

BODY AND LIMB SIZE DISSOCIATION AT THE ORIGIN OF BIRDS: UNCOUPLING ALLOMETRIC CONSTRAINTS ACROSS A MACROEVOLUTIONARY TRANSITION

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The origin of birds and powered flight is a classic major evolutionary transition. Research on their origin often focuses on the evolution of the wing with trends of forelimb elongation traced back through many nonavian maniraptoran dinosaurs. We present evidence that the relative forelimb elongation within avian antecedents is primarily due to allometry and is instead driven by a reduction in body size. Once body size is factored out, there is no trend of increasing forelimb length until the origin of birds. We report that early birds and nonavian theropods have significantly different scaling relationships within the forelimb and hindlimb skeleton. Ancestral forelimb and hindlimb allometric scaling to body size is rapidly decoupled at the origin of birds, when wings significantly elongate, by evolving a positive allometric relationship with body size from an ancestrally negative allometric pattern and legs significantly shorten by keeping a similar, near isometric relationship but with a reduced intercept. These results have implications for the evolution of powered flight and early diversification of birds. They suggest that their limb lengths first had to be dissociated from general body size scaling before expanding to the wide range of fore and hindlimb shapes and sizes present in today's birds.

KEY WORDS: Allometry, aves, constraint, macroevolution, theropoda.

The history of vertebrates is marked by several major evolutionary transitions where the generation of novel functions and/or ecologies are due to large-scale alterations of the limb skeleton (e.g., origin of tetrapods, whales, snakes; Hall 2007). Plesiomorphically tetrapods are suspected to have had their limb evolvability restricted by developmental constraints linking the entire fore and hindlimbs and individual segments (stylo-, zeugo-, and autopodium) to one another and across each limb (Capdevila and Izpisua Belmonte 2000; Young and Hallgrímsson 2005). Decoupling these modules is central to dramatically altering limb phenotypes and permitting functional specialization and diversification (Schmidt and Fischer 2009; Young et al. 2010; Bell and Goswami 2011). The origin of birds and powered flight presents

a case where a lineage evolved a novel locomotory mode with divergent functional demands that may have been strong enough to break ancestral developmental covariation patterns in the limbs.

Extant birds have remarkable variation in limb proportions (Zeffer et al. 2003). This variation has been suggested to be the result of its dissociation from the tail (Gatesy and Middleton 1997) and its reorientation to support an anteriorly shifted center of mass (Gatesy 2002), whereas forelimb variation is associated with different flight locomotory modes and relaxed selection in flightless birds (Middleton and Gatesy 2000).

Bird ancestry lies in theropod dinosaurs and the fossil record of this transition has expanded greatly in recent years (Padian and Chiappe 1998; Xu et al. 2010a). Nonavian theropods spanned



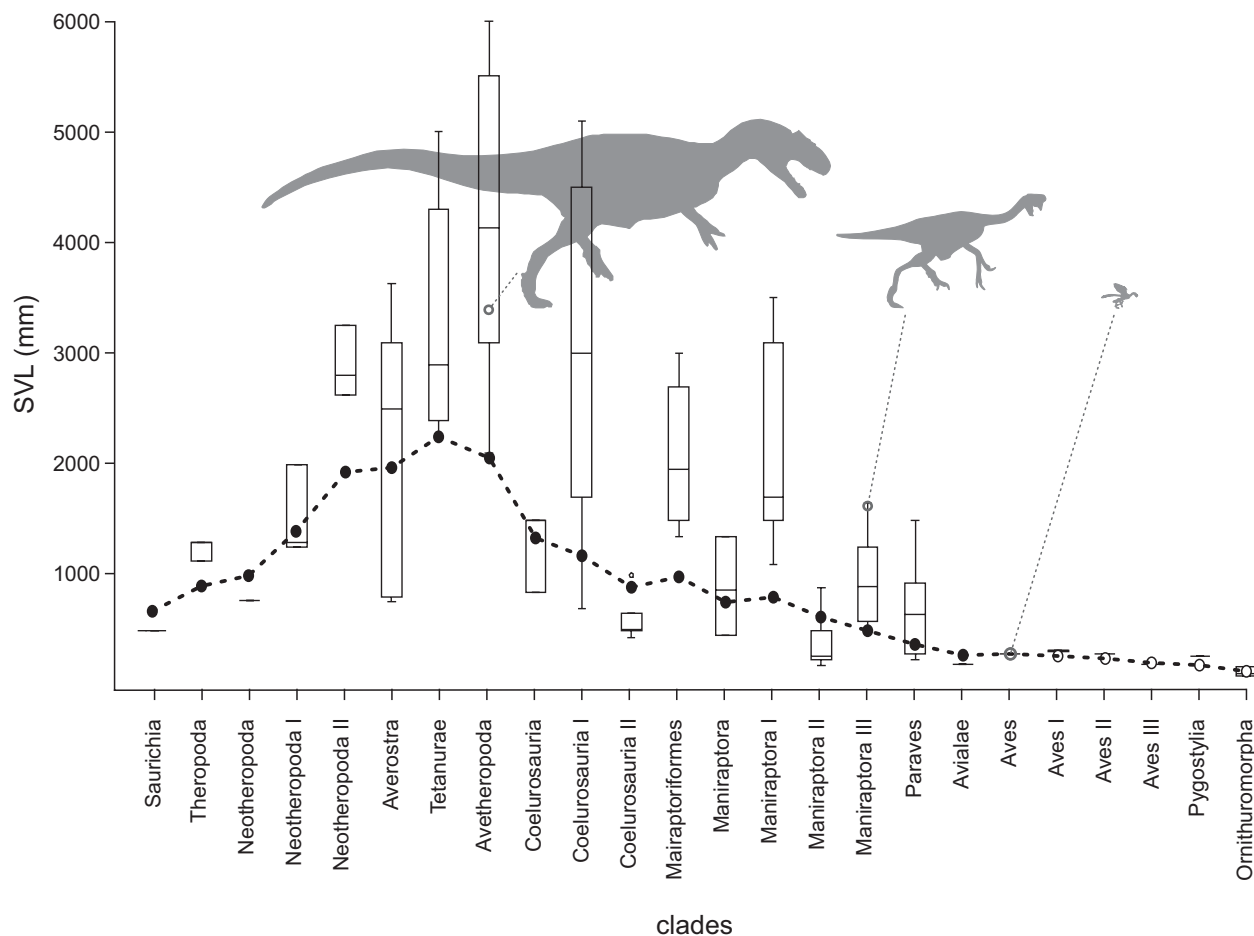


Figure 1. Evolution of body size in Theropoda. SVLs for individual theropod lineages (boxplots) and nodes (dashed line, closed circles for nonavian theropod clades, open circles for avian clades) between Theropoda and Aves are plotted along the phylogenetic backbone from Theropoda to Ornithuromorpha. Data are given in Table 1 and Table S1 and the phylogeny is based on Figure S1(B). Silhouettes of *Allosaurus*, *Citipati*, and *Archaeopteryx* are shown to relative scale.

four orders of magnitude in body size, with species masses estimated to range from less than 1 kg to greater than 5000 kg (Turner et al. 2007; Hutchinson et al. 2011; Fig. 1). A pattern of body size reduction has been described within coelurosaurian theropods preceding the origin of birds (Carrano 2006; Turner et al. 2007). Coincident with this size reduction is an apparent trend of forelimb elongation within maniraptoran theropods (Chatterjee and Templin 2004; Bybee and Lee 2006; Novas et al. 2009; Xu et al. 2011) that continued into the earliest avians, which had relatively longer and more robust forelimbs than nonavian theropod antecedents (Zhou and Zhang 2003; Xu et al. 2011). Prey capture has been suggested to have been the adaptive driver of forelimb elongation within the clade (Ostrom 1969; Carpenter 2002; Senter 2006), with the flight stroke ultimately derived from this function (Padian and Chiappe 1998). Arboreality has also been proposed as a driver for forelimb elongation (Chatterjee and Templin 2004; Xu et al. 2010a), although no evidence for arboriality is present in the hindlimbs (Dececchi and Larsson 2011). Regardless of the

favored scenario, all maintain that directed selection drove forelimb elongation in avian antecedents and was later exapted to perform as a sufficiently sized aerofoil, permitting the evolution of powered flight (Chatterjee and Templin 2004).

Given the degree body size influences estimates of extant systematic and functional relationships (Schmidt-Nielsen 1984; Gilbert et al. 2009), allometry must be examined and accounted for before any long-term adaptive trends across the origin of birds are proposed. This is not to say that allometric relationships are not adaptive (Bertram and Biewener 1990), but rather that significant divergences from a historical allometry imply a focused evolutionary change (e.g., Thörington and Santana 2007; Young et al. 2010). Understanding the allometric biases of limb proportions is fundamental to creating testable hypothesis to determine the evolutionary drivers of the nonavian theropod to bird transition. We use a large compilation of new fossil data to examine the evolution of limb lengths and body size across the origin of birds to identify significant nonallometric evolutionary changes that

could be associated with the decoupling of the ancestral theropod developmental and functional regimes.

Materials and Methods

MEASUREMENTS

Two datasets of fossil measurements were used. The first included 67 nonavian theropods and basal birds' specimens representing 53 different genera. Complete skull and precaudal vertebral series were obtained from the literature, personal communications, and personal measurements (see electronic Supporting Information). All but 17 are considered adults. The avian *Dalianraptor* was not included with the phylogenetic analysis, because its relationship within Aves is uncertain (O'Connor et al. 2011). Representative taxa from all major clades, with the exception of Therizinosauria, were included. Therizinosaurs were excluded due to the lack of any sufficiently complete single individual specimens. Individual bone lengths and four composite measurements were used: snout–vent lengths (SVLs) (skull plus cervical plus trunk lengths), trunk length (dorsal vertebral series plus sacral series lengths), total forelimb (humerus plus radius plus metacarpal II lengths), and total hindlimb (femur plus tibia plus metatarsal III lengths). The second dataset of 132 species including incomplete specimens was used to increase sampling within Theropoda (see electronic Supporting Information). This taxon set included six therizinosaurs to completely survey all major nonavian theropod clades. SVLs for specimens without completely preserved precaudal vertebral series in our larger dataset were estimated using the four lengths that had the strongest correlation with body size or through comparisons to related taxa with known measurements (see Results section and electronic Supporting Information).

TAXONOMY OF BIRDS

We use the taxonomic terms Aves and Avialae as per Zhang et al. (2008). Avialae includes all maniraptoran theropods closer to modern birds than *Deinonychus antirrhopus*, whereas Aves is the clade containing the last common ancestor of *Archaeopteryx lithographica* and *Vultur gryphus*.

JUSTIFICATION OF SVL

Snout–vent length was used to standardize body size in our analysis to avoid the confounding effects of nonallometric adaptations in limb lengths associated with functional differences (Norberg 1979; Thorington and Heaney 1981; Kohlsdorf et al. 2001; Zeffert et al. 2003; Samuels and van Valkenburgh 2008; Bell and Chiappe 2011; Dececchi and Larsson 2011). In neontological studies, these differences are assessed after the limb has been standardized against a measure of body size, either body mass or a body length, such as SVL, which are highly correlated to each

other (Thorington and Heaney 1981; Hutton 1987; Deichmann et al. 2008; Meiri 2010).

PHYLOGENETIC TOPOLOGIES AND REGRESSION ANALYSES

Five taxonomic permutations of regression analysis were performed: including all specimens; excluding juvenile and duplicate specimens; excluding birds; excluding birds, juveniles, and duplicate specimens; and including only birds. The scansoriopterygian *Epidexipteryx* was included as a nonavian theropod in our analysis. The inclusion/exclusion of avians allowed us some degree of phylogenetic control, without the limitations imposed by phylogenetic independent contrast (PIC). For the relative length dataset, only ordinary least square (OLS) regression model was run because the *Y* variable (element length relative to SVL) is directly dependent on the value of *X* (SVL).

Nodal reconstructions were calculated based on a relaxed supertree constructed from multiple sources (see electronic Supporting Information) where branch lengths were treated as equal. To account for evolutionary distance between clades, a secondary analysis was performed with branch lengths derived from the matrix of Xu et al. (2009) and Choiniere et al. (2010) (see electronic Supporting Information). Branch lengths for each permutation were reconstructed in Winclada (64) under unambiguous character optimization (Nixon 2002).

Three tree topologies were used to account for the uncertainty of the phylogenetic position of Scansoriopterygidae: Scansoriopterygidae as sister to Aves (Zhang et al. 2008); Scansoriopterygidae as an avian more derived than *Archaeopteryx* (Choiniere et al. 2010; Xu et al. 2011); and Scansoriopterygidae as sister to Oviraptorosauria with deinonychosaurs as the sister group to avians (Xu et al. 2009; Agnolin and Novas 2011). Nodal reconstructions were performed in Mesquite 2.7.5 (Maddison and Maddison 2011; see electronic Supporting Information). Relative limb length estimates at nodes were derived using SVL reconstruction for said node as the *X* variable in the relative limb length OLS regression (see Tables S2 and S5).

PIC methods were not used for our regression analyses. PIC methods were not used because accurate approximations of branch lengths for the regression tree are not attainable. Incorrect branch lengths have been shown to dramatically influence PIC results (Díaz-Uriarte and Garland 1998) and should not be used casually with fossil-based analyses. In PIC, branch length measures (Díaz-Uriarte and Garland 1998) and the exact nature of the leaf arrangement (Garland et al. 2005) significantly affect the reconstruction of the primary data used in the regression analysis. Here, we use raw regression values and compare them to nodal reconstructions along the phylogenetic backbone that allows us to account for phylogeny but, due to the nature of square change parsimony, not be overly influenced by perturbations in

distal branch while reducing the “averaging” effect that may dilute a signal in ancestor-descendant pairs along a tree (Carrano 2006). As our trend analysis concentrated on the backbone nodes, inconsistencies in branch lengths of tips or perturbations of leaf arrangement were not a significant factor in influencing the clade to clade relationships that are the core of our results (see Supporting Information for comparison of nodal reconstructions under all branch length models).

Although the use of morphological character changes as a proxy for branch length is controversial (given the problems of independence, large degrees of missing data, and unequal sampling through the taxon set), we use them here on nodal reconstructions only to provide a range of values and to insure that specific topologies do not constrain the implication of our results. In a PIC regression, these challenges to the character count as branch length provide not just a series of hypothesis to test against regression values, but a potentially highly significant bias to regression values (Díaz-Uriarte and Garland 1998).

Other methods of obtaining branch lengths for PIC such as stratigraphic distances are hindered by the fact that most of the taxa included here come from only four localities, due to preservation biases. In addition, the oldest coelurosaurian theropod, *Epidexipteryx* at approximately 162–168 million years old (Zhang et al. 2008), is also one of the most derived and single handedly collapses all major branches within Coelurosauria to this age. A final possible solution to the PIC branch length challenge is using all branch lengths equal to 1, yet this too has its own severe problems. For example, branches to each of the two species of *Microraptor*, which are from the same geological formation, would be equivalent to the branch leading to *Buitreraptor*, a taxon separated from its sister group in this analysis by at least 90 million years, based on the Laurasian–Gondwana split dates (Torsvik et al. 2012) as stated in Makovicky et al. (2005). Another complication is the underlying trend in body size reduction toward node Aves, which potentially biases the results of a PIC analysis (Garland et al. 2005). Evidence for this is a nonzero slope of absolute values of standardized contrasts versus their standard deviations in the main dataset when both missing taxa and polytomies are accounted for in the analysis (results not shown).

Results

CORRELATIONS

In general, limb lengths are strongly and significantly correlated with SVL (Fig. 2; Table 1; electronic Supporting Information). With the sole exception of the metatarsus in the avian only analysis, all hindlimb elements have higher coefficients of determination (r^2 of 0.9 or greater) than any in the forelimb (r^2 of 0.55 or greater). There is a decrease in correlation proximodistally

in the forelimb, and between the femur and metatarsus in the hindlimb. Overall, avian forelimb lengths show a positive allometric scaling value versus SVL (slope = 1.28) and are significantly higher than that of nonavian theropods (slope = 0.70; Fig. 2C). In the hindlimb, avian and the total nonavian theropod datasets have scaling values that are similar (slope = 0.96 and 0.88, respectively). When only similar-sized avian and nonavian theropods are compared (~350 mm SVL and smaller), the latter shows a much higher slope ($\text{Log}_{\text{HL}} = 1.1267 [\pm 0.2418]$ $\text{Log}_{\text{SVL}} - 0.38045 [\pm 0.33125]$, $n = 12$, $r^2 = 0.54$). Using the total nonavian theropod dataset, the marked lower than expected values in most avian taxa (average difference –24%) is likely due to the difference in the intercept between the two regressions (nonavian theropods = 0.1974 ± 0.007 , avians = -0.0712 ± 0.023).

As suggested in previous studies (Farina and Christiansen 2004; Therrien and Henderson 2007), femur and skull lengths are significantly correlated with body size. In addition, the scapula and ilium both show r^2 values of 0.93 or greater under all permutations, except in the avian only dataset (Table 1; electronic Supporting Information). The strong correlation between scapular length and SVL is not due to passive effects of the scapula being bound to the forelimb as under all five permutations the scapula records higher correlation coefficients. Partial correlation analysis found that scapular length shows a stronger association to SVL or femur length than either humeral or total forelimb length in theropods, including or excluding birds (Table 2; electronic Supporting Information).

RELATIVE LIMB LENGTHS

Relative measurements of the forelimb against SVL show higher correlation values, and significantly higher slopes than the hindlimb (Table 1; electronic Supporting Information). When avians are excluded, regression analysis shows stronger correlations than when avians are included. Direct comparisons between avian and Deinonychosauria of similar SVL indicate that the latter have significantly longer hindlimbs, both in relative and absolute terms. Small-bodied paravians had relative hindlimb lengths (83–104% SVL, mean 94%) that were significantly longer than those of avians of a similar body size (59–86% mean = 68%; uneq var. T -test = 8.839, $P(\text{same}) < 0.0001$). Other small-bodied (SVL less than 500 mm) nonparavian theropods did not have similarly elongated hindlimbs. Both *Microraptor* sp. and *Anchiornis* had relative levels of forelimb elongation (60–72% of SVL) equal to those present in the basal birds *Archaeopteryx* and *Confuciusornis* (see electronic Supporting Information). These paravian taxa show level of forelimb elongation that is not significantly different from the avian dataset.

To account for the possibility that there were errors in our SVL reconstructions, we ran a complimentary analysis using humeral to femur ratios (H:F) and residuals from regression of

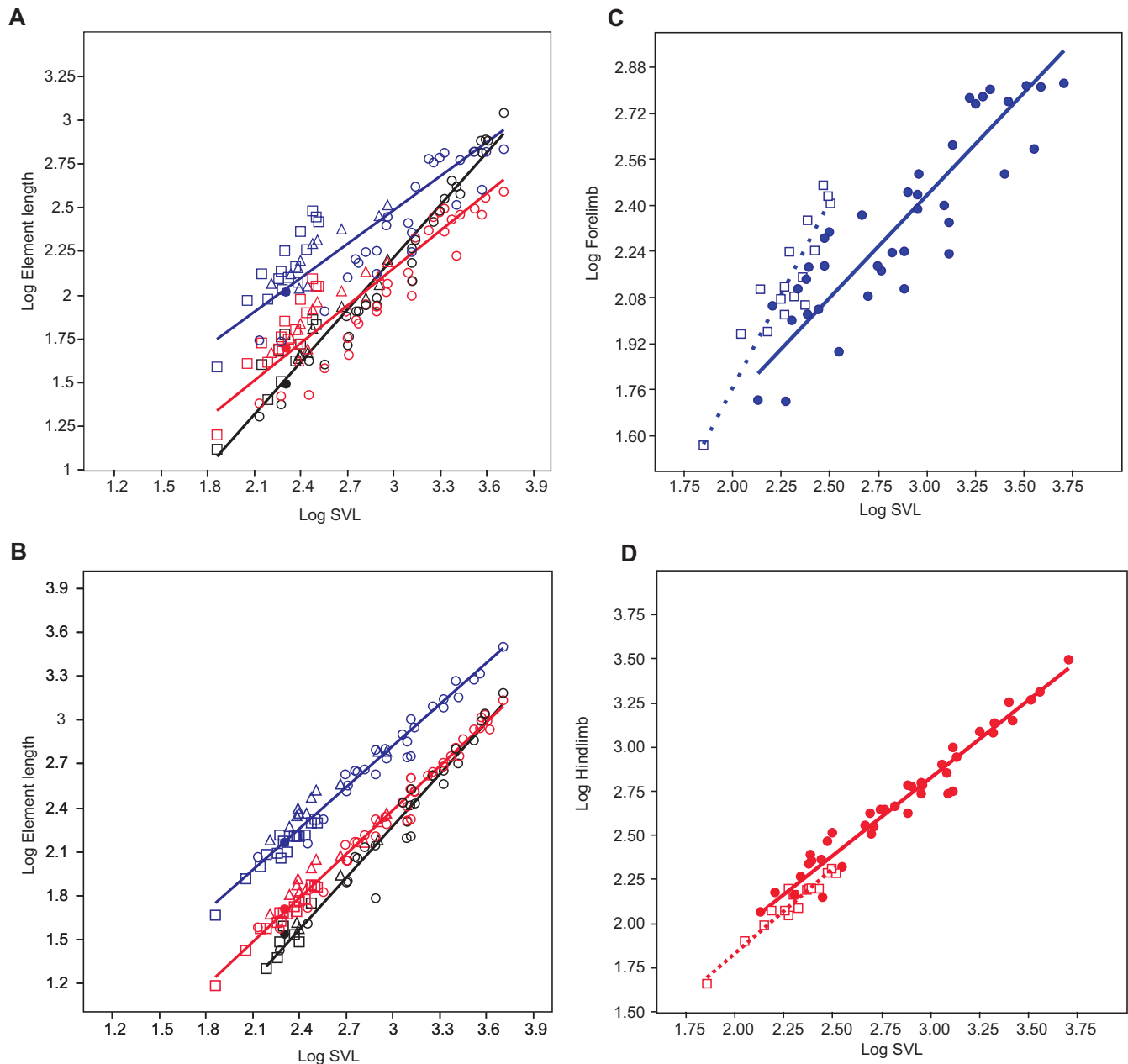


Figure 2. Regressions of theropod forelimb and hindlimb bones against SVL. Log-log reduced major axis regressions of limb bone length versus SVL for all specimens used here, forelimb data are presented in (A) and hindlimb data in (B). Red denotes the stylopodial element (humerus and femur), blue the entire limb length, and black the girdle elements (scapula and ilium). Open squares denote birds, triangles represent paravians (deinonychosaurs), and all other nonavian theropods are circles. Due to its uncertain affinities, *Epidexipteryx* is denoted by a filled circle. (C) and (D) compare nonavian (solid line) versus avian (dashed line) forelimb (C) and hindlimb (D) regressions using all measured individuals for each category. Open squares denote avians specimens, while closed circles nonavian theropods.

H on F length for 95 nonjuvenile taxa (see electronic Supporting Information). These scores were mapped onto the larger uniform dataset (Fig. 3; electronic Supporting Information). Although the H:F ratio analysis shows a trend of increasing values within Maniraptora (Fig. 3A), the residual value shows no pattern until Aves (Fig. 3B).

PHYLOGENETIC RECONSTRUCTIONS

All permutations and branch length settings revealed a strong signal of body size reduction within Coelurosauria (see electronic Supporting Information). Nodal reconstructions are broadly similar across topologies and datasets. The SVL of node Paraves is reconstructed at approximately 350 and 500 mm, and node

Table 1. Linear regression analyses of absolute (A) and relative (B) values from the total measured dataset. See text for reasoning behind use of OLS for relative measurement data. For all other permutations, see Table S2 in electronic Supporting Information. All errors are standard errors. F = femur, FL = forelimb (H + R + MC), H = humerus, HL = hindlimb (F + T + MT), IL = ilium, MC = metacarpal II, MT = Metatarsal III, R = radius, SC = scapula, SK = skull, TR = trunk axial series. Asterisks denote those scaling relationships that are significantly different from isometry using a Student's *T*-test.

(A)										
	RMA					OLS				
	<i>N</i>	Slope	error	Inter	error	Slope	error	Inter	error	<i>r</i> ²
TR*	64	1.042	0.010	−0.40314	0.001	1.0312	0.010	−0.3947	0.028	0.99
H*	60	0.71009	0.041	0.026928	0.013	0.63805	0.041	0.22246	0.114	0.81
R*	57	0.62185	0.054	0.15629	0.022	0.47558	0.055	0.54025	0.150	0.58
MC*	56	0.63894	0.057	−0.17711	0.024	0.48195	0.057	0.24516	0.156	0.57
FL*	54	0.64261	0.046	0.55803	0.016	0.55022	0.046	0.80692	0.126	0.73
F	65	1.0001	0.017	−0.61442	0.002	0.99093	0.017	−0.58906	0.047	0.98
T*	59	0.89102	0.022	−0.24486	0.004	0.87494	0.022	−0.20089	0.062	0.96
MT*	57	0.93282	0.031	−0.61494	0.007	0.90356	0.031	−0.53558	0.086	0.94
HL*	55	0.93612	0.024	0.013854	0.004	0.9203	0.024	0.05642	0.064	0.97
SC	49	0.99191	0.033	−0.75908	0.009	0.966	0.033	−0.68686	0.093	0.95
SK	67	0.9361	0.030	−0.48827	0.007	0.90501	0.030	−0.40134	0.084	0.93
IL*	38	1.1722	0.036	−1.2401	0.011	1.1525	0.036	−1.184	0.103	0.97

(B)						
	Slope	error	Intercept	error	<i>r</i> ²	<i>N</i>
TR*	0.0312	0.01004	1.6053	0.02838	0.1344	64
SK*	−0.0950	0.02968	1.5987	0.08418	0.1362	67
H*	−0.3620	0.04092	2.2225	0.1126	0.5743	60
R*	−0.5244	0.05403	2.5516	0.1480	0.6314	57
MC*	−0.5281	0.05577	2.2734	0.1523	0.6267	56
FL*	−0.4498	0.04604	2.8069	0.12578	0.6474	54
F*	−0.0091	0.01687	1.4109	0.04744	0.0045	66
T*	−0.1251	0.02232	1.7991	0.06186	0.3552	60
MT*	−0.0964	0.03126	1.4644	0.08589	0.1475	58
HL*	−0.0797	0.02354	2.0564	0.06414	0.1778	56
SC*	−0.0304	0.03286	1.3131	0.0929	0.0223	49

Aves between 260 and 320 mm. All permutations showed a consistent trend of increasing relative forelimb lengths within Coelurosauria peaking in basal birds. The hindlimb also shows a progressive increase reaching its maximum value at Paraves, followed by a marked decrease in avians (see electronic Supporting Information).

Node reconstructions for SVL and limb length reveal a close fit between reconstructed limb values and those generated from OLS relative length regression equations (see electronic Supporting Information). This was observed for nonparavian nodes, followed by a marked divergence within Aves for all reconstruction equations (Fig. 4, see electronic Supporting Information). Both parametric (Pearson's) and nonparametric (Spearman's and Kendall's τ) tests indicated significant correlations between the expected and phylogenetically reconstructed values (see electronic Supporting Information). These correlations are stronger in the

forelimb and humerus than the hindlimb was and were similar across topologies.

Within paravian theropods, there is no consistent pattern of elongation within the forelimbs beyond those expected through negative scaling. Maniraptora had expected or slightly reduced relative forelimb lengths, depending on the placement of Compsognathidae. The hindlimb shows two distinct regions of overestimation by the curves: one at Neotheropoda to Ceratosauria and a second within Aves. This pattern differs markedly from that in nonavian maniraptorans indicating a fundamental shift in hindlimb scaling coincident with the origin of birds.

Discussion

Body size significantly affects organ scaling and must be accounted for before any comparative analysis can be performed.

Table 2. Partial correlation scores comparing strength of correlation of the scapula (SC) to body size as represented by SVL(A) or F(B), Humerus (H), and Forelimb (FL) for all specimen database ($N = 4$). All data were logged before analysis was performed. Vertical values below the X denote r score, and horizontal values above the X denote probability that two elements are not correlated. For all other permutations, see Table S3 in electronic Supporting Information.

(A)				
	SVL	SC	H	FL
SVL	X	0.0000	0.0012	0.0002
SC	0.7518	X	0.7133	0.447
H	0.5009	0.0608	X	0.0000
FL	-0.5675	0.1254	0.9642	X
(B)				
	F	SC	H	FL
F	X	0.0000	0.0033	0.0004
SC	0.8085	X	0.8875	0.299
H	0.4645	0.0237	X	0.0000
FL	-0.5482	0.1729	0.9597	X

Although we are not discounting the role of adaptation, we suggest that other nonadaptive factors play a larger role than generally appreciated. Femoral length remains an accurate proxy of SVL in many nonavian theropods; however, there are some notable exceptions (e.g., small-bodied basal deinonychosaurs and avians). Our results support previous findings that skull length can be an effective body size proxy across Theropoda (Therrien and Henderson 2007), with some caveats. Although skull length did demonstrate a strong relationship with body size, other skeletal elements (femur, scapula) showed higher correlations and these elements may be less susceptible to phylogenetic biases within nonavian theropods than the skull (Brusatte et al. 2012). Hindlimb segmental and total lengths are strongly correlated with SVL in nonavian theropods, whereas forelimb values are less so, although they remain statistically significant. We suggest that this pattern is the result of the bipedal, terrestrial locomotory constraints on the hindlimb, and differential selection on forelimb functions in these taxa. Our results support earlier hypotheses that the non-locomotory function of nonavian theropod forelimbs may have been a driver for higher forelimb variation in these taxa due to relaxed functional constraints (Gatesy and Dial 1996; Gatesy and Middleton 1997).

THE SCAPULA

The robust correlation between scapular length and body length, especially in nonavian taxa, was unexpected (but see Dececchi et al. 2012). Within nonavian theropods, scapula lengths are more tightly correlated to SVL (or F) than forelimb length (see

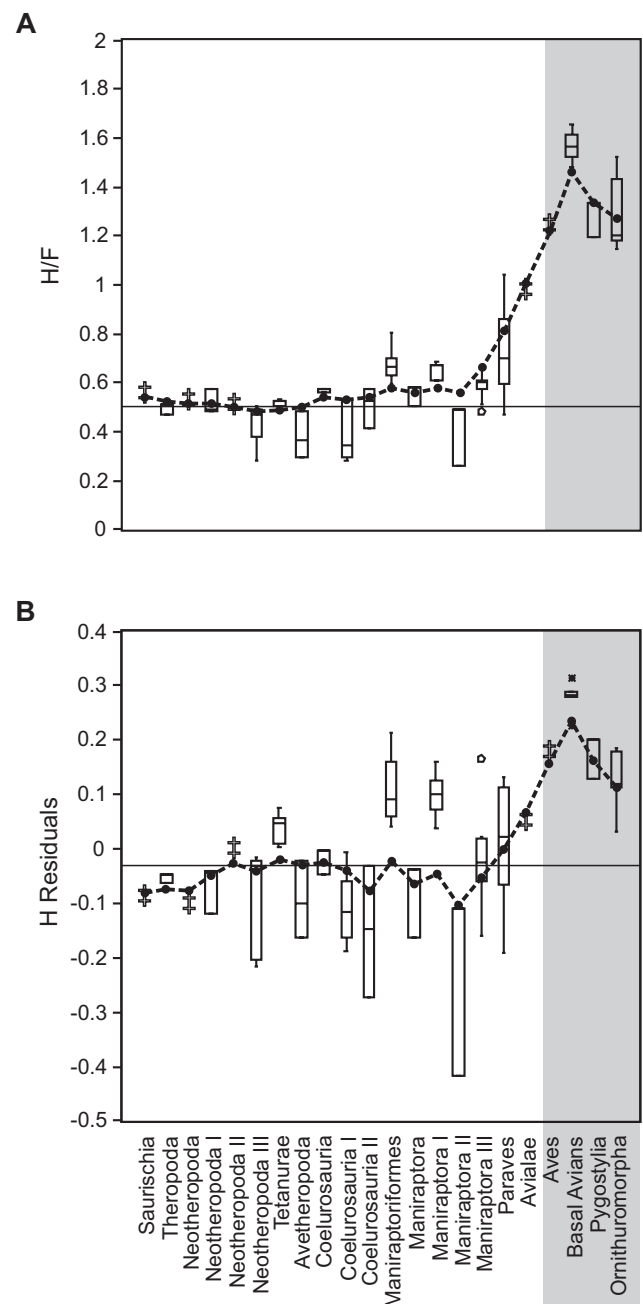


Figure 3. Plots of individual clades (boxplots) and nodal reconstructions along the phylogenetic trajectory through the origin of birds (dashed line) for the humerus to femur ratio (A) and humerus to SVL residuals (B) using the largest dataset topology. The gray box highlights Aves. The solid horizontal line represents the average value for noncolurosaurian theropods. When corrected for body size, humeral lengths in maniraptorans deviate in herbivorous (lengthening) and myrmecophagous (shortening) clades.

electronic Supporting Information). We suggest that the close association between scapula length and SVL may be due to the developmental origins of the scapula. The avian scapula develops from two separate condensations. The scapular blade is

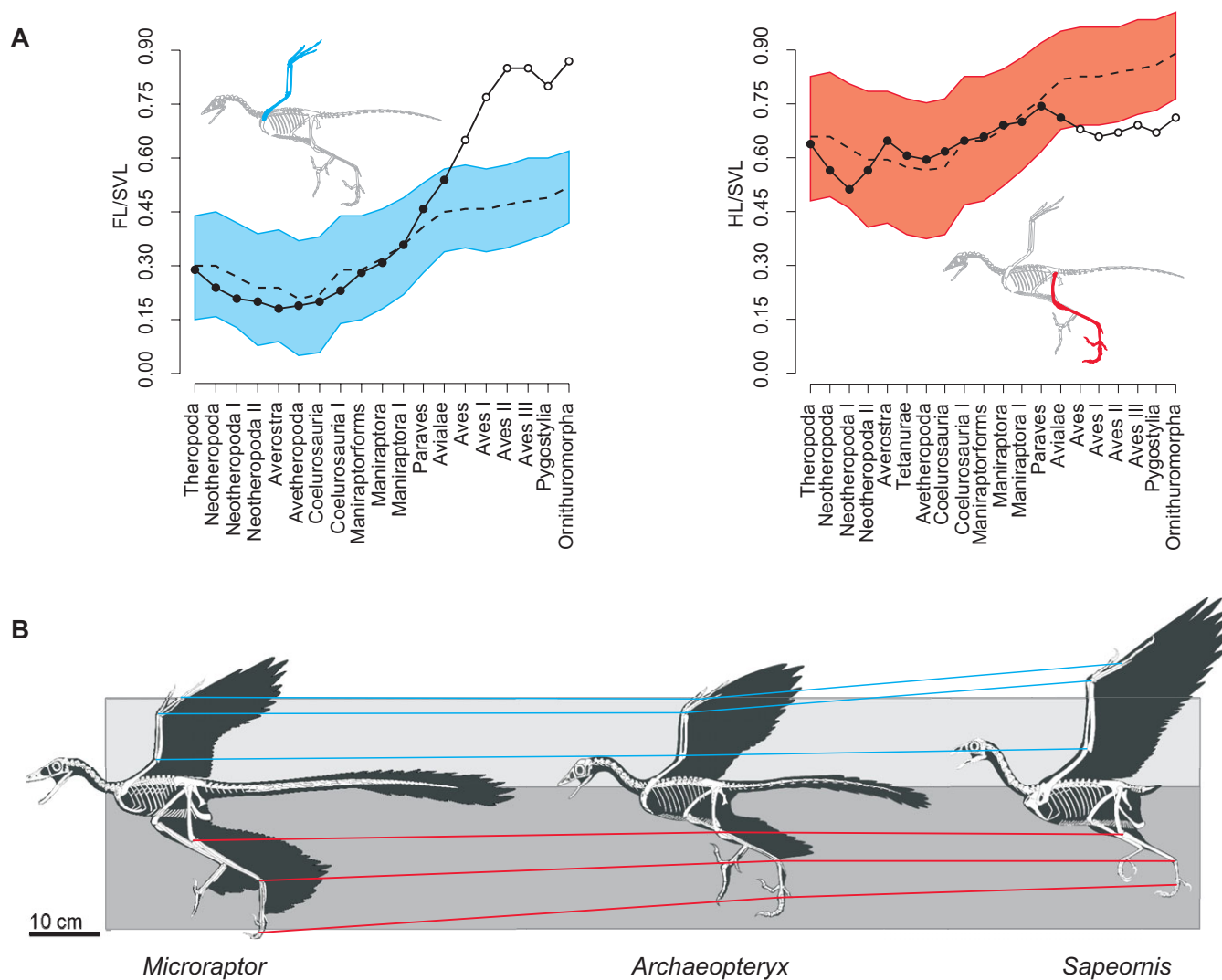


Figure 4. Evolution of forelimb and hindlimb lengths corrected for body size across the nonavian theropod to bird transition. (A) Nodal reconstructions (solid line) for relative forelimb (FL) and hindlimb (HL) lengths to SVL using the measured taxon dataset and *Epidexipteryx* as the sister taxon to Aves tree topology. Estimated expected lengths are derived from linear regressions (dashed lines) with corresponding 95% error bounds (shaded region) using the adult nonavian theropod dataset. Nonavian thereopod nodes are closed circles and avian nodes are open circles. See electronic Supporting Information for other phylogenetic permutations. (B) Direct comparison of fore and hindlimbs across similar sized paravian and avian taxa. Silhouette reconstructions are based on *Microraptor zhaoianus*, *Archaeopteryx lithographica*, and *Sapeornis angustus* to illustrate each limb bone in the same orientation. Fore and hindlimbs are positioned in the paraxial plane for comparison, although this orientation would not have been permissible in life in the former two taxa. Despite that all three have similar SVL values (240, 231, and 247 mm, respectively), the origin of birds corresponds with a significant lengthening of the forelimb and shortening of the hindlimb.

derived primarily from the sclerotome of somites 17–24, whereas the glenoid region and coracoid are derived from the lateral plate mesoderm (Huang et al. 2000, 2006; Valask et al. 2011). Thus, the close association between axial column and scapular blade length may be due, in part, to their common somitic origins. As both SVL and femur length are strongly correlated to body size, they are also highly correlated to scapula length. Integration between scapula length and SVL becomes weaker, whereas that between the forelimb and scapula and the relative scapular length

increases in birds (mean value of scapula length/SVL for nonavian theropods = 15.6%, avians = 22.2%) (unequal var. T -test = -4.0216 , P (same mean) = 0.0001). Although the scapula blade is derived from largely somitic tissue, the girdle's musculature is influenced by factors in the forelimb (Kuijper et al. 2005; Valask et al. 2011). Superficial forelimb muscles (e.g., pectoralis and latissimus dorsi) in birds develop from lateral plate mesoderm, whereas the deeper girdle musculature is derived from somites by the forelimb field (Valask et al. 2011). This linkage

may help explain the differences in integration between the forelimb and scapula in birds. Pectoral and forelimb musculature becomes increasingly hypertrophied within birds, with pectoral depressor muscles averaging 10–13% of extant bird body mass (Biewener 2011). Scapula lengthening and pectoral muscle mass enlargement are probably initiated during avian embryogenesis because both systems are well developed in ovo (Nakane and Tsudzuki 1999). In ovo muscle size and activity significantly affect both scapula and forelimb development, including scapula length (Nowlan et al. 2010a, b) and the enlargement of the flight-related musculature may have lead to a more integrated pectoral-forelimb system with these muscles inducing novel biomechanical stress on the developing embryo.

ALLOMETRY AND THEROPOD LIMBS

Given the close association of limb length and body size, it is not unexpected that the trend of body size decrease in coelurosaurs is associated with an elongation of their appendicular skeleton, most notably in the forelimb (Figs. 3 and 4). The phylogenetic axis from node Theropoda to node Aves does not deviate from the 95% confidence bounds of the expected fore and hindlimb lengths using the nonavian theropod allometric regression. Although perhaps not surprising, this pattern indicates that the relative lengthening of the forelimb through maniraptoran evolution is coupled with an evolution of body size reduction. This pattern is significantly disrupted at node Aves, suggesting that scaling factors have changed for limb growth in this clade.

Our findings do not support an evolutionary trend in increasing forelimb length throughout Coelurosauria to Aves. We stress that our findings do not suggest that individual lineages did not deviate from this general trend. For example, the ornithomimosaurs show significantly elongated forelimbs (Fig. 3). What our findings do challenge is the notion that there is a trend of forelimb elongation within coelurosaurs beyond what is expected due to concurrent body size decrease in this lineage. Individual elongation (and reduction) events within derived nonavian theropods were likely driven by lineage specific adaptive scenarios, rather than an overarching single clade wide evolutionary or allometric driver. Of note is the level of elongation present in the herbivorous (Zanno and Makovicky 2011), terrestrial (Makovicky et al. 2004; Kirkland et al. 2005) coelurosaurian clades the Ornithomimosauria and Therizinosauria (Fig. 3B), among the highest for nonavian theropods.

Our use of humerus to femur (H:F) residuals should not be taken as support for the use of raw H:F ratios as a determination of relative forelimb length (Chatterjee and Templin 2004; Bybee and Lee 2006; Zhang et al. 2008; Novas et al. 2009). We caution against the use of this metric because of the significant allometric nature of both bones and the dramatic deviations in specific clades, including Aves. As illustration, compare three nonavian

taxa (*Citipati*, *Coelophysus*, and *Coelurus*) with identical H:F values (0.57), despite having radically different forelimb lengths relative to SVL (*Citipati* 117%, *Coelurus* 100%, and *Coelophysus* 73% of expected).

PARAVIANS

Basal deinonychosaurs have hindlimb elongations equal to or greater than those in highly cursorial taxa such as ornithomimosaurs and parvicursorines (Makovicky et al. 2004; Xu et al. 2010b). Although basal deinonychosaurs do not have the extremely elevated metatarsal to femoral (Mt:F) length ratios preset in parvicursorines, they do possess values similar to ornithomimids, *Caudipteryx* or *Limusaurus*. In either case, total hindlimb length is a stronger correlate with running ability and speed than Mt:F (Garland and Janis 1993; Christiansen 2002) and elongation of the metatarsals is more closely linked to home range size (Garland and Janis 1993). The presence of elongate metatarsals in parvicursorines may be due to the unique requirements of their suspected myrmecophagy (Xu et al. 2010b). Like equivalent sized extant mammalian carnivores (Carbonne et al. 2007), basal deinonychosaurs likely did not partake in long pursuit hunts that favor the evolution of elongate distal limb segments, but relied primarily on ambush or low-cost hunts techniques (Fowler et al. 2012).

The level of hindlimb elongation in this clade affects mass estimate calculations that reconstruct paravians as significantly heavier than similar size avians (Turner et al. 2007). *Microraptor zhaoianus* or *Mei long* are estimated to be 320% and 410% larger, respectively, than the Berlin example of *Archaeopteryx* although all three animals differ by less than 5% in SVL. Similar distortions are seen when comparing *Mei long* to the other basal troodontids in this analysis (*Anchiornis* and *Jinfengopteryx*). Reconstructions for *Archaeopteryx* and small deinonychosaurs show similar outline and body volume (Hu et al. 2009), and they likely had similar tissue density (Hutchinson et al. 2007). We find no plausible explanation for this proposed difference in body mass, and believe it to be solely caused by overestimations due to femoral length differences.

AVES

Avians break the theropod appendicular scaling pattern in the forelimb and hindlimb. The forelimb scaling to SVL changes from negative to a positive allometry in birds. In *Archaeopteryx*, the most basal bird, this difference is not as pronounced, as it shares similar forelimb proportions to similar sized deinonychosaurs such as *Microraptor* (Fig. 4), although its hindlimbs are relatively shorter (Figs. 2, D, 4B). This may be linked to the limited flight capacity, if any, of *Archaeopteryx* compared to more derived basal avians such as *Sapeornis* (see Wang et al. 2011 and references therein). In volant basal avians, the extreme size of the forelimb

may have been driven by the need to compensate for their large body size, relatively short primaries and unrefined flight anatomy (Clarke and Middleton 2008; Wang et al. 2011).

Avians also show a reduction in their hindlimbs compared to expected theropod values at that body size. Birds achieved this by retaining a near-isometric hindlimb to SVL scaling relationship but with a reduced intercept. All avians in our dataset show hindlimb lengths that are at least 30% smaller than a comparable sized paravian. As early avians are reconstructed as having similar limb mechanics as nonavian theropods (Hutchinson and Allen 2009), it begs the question: why do they not retain the paravian hindlimb scaling factor?

One possible solution is that long limbs would hinder perching and movement along tree branches. Basal birds, such as *Archaeopteryx*, and the origin of birds are hypothesized to have been terrestrial (Bell and Chiappe 2011; Dececchi and Larsson 2011). However, birds rapidly evolved adaptations for perching in trees, with taxa such as *Jeholornis* and *Sinornis* having a fully reversed hallux for small-diameter branch grasping (Dececchi and Larsson 2011). By reducing hindlimb length, arboreal taxa decrease torsional forces when perching or moving along thin diameter perches (Cartmill 1985), a useful trait if avians spent more time within the canopy. Reducing limb length would also likely decrease total mass and facilitate the tucking of hindlimbs when flying. Tucking smooths the profile and reduces the amount of parasitic drag experienced during flight by more than four times (Pennycuik 1971; Tucker 1988).

Conclusion

Interlimb length ratios are widely used as the basis for phylogenetic characters and to derive evolutionary scenarios (Padian and Chiappe 1998; Chatterjee and Templin 2004; Bybee and Lee 2006; Novas et al. 2009; Xu et al. 2009; Choiniere et al. 2010; Xu et al. 2010a) without accounting for potential allometric effects. However, we show that it is necessary to establish a pre-transition baseline for appendicular evolution before examining limb evolution through the nonavian theropod to avian transition. Here, we have demonstrated that the previously reported trend of forelimb lengthening in maniraptorans is an allometric consequence of reduced body size, and not a size-independent pattern. Additionally, we have demonstrated that early birds diverged radically from both the forelimb and hindlimb bauplan of nonavian theropods. The first birds have a marked elongation and integration of the forelimb and pectoral unit that is not present in nonavian theropods. These results signal a fundamental shift in the appendicular skeletal development between avian and nonavian theropods and suggest significant behavioral and ecological divergence between these clades.

Our results reinforce previous findings of a disintegration of the ancestral forelimb and hindlimb system within theropods (Gatesy and Dial 1996; Gatesy 2002), although we suggest that there remained a significant degree of integration mediated through allometry until the origin of birds. Although nonavian theropods were terrestrial cursors (Gatesy and Middleton 1997; Dececchi and Larsson 2011), birds rapidly diversified ecologically (i.e., swimming, perching, wading, etc.) and show evidence for a further decoupling of within limb modules (Gatesy and Middleton 1997; Middleton and Gatesy 2000; Gatesy 2002; Zeffer et al. 2003). This decoupling began with the freeing of the limbs from the ancestral scaling relationship of nonavian theropods, allowing each limb module a new degree of selective freedom. This result suggests a more independent control of limb development evolved at the origin of birds to dissociate forelimb and hindlimb lengths from body size. This dissociation, followed by similar breaks in intralimb integration, may be fundamental to the initial diversification of birds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Linear measurements of theropods elements used in “measured” dataset analysis.

Table S2. Linear regression analyses of absolute (A–E) and relative (F–I) values from measured dataset.

Table S3. Partial correlation scores comparing strength of correlation of the scapula length (SC) to body size (as represented by SVL or F), Humerus (H), or Forelimb (FL) length.

Table S4. Nodal reconstructions, SVL (in mm) has been logged, all other measurements expressed as a fraction of SVL.

Table S5. Nodal reconstructions of relative element length (element length/SVL) compared to values estimated based on OLS regression at reconstructed nodal body size (based on SVL).

Table S6. Parametric (Pearson's ρ) and nonparametric (Spearman's D and Kendall's τ) correlation comparisons between nodal reconstructed values for and those estimated through allometric regression.

Table S7. (A) Comparison of H:F ratio and residual produced by regressing log humeral length on log femoral length. $\log_H = 0.77368(\pm 0.0305) \times \log_F + 0.32768 (\pm 0.0054)$, $n = 95$, $r^2 = 0.855$. (B) Nodal humeral residual reconstructions using the larger dataset length topology.