The Geometry of Taking Flight: Limb Morphometrics in Mesozoic Theropods

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ABSTRACT Theropoda was one of the most successful dinosaurian clades during the Mesozoic and has remained a dominant component of faunas throughout the Cenozoic, with nearly 10,000 extant representatives. The discovery of Archaeopteryx provides evidence that avian theropods evolved at least 155 million years ago and that more than half of the tenure of avian theropods on Earth was during the Mesozoic. Considering the major changes in niche occupation for theropods resulting from the evolution of arboreal and flight capabilities, we have analyzed forelimb and hindlimb proportions among nonmaniraptoriform theropods, nonavian maniraptoriforms, and basal avialans using reduced major axis regressions, principal components analysis, canonical variates analysis, and discriminant function analysis. Our study is the first analysis on theropod limb proportions to apply phylogenetic independent contrasts and size corrections to the data to ensure that all the data are statistically independent and amenable to statistical analyses. The three ordination analyses we performed did not show any significant groupings or deviations between nonavian theropods and avian maniraptorans when including all limb elements. However, the bivariate regression analyses did show some significant trends between individual elements that suggested evolutionary trends of increased forelimb length relative to hindlimb length from nonmaniraptoriform theropods to nonavian maniraptoriforms to basal avialans. The increase in disparity and divergence away from the nonavian theropod body plan is well documented within Cenozoic forms. The lack of significant groupings among Mesozoic forms when examining the entire theropod body plan concurrently suggests that nonavian theropods and avian theropods did not substantially diverge in limb proportions until the Cenozoic. J. Morphol. 276:152–166, 2015. © 2014 Wiley Periodicals, Inc.

KEY WORDS: Theropoda; evolution of flight; ordination analyses; limb morphometrics

INTRODUCTION

The first 80 million years of the evolution of Theropoda was largely terrestrial, starting with forms such as Herrerasaurus and Eudromaeus in the Late Triassic and culminating with Archaeopteryx in the Late Jurassic (von Meyer, 1861; Sereno and Novas, 1992; Novas, 1993; Martinez et al., 2011). For the past 155 million years, Theropoda has been a successful clade consisting of both terrestrial and volant forms, with nearly 10,000 extant representatives (Jetz et al., 2012). Based on key fossil evidence found in the past 20 years in China, Spain, and Argentina, it is largely accepted that birds evolved from theropod dinosaurs (see Chiappe and Dyke, 2002 for review). The synapomorphies that basal birds share with ancestral nonavian theropods also strongly support nonavian maniraptorian theropods as the group that gave rise to birds (Gauthier, 1986). The elongated forelimb of Maniraptora (literally “hand-thief”) aptly defines this group, but this is only one of many characters that nonavian maniraptorans share with their avian descendants (Gauthier, 1986).

To better understand the relationship between nonavian theropods and avialans, many workers have examined relevant limb proportions to evaluate transitions between these two groups with regard to the origin of flight (Holtz, 1995; Gatesy and Dial, 1996; Gatesy and Middleton, 1997; Middleton and Gatesy, 2000; Dececchi and Larsson, 2011). Coombs (1978) conducted the first large-scale analysis of nonavian dinosaurian limb proportions to interpret cursorial ability on the grounds that longer distal limb elements relative to the femur were indicative of advanced cursoriality. After the nesting of Avialae within Maniraptora was considered strongly supported (Gauthier,
1986), limb proportion analysis was done on both nonavian and avian theropods together to examine the transition from nonavian theropod groups to birds (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000). These studies demonstrated that avian theropods occupied a much larger morphospace in forelimb and hindlimb proportions than nonavian theropods and suggested that the evolution of a forelimb locomotor module in combination with the decoupling of the hindlimb and tail modules allowed for this larger morphospace occupation (Gatesy and Dial, 1996; Gatesy and Middleton, 1997; Middleton and Gatesy, 2000). However, they also found a substantial degree of overlap between the morphospaces of nonavian and avian theropods (Middleton and Gatesy, 2000). A more recent study by Dececchi and Larsson (2011) evaluated the evolution of arboreality in nonavian Theropoda using a combination of qualitative and quantitative metrics, including limb proportions. They found that nonavian theropods including derived nonavian maniraptorans clustered with basal and ground-dwelling birds and were unlikely to be arboreal (Dececchi and Larsson, 2011). This suggests a potential morphological dichotomy between terrestrial nonavian theropods and volant Mesozoic avian theropods.

Since the pioneering studies of Gatesy and Middleton, many basal nonavian and avian theropods have been discovered, primarily from China (Xu and Norell, 2006). The wealth of new data permits fresh insight into the morphometric and functional aspects of the nonavian theropod-avian transition. This study focuses on Mesozoic theropods and, in particular, nonavian theropods, rather than Cenozoic birds as in previous studies (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000). Further, previous studies did not use phylogenetic independent contrasts (PICs) or size correction when evaluating their data (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000). Although ternary diagrams are an effective method for circumventing size-based issues, it is critical to use PICs when evaluating a taxonomically diverse dataset because the data otherwise fail to meet the criteria of statistical independence and cannot be subjected to rigorous statistical testing.

This study re-evaluates earlier limb proportion research on the evolution of flight by examining 136 Mesozoic theropod specimens, including both nonavian and avian theropods. We do not include Cenozoic specimens so as to better understand the transition during the Mesozoic and to avoid overwhelming the dataset with modern avians. Using reduced major axis (RMA) regressions, principal components analysis (PCA), canonical variates analysis (CVA), and discriminant function analysis (DFA), we examine the presence or absence of a directional trend and significant groupings in the forelimb and hindlimb proportions between non-

maniraptoriform Theropoda, nonavian Maniraptoriformes, and basal Avialae after applying both phylogenetic and size corrections. We hypothesize that our results will be consistent with previous papers and find little separation between Mesozoic nonavian and avian theropods, especially considering the elimination of phylogenetic covariance in this study using independent contrasts. However, the use of more advanced statistical testing is necessary to fully evaluate trends in limb proportions among Mesozoic theropods. Our results have implications for mapping osteological trends in the origins of flight, allowing for quantification of the disparity of limb proportions for both avian and nonavian theropods during the Mesozoic.

MATERIALS AND METHODS

Material

One hundred and thirty-six Mesozoic theropod specimens were grouped into three categories: nonmaniraptoriform Theropoda (n = 36), nonavian Maniraptoriformes (n = 59), and basal Avialae (n = 41). The generality of the groups was necessary to produce large enough sample sizes to perform meaningful statistical tests. Nonmaniraptoriform Theropoda includes Herrerasaurus and taxa more derived than Herrerasaurus, but outside of Maniraptoriformes. Nonavian Maniraptoriformes includes ornithomimosaur and maniraptorans not including Archaeopteryx. Compagnolithids are included as nonavian maniraptoriforms in this study based on Gólich and Chiappe (2006), though this group is not phylogenetically stable and may be outside of Maniraptoriformes. Basal Avialae includes Archaeopteryx and all Mesozoic theropod taxa more derived than Archaeopteryx. We also examined subgroups to identify qualitative trends between and within the three larger groups. Subgroups examined include basal Theropoda (n = 8), Megalosaurus (n = 3), Sinosauroidea (n = 2), Cerasauridae (n = 3), Allosauroidea (n = 7), Abelisauridae (n = 2), basal Tetanurae (n = 2), Tyrannosauroidea (n = 9), Compsognathidae (n = 5), Ornithomimosauria (n = 9), Alvarezsauroidea (n = 2), Therizinosauridae (n = 1), Oviraptorosauria (n = 19), Troodontidae (n = 7), Dromaeosauridae (n = 14), basal Avialae (n = 8), Confuciusornithidae (n = 3), Enantiornithes (n = 13), Omniporopterygidae (n = 1), Ornithuromorpha (n = 10), Longipterygidae (n = 4), and basal Ornithurae (n = 2).

Allometric changes in the vertebrate skeleton are often a function of ontogeny (Thompson, 1917; Gould, 1966; Houck et al., 1990). For example, juveniles of some extinct flightless birds have limb ratios that misleadingly suggest flight capability (Middleton and Gatesy, 2000), so the use of juveniles in our analyses may not have provided accurate determination of limb length and/or ratios in the adult animal. To avoid such bias in our data, only subadult or adult specimens were used with relative age determination based on original descriptions of each specimen. We also omitted composite skeletons from the study so that all calculated limb proportions accurately and reliably reflect the morphology of a single individual.

Methods

We obtained measurements of forelimb and pectoral girdle elements (scapula, humerus, radius, ulna, metacarpal III), hindlimb and pelvic girdle elements (ilio, femur, tibia, metatarsal III), and total skull length (rostrum to occipital condyle). Measurements were derived either from specimen data cited in primary literature or direct measurement using 300 mm Mitutoyo™ 500-173 digital calipers and cloth tape measure for bones longer than 300 mm. Measurements were repeated three times to verify each value and the resulting averages were
used in subsequent analyses. Measurements taken from literature that were considered estimates were noted as such, and inclusion in our dataset was contingent on specimen completeness. The supporting information includes a full list of specimens analyzed in our study with associated measurements (Supporting Information Table S1). The measurements included total forelimb (humerus + ulna), hindlimb (femur + tibia + metatarsal III), skull, humerus, ulna, femur, tibia, and metatarsal III length.

Two complicating factors associated with analyses of this type exist: size and phylogeny. PICs are necessary when evaluating data across a broad taxonomic range, as genera tend to demonstrate stronger covariance with increasing phylogenetic closeness (Felsenstein, 1985, 2004; Garland et al., 1992). PICs account for this covariance and make the data independent and amenable to statistical testing. To generate PICs (Felsenstein, 1985), we created an informal supertree in Mesquite (Maddison and Maddison, 2011) based on a number of recent phylogenies: basal Theropoda (Nesbitt et al., 2009), Cetarsauria (Carrano and Sampson, 2008), Allosauroidea (Brusatte and Sereno, 2008; Benson, 2010), Abelisauridae (Pol and Rauhut, 2012), basal Tetanurae (Carrano et al., 2012), Tyrannosauroidae (Brusatte et al., 2010), Compsognathithidae (Chiappe and Gökül, 2010), Alveareauroidea (Choiniere et al., 2010), Ornithomimosauria (Lignola and Lopez, 2011), Therizinosauria (Norell et al., 2000), basal Ornithopoda (Lamanna et al., 2014), Troodontidae (Turner et al., 2007; Gao et al., 2012), Dromaeosauridae (Turner et al., 2007), and basal Avialae (O'Connor and Zhou, 2013). Any genera that were not included in the above analyses were assigned based on their most recent inclusion in a systematic phylogeny. Phylogenies used for each individual taxon and the generated informal supertree are included in the Supporting Information Table S1 and Fig. S15.

PICs were generated using the Phenotypic Diversity Analysis Programs (PDAP) module in Mesquite (Midford et al., 2005). The PDAP module outputs raw contrasts as well as their associated standard deviations, which are based on branch lengths. Branch lengths used here are in millions of years before present and were calculated using known geochronological ages for the formations in which the specimens were found or the mean of the geologic stages associated with those formations. Ages and formations for each specimen are listed in the Supporting Information Table S1. We calculated contrasts for the forelimb (humerus + ulna), hindlimb (femur + tibia + metatarsal III), skull, humerus, ulna, femur, tibia, and metatarsals lengths to statistically evaluate changes between and within the forelimb, hindlimb, and skull across the three groups.

Once we accounted for phylogeny, it was necessary to correct for size using the phylogenetically corrected data (Garland et al., 1992). Size can best be accounted for by taking the residuals of each element when regressed against body mass. Previous studies have aimed to estimate body mass in dinosaurs by finding skeletal correlates (Henderson, 1999; Christiansen and Fariña, 2004; Packard et al., 2009; Campione and Evans, 2012; Kubo and Kubo, 2012). Many have demonstrated that femoral length scales with body mass with a high correlation (Anderson et al., 1985; Christiansen, 1999; Christiansen and Fariña, 2004), though femoral circumference data have a higher correlation with body mass than does femoral length (Campione and Evans, 2012). Because our dataset was primarily generated from the literature, femoral length data were often available and femoral circumference data were rarely reported. Therefore, we used the length of the femur as a proxy for body size and the residuals of RMA regressions, regressed through the origin, of each variable on femur length as our size-free data. RMA regressions are preferred over ordinary least-squares regressions when both axes are subject to error (Sokal and Rohlf, 2011), as is the case with limb measurements. As the length of the femur is included in the hindlimb metric, there is covariance between our metrics for body mass and the hindlimb. This was also the case for Kubo and Kubo (2012) who used the geometric mean of the hindlimb as their body mass metric. Following their example, we use femoral length in spite of the associated covariance due to lack of a better available metric for determining body mass. RMA regressions were performed in both MATLAB (Mathworks, 2012) using the custom gmreregress function written by Antonio Trujillo-Ortiz (www.mathworks.com/matlabcentral) and in Paleontological Statistics (PAST; Hammer et al., 2001). Residuals were calculated in PAST.

After correcting for size and phylogeny, we could then confidently subject our data to statistical analyses. Because there is no independent variable in the analyses and both axes are subject to error, it was not possible to test for statistical significance using a classical analysis of covariance (ANCOVA). Instead, we performed RMA regressions to check for correlation between elements for each group and constructed 95% confidence intervals for the resulting slopes based on 1999 bootstraps. We based significance of between-group difference on the overlap of these confidence intervals. We performed PCA and CVA to identify trends in our data for all elements simultaneously. These analyses included the size-corrected humeri, ulnae, tibiae, and metatarsi independent contrasts. Both PCA and CVA look for differences in data by creating a new set of variables that are linear combinations of the original variables. The primary difference between PCA and CVA is that PCA maximizes variation between individuals, whereas CVA maximizes variance between predefined groups. We defined three a priori categorical groups for our CVA: nonmaniraptoriform theropods, nonavian maniraptoriforms, and basal avialans. Further, principal components are mutually orthogonal to the original variables, while canonical variates are not because the original space is rescaled in the process of maximizing between-group variation. As the axes that maximize differences between group means are not necessarily identical to those that maximize differences between individual means, we performed both PCA and CVA and compared the results. Finally, we performed a DFA on the size-corrected humeri, ulnae, tibiae, and metatarsi independent contrasts to classify each individual within one of the three a priori groups based on the CVA. By this method, each contrast is assigned to the group with the least Mahalanobis distance between its centroid and the contrast (Hammer et al., 2001).

RESULTS

The analyses can be grouped into three categories: regression analysis between elements, regression analysis of elements against body mass, and ordination analyses. The first group of analyses evaluates how the elements interact across the three major phylogenetic groups and demonstrates statistical significance after applying body mass corrections. The second group of analyses evaluates statistically significant changes in element lengths with body mass between the three groups. The third group of analyses tests all elements at once to find any meaningful groupings using a multivariate approach.

Regression Analyses

After correcting the forelimb and hindlimb metrics for body mass, we found that basal avialans and nonmaniraptoriform theropods were statistically significantly different from each other, though neither was significantly different from nonavian Maniraptoriformes (Table 1, Fig. 1B, Supporting Information Fig. S1). All three groups demonstrated negative correlations, which are not statistically significantly different from zero, and
low $R^2$ values (Table 2). Within the forelimb, no group was statistically significantly different from any other group (Table 1, Fig. 2A, Supporting Information Fig. S2). Confidence intervals for the slopes were particularly large for the humerus-ulna analysis, especially for nonavian maniraptoriforms, and all had positive correlations (Table 2). Both nonmaniraptoriform theropods and basal avialans had statistically significant slopes and reasonably high $R^2$ values, but nonavian maniraptoriforms did not (Table 2). The humerus-tibia analysis showed that nonmaniraptoriform theropods were statistically significantly different from both nonavian maniraptoriforms and basal avialans, but nonavian maniraptoriforms and basal avialans did not differ significantly from one another (Table 1, Fig. 2C, Supporting Information Fig. S4). Nonmaniraptoriform theropods showed a positive correlation

### Table 1. The significance of three theropod groups based on bootstrapped RMA regression 95% confidence intervals for nonmaniraptoriform Theropoda, nonavian Maniraptoriformes, and basal Avialae

| Between elements          | Nonmaniraptoriform Theropoda (NM) | Nonavian Maniraptoriformes (MF) | Basal Avialae (BA) |
|--------------------------|-----------------------------------|----------------------------------|--------------------|
| Forelimb-hindlimb        | BA                                | BA                              | NM                 |
| Skull-forelimb           | BA                                | BA                              | NM                 |
| Skull-hindlimb           | MF                                | NM                              | NM, MF             |
| Humerus-ulna              | BA                                |                                  |                    |
| Humerus-tibia             | BA                                |                                  |                    |
| Humerus-metatarsus        | MF, BA                            | NM                              | NM                 |
| Ulna-tibia                | BA                                |                                  |                    |
| Ulna-metatarsus           | MF, BA                            | NM                              | NM                 |
| Tibia-metatarsus          | BA                                |                                  |                    |
| Forelimb/hindlimb-femur  | MF, BA                            | NM                              | NM                 |
| Forelimb-femur            |                                  |                                  |                    |
| Hindlimb-femur            |                                  |                                  |                    |
| Skull-femur               |                                  |                                  |                    |

Statistically significant between-group differences are indicated for each variable by the presence of the significantly different group’s acronym in each column.
between humerus and metatarsus lengths, while nonavian maniraptoriforms and basal avialans presented negative correlations between the two elements. All had low \( R^2 \) values and were not statistically significant from zero (Table 2). Nonmaniraptoriform theropods and basal avialans were statistically significantly different from one another in the ulna-tibia analysis, but neither differed significantly from nonavian maniraptoriforms (Table 1, Fig. 3A, Supporting Information Fig. S5). All groups demonstrated positive correlations, and while nonmaniraptoriform theropods had a slope significantly different from zero, the slopes for nonavian maniraptoriforms or basal avialans did not differ significantly from zero (Table 2). In the ulna-metatarsus analysis, nonmaniraptoriform theropods were statistically significantly different from both nonavian maniraptoriforms and basal avialans, though they were not significantly different from each other (Table 1, Fig. 3B, Supporting Information Fig. S6). As with the humerus-metatarsus analysis, nonmaniraptoriform theropods had a negative correlation in the ulna-metatarsus analysis, while nonavian maniraptoriforms and basal avialans demonstrated negative correlations (Table 2). All three groups had low \( R^2 \) values and slopes that did not differ significantly from zero (Table 2). Within the hindlimb, the tibia-metatarsus analysis showed nonmaniraptoriform theropods and nonavian maniraptoriforms to be statistically significant from basal avialans (Table 1, Fig. 4, Supporting Information Fig. S13). All three had slopes that did differ significantly from zero (Table 2).

In the skull-forelimb analysis, basal avialans differed significantly from both nonmaniraptoriform theropods and nonavian maniraptoriforms, but nonmaniraptoriform theropods and nonavian maniraptoriforms did not differ from one another (Table 1, Fig. 5B, Supporting Information Fig. S7). Both nonmaniraptoriform theropods and nonavian maniraptoriforms had negative correlations, while basal avialans had a positive correlation between skull and forelimb length (Table 2). No group had

### Table 2. The 95% bootstrapped slope confidence interval, \( R^2 \) value, and \( P \)-value of each RMA regression done for each set of elements for each group

|                        | Nonmaniraptoriform Theropoda | Maniraptoriformes | Basal Avialae |
|------------------------|------------------------------|-------------------|--------------|
| Forelimb-hindlimb      |                              |                   |              |
| Confidence interval    | \((-0.074, 0.468)\)          | \((-1.684, -0.0326)\) | \((-0.150, -0.281)\) |
| \( R^2 \)              | 0.040                        | 0.039             | 0.026        |
| \( P \)-value          | 0.580                        | 0.502             | 0.498        |
| Skull-forelimb         |                              |                   |              |
| Confidence interval    | \((-6.256, -0.335)\)         | \((-2.7369, -0.4756)\) | \((-0.0596, 2.0834)\) |
| \( R^2 \)              | <0.001                       | <0.001            | 0.008        |
| \( P \)-value          | 0.998                        | 0.945             | 0.793        |
| Skull-hindlimb         |                              |                   |              |
| Confidence interval    | \((-0.0362, 0.636)\)         | \((-0.9377, -0.093)\) | \((-1.0894, 0.21)\) |
| \( R^2 \)              | 0.366                        | 0.075             | <0.001       |
| \( P \)-value          | 0.086                        | 0.339             | 0.962        |
| Humerus-ulna            |                              |                   |              |
| Confidence interval    | \((1.1727, 2.2865)\)         | \((0.8675, 7.0058)\) | \((1.628, 3.084)\) |
| \( R^2 \)              | 0.845                        | 0.070             | 0.369        |
| \( P \)-value          | <0.001                       | 0.189             | <0.001       |
| Humerus-tibia           |                              |                   |              |
| Confidence interval    | \((-0.0126, 0.4029)\)        | \((0.3073, 1.5047)\) | \((0.5759, 2.7091)\) |
| \( R^2 \)              | 0.177                        | 0.072             | 0.007        |
| \( P \)-value          | 0.103                        | 0.161             | 0.722        |
| Humerus-metatarsus      |                              |                   |              |
| Confidence interval    | \((0.1935, 1.47)\)           | \((-3.2273, -0.4208)\) | \((-2.5286, -0.5338)\) |
| \( R^2 \)              | 0.095                        | <0.001            | 0.106        |
| \( P \)-value          | 0.264                        | 0.949             | 0.136        |
| Ulna-tibia              |                              |                   |              |
| Confidence interval    | \((-0.0461, 0.2581)\)        | \((0.2227, 1.3849)\) | \((0.5914, 3.2607)\) |
| \( R^2 \)              | 0.392                        | 0.034             | <0.001       |
| \( P \)-value          | 0.014                        | 0.402             | 0.968        |
| Ulna-metatarsus         |                              |                   |              |
| Confidence interval    | \((0.02306, 1.3056)\)        | \((-4.3098, -0.5749)\) | \((-2.7613, -0.5366)\) |
| \( R^2 \)              | 0.086                        | 0.110             | 0.091        |
| \( P \)-value          | 0.274                        | 0.195             | 0.147        |
| Tibia-metatarsus        |                              |                   |              |
| Confidence interval    | \((1.5565, 2.4924)\)         | \((1.1857, 2.5921)\) | \((0.605, 1.148)\) |
| \( R^2 \)              | 0.493                        | 0.280             | 0.600        |
| \( P \)-value          | 0.001                        | 0.006             | <0.001       |

All regressions have been corrected for both phylogeny and body size.
high $R^2$ values or slopes that differed significantly from zero (Table 2). The skull-hindlimb analysis was the only analysis in which nonmaniraptoriform theropods and nonavian maniraptoriforms significantly differed from one another, but where neither was significantly different from basal avialans (Table 1, Fig. 5C, Supporting Information Fig. S8). Nonmaniraptoriform theropods and basal avialans had a slope near zero, but skull and hindlimb length for nonavian maniraptoriforms were negatively correlated (Table 2). All groups had low $R^2$ values and slopes that were not statistically significantly different from zero (Table 2).

When evaluating individual elements or sets of elements (i.e., hindlimb and forelimb) against body mass (i.e., femur length), we did not first correct the elements and sets of elements for body mass by taking residuals of elements (or sets of elements) against femur length. In the analysis of forelimb-hindlimb ratio against body mass, nonmaniraptoriform theropods were statistically significantly different from both nonavian maniraptoriforms and basal avialans (Table 1, Fig. 1A, Supporting Information Fig. S9). Nonavian maniraptoriforms and basal avialans were not statistically significantly different from one another. Nonmaniraptoriform theropods had a negative slope, while both nonavian maniraptoriforms and basal avialans had positive slopes (Table 3). However, the bootstrapped confidence intervals for both nonmaniraptoriform theropods and nonavian maniraptoriforms were very large. All groups had small $R^2$ values, though both nonmaniraptoriform theropods and basal avialans had...
slopes that were statistically significantly different from zero (Table 3). The three groups did not significantly differ in the forelimb-femur, hindlimb-femur, or skull-femur analyses (Table 1, Figs. 5A, 6, Supporting Information Figs. S10, S11, S12). All three of these analyses had high $R^2$ values and significant correlations for each group (Table 2).

**Ordination Analyses**

The first two components of the PCA summarized 92.80% of the total variance, with the first and second principal components accounting for 67.43% and 25.37% of the total variance, respectively. The third and fourth principal components accounted for less than 8% of the total variance. The broken stick method indicates that they do not account for more variation than would be expected by chance and so were excluded from our interpretations (Supporting Information Fig. S14).

All three groups overlapped substantially in morphospace and demonstrated no clear groupings (Fig. 7A). The basal contrast plotted near the center of the morphospace. CVA summarized 96.79% of the total variance in the first two axes, with the first and second axes accounting for 86.53% and 10.26% of the total variance, respectively. There was overlap between the contrasts of all three groups and substantial overlap of 95% confidence ellipses (Fig. 7B). The confidence ellipses for nonmaniraptoriform theropods and basal avialans are entirely encircled by the nonavian maniraptoriform confidence ellipse. The total variance explained for both the PCA and CVA as well as a scree plot can be found in the Supporting Information Table S2 and Fig. S14.

DFA attempted to classify each contrast into the given phylogenetic groups: nonmaniraptoriform Theropoda, nonavian Maniraptoriformes, and basal Avialae. Fifty percent of the 46 total contrasts were correctly classified (Table 4). Nonmaniraptoriform Theropoda and basal Avialae demonstrated particularly poor identification accuracy, with only 41.7% of nonmaniraptoriform Theropoda and 40.0% of basal Avialae correctly classified. Conversely, 71.4% of nonavian Maniraptoriformes were correctly classified.

**DISCUSSION**

The majority of between-elements analyses demonstrate a statistically significant separation of nonmaniraptoriform theropods from Mesozoic avialans with nonavian maniraptoriforms intermediate between the two. Only the skull-hindlimb analysis results in significant differentiation between nonmaniraptoriform theropods and nonavian maniraptoriforms with neither being significantly different from basal avialans. Despite these relationships, the three phylogenetic groups were not clearly distinguished by PCA, CVA, or DFA. It appears that though the between-elements regressions show a generally significant trend in pairwise limb proportions among the theropod groups considered, these relationships collapse and the groups become indistinguishable in morphospace when all the elements are included in ordination analyses. This discrepancy between bivariate limb proportions is likely due to the high degree of allometric variation in theropod morphology and the complex evolutionary relationships of these groups.
proportions and multivariate analyses that consider all the included limb proportions simultaneously suggests that there are small-scale trends between the groups, but not a massive directional change in the overall theropod body plan during the Mesozoic. Previous studies have shown similar morphological overlap between nonavian theropods and Mesozoic birds (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000; Dececchi and Larsson, 2011), though these analyses incorporated a much larger number of Cenozoic forms than Mesozoic forms making it difficult to examine Mesozoic-specific changes. Our study demonstrates that there are statistically significant changes in theropod appendicular proportions during the Mesozoic, trending from short-armed nonmaniraptoriform theropods to longer-armed Mesozoic birds, but that the overall body plan of Theropoda within the Mesozoic had not yet significantly diverged from the nonmaniraptoriform condition in terms of limb proportions. Lack of a major directional trend in both fore- and hindlimb proportions, which we originally hypothesized to reflect the evolution of flight adaptations, was not apparent and is likely due to high disparity of limb proportions in the three theropod groups we examined and the niche specializations of individual species within those major groups.

The ratio of forelimb to hindlimb length quantifies and compares the total length of the forelimb and hindlimb, ignoring the proportions of the individual elements comprising each limb, and reflects the interplay of the theropod body plan in such behaviors as locomotion and prey capture (Fig. 1B). We might expect significant differences in forelimb-hindlimb proportions between terrestrial and volant species. As with the majority of the analyses we performed, Mesozoic birds have a comparatively long forelimb relative to the hindlimb (0.61–1.12), while nonmaniraptoriform theropods present a smaller ratio (0.14–0.43) and nonavian maniraptoriforms are intermediate (0.28–0.55). Basal avialans are statistically significantly different from the more basal nonmaniraptoriform theropods in this proportion, and neither is significantly different from the intermediate nonavian maniraptoriforms (Table 1).

The appearance of a directional trend from relatively short to long forelimbs is in part due to the inclusion of disproportionately short-armed tyrannosauroids. Four of 12 nonmaniraptoriform theropods are tyrannosauroids with forelimb-hindlimb ratios that range from 0.14 to 0.19 (Fig. 7A). Although this group may represent an extreme specialization, the next nonmaniraptoriform theropod with the largest forelimb-hindlimb ratio is Allosaurus (0.30), which overlaps with the low-end nonavian maniraptoriforms, Caudipteryx (0.28), Hoplocheirus (0.31), and Compsognathus (0.32). Basal nonavian maniraptoriforms (ornithomimids, compsognathids, alvarezsaurids, and oviraptorosaurs) dominate low-end values of this ratio, while high-end values are displayed by troodontids and dromaeosaurs (0.54–0.55). Despite the lack of significant difference between nonavian maniraptoriforms and Mesozoic birds in phylogenetically-corrected regressions of forelimb and hindlimb, the raw ratios for Mesozoic birds do not overlap with those of either nonavian theropod group (Fig. 7A).

Interestingly, there were no significant differences between any of the three groups in proportions relating the forelimb elements (humerus, ulna; Fig. 2A, Table 1). A wide range of variation in the humerus-ulna ratio exists within nonmaniraptoriform theropods, ranging from Eoraptor (1.01) to Carnotaurus (3.65) (Bonaparte et al., 1990; Sereno et al. 2012). Apart from the aberrant ratio of Carnotaurus, nonavian maniraptoriforms present a similarly diverse range (1.02–1.44) to nonmaniraptoriform theropods. Basal Avialae is on the lower end of the spectrum (0.73–1.16), but does not differ significantly from the other two groups (Table 1). Otohornis (0.73) has a much lower humerus-ulna ratio than other Cretaceous birds (Dong, 1993) with all other birds we examined having ratios greater than 0.91. The elongation of the ulna relative to the humerus has previously been considered to aid in flight ability, such that birds with shorter humeri relative to other forelimb elements (i.e., a humerus-ulna ratio <1.0) are capable of increased flight maneuverability (Rayner, 1988;
The smaller humerus-ulna ratios exhibited by Mesozoic birds relative to nonavian theropods in our analysis support the hypothesis that evolution toward flight-capable limb proportions was well underway by the end of the Mesozoic, though Mesozoic birds had not yet reached the level of flight specialization or disparity characteristic of modern birds.

Middleton and Gatesy (2000) recognized *Carnotaurus* to have a humerus-ulna ratio similar to that of extant birds with reduced forelimb function, though Senter and Parrish (2006) argued that the extent of the humeral head in *Carnotaurus* suggests that its forelimb may not have been functionless despite its reduction. *Carnotaurus* is considered to have evolved reduced forelimbs convergently with tyrannosaurs because some animals closely related to *Carnotaurus* have unreduced forelimbs (Middleton and Gatesy, 2000; Senter and Parrish, 2006). *Tyrannosaurus* and other derived tyrannosaurids range in humerus-ulna proportions from 1.8 to 1.96, much lower than that of *Carnotaurus* (3.65). Therefore, it is evident that the convergent evolution of forelimb reduction in these two groups proceeded differently and perhaps should not be conflated.

The humerus-tibia and ulna-tibia analyses both found basal avialans and nonmaniraptoriform theropods to be statistically significantly different from one another (Figs. 2B, 3B; Table 1). This is
not surprising given that the distal limb element in birds is intrinsically lengthened in part due to fusion of the tarsals with the tibia to form the avian tibiotarsus. Both nonavian theropod groups have similarly shorter humeri relative to their tibiae with nonmaniraptoriform theropods and nonavian maniraptoriforms ranging from 0.26 to 0.61 and 0.21 to 0.78, respectively. In contrast, Mesozoic birds range from 0.68 to 1.55, resulting from an increase in the length of the humerus relative to the tibiotarsus despite the already lengthened hindlimb element due to incorporation of the tarsal bones. Basal forms such as *Archaeopteryx* occupy the lower end of the humerus-tibia range (0.77), while the more derived *Sapeornis* is at the higher end (1.54), leading Zhou and Zhang (2003) to conclude *Sapeornis* was a soaring species.

The ulna-tibia analysis paints a similar picture in which nonmaniraptoriform theropods range from 0.14 to 0.54, nonavian maniraptoriforms range from 0.20 to 0.63, and basal avialans range from 0.63 to 1.62. Similar to the humerus-tibia analysis, *Archaeopteryx* and other more basal birds are on the low end for Mesozoic birds (0.80), while *Sapeornis* has the largest humerus-tibia ratio (1.62). Our results are consistent with previous

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**TABLE 3.** The 95% bootstrapped slope confidence interval, $R^2$ value, and $P$-value of each RMA regression done for each set of elements for each group against body size (femur length)

|                        | Nonmaniraptoriform Theropoda | Maniraptoriformes | Basal Avialae |
|------------------------|-------------------------------|------------------|--------------|
| Forelimb/hindlimb-femur| ($-23.14, -2.16$)            | (0.929, 21.4)    | (1.538, 3.26) |
| $R^2$                  | 0.4290                        | 0.0310           | 0.3540       |
| $P$-value              | 0.029                         | 0.547            | 0.008        |
| Forelimb-femur         | ($0.4849, 1.8418$)            | (0.7919, 0.9886) | (0.7214, 0.9056) |
| $R^2$                  | 0.4186                        | 0.9176           | 0.9363       |
| $P$-value              | 0.009                         | <0.001           | <0.001       |
| Hindlimb-femur         | ($0.9866, 1.0913$)            | (1.045, 1.1588)  | (0.7690, 1.0266) |
| $R^2$                  | 0.9879                        | 0.9847           | 0.9237       |
| $P$-value              | <0.001                        | <0.001           | <0.001       |
| Skull-femur            | ($0.7301, 1.0842$)            | (0.8069, 1.3401) | (0.6862, 1.5427) |
| $R^2$                  | 0.9200                        | 0.7811           | 0.7159       |
| $P$-value              | <0.001                        | <0.001           | <0.001       |

All regressions have been corrected for both phylogeny.

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Fig. 6. Forelimb and hindlimb with body size. **A:** The forelimb plotted against the femur showing how forelimb length changes with body size in the three groups. **B:** The hindlimb plotted against the femur showing how hindlimb length changes with body size in the three groups. Red lines indicate RMA regressions for all three groups together. The cross is the basal contrast, black circles are nonmaniraptoriform theropods, plus signs are nonavian maniraptoriform theropods, and open squares are basal avialans. The color of the letters reflects significances found in Table 1 (NM – nonmaniraptoriform theropods, MF – maniraptoriforms, BA – basal avialans). Different colors (red – blue) indicate statistical significant differences between those groups, black indicates no significant difference with any other group, and abbreviations of the same color (red – red, blue – blue) indicates no statistical difference between those groups.
analyses, which found *Archaeopteryx* to overlap with nonavian theropods (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000; Dececchi and Larsson, 2011). Although the flight capabilities of *Archaeopteryx* are hotly debated and as yet unresolved (Ostrom, 1974; Olson and Feduccia, 1979; Ruben, 1993; Speakman and Thomson, 1994; Yalden, 1997; Longrich, 2006; Nudds and Dyke, 2010), it is clear that the appendicular proportions of *Archaeopteryx* were quite similar to nonavian theropods.

The humerus-metatarsus and ulna-metatarsus analyses both found basal avialans and nonavian maniraptoriforms to be statistically significantly different from nonmaniraptoriform theropods (Figs. 2C, 3C; Table 1). Similar to the humerus-tibia and ulna-tibia analyses, there is no overlap between nonmaniraptoriform theropods and basal avialans, while nonavian maniraptoriforms are intermediate in proportion. Basal avialans and nonavian maniraptoriform theropods both present higher ulna-metatarsus ratios than nonmaniraptoriform theropods. Further, analysis of the tibia-metatarsus ratio (Fig. 4) found basal avialans to be statistically significantly different from both groups of nonavian theropods (Table 1) despite substantial overlap in the tibia-metatarsus ratios for all three groups: nonmaniraptoriform theropods (1.39–2.18), nonavian maniraptoriforms (1.31–3.04), and basal avialans (1.39–2.53). The statistical difference is likely related to the incorporation of the tarsal bones into both the tibia and metatarsus by some maniraptorans and basal avialans, which change the overall configuration of the lower hindlimb. Longer distal limb elements are traditionally considered to reflect enhanced cursoriality (Coombs, 1978; Garland and Janis, 1993; Carrano, 1998). In the case of theropods, the decoupling of the hindlimb and tail locomotor modules in association with the origins of flight allowed theropods to expand into noncursorial locomotor modes (Gatesy and Dial, 1996; Gatesy and Middleton, 1997) and reduced the importance of a relatively long metatarsus, especially in comparison with the length of forelimb elements. These modifications are key to flight capability. According to our study, such modifications had already occurred within nonavian maniraptoriforms, which minimally overlap with nonmaniraptoriform theropods in their tibia-metatarsus ratios (0.58–1.97 and 0.42–1.07, respectively). Such developments as

### TABLE 4. A classifier matrix based on discriminant function analysis. Rows are the given groups and columns are the groups predicted by the discriminant function analysis.

|                     | Nonmaniraptoriform Theropoda | Maniraptoriforms | Basal Avialae | Total |
|---------------------|------------------------------|-----------------|---------------|-------|
| Nonmaniraptoriform Theropoda | 5                            | 2               | 5             | 12    |
| Maniraptoriforms    | 2                            | 10              | 2             | 14    |
| Basal Avialae       | 6                            | 6               | 8             | 20    |
| Total               | 13                           | 18              | 15            | 46    |

Percent correctly classified: 50%.

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wing-assisted incline running in extant flightless chicks suggest possible increased arboreal capabilities for nonavian maniraptoriforms that clearly lacked powered flight (Dial, 2003; Bundle and Dial, 2003; Hutchinson, 2003; Tobalske and Dial, 2007). Increased arboreal capabilities, in turn, made possible by the precursors to fully developed wings in nonavian maniraptoriforms may be the cause for the statistical grouping of nonavian maniraptoriforms and Mesozoic birds in the humerus-metatarsus and ulna-metatarsus analyses.

In addition to appendicular proportions, we also examined how total skull length changed relative to both forelimb and hindlimb length (Fig. 5; Table 1). Unlike the analyses on limb proportions, the skull-forelimb ratio statistically differentiated both groups of nonavian theropods from basal avialans, though not from each other, while the skull-hindlimb ratio significantly differed between the two nonavian theropod groups, but not between either group and basal avialans (Table 1). Clearly, there were different factors driving evolutionary changes in skull length and forelimb-hindlimb proportions in theropods. Specifically, nonmaniraptoriform theropods have much larger skull-forelimb ratios (0.73–2.35) than either nonavian Maniraptoriformes (0.36–1.72) or basal Avialae (0.28–0.78). The reduction in forelimb in favor of an increase in not only skull length but also skull robusticity, has been well documented in tyrannosaurs with the skull replacing the forelimbs as the primary prey-capture device (Carpenter and Smith, 2001; Lipkin and Carpenter, 2008; Lockley et al., 2008), though the usefulness of tyrannosaur forelimbs is still debated (Lipkin and Carpenter, 2008). The large range of values for nonmaniraptoriform theropods (0.73–2.35) is indicative of the fact that many nonmaniraptoriform theropods had un reduced forelimbs as compared with tyrannosaurs (Lipkin and Carpenter, 2008). Still, the lowest skull-forelimb values for nonmaniraptoriform theropods overlap the high-end for basal avialans, clearly indicating some change from basal to more derived theropods. However, the significant difference appears to be driven both by the disproportionately small forelimbs of tyrannosaurs and Carnotaurus as well as a low sample size for the nonmaniraptoriform theropod dataset (n = 9). In contrast, the skull-hindlimb analysis yielded substantial overlap between all three groups with nonmaniraptoriform theropods ranging from 0.32 to 0.45, nonavian maniraptoriforms from 0.17 to 0.57, and basal avialans from 0.28 to 0.61, though the majority of nonavian maniraptoriforms are below 0.37 with Juravenator an obvious outlier due to its large skull (Göhlich and Chiappe, 2006; Göhlich and Chiappe, 2010). Overall, the analyses considering skull length and limb lengths indicate that skull length in Theropoda is not directly related to either forelimb or hindlimb modules given the substantial overlap between groups in the skull-hindlimb analysis and the fact that significant differentiation demonstrated by the skull-forelimb analysis seems to be controlled by the short forelimbs of derived tyrannosaurs.

Both the principal components and canonical variates analyses show strong overlap between the three phylogenetic groups (Fig. 7). Further, the DFA only correctly classified 50% of the contrasts based on the canonical variate scores (Table 4). Within the CVA, the 95% confidence ellipses for nonmaniraptoriform theropods and basal avialans fit completely within the nonavian maniraptoriform confidence ellipse, and all but two nonavian maniraptoriforms fall within either the basal avialan or nonmaniraptoriform theropod confidence ellipses (Fig. 7B). In spite of the statistically significant bivariate plots showing some degree of separation between nonmaniraptoriform theropods and basal avialans with nonavian maniraptoriforms as intermediate, ordination analyses including all size-corrected appendicular elements (i.e., humeri, ulnae, tibiae, metatarsi) produce no such separation. This is also evident when comparing the forelimb and hindlimb before and after data have been phylogenetically corrected. Before calculating PICs, there is no overlap between nonavian and avian theropods in the forelimb-hindlimb ratio (Fig. 8A). However, this differentiation is lost after phylogenetically correcting the data (Fig. 8B) despite significant difference in some ratios between nonmaniraptoriform theropods and basal avialans (Table 1). Lack of significant differentiation of the groups in ordination analyses considering all limb proportions of interest suggests that no major change in the body plan of theropods in terms of limb proportions occurred during the Mesozoic. Our results are consistent with those of previous analyses examining all Theropoda including Cenozoic avian theropods (Gatesy and Midlenton, 1997; Midlenton and Gatesy, 2000; Dececchi and Larsson, 2011).

To better test how the forelimb, hindlimb, and skull change with respect to body size, we regressed forelimb length, hindlimb length, skull length, and the forelimb-hindlimb ratio against femur length, as a measure of body mass, for each group. Rather unsurprisingly, the forelimb-femur (Fig. 6A), hindlimb-femur (Fig. 6B), and skull-femur (Fig. 5A) analyses did not demonstrate any statistically significant differences between the three groups (Table 1), and all slopes were positive, differed significantly from zero, and were associated with high $R^2$ values (Table 3). Generally, as the animals increased in size, so did the lengths of their respective limb elements. The forelimb-hindlimb ratio was the only variable that differed significantly between groups (Fig. 1A). Specifically, nonmaniraptoriform theropods were statistically significantly different from both nonavian maniraptoriforms and basal
Avialans (Table 1). Nonmaniraptoriform theropods presented a negative slope, while regressions for both nonavian maniraptoriforms and basal avialans had a positive slope (Table 3). These results indicate that as nonmaniraptoriform theropods increased in size, their forelimbs decreased in length relative to their hindlimbs, with the opposite trend true for nonavian maniraptoriforms and basal avialans. That is, those theropods in the lineage leading to modern day birds tend to display a co-occurring decrease in size and increase in forelimb length relative to hindlimb length. The largest nonmaniraptoriform theropods were the tyrannosaurids with their famously short arms, and their derived form likely plays a role in driving this statistical trend.

**CONCLUSION**

Theropoda is a very long-lived clade evolving first in the Late Triassic, becoming the dominant carnivores throughout the Mesozoic, and remaining successful throughout the Cenozoic with nearly 10,000 extant descendants (Jetz et al., 2012). Though previous analyses have examined a large sample of the then-known Theropoda from both the Mesozoic and Cenozoic (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000), the vast majority of theropod specimens that can be analyzed are represented by modern birds making the datasets strongly affected by the pull of the Recent. Consequently, inclusion of recent species in large-scale analyses of evolutionary change in theropod morphology likely overwhelms any trends that had developed during the Mesozoic. When we consider the limb proportions of Mesozoic forms only, it is evident that Jurassic and Cretaceous avians plot on top of nonavian theropods using multivariate ordination analyses. Though the overall theropod body plan in terms of limb proportions does not significantly differentiate Mesozoic clades, certain elements differ significantly relative to others, especially between the forelimb and hindlimb. Specifically, our results show a general trend of increasing elongation of the forelimb relative to the hindlimb length with increasingly derived theropods from nonmaniraptoriform theropods to nonavian maniraptoriforms to basal avialans. Ours is the first study examining theropod proportional changes using PICs, body size corrections, RMA regressions, and ordination analyses. Using this complement of data corrections and analyses, it is possible to make the data amenable to statistical analyses and accurately examine the changes within Mesozoic theropods from a
statistical vantage. Though the evolutionary transition from nonavian theropods to avians occurred during the Oxfordian stage of the Jurassic, ~90 million years before the extinction of nonavian dinosaurs, the overall limb proportions and body plan of theropods did not substantially diverge from the nonmaniraptoriform theropod condition until the Cenozoic, with only subtle element by element trends apparent between nonmaniraptoriform Theropoda, nonavian Maniraptoriformes, and basal Avialae during the Mesozoic.

Future studies can focus on comparisons between the morphospace occupation and relative disparity of all major vertebrate fliers, including gliding and flying mammals and pterosaurs, as well as the occupation of morphospace for these groups across time (i.e., Mesozoic birds and Cenozoic birds, early Cenozoic bats and recent bats). Further, limb proportions are just one morphological change leading to increased flight capability. The morphological changes leading to the development of feathers, the reduction of the caudal series and formulation of the pygostyle, the location of the center of mass, and many others were necessary in conjunction for theropods to ultimately develop successful flight. It is important to remember that each of these individually represents only one small piece of the puzzle in the development of flight.

ACKNOWLEDGMENTS

We would like to thank Zhang Fang (IVPP), Xu Xing (IVPP), Zhang Fengjiao (Dalian Museum of Natural History), and Gao Chunling (Dalian Museum of Natural History) for specimen access. We would like to thank the University of Pennsylvania Paleobiology Stipend, the Gregory and Susan Walker Fund, the University of Pennsylvania Research Foundation, and NSF EAR 1024671 awarded to P. D. for help funding this research. Finally, we would like to thank Matthias Starck (editor), Matthew Bonnan, and Dennis Evangelista for very helpful reviews and Adam Laing, Warren Evans, Eric Morschhauser, Andrew McDonald, Colin Phillips, and David Vann for helpful discussions relating to both statistics and dinosaur taxonomy. We would also like to thank Jennifer Hall illustrating the silhouettes in Figures 7 and 8.

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