in extremely small, large, or specialized taxa). Again, future research into these applications is warranted.

If the relatively isometric pattern we report for *A. mississippiensis* is plesiomorphic for archosaurs generally, this might suggest that the difference in length between the forelimbs and hindlimbs had a more basal origin, perhaps among the archosauromorphs or even within more basal members of the Sauropsida or Amniota. In fact, among a diverse range of amniotes, the forelimb is typically shorter than the hindlimb except for specialized forms such as fliers, climbers, and swimmers (see for example: Middleton and Gatesy, 2000 [birds]; Llorente et al., 2008 [turtles]; Kohlsdorf et al., 2001 [lizards]; Ruff, 2003 [humans and baboons]; Young and Hallgrímsson, 2005 [therian mammals]). Therefore, the simplest explanation for the observation that the forelimbs of *A. mississippiensis* are shorter than the hindlimbs is that they retain a developmental pattern basal to all amniotes. Whether or not such a pattern is static across most amniotes (forelimbs remain relatively shorter than hindlimbs throughout development) or occurs because of heterochronic processes during ontogeny remains to be investigated in more detail.

However, comparison of our data with that of Reisz et al. (2005) for *Massospondylus* offers additional insights. We found it of interest that the only forelimb bone measured beyond the humerus in the Reisz et al. (2005) study was the ulna. This is not a criticism, as we fully appreciate the fragmentary nature of fossil specimens and their incomplete preservation. However, our data on *A. mississippiensis* show that although the ulna scales with negative allometry in relation to the femur, humerus, and forelimb, the radius scales isometrically and metacarpal III scales, at least embryonically, with positive allometry. If a similar pattern were present in *Massospondylus*, this would suggest that, as with *A. mississippiensis*, the negative allometry of the ulna is not indicative of overall forelimb scaling but is related to other functional or phylogenetic processes.

One of us (MFB) collected additional long bone length data on *Massospondylus* and added it to the data reported by Reisz et al. (2005). In particular, we included, where possible, length measurements of the radius. Too few third metacarpals were available to generate valid statistical results. Even with the radius, only a small number of reasonably complete associated forelimbs and hindlimbs of these sauropodomorphs were available with radii ( $n = 5$ ). However, RMA regression analyses of these data support the claim by Reisz et al. (2005) for *Massospondylus* that the forelimb scales with negative allometry in relation to the femur. Moreover, despite the small sample size and rather large 95% confidence intervals, the radius scales negatively along with the ulna against femur length, a pattern different from the one reported by us for *A. mississippiensis* (Table 6). When ulna and radius length are regressed against humerus length, the ulna scales with isometry whereas the radius shows a negative allometric trend (Table 6). This trend is opposite of what we report for the *A. mississippiensis* forelimb, again suggesting something different is occurring in the forelimb of *Massospondylus*.

These data suggest three intriguing possibilities to us. The first possibility is that in various archosaur lineages

**TABLE 6. Regression of forelimb and hindlimb elements on femur and humerus length in the sauropodomorph *Massospondylus***

Comparison	n	Slope	r <sup>2</sup>	95% CI
Humerus/Femur <sup>a</sup>	10	0.9003	0.995	0.8504–0.9503
Ulna/Femur <sup>a</sup>	8	0.8782	0.994	0.8098–0.9466
Radius/Femur <sup>a</sup>	4	0.5190	0.932	0.1060–0.9319
Tibia/Femur	11	0.9694	0.994	0.911–1.028
Ulna/Humerus	8	0.9758	0.993	0.901–1.050
Radius/Humerus <sup>a</sup>	5	0.7006	0.956	0.4315–0.9698

<sup>a</sup>A negative slope. Data from Reisz et al. (2005) and MFB. Note the negative allometry that is prevalent for the humerus, radius, and ulna, in contrast to the generally isometric pattern we report for *Alligator mississippiensis*.

that became bipedal, such as dinosaurs, negative allometric growth of the forelimb relative to the hindlimb was part of a suite of adaptations for bipedalism. In other words, as Reisz et al. (2005) have proposed for *Massospondylus*, perhaps embryonically quadrupedal limb proportions were subsequently modified during ontogeny such that larger individuals had bipedal limb ratios. Such a trend might be postulated to characterize the evolution of bipedalism in various archosaur lineages, but this hypothesis requires further investigation. For example, it should be noted that in the ornithischian dinosaur *Maiasaura* the same general limb proportions are retained throughout ontogeny whereas the cross-sectional robustness of the forelimbs increases (Dilke, 2001). This finding suggests that quadrupedal locomotion was favored more often in adult *Maiasaura* than in juveniles (Dilke, 2001) with no significant change in limb ratios.

A different possibility is that, for secondarily quadrupedal archosaurs such as many dinosaurs and perhaps crocodylians, an original trend of negative forelimb allometry was changed via isometric or near-isometric growth of the forelimb relative to the hindlimb. We find it significant that sauropod dinosaur long bones show distinctly isometric scaling trends (Bonnar, 2004, 2007; Wilhite, 2003, 2005), a pattern of growth that would ensure the quadrupedal proportions of the limbs were maintained into adulthood. Because of the complex locomotor history of crocodylians, it remains difficult to resolve whether these animals reverted from bipedalism to a secondarily quadrupedal posture, or whether the lineage ultimately leading to *A. mississippiensis* has always retained a quadrupedal posture. Either scenario we suggest here could account for the trends in American alligators, but further research is required to determine which hypothesis best accounts for crocodylian limb growth.

A third possibility is that a trend toward negative forelimb allometry is only ever achieved in archosaurs when other locomotor changes in the pelvis and hindlimb (e.g., erect, parasagittal gait) allow the forelimb to be removed from locomotor constraints. It is generally assumed that most bipedal nonavian dinosaurs walked with a horizontal vertebral column and that the large tail was held off the ground (Carrier et al., 2001). A change in hindlimb posture coupled with the absence of significant tail drag (see Willey et al., 2004 for the effects of tail drag on alligator locomotion) may free the

forelimb to scale with more negative or positive trends. In other words, the negative forelimb allometry reported for some nonavian dinosaurs may be an aftereffect of bipedalism, not necessarily its primary cause. Whether such trends are more widespread among archosaurs generally remains to be investigated.

In summary, we find that the general long bone proportions of *Alligator mississippiensis* scale at or near isometry from embryonic to adult size. The major exceptions to these trends are seen in the ulna, where negative allometry prevails, and in the embryonic positive allometry of the third metapodials. These trends, however, seem less correlated with changing limb proportions than with maintaining the functional integrity of the limbs throughout ontogeny. Our data suggest that if bipedalism in archosaurs is tied, in part, to negative forearm allometry, it was either secondarily lost in *A. mississippiensis* through isometric scaling, or was never present in this lineage (i.e., differential forelimb and hindlimb proportions were a plesiomorphic feature inherited from a distant common ancestor). Ultimately, more data are required to elucidate ontogenetic trends in limb proportions among archosaurs and amniotes more broadly, an area of research we suspect will be very fruitful.

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