



USING LINEAR AND GEOMETRIC MORPHOMETRICS TO DETECT INTRASPECIFIC VARIABILITY AND SEXUAL DIMORPHISM IN FEMORAL SHAPE IN *ALLIGATOR MISSISSIPPIENSIS* AND ITS IMPLICATIONS FOR SEXING FOSSIL ARCHOSAURS

MATTHEW F. BONNAN,^{*1} JAMES O. FARLOW,² and SIMON L. MASTERS^{1,†}

¹Department of Biological Sciences, Western Illinois University, Macomb, IL 61455 USA;

²Department of Geosciences, Indiana Purdue University / Fort Wayne, 2101 Coliseum Boulevard East, Fort Wayne, IN 46805 USA

ABSTRACT—Sexual size dimorphism (SSD) is prevalent among extant vertebrates and presumably was as common among fossil archosaurs. Here, we test the hypothesis that femur shape is a reliable indicator of sex among archosaurs using linear and geometric morphometric analyses on a large sample of sexed *Alligator mississippiensis* femora. Linear regression of femoral dimensions onto femur length in alligators shows that male femora are the largest and stoutest in midshaft and articular dimensions, whereas females show more variation in their midshaft dimensions. Using thin-plate splines analyses, regression of partial warps onto alligator femur length revealed that with increasing size the midshaft expands whereas shaft torsion diminishes, that femur shape differs according to sex, and that females show the maximum amount of shape variation at a size 72% that of the largest males. However, sexual dimorphism accounts for only 3% of the total femur shape variation in the sample. Differences in reproductive physiology (e.g. shelling eggs in females) may account for some of the fine morphological differences between males and females. However, size and individual variation appear to effect femur shape the most. These results have significant implications for inferring fossil archosaur sex from femoral dimensions and shape.

INTRODUCTION

Sexual size dimorphism (SSD) is common among vertebrates and influences many aspects of their biology (see Fairbain [1997] and Blackenhorn [2005] for overviews). Among many lizards, snakes, turtles, and birds, females are typically larger than males (Storrier, 1971; Pough et al., 1998; Liem et al., 2001). Although increased egg carrying capacity is often correlated with larger female body size, the biological factors underlying SSD are complex (e.g., Storrier, 1971; Fairbain, 1997; Pough et al., 1998; Dunn et al., 2001; Blackenhorn, 2005; Schwartzkopf, 2005). For example, territorial behaviors in males tend to favor larger body sizes relative to females in some lizards as well as in crocodylians (Pough et al., 1998).

Presumably, SSD was as prevalent among non-avian dinosaurs and other extinct archosaurs as it is among extant sauropsids, but detecting differences between the sexes based on skeletal morphology remains difficult. SSD in postcranial anatomy or bone growth pattern has been hypothesized for several species of dinosaurs (Carpenter, 1990, 1999; Raath, 1990; Rowe and Gauthier, 1990; Weishampel and Chapman, 1990; Larson, 1994, 1997; Chapman et al., 1997; Galton, 1997; Heerden and Galton, 1997; Benton et al., 2000; Sander, 2000; Brochu, 2003; Erickson et al., 2005; Molnar, 2005; Wilhite, 2005). Commonly individuals of a presumed species are interpreted as comprising two sexual morphs, a gracile and a robust form, with the latter usually identified as the female (see preceding references). The relative massiveness of the articular ends or the midshaft of limb bones are among the features in which the sexes are thought to have dif-

fered. How reliable are these inferences and do they reflect patterns of limb morphology observed in extant archosaurs?

The role of the femur in weight support and locomotion as well as its strong correlation with body size in archosaurs as well as tetrapods generally (Farlow et al., 2005 and references cited therein) make it an excellent appendicular element with which to investigate and quantify SSD in extant archosaurs and dinosaurs. Moreover, the femur is one of the best preserved and least distorted elements in fossil assemblages.

Here, we test the hypothesis that femur shape is a reliable indicator of sex in a well-known, extant archosaur, the American alligator (*Alligator mississippiensis*). A large sample of femora from individuals of known sex and provenance provided an unprecedented opportunity to test this hypothesis. Ultimately, we predict that if previous speculations about articular end and midshaft robustness are correct, these shape differences should reliably separate the sexes among extant and extinct archosaurs.

Institutional Abbreviations—RWR, Rockefeller Wildlife Refuge, Louisiana.

MATERIALS AND METHODS

Most of the alligator femora measured and digitized during this study were collected by personnel of Rockefeller State Wildlife Refuge (RWR) from animals taken from RWR, Sabine National Wildlife Refuge, Lacassine National Wildlife Refuge, Marsh Island State Wildlife Refuge, and Pecan Island in southern Louisiana. One large male was captured near Vicksburg, MS, but was included with the Louisiana sample for data analysis. About a third of these specimens were collected in 1999 (Farlow and Britton, 2000), with unambiguous information about whether the alligators were captive or wild individuals. The remainder was a large sample of femora collected during the 1980s, and for many of these bones information about the captivity status of the animals was not recorded. However, most or all of these were

*Corresponding author.

†Current address: Intermountain Paleo Consulting, 461 W. 2005, Vernal, UT 84078.

probably wild individuals, and were included with known wild alligators in our analyses. We also measured femora of alligators collected from sites in Louisiana, Florida, and Virginia in the collections of the Florida Museum of Natural History (Gainesville), National Museum of Natural History (Smithsonian Institution), Royal Ontario Museum, Field Museum of Natural History, University of Michigan, and Michigan State University. Our sample included animals with a minimum size range of 27–427 cm total length (some of the femora in museum collections were from animals whose overall size was not measured).

Femur length, maximum diameter of the proximal end of the bone, minimum proximal diameter, distal width, distal height, length from the proximal end to the fourth trochanter, and minimum midshaft circumference were measured for *Alligator mississippiensis* as described by Farlow and Eelsey (2004) and Farlow et al. (2005). We examined bivariate relationships between femur length and the other femoral dimensions. Moreover, bivariate relationships between distal width and distal height, and between maximum and minimum proximal width were further investigated in our alligator sample.

Long bones are living tissues that respond to the major forces acting on them by changing their shape (Vogel, 2003; Biewener, 2005). It follows that different loading regimes in wild and captive animals may potentially induce significant differences in long bone shape. Therefore, only data for wild or probable wild individuals were used in these analyses. However, given the uncertainty of captivity status in the museum-measured specimens, two separate analyses were performed: one for the Louisiana (plus Mississippi) sample alone to be certain that the trends reported here applied to known wild individuals, as well as another combining all the individuals to see if similar trends emerged regardless of captivity status. In the geometric morphometric analyses (described below), only a sub-sample of the wild Louisiana population was analyzed.

Femoral measurements were log-transformed before analysis. Reduced major axis (RMA) analyses were used to fit lines to data. Bivariate relationships were identified as allometric if the 95 % confidence interval of the RMA slope (Leduc, 1987) did not include 1. Bivariate femoral shape variability was expressed as the relative dispersion about the reduced major axis (D_d ; Imbrie 1956), a parameter akin to a two-dimensional coefficient of variation:

$$D_d = 100 * \text{square root} \left(\frac{(2 * (1 - r) (S_x^2 + S_y^2))}{((\text{mean } x)^2 + (\text{mean } y)^2)} \right),$$

where x = independent variable, y = dependent variable, S_x^2 = variance of the independent variable, S_y^2 = variance of the dependent variable.

Analyses of covariance were used to test for SSD in femoral shape in alligators.

Linear measurements are not independent of size, and as a consequence it is often difficult to separate size from shape effects in a given sample (see Somers, 1989). Moreover, linear measurements may not capture more subtle information about bone shape, especially regions with curves or other non-linear features. To compare shape independent of size, several statistical approaches known collectively as geometric morphometrics are utilized (see Zelditch et al. [2004] and Slice [2005] for excellent, recent overviews). Many geometric morphometric techniques examine differences in coordinate distances between homologous sets of landmarks among a sample of specimens (see Chapman, 1990a, 1990b; Chapman and Weishampel, 1997; Zelditch et al., 2004; Slice, 2005; and references therein). Here, thin-plate splines (TPS) is preferred because this technique is ideal for analyzing a set of objects (alligator femora) that are similar in overall morphology and in which the detection of more subtle shape differences is desired (Bookstein, 1991, 1996; Rohlf, 1993; Zelditch et al., 2004; Slice, 2005).

In a TPS analysis, homologous landmark coordinates of all specimens are aligned, rotated, and scaled into a grand mean reference form via generalized least-squares Procrustes superimposition (Bookstein, 1991; Zelditch et al., 2004; Slice, 2005). Differences in the sum of squared Procrustes distances between the homologous landmark coordinates of each specimen and the reference form are calculated to reveal changes in shape. These shape differences can be analyzed mathematically and visualized as a deformation grid or thin-plate spline (Bookstein, 1991). Partial warps (shape coefficients generated from the sum of squared Procrustes distances) are correlated, dependent variables that collectively describe shape and have the appropriate degrees of freedom to be analyzed with standard multivariate statistics including multivariate regression (Bookstein, 1991, 1996; Rohlf, 1993; Zelditch et al., 2004; Slice, 2005). An extensive literature exists on the mechanics and mathematical theory underlying thin-plate splines, and readers are referred to Bookstein (1991, 1996 and references therein), Zelditch et al. (2004 and references therein), and Slice (2005 and references therein) for more detailed information. Birch (1997), Monteiro (1999), and Bonnan (2004) provide applied biological and paleontological examples and overviews of TPS analyses.

Femora of *Alligator mississippiensis* were photographed from their caudal sides for digitization through a standard method described previously by Bonnan (2004) for sauropod dinosaurs. The program tpsDig2 (version 2.04) (Rohlf, 2005) was used to digitize the standardized photographs of the femora. The landmarks selected for digitization followed the protocol of Bonnan (2004) and are shown in Figure 1. Most of the selected landmarks are related to areas of muscle insertion or origin (e.g., greater and lesser trochanters, fourth trochanter) or represent the maxima or minima of various homologous regions of the femur.

We are using TPS to infer gross morphological changes associated with the femur that are probably associated with changes in the mechanical advantage of certain muscles. It is therefore important to briefly designate which muscles are associated with these selected landmarks and the gross actions of these muscles.

Landmarks 1 and 2 and their intervening semi-landmarks are

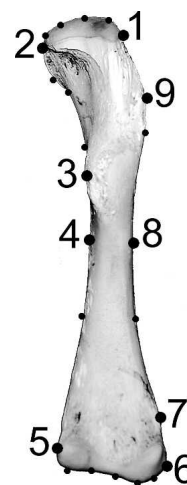


FIGURE 1. Caudal view of a right *Alligator mississippiensis* femur showing the major landmarks selected for the study (large and numbered) as well as the semi-landmarks (smaller points). Landmarks 1, 2, and their intervening semi-landmarks encompass the femoral head; landmark 3 denotes the fourth trochanter; landmarks 4 and 8 designate the minimum midshaft constriction; landmarks 5, 6, and their intervening semi-landmarks demarcate the distal end and condyles; landmark 7 denotes the region of origin for the lateral head of the M. gastrocnemius; landmark 9 indicates the distal edge of the region encompassing the greater and lesser trochanters. Other semi-landmarks refine the shape of the femoral shaft.

associated with the shape of femoral head and its orientation. The femoral head is not always oriented in parallel to the distal end of the femur and the medial side is twisted cranially to various degrees in different specimens. As a consequence, when compressed into two dimensions, the more cranially the femoral head is twisted relative to the distal condyles, the more “narrow” the space and shape between landmarks 1 and 2 will appear in the analysis. Therefore, “narrowing” or “widening” of the femoral head in this analysis actually corresponds to how far cranially the femoral head is twisted out of the plane parallel to the distal condyles.

Landmark 3 is associated with the fourth trochanter, a landmark well-correlated with the insertion of the Mm. caudofemorales that retract or extend the femur about the acetabulum (Gatesy, 1990, 1997). Landmarks 4 and 8 designate the narrowest point of the midshaft and the proximally and distally intervening lateral and medial semi-landmarks on the femoral shaft help define its gross curvature. Landmarks 5 and 6 and the intervening semi-landmarks are associated with the shape and extent of the distal condyles. Landmark 7 is typically not named in the available literature, but it is a prominent, homologous region in alligator femora. We will not name landmark 7, but it is a distal, lateral scarred and rugose area on alligator femora that appears to be associated with the origin of the lateral head of the M. gastrocnemius (MFB, pers. obs.). That this muscle arises in this region is corroborated by other sources (Gatesy, 1997; Carrano and Hutchinson, 2002) although these authors do not specifically call attention to this region of the femur. Landmark 9 is associated with the distal extent of the region that encompasses the greater and lesser trochanters of the femur. This region between landmarks 1 and 9 is associated with M. iliofemoralis and Mm. puboischiofemorales internus (Gatesy, 1997), muscles that abduct the femur during the swing phase of locomotion.

In the results, discussion, and tables, changes in morphology associated with landmarks will be indicated by numbers in parentheses. Some landmarks selected for our analyses were geometrically but not strictly anatomically homologous (as indicated in Figure 1). However, as Bonnan (2004) noted, many morphometric analyses use both geometric and biological landmarks (see MacLeod, 2002 as well). Moreover, we are not utilizing these methods to establish phylogenetic relationships. Therefore, we do not anticipate that the incorporation of geometrically homologous landmarks would be problematic. A number of sliding semi-landmarks were also digitized to capture the curved surfaces of the proximal and distal ends and the midshaft curvature (see Zelditch et al., 2004 for an overview).

The programs tpsSmall, tpsRelw, and tpsRegr (Rohlf, 2005) were used to generate the partial warps and deformation grids. The tpsSmall (Rohlf, 2005) program was used to calculate the mean variation of Procrustes distances from the reference form, and showed that sample variation was very small and appropriate for TPS analysis (correlation > 0.99; high correlation values between specimen Procrustes distances and the reference form).

Significant differences between the sexes for *Alligator* were determined via MANOVA of the partial warp data exported to the SPSS statistical package (SPSS version 15, 2006), whereas visualization of shape differences were obtained through relative warp plots in the TPS statistical packages. Overall sample variation was determined through a principal components analysis of the partial warps on a variance/covariance matrix, generating orthogonal principal components of shape (Bookstein, 1991; Rohlf, 1993; Zelditch et al., 2004; Slice, 2005). An application of Anderson's test derived from Zelditch et al. (2004) was used to determine which extracted shape components (relative warps or PRINs) were “biologically” meaningful.

Regression of partial warps onto log-transformed femur length was used to determine the contribution of ontogeny to shape variation in the sample. Multiple regression of the partial warps

on log-transformed femur length was used to determine how well the data fit a linear model, generating multiple r^2 values for non-uniform, uniform, and total shape change fit. It is the total shape change r^2 value that shows how well or how poorly the predicted shape change of the femur fits the data.

Centroid size, rather than a linear size measurement (i.e., femur length), is often used in geometric morphometrics because it represents a pure geometric scaling variable with mathematical independence from shape (Bookstein, 1991; Zelditch et al., 2004). Here, length was chosen instead of centroid size to simplify comparisons of these results with previous, non-geometric morphometric studies. Moreover, femur length is a variable well-correlated with the mechanical properties of long bones (Vogel, 2003; Biewener, 2005) as well as with body size (Farlow et al., 2005).

Multivariate regression of the partial warps on log-transformed femur length were used to test for allometry and to produce thin-plate splines deformations. Unlike linear regression, allometry is not reported as a slope value. Instead, against a null model of isometry (i.e., no significant shape difference between the specimens and the mean with increasing length), a significant, multivariate difference ($P < .05$ based on Wilk's Lambda) in partial warp scores from the predicted mean indicates femur allometry (significant shape change). Goodall's F-test, a statistic designed specifically for geometric morphometric regression (Goodall, 1991) was used to generate a coefficient of determination (R^2) which, following Monteiro (1999), is expressed as a percentage of shape change explained by increasing femur length.

Finally, a discriminant function analysis (DFA) was performed on the partial warp data in SPSS to yield canonical variates (CV). Canonical variates are independent, orthogonal vectors similar to principal components that describe the greatest amount of variation which best separates predetermined groups. In our alligator sample, a DFA was run to determine where alligator femora differ most in their shape based on sex. Once CVs are generated, partial warps are regressed onto each CV (see Rohlf et al., 1996 for details and an example), thereby generating thin-plate spline visualizations that show what femoral shape changes best separate male and female alligators.

RESULTS

Linear Analyses

The relationship between femur length (independent variable) and all other femoral dimensions shows strong positive allometry (slope = 1.1–1.3; Table 1); with increasing size, alligator femora become relatively stouter bones. Slopes for the Louisiana sample alone are consistently slightly steeper than for the entire sample of wild and probable wild alligators, possibly because the all-wild-alligator sample includes many more young individuals than the Louisiana sample alone. Slopes of relationships comparing the distal transverse dimensions or minimum proximal diameter with femur length tend to be somewhat higher than slopes comparing midshaft circumference or the distance from the proximal end of the bone to the fourth trochanter with femur length. Dodson (1975) found positive allometric relationships between a proxy for overall alligator size (axis-sacrum length) and femoral proximal width, minimum shaft width, and length from the proximal end to the fourth trochanter, results not entirely equivalent to, but consistent with, ours.

Distal height may show very slight positive allometry with distal width, but the relationship between minimum and maximum proximal width appears to be isometric.

Most D_a values are greater for the entire sample of wild alligators than for Louisiana alligators alone (Tables 2, 3). Bivariate comparisons involving distal width or height, or minimum proxi-

TABLE 1. Bivariate relationships between log-transformed femoral dimensions of wild and probable wild alligators.

Femur size measure	Femoral dimension	Sample	r	Slope (95% CI)	N
Length	Distal width	LA	0.977	1.185 (1.110–1.265)	172
		All	0.991	1.136 (1.096–1.179)	214
	Distal height	LA	0.979	1.294 (1.216–1.377)	172
		All	0.990	1.207 (1.161–1.254)	212
	Maximum proximal diameter	LA	0.987	1.178 (1.123–1.236)	172
		All	0.993	1.143 (1.106–1.182)	213
	Minimum proximal diameter	LA	0.971	1.243 (1.154–1.338)	172
		All	0.987	1.163 (1.113–1.215)	214
	Minimum midshaft circumference	LA	0.975	1.163 (1.086–1.247)	172
		All	0.990	1.131 (1.089–1.176)	214
Distance from femoral head to fourth trochanter	LA	0.988	1.145 (1.092–1.200)	172	
		0.995	1.109 (1.081–1.138)	213	
	All	1.092	1.092 (1.023–1.165)	174	
		0.992	1.062 (1.026–1.099)	214	
Distal width	Distal height	LA	0.977	1.055 (0.989–1.126)	175
		All	0.989	1.017 (0.978–1.058)	216

P < .001 in all relationships.

Abbreviations: **LA** = Louisiana and Mississippi alligators; **All** = alligators from all geographic areas.

mal width, generally show the greatest variability. Surprisingly—given the uncertainty involved in its measurement (Farlow et al., 2005)—the distance from the femoral head to the fourth trochanter, compared with femur length, is the least variable relationship.

ANCOVAs revealed only one sexual difference in alligator femoral shape (Table 4): Male femora of a given length have a relatively larger minimum midshaft circumference than female femora. The sexual difference is significantly different both for the entire wild alligator sample and the wild Louisiana sample alone, but the difference is subtle: for a given femur length, males have a midshaft circumference 3–4% larger than that of females. Furthermore, there is considerable overlap between the sexes in the midshaft circumference-femur length relationship, and the difference between the sexes is only seen in large alligators. For Florida Museum of Natural History alligators alone, the ANCOVA is not significant (but in the direction of males having relatively stouter femora; Table 4), but the sample size here is small. Male alligators reach much larger sizes than do females. If the ANCOVA for Louisiana alligators is restricted to reptiles in the size range of females, the difference between the sexes remains statistically significant (Table 4).

One particular trend observed in the bivariate plots of femur length versus midshaft circumference is a clustering of individuals with femora at approximately 72% (189 mm / 236 mm) the size of the largest femur in the sample (Fig. 2A). At this point, the maximum amount of variation in midshaft circumference occurs, with the most variation occurring in female femora. Ap-

parently, although the female femora do not grow longer than approximately 189 mm in this sample, there appears to be more variation in minimum midshaft circumference in the largest females.

However, is the apparently greater midshaft circumference variation in females a real signal? One could suspect that the greater midshaft circumference variation in the larger females is simply a reflection of the greater number of large female alligators or even of differences in mass. If this is indeed the case, it would be predicted that the *D_d* values would be greater for the large females than for the small females. To test this, we first subdivided the wild and probable wild Louisiana females into “small” (110.10–150.00 mm; *n* = 17) and “large” (150.10–190.00 mm; *n* = 34) groups and calculated the coefficient of variation for midshaft circumference. In this case, the largest females in the sample show more variation than the smaller group (Table 3). To ensure that this increased variation was not due to the greater number of individuals in the “large” sub-sample, we randomly selected 17 individuals from the “large” group (to match the number of individuals in the “small” sub-sample) over 30 replicates and calculated the coefficient of variation. In 29 of 30 trials, the “large” sub-sample consistently showed more variation in the minimum midshaft circumference than the “small” sub-sample. Finally, the *D_d* values for the “large” group are lower than for the “small” group (Table 3), which suggests that the increased midshaft circumference variation is not simply an artifact of the larger sample size.

A plot of the sub-sample (*n* = 101, the sample used for TPS;

TABLE 2. Coefficients of relative dispersion about the reduced major axis for alligator log-transformed femoral dimensions.

Femur size measure	Femoral dimension	Treatment	<i>D_d</i>	N
Length	Distal width	LA	1.285	172
		All	1.367	214
	Distal height	LA	1.340	172
		All	1.507	212
	Maximum proximal diameter	LA	0.964	172
		All	1.193	213
	Minimum proximal diameter	LA	1.572	172
		All	1.763	214
	Distance from femoral head to fourth trochanter	LA	0.871	172
			0.961	213
All		1.869	174	
		1.791	214	
Distal width	Distal height	LA	1.892	175
		All	2.165	216

Abbreviations: **LA** = wild and probable wild Louisiana and Mississippi alligators; **All** = wild and probable wild alligators from all geographic areas.

TABLE 3. Coefficients of relative dispersion about the reduced major axis (D_d) for log-transformed values of femoral minimum midshaft circumference and length in *Alligator mississippiensis*.

Sample (femur length size range)	Mx/Mn	D_d	N
All wild and probable wild alligators (39.7–263 mm)	6.6	1.388	214
Wild and probable wild LA alligators (39.7–263 mm)	6.6	1.281	172
Wild and probable wild LA alligators in female femur length size range (81–189 mm)	2.3	1.272	147
Wild and probable wild LA females (81–189 mm)	2.3	0.997	53
Wild and probable wild LA males (39.7–263 mm)	6.6	1.158	62
Wild and probable wild LA females (110.10–150.00 mm)	1.36 (6.59)	5.042	17
Wild and probable wild LA females (150.10–190.00 mm)	1.26 (8.51)	3.017	34

Coefficient of variation values for log-transformed femoral minimum midshaft circumference in wild and probable wild Louisiana female alligators are reported in parentheses for the last two subsets, showing how midshaft variation changes with increasing femur size. Each subset was divided into the smallest (110.10–150.00 mm) and largest Louisiana wild/probable wild females (150.10–190.00 mm). Note that more variation in minimum midshaft circumference is present in the largest females, but that the relative dispersion is lowest in the largest females as well (see text for more information).

Abbreviations: **All** = alligators from all geographic areas; **LA** = Louisiana; **Mx/Mn** = ratio of the largest femur length in the sample to the smallest.

see below) of larger females with the larger males in the sample again shows slightly more variation in females than males near the upper limit of female femur length (Fig. 2B). One would predict that the most variation would occur in females known to be producers (i.e., reproductively active egg layers) because of the potential for calcium reallocation for shelling eggs (see discussion). However, neither producers nor known non-producing females show much variation in the plot, and it is females of unknown reproductive status that actually appear to contribute to most of the femoral midshaft circumference variance (Fig. 2B).

Thus, the linear data show that the femora of male alligators reach the largest sizes and are the stoutest over their size range, whereas the femora of females in the sample never exceed 72% of the maximum femur size but do vary more in their midshaft dimensions at and around this size. However, this slight increase in midshaft minimum circumference variation does not appear to be correlated with reproductive status.

Thin-Plate Splines

A sub-sample of 101 individuals was photographed, digitized, and analyzed for shape variation using the TPS programs described above. A MANOVA of the partial warp scores showed a significant difference in femur shape between males and females (Wilk's Lambda = 0.362; $F = 2.245$; $df = 44, 56$; $P = .002$). These differences in femur shape were analyzed in three subsequent ways.

First, a PCA of the partial warp scores was used to examine the maximum overall shape variation in the sample. Using Anderson's test (see materials and methods), the PCA of partial warps yielded only one distinct shape component, principal component or relative warp (PRIN) 1, which accounted for approximately 41% of the total shape variation. This component appears to reflect overall femoral robustness (Fig. 3). As specimens plot negatively along the PRIN 1 axis, the proximal end (1,2 and intervening semi-landmarks) "expands" and becomes more convex, the distal end (5,6 and intervening semi-landmarks) expands and the lateral condyle becomes more distinct, the landmark 7 shifts proximally, the fourth trochanter (3) shifts distally, and the midshaft expands (4,8). As specimens plot positively along this axis, we see a reversal from the positive trend: proximal end (1,2 and intervening semi-landmarks) "narrowing," distal end (5,6 and intervening semi-landmarks) narrowing, landmark 7 shifts distally, the fourth trochanter (3) shifts proximally, and the midshaft (4,8) narrows.

The "expansion" and "narrowing" of the proximal end corresponds to the orientation of the femoral head in three-dimensional space relative to the distal end. As specimens plot more negatively (which tend to be the larger alligator femora), the femoral head becomes more aligned (in parallel with) the distal condyles. Put another way, larger alligator femora tend to have less proximodistal shaft torsion than those of smaller individuals.

Second, femur shape was regressed against femur length. Multiple regression of all partial warps onto femur length shows a

TABLE 4. Effects of sex on femoral shape in wild and probable wild alligators. All parameters were log-transformed prior to analysis.

Dependent variable	Covariate	Treatment	Probability associated with F test:			
			Levene's test of equality of variances	Lack of fit test	Effect of sex	N of alligators (females: males)
Distal width	Length	LA	0.837	0.030	0.128	53:62
Distal height		LA	0.776	0.174	0.626	53:62
Maximum proximal diameter	Minimum proximal diameter	LA	0.465	0.086	0.237	53:62
Minimum proximal diameter		LA	0.430	0.003	0.589	53:62
Minimum midshaft circumference		LA	0.265	0.218	<0.001	53:62
		LA in female femur length range (81–189 mm)	0.385	0.247	0.020	53:43
Distance from femoral head to fourth trochanter			All	0.081	0.119	0.002
	FL		0.171	—	0.759	14:13
	LA		0.698	0.911	0.757	53:62
Distal height	Distal width	LA	0.895	0.611	0.430	53:63
Minimum proximal diameter	Maximum proximal diameter	LA	0.049	0.996	0.211	53:64

Probability values associated with the effect of the covariate were < .001 in all cases.

Abbreviations: **FL** = Florida alligators; **LA** = Louisiana and Mississippi alligators; **All** = alligators from all geographic areas.

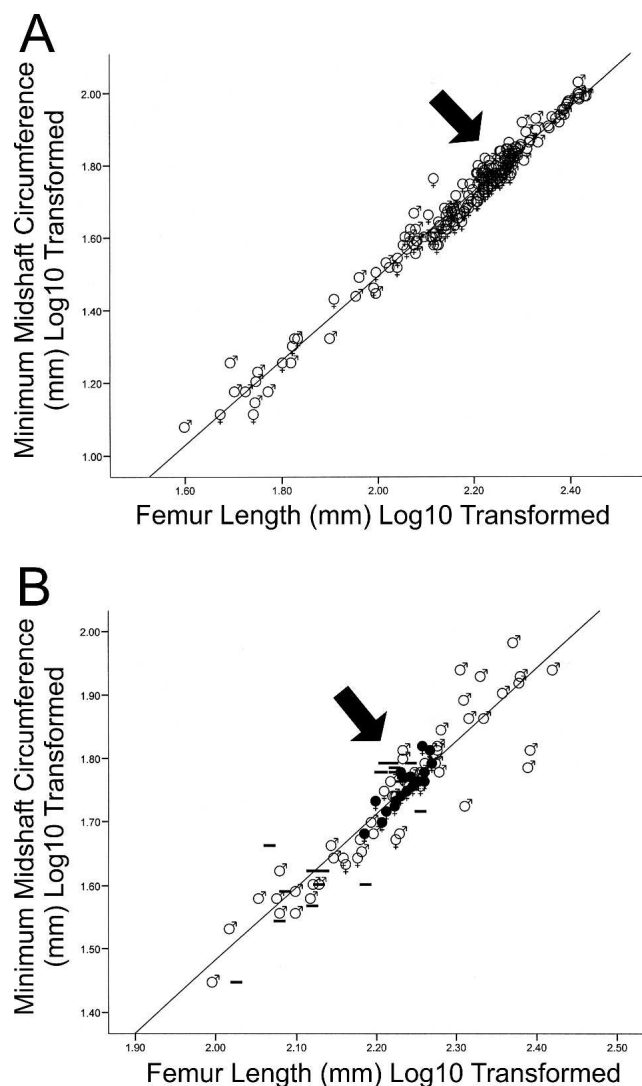


FIGURE 2. Bivariate plots of log₁₀-transformed femur length against minimum circumference using RMA regression. **A**, all alligator femora (wild and captive) in the sample, showing the distribution of males and females. **B**, the subset of alligator femora used in the thin-plate splines analysis showing males and females of varying reproductive status: known producers (filled female symbols), known non-producers (open female symbols), and unknown reproductive status (dashes). Lines in both figures are regression lines. Arrows indicate the region of the largest females in the sample and the greatest midshaft circumference variation.

good fit with the predicted shape change (multiple $r^2 = 0.8002$ for all partial warps). For *Alligator mississippiensis*, multivariate regression of the partial warps onto femur length reveals a statistically significant difference in femur shape with increasing size (Table 5). Regression of the partial warps onto femur length reveals that with increasing size most femoral shape change occurs at the proximal (1,2 and intervening semi-landmarks) and distal ends (5,6 and intervening semi-landmarks) of the femur and in midshaft stoutness (5,8) (Fig. 4), a trend that agrees with and enhances both our linear and TPS PCA results. As alligator femora increase in size, the proximal end aligns more in parallel with the distal end, the distal end expands, and the midshaft becomes more “stout.” Moreover, the fourth trochanter (3) shifts distally and landmark 7 shifts proximally with increasing size.

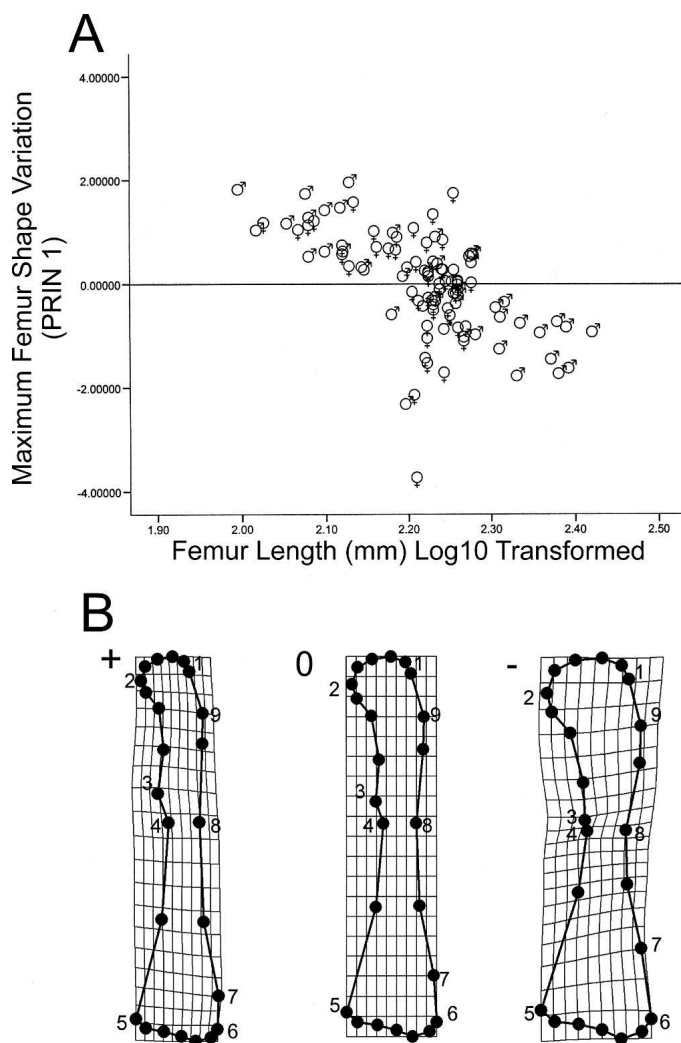


FIGURE 3. Maximum femur shape variation in relation to femur size. **A**, plot of maximum femur shape variation (PRIN 1 of partial warps) against log₁₀ transformed femur length (mm) showing the distribution of males and females. Note that the most shape variation occurs at a sub-maximal size and that the largest individuals in the sample are all male. **B**, deformation grids depicting the shape changes associated with the PRIN 1 axis based on the landmarks and semi-landmarks selected for the femur. The major landmarks are numbered and correspond to their designations in the text and in Figure 1. The semi-landmarks are unlabelled. Abbreviations: 0, the reference form; -, the negative end of the PRIN 1 axis; +, the positive end of the PRIN 1 axis.

Again, most of the variation in femoral shape occurs at approximately 72% of the maximum size in the sample, and is most variable among females (Fig. 5A). However, it should be noted that shape change associated with size only accounted for approximately 18% of the total shape change in the sample (Table 5). Moreover, as with the linear data, the known female producers show the least amount of femoral shape variation compared with the non-producers and unknowns (Fig. 5B).

Finally, third, a DFA of the partial warps discriminated sex correctly approximately 88% of the time and generated a single canonical variant (CV 1) (Table 5). Regression of CV 1 on femur length reveals that most shape differences between the sexes are subtle (Fig. 6). Compared to the reference form, in females the proximal end (1,2 and intervening semi-landmarks) is slightly more “narrow,” the fourth trochanter (3) is more medially situated, the lateral condyle (6 and related semi-landmarks) is

TABLE 5. Multiple regression of partial warps on log-10 femur length (mm) and CV 1 (sex).

Regression	Multiple r^2	Wilk's lambda	F	df	P	R ²
Log10 femur length (mm)	0.8032	0.19976825	5.098	44, 56	<.000001	18.2%
CV 1 (sex)	—	0.00000014	9060227.557	44, 56	<.000001	3%
Males (38/47)						
Females (51/54)						

Multiple r^2 values show how well the regression fits the assumption of multivariate linearity. No multiple r^2 is reported for CV 1 because this variable is already correlated entirely with sex. A significant difference ($P < .05$) indicates allometry or a significant shape change due to size increase or sex. R^2 is the coefficient of determination (after Montiero, 1999), which reflects the percentage of shape variability in the sample explained by the regression. It should be noted that only 3% of the total sample variation is due to shape differences in the femur related to sex. The number of male and female specimens correctly assigned to sex based on femur shape (88%) are reported under CV 1 (number correctly assigned / total number).

slightly more distally placed, and the region of the greater and lesser trochanters (1,9) is subtly truncated. For male femora, the proximal end (1,2 and intervening semi-landmarks) is more “expanded,” the midshaft is subtly expanded (4,8), the fourth trochanter has shifted more laterally (3), and the region of the greater and lesser trochanters (1, 9) is expanded. These results show that male femora are perhaps subtly more robust than those of females, that the femoral head is less “twisted” out of plane with the distal condyles (as the “expansion” of this region would indicate), and that the fourth trochanter has shifted somewhat laterally. However, these sex-related shape changes are very subtle and account for only 3% of the total shape change in the alligator sample.

Therefore, most of the shape variation in the sample appears to be related to allometry and individual variation. Taken in total, the thin-plate splines analyses show there are subtle but significant differences in femur shape between males and females in *Alligator mississippiensis*. However, shape change associated with size increase and individual variation appears to account for most of the sample signal.

DISCUSSION

Previous studies have hypothesized SSD in various archosaurs based on the presence of gracile and robust morphs. In particular, the robust morph has usually been presumed to be female, with generally stouter limbs characterized by expanded articular surfaces and midshaft regions. It is therefore interesting that using linear measurements of the femur of *Alligator mississippiensis*

the sexes seem not to differ in the relative stoutness (compared with femur length) of the proximal or distal articular ends, but do differ in the relative stoutness of the femoral midshaft, with femora of males having slightly larger midshaft circumferences than female femora of comparable length. This sexual difference can be seen in intraspecific variability in femur shape; the coefficient of dispersion about the reduced major axis is less for

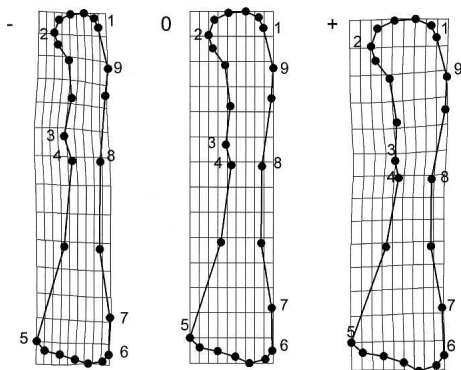


FIGURE 4. Deformation grids depicting the shape changes associated with the regression of the partial warp scores onto log-10 transformed femur length (mm). Note the expansion of the proximal and distal ends (1,2 and intervening semi-landmarks), the subtle increase in femoral midshaft width (4,8), the distal shift in the fourth trochanter (3) and greater/lesser trochanter region (1,9), and the expansion of the region for *M. gastrocnemius* origin (6,7) with increasing size. The major landmarks are numbered and correspond to their designations in the text and in Figure 1. The semi-landmarks are unlabelled. Abbreviations: 0, the reference form; -, the smallest individual in the sample; +, the largest individual in the sample.

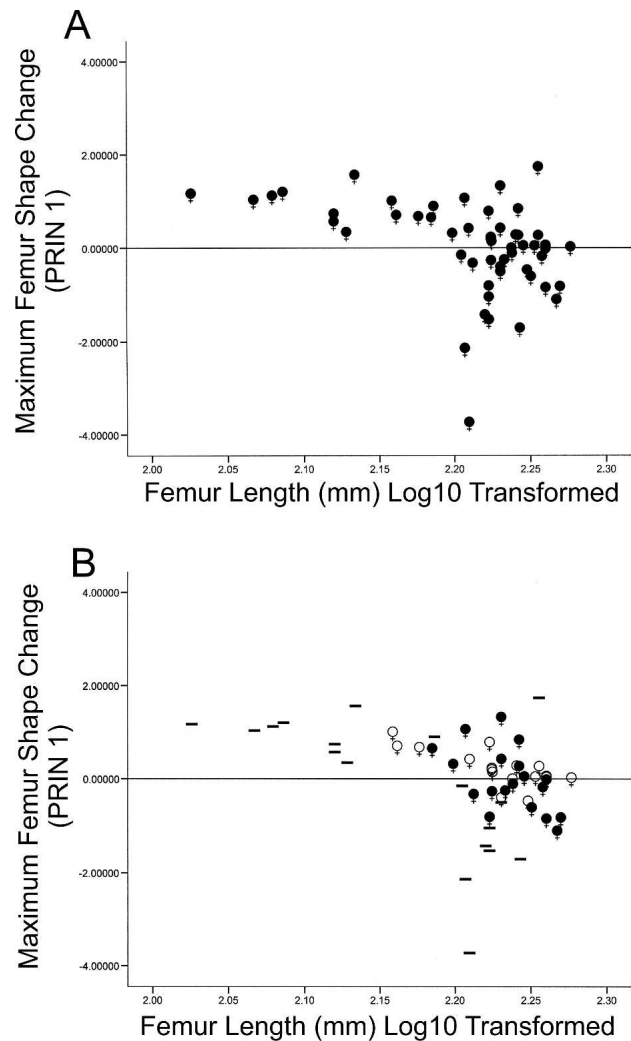


FIGURE 5. Maximum femur shape variation in relation to femur length in females. Plots of maximum femur shape variation (PRIN 1 of partial warps) against log10-transformed femur length (mm) in females only showing: **A**, all females in the subsample; and **B**, all females in the subsample designated as known producers (filled female symbols), known non-producers (open female symbols), or unknown reproductive status (dashes). Note that most of the sample shape variation occurs in the females of unknown reproductive status.

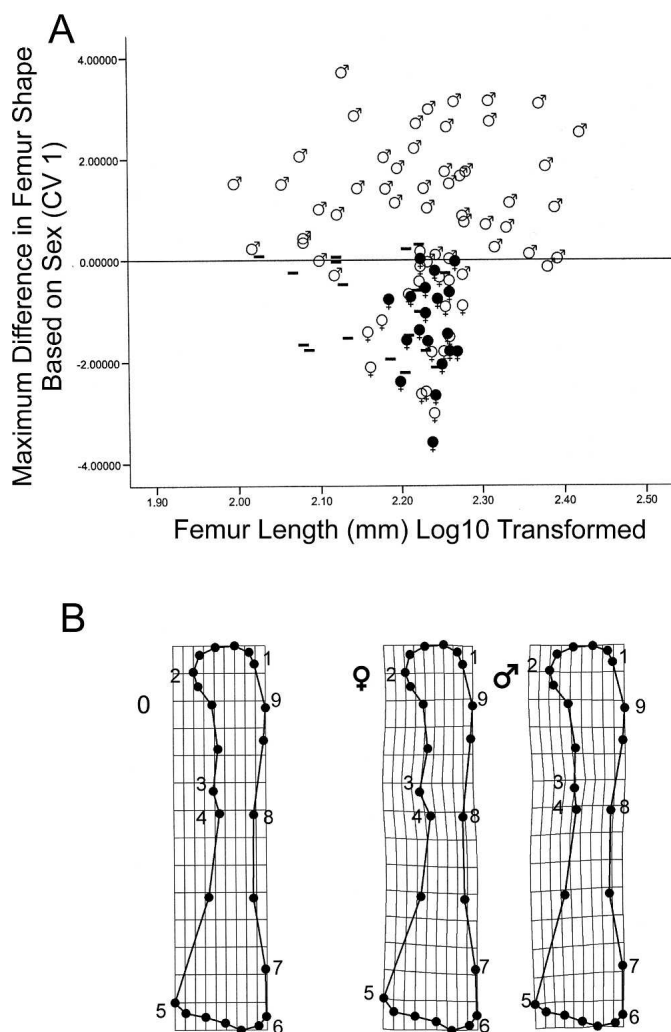


FIGURE 6. Discriminant function analysis (DFA) plot of Canonical Variate (CV) 1 which best separates out femur shape by sex against log₁₀-transformed femur length (mm). **A**, plot of males and females of various reproductive status (see Figs. 2 and 5 for legend). **B**, deformation grids reflecting shape changes in the femur between male and female specimens. Note that the shape differences between male and female alligator femora are subtle and relatively small. Abbreviations as per Fig. 4.

the individual sexes than for both sexes combined. The sexes also differ in absolute size, and so femora of male alligators become larger than female femora. In *Alligator mississippiensis*, selection for larger males is apparently associated with territorial defense (cf., Chabrek and Joanen, 1979; Joanen and McNease, 1980; Pough et al., 1998).

The thin-plate splines results corroborate and enhance our linear analyses for *Alligator mississippiensis*. These data show the greatest variation in femoral shape at a size below that of the largest individuals. The midshaft (4,8) and articular ends (1,2 and intervening semi-landmarks; 5,6 and intervening semi-landmarks) expand and become more aligned with one another as size increases, and overall femur shape shows the most variation at a particular sub-maximal size. In the largest males and females, the femur is less “twisted” than in smaller individuals. The femur of female individuals in the sample never exceeds 189 mm and around this range there is a large spread in overall femur shape. As in the linear analyses, there is much less shape change

for male alligators as the maximum recorded femur length in the sample is approached.

The greater amount of relative variation in midshaft dimensions and overall femur shape in female alligator femora may be related to the physiological consequences of shelling eggs. As Wink and Elsey (1986) and Schweitzer et al. (2005, 2007) have demonstrated, female alligators do not store and resorb medullary calcium in their long bones as female birds do to provide calcium for their egg shells. Instead, like turtles, female alligators must resorb and utilize structural bone in order to mobilize enough calcium to shell their eggs (Wink and Elsey, 1986; Schweitzer et al., 2005, 2007). These data are suggestive for our results, and it is tempting to suggest that the greater variability observed in female alligator femora is related, in part, to how often particular individuals reproduced and shelled eggs.

However, if this is the case, it is important to note that the laying females and the known non-producers show the least shape variability in this sample. In fact, the most robust female femora in the sample are those of unknown reproductive status (Figure 5). The laying females and known non-producers show the least shape variation in the sample and more-or-less follow the pattern of the males. Thus, where the reproductive status of the female is known, there is no discernible difference in shape between producers and non-producers. Therefore, it remains unknown if shelling of eggs affects female femora shape in a significant way. It is certainly possible that the most robust female femora are those of producers who have “stockpiled” more calcium reserves, but it is equally plausible that these robust individuals are non-producers that can become more robust because less of their calcium has been diverted to egg shelling. Future analyses of known producers and non-producers may shed additional light on this pattern.

Significantly, size and individual variation appear to have a greater impact on femur shape than sex. As femur size increases, areas associated with muscular insertion shift in their relative positions, which probably changes the mechanical advantage of these tissues. For example, the fourth trochanter (3) shifts relatively more distally in larger individuals. Based on the principles of a second-order lever system, this would suggest the mechanical advantage of the *Mm. caudofemorales* increases with increasing size whereas the relative range of movement and/or speed of the femur would decrease (see Bonnan, 2004 for a discussion of these systems in a thin-plate splines context). Under similar principles, the relatively more distal position of the greater and lesser trochanter region (1,9) with increasing size also suggests “improved” mechanical advantage for the *M. iliofemoralis* and *Mm. puboischiofemorales internus* in larger individuals. We note that the expansion of the area between landmarks 6 and 7, a region shown to serve, in part, as the origin of the lateral head of the *M. gastrocnemius*, may indicate the increasing size of this primary plantarflexor in larger individuals. Certainly, differences in activity and diet among individuals in the sample must also have a significant impact on shape variation in the population of alligator femora.

We have hypothesized that femur shape is a reliable indicator of sex in archosaurs and that variation in the expansion of the midshaft and articular surfaces might be reliable, distinguishing features that would separate sexes in extinct archosaurs. Our data suggest this hypothesis is, at first consideration, correct in that alligators show sex-specific but subtle differences in femoral shape associated with midshaft stoutness, proximal and distal end shape and orientation, and regions of muscular attachment. Moreover, there is a sub-maximal size at which both the greatest variation in femoral shape occurs and where the largest sex departs company with the smaller gender. However, we would be remiss if we did not acknowledge that these signals comprise but a small fraction (3%) of the total shape change in a given femur sample.

The sprawled position of alligator femora may cause other changes in shape that may not necessarily occur in the parasagittal limbs of archosaurs such as non-avian dinosaurs and birds (see, for example, work by Blob [2000] and Meers [2002] on femoral and humeral cortical area, respectively). Future investigations into SSD and long bone shape in non-avian dinosaurs and birds promises to shed additional light on these concerns.

Although there are distinct differences in femur shape between male and female alligators, these differences are small and require a large sample size to detect, a requirement that is often difficult or impossible to meet with fossil archosaurs. We doubt that we would have noted the finer differences between the sexes shown in the DFA of the thin-plate splines analyses had we not known the sexual identity of each individual *a priori*. This difficulty is probably greater for fossil archosaur samples. The most reliable signal in our data is probably midshaft stoutness: males have a slightly greater femoral midshaft circumference for a given femur length than do females. Another promising signal in our data for fossil archosaurs is the apparently greater variation in female femora at or near their maximum size. In a larger sample of fossil archosaur femora, it might be possible to infer sex from plots of the robustness of the midshaft and shape variation, with the males being the larger and stouter in midshaft circumference. However, one must be careful even here, for other archosaurs show reversed SSD trends. For example, in many raptorial birds and the extinct moa, the female is the larger and more robust form (Dunn et al., 2001; Worthy et al., 2005).

Our data suggest that a significant but subtle shape difference is present in the femora of male and female alligators. If the alligator model of growth and SSD is applicable to other fossil archosaurs, such data could have significant implications for studies of fossil archosaur growth and histological interpretation. Perhaps in cases where a large number of femora are preserved over an ontogenetic series, such data could elucidate shape trends correlated with SSD. However, at this time, our data can only detect subtle shape differences and we must be cautious not to over-extend alligator ontogenetic and sex trends too broadly. For example, the presence of medullary bone in certain non-avian dinosaurs (e.g., *Tyrannosaurus rex*; Schweitzer et al., 2005) suggests morphological differences in the femur between males and females may follow trends closer to those of birds.

Our data also raise a significant point for consideration. The subtle pattern of SSD we report for alligator femora is not of the degree commonly postulated for many extinct archosaurs, such as non-avian dinosaurs. If the alligator pattern of SSD is applicable more broadly to extinct archosaurs, it could be that what has been previously described as SSD is actually a different signal. For example, the "robust" and "gracile" femora of many non-avian dinosaurs might reflect differences in life histories other than SSD. Ultimately, any future study of SSD in fossil archosaurs must first address these patterns in the linear and geometric morphometric data of other archosaurs, including birds, before more robust conclusions can be inferred.

ACKNOWLEDGMENTS

We benefited from the reviewer comments of David C. Evans, Ralph E. Chapman, Johannes Müller, and Robert Reisz. We thank Ruth Elsey of the Rockefeller Wildlife Refuge for access to specimens, and wish the refuge a speedy recovery from the effects of Hurricane Rita. We also thank Jennifer Sandrik for her insight on alligator femoral "twisting." This research was supported by NSF grant EAR-0207182 to Farlow and from a University Research Council (URC) grant 3-30185 from Western Illinois University to Bonnan.

LITERATURE CITED

- Benton, M. J., L. Juul, G. W. Storrs, and P. M. Galton. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology* 20:77–108.
- Biewener, A. A. 2005. Biomechanical consequences of scaling. *Journal of Experimental Biology*, 208:1665–1676.
- Birch, J. M. 1997. Comparing wing shape of bats: the merits of principal-components analysis and relative-warp analysis. *Journal of Mammalogy*, 78(4):1187–1198.
- Blackenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111:977–1016.
- Blob, R. W. 2000. Interspecific scaling of the hindlimb skeleton in lizards, crocodylians, felids and canids: does limb bone shape correlate with limb posture? *Journal of Zoology, London*, 250:507–531.
- Bonnan, M. F. 2004. Morphometric analysis of humerus and femur shape in Morrison sauropods: implications for functional morphology and paleobiology. *Paleobiology*, 30(3):444–470.
- Bonnan, M. F. and Senter, P. 2007. Were the basal sauropodomorph dinosaurs *Plateosaurus* and *Massospondylus* habitual quadrupeds?; pp. 139–155 in P. M. Barrett and D. J. Batten (eds.), *Evolution and palaeobiology of early sauropodomorph dinosaurs*. *Special Papers in Palaeontology*, 77.
- Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. New York: Cambridge University Press.
- Bookstein, F. L. 1996. Combining the tools of geometric morphometrics; pp. 131–151 in L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice (eds.), *Advances in Morphometrics*. New York: Plenum Press.
- Brochu, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Memoir 7, Society of Vertebrate Paleontology Volume 22, Supplement to Number 4*, 138 pp.
- Carpenter, K. 1990. Variation in *Tyrannosaurus rex*; pp. 141–145 in K. Carpenter and P. J. Currie (eds.), *Dinosaurs Systematics: Perspectives and Approaches*. New York: Cambridge University Press.
- Carpenter, K. 1999. *Eggs, Nests, and Baby Dinosaurs: A Look at Dinosaur Reproduction*. Indiana University Press, Bloomington, IN, 338 pp.
- Carrano, M. T. and Hutchinson, J. R. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology*, 253:207–228.
- Chabrek, R. H. and T. Joanen. 1979. Growth rates of American alligators in Louisiana. *Herpetologica*, 35:51–57.
- Chapman, R. E. 1990a. Shape analysis in the study of dinosaur morphology; pp. 21–42 in K. Carpenter, and P. J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge: Cambridge University Press.
- Chapman, R. E. 1990b. Conventional Procrustes approaches; pp. 251–267 in F. J. Rohlf, and F. L. Bookstein (eds.), *Proceedings of the Michigan Morphometrics Workshop*. Ann Arbor: University of Michigan Museum of Zoology.
- Chapman, R. E. and Weishampel, D. B. 1997. Biometrics; pp. 59–62 in P. J. Currie, and K. Padian (eds.), *Encyclopedia of Dinosaurs*. New York: Academic Press.
- Chapman, R. E., D. B. Weishampel, G. Hunt, and D. Rasskin-Gutman. 1997. Sexual dimorphism in dinosaurs; pp. 83–93 in Wolberg, D. L., E. Stump, and G. D. Rosenberg (eds.), *Dinofest International*. Philadelphia: Academy of Natural Sciences.
- Dodson, P. 1975. Functional and ecological significance of relative growth in *Alligator*. *Journal of Zoology, London* 175:315–355.
- Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, 55(1):161–175.
- Erickson, G. M., A. Kristopher Lappin, and P. Larson. 2005. Androgynous rex—the utility of chevrons for determining the sex of crocodylians and non-avian dinosaurs. *Zoology*, 108(4):277–286.
- Erickson, G. M., P. J. Currie, B. D. Inouye, and A. D. Winn. 2006. *Tyrannosaurus* life tables: an example of nonavian dinosaur population biology. *Science*, 313:213–217.
- Fairbain, D. J. 1997. Allometry of sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*, 27:659–687.
- Farlow, J. O., and A. Britton. 2000. Size and body proportions in *Alligator mississippiensis*: implications for archosaurian ichnology. *Paleontological Society of Korea Special Publication* 4:189–206.

- Farlow, J. O., and R. M. Elsey. 2004. Femoral dimensions and mid-thigh circumference in *Alligator mississippiensis*. *Lethaia* 37:401–405.
- Farlow, J. O., G. R. Hurlburt, R. M. Elsey, A. R. C. Britton, and W. Langston, Jr. 2005. Femoral dimensions and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. *Journal of Vertebrate Paleontology* 25:354–369.
- Galton, P. M. 1997. Comments on sexual dimorphism in the prosauropod dinosaur *Plateosaurus engelhardti* (Upper Triassic, Trossingen). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1997: 674–682.
- Gatesy, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology*, 16(2):170–186.
- Gatesy, S. M. 1997. An electromyographic analysis of hindlimb function in *Alligator mississippiensis* during terrestrial locomotion. *Journal of Morphology*, 234: 197–212.
- Goodall C. 1991. Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society*, 53(2):285–339.
- Heerden, J. Van, and P. M. Galton. 1997. The affinities of *Melanorosaurus*—a Late Triassic prosauropod dinosaur from South Africa. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1997:39–55.
- Imbrie, J. 1956. Biometrical methods in the study of invertebrate fossils. *Bulletin American Museum of Natural History* 108:213–252.
- Joanen, T. and MacNease, L. 1980. Reproductive biology of the American alligator in southwest Louisiana. Pp. 153–159 in J. B. Murphy and J. T. Collins (eds.), *Reproductive Biology and Diseases of Captive Reptiles*. Contributions to Herpetology 1, Society for the Study of Amphibians and Reptiles. Lawrence, KS.
- Larson, P. L. 1994. *Tyrannosaurus* sex; pp. 139–155 in G. D. Rosenberg and D. L. Wolberg (eds.), *Dino Fest*. Paleontological Society Special Publication 7, University of Tennessee, Knoxville, TN.
- Larson, P. L. 1997. The king's new clothes: a fresh look at *Tyrannosaurus rex*; pp. 65–71 in D. L. Wolberg, E. Stump, and G. D. Rosenberg (eds), *Dinofest International*. Flagstaff, Ariz: Arizona State University.
- Leduc, D. J. 1987. A comparative analysis of the reduced major axis technique of fitting lines to bivariate data. *Canadian Journal of Forestry Research* 17:654–659.
- Liem, K. F., W. E. Bemis, W. F. Walker, and L. Grande. 2001. *Functional Anatomy of the Vertebrates*. Third edition. Harcourt College Publishers, New York, 703 pp.
- MacLeod, N. 2002. Phylogenetic signals in morphometric data; pp. 100–138 in N. MacLeod and P. L. Forey (eds.), *Morphology, Shape, and Phylogeny*. Taylor and Francis, New York.
- Meers, M. 2002. Cross-sectional geometric properties of the crocodylian humerus: an exception to Wolff's Law? *Journal of Zoology*, London, 258:405–418.
- Molnar, R. E. 2005. Sexual selection and sexual dimorphism in theropods; pp. 284–312 in K. Carpenter (ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington, IN.
- Monteiro L. R. 1999. Multivariate regression models and geometric morphometrics: the search for causal factors in the analysis of shape. *Systematic Biology*, 48(1):192–199.
- Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, K. D. Wells. 1998. *Herpetology*. Prentice Hall, New Jersey, 577 pp.
- Raath, M. A. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*; pp. 91–105 in K. Carpenter and P. J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge, U.K.
- Rohlf, F. J. 1993. Relative Warp Analysis and an example of its application to mosquito wings; pp. 131–159 in L. F. Marcus, E. Bello, and A. Garcia-Valdescasas (Eds.), *Contributions to Morphometrics*. Madrid: CSIC.
- Rohlf, F. J. 2005. Thin-plate splines (TPS) software family: TPSDIG, TPSRELW, TPSREGR, TPSUTIL. SUNY, Stony Brook.
- Rohlf, F. J., A. Loy, and M. Corti. 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. *Systematic Biology*, 45(3):344–362.
- Romer, A. S. 1956. *Osteology of the Reptiles*. Chicago: University of Chicago Press, 772 pp.
- Rowe, T., and J. Gauthier. 1990. Ceratosauria; pp. 151–168 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley.
- Sander, P. M. 2000. Longbone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* 26:466–488.
- Schwartzkopf, L. 2005. Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). *Herpetologica*, 61(2):116–123.
- Schweitzer, M. H., J. L. Wittmeyer, and J. R. Horner. 2005. Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. *Science* 308:1456–1460.
- Schweitzer, M. H., R. M. Elsey, C. G. Dacke, J. R. Horner, and E.-T. Lamm. 2007. Do egg-laying crocodylian (*Alligator mississippiensis*) archosaurs form medullary bone? *Bone*, 40:1152–1158.
- Slice, D. E. 2005. *Modern Morphometrics in Physical Anthropology*. New York: Kluwer Academic Publishers.
- Somers, K. M. 1989. Allometry, isometry, and shape in principal components analysis. *Systematic Zoology*, 38(2):169–173.
- SPSS. 2006. SPSS release 15.0 for Windows.
- Storror, R. W. 1971. Adaptive radiation of birds; pp. 149–188 in D. S. Farmer and J. R. King (eds.), *Avian Biology*, Volume 1. New York: Academic Press.
- Vogel, S. 2003. *Comparative Biomechanics: Life's Physical World*. Princeton University Press, Princeton, NJ, 580 pp.
- Weishampel, D. B., and R. E. Chapman. 1990. Morphometric study of *Plateosaurus* from Trossingen (Baden-Württemberg, Federal Republic of Germany); pp. 43–51 in K. Carpenter and P. J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge, UK.
- Wilhite, D. R. 2005. Variation in the appendicular skeleton of North American sauropod dinosaurs: taxonomic implications; pp. 268–301 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, IN.
- Wink, C. S. and R. M. Elsey. 1986. Changes in femoral morphology during egg-laying in *Alligator mississippiensis*. *Journal of Morphology*, 189(2):183–188.
- Worthy, T. H., M. Bunce, A. Cooper, and A. Scofield. 2005. *Dinornis*—an insular oddity, a taxonomic conundrum reviewed. *Monografies de la Societat d'Història Natural de les Balears* 12:377–390.
- Zelditch, M.L., D.L. Swiderski, H.D. Sheets, and W.L. Fink. 2004. *Geometric Morphometrics for Biologists: A Primer*. New York: Elsevier Academic Press.

Submitted October 3, 2007; accepted November 19, 2007.