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Phylogeny, function and ecology in the deep evolutionary history of the mammalian forelimb

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Mammals are the only living members of the larger clade Synapsida, which has a fossil record spanning 320 Ma. Despite the fact that much of the ecological diversity of mammals has been considered in the light of limb morphology, the ecological comparability of mammals to their fossil forerunners has not been critically assessed. Because of the wide use of limb morphology in testing ecomorphological hypothesis about extinct tetrapods, we sought: (i) to estimate when in synapsid history, modern mammals become analogues for predicting fossil ecologies; (ii) to document examples of ecomorphological convergence; and (iii) to compare the functional solutions of distinct synapsid radiations. We quantitatively compared the forelimb shapes of the multiple fossil synapsid radiations to a broad sample of extant Mammalia representing a variety of divergent locomotor ecologies. Our results indicate that each synapsid radiation explored different areas of morphospace and arrived at functional solutions that reflected their distinctive ancestral morphologies. This work counters the narrative of non-mammalian synapsid forelimb evolution as a linear progression towards more mammalian morphologies. Instead, a disparate array of early-evolving shapes subsequently contracted towards more mammal-like forms.

1. Introduction

Morphological comparisons between extant and extinct animals are fundamental to inferences about the locomotion and ecologies of fossil taxa. When consistent ecomorphological relationships are identified in extant taxa, hypotheses can be tested about organisms for which ecology cannot be observed directly. A conceptual foundation of ecomorphology is the overlap between ecology and morphology [1,2], but the interplay of these factors with the details of biomechanical function and phylogenetic history is critical because it can result in an imperfect match between shape and function. To consider these issues more deeply, we conducted a two-dimensional geometric morphometric analysis of forelimb shape in the clade Synapsida with three interrelated goals: (i) to estimate when in synapsid phylogenetic history, modern mammals become useful analogues for predicting ecologies of extinct taxa; (ii) to investigate individual examples of morphological convergence within this conceptual framework; and (iii) to determine if members of the distinct evolutionary radiations of synapsids evolved comparable functional solutions to shared ecological problems.

Synapsida, the amniote clade that includes all living mammals and their extinct forerunners, spans an estimated 320 Myr of evolutionary history [3,4], three major mass extinctions and several consecutive adaptive radiations [5–9]. Highly specialized morphologies can be observed among the Mesozoic mammaliaforms [10–12] (see *Methods* for group definitions used in this study), with other notable examples dating to at least the Permian [13–16], thus providing evidence of a deep evolutionary origin of derived

ecomorphologies. The high ecomorphological disparity of mammals makes them tempting models for their fossil ancestors, yet the very depth of synapsid history makes particularly acute the question of whether crown-group mammals are instructive analogues for early members of Synapsida [17,18]. Studies comparing fossil synapsids directly to crown mammals have focused primarily on the closest non-mammalian fossil relatives of extant Mammalia from the mid to late Mesozoic. Research on teeth [19,20], jaws [21–23] and forelimb metrics [11] has demonstrated that the ecology and morphologies of Jurassic and Cretaceous mammaliaforms can be compared to many extant groups despite the existence of some morphological differences. However, these studies are restricted in their phylogenetic scope, limiting their applicability to the ecomorphology of the appendicular skeleton in the most ancient members of fossil Synapsida.

Here, we undertake a detailed comparison of forelimb morphology between a sample of extant Mammalia and a large dataset of fossil non-mammalian synapsids spanning most of the group's geologic history. To test whether phylogenetic history determines available functional solutions, as well as the utility of ecomorphological approaches, we use shape analysis of the humerus and the ulna. Many extant ecomorphologies can be identified and quantified through forelimb shape even when constituent bones are considered in isolation. It has been shown that humeral and ulnar morphology, for example, are reliable predictors of ecologies such as burrowing and cursoriality [24–28]. Combined with this functional system's critical importance to quadrupedal locomotion and the lack of functional morphometric research conducted specifically on early synapsid forelimbs, the humerus and ulna represent a uniquely powerful system with which to address the three questions of this study. Finally, although extant mammals are noteworthy for their ecological diversity, forelimb skeletal elements are homologous across the entire history of Synapsida, facilitating direct comparison across the wide temporal, phylogenetic, and morphological disparities that are encompassed by our novel dataset.

We conducted a two-dimensional geometric morphometric analysis comparing humerus and ulna shapes of extant mammals to specimens representing four major evolutionary radiations from the earliest members of Synapsida (pelycosaurs) through to the evolutionary origin of Theria (defined in our data by the divergence of Marsupialia and Placentalia). We found that throughout the long and diverse history of Synapsida, stemward members of the clade did not repeatedly evolve mammalian ecomorphotypes in response to similar ecological needs. Instead, phylogenetic position is a stronger predictor of forelimb shape, even in ecologically specialized taxa. Further, we show the use of extant mammalian forelimb shapes to predict the ecomorphology of extinct synapsids is not viable until the origin of mammaliaforms.

2. Methods

(a) Taxonomic sampling

We conducted geometric morphometric analyses on proximal and distal humeri and proximal ulnae. Our taxon sample comprises five radiations within Synapsida: (i) the Pennsylvanian and early Permian 'pelycosaur'-grade synapsids (hereafter pelycosaurs), (ii) the middle Permian through Late Triassic non-cynodont

therapsids (therapsids), (iii) non-mammalian members of Cynodontia (cynodonts), (iv) mammaliaforms, here defined as all extinct taxa from the base of Mammalia to the base of crown Theria, and (v) extant representatives of Mammalia, including sampled members of Monotremata, Marsupialia and Placentalia. We use these paraphyletic grades as our units of comparison because they are temporally and morphologically distinct radiations of synapsids, analogous to the more familiar radiations of dinosaurs and birds. Nonetheless, it should be noted that the 'mammaliaform' radiation, broadly stated, consisted of multiple, successive adaptive radiations of different mammaliaform lineages [5]. Because a goal of this study is to better understand the effectiveness of ecomorphological comparisons between extant and fossil animals, we considered it necessary to place all extant taxa within one group, even though some of the members of our (completely extinct) mammaliaform group fall between monotremes and therians on the phylogeny of mammals, whereas others fall outside of crown Mammalia. Group assignments for all taxa are presented in electronic supplementary material, S1. We also included a small sample of extant and extinct reptiles and amphibians to assess the similarity of early synapsids to potential outgroups. In total, our dataset comprises 1870 individual specimens representing 218 genera (electronic supplementary material, S2).

Our sample prioritized taxa that we hypothesized would best represent extinct ecomorphologies, and we classified taxa in the following ecomorphological categories: fully fossorial, semi-fossorial, generalist, large-bodied herbivore, semi-aquatic, cursorial and arboreal. We specifically excluded groups for which there is no evidence of numerous extinct analogues (e.g. volant, fully pelagic and bipedal mammals). Although a small number of gliding mammaliaforms have been described [10,29], there is no strong evidence of gliding locomotion in synapsids more stemward than mammaliaforms. Therefore, we did not target gliding as an ecomorphology of interest, given the phylogenetic and temporal focus of this study. A detailed description of the ecomorphological categorizations can be viewed in electronic supplementary material, S1.

(b) Geometric morphometric analyses

We digitized landmarks and semi-landmarks, and recorded scale, on photographs taken by the authors and a number of high-quality published images (list of image citations in electronic supplementary material, S1) using tpsDIG2ws [30]. Type II landmark and semi-landmark numbering is as follows: proximal humerus—four landmarks, 19 semi-landmarks; distal humerus—eight landmarks, 26 semi-landmarks; proximal ulna—five landmarks, 22 semi-landmarks (figure 1) (further details in electronic supplementary material, S1). The landmarks represent consistently recognizable extrema on the outlines of the humerus and ulna because there are no usable internal landmarks across the breadth of morphological disparity and diversity of preservation styles present in our sample. Our method of separately photographing, digitizing and analysing the two functional ends of the humerus allowed us to consider the morphology of each region as independently as possible and minimize potential distorting influences such as torsion, damage or incomplete preparation. We analysed the proximal humerus in posteroventral view, emphasizing the perspective that maximized the total width of the proximal end and provided the best view of the delto-pectoral crest (figure 1). In the extant sample, we used the anterior view for the proximal humerus because this perspective includes the deltoid tuberosity, making it a most morphologically analogous viewpoint. We analysed the distal humerus in dorsal view, although all relevant morphology is visible in either dorsal or ventral view. Our analysis of the ulna focused solely on the proximal end and the shape of the olecranon process in lateral view. Examples of the landmark

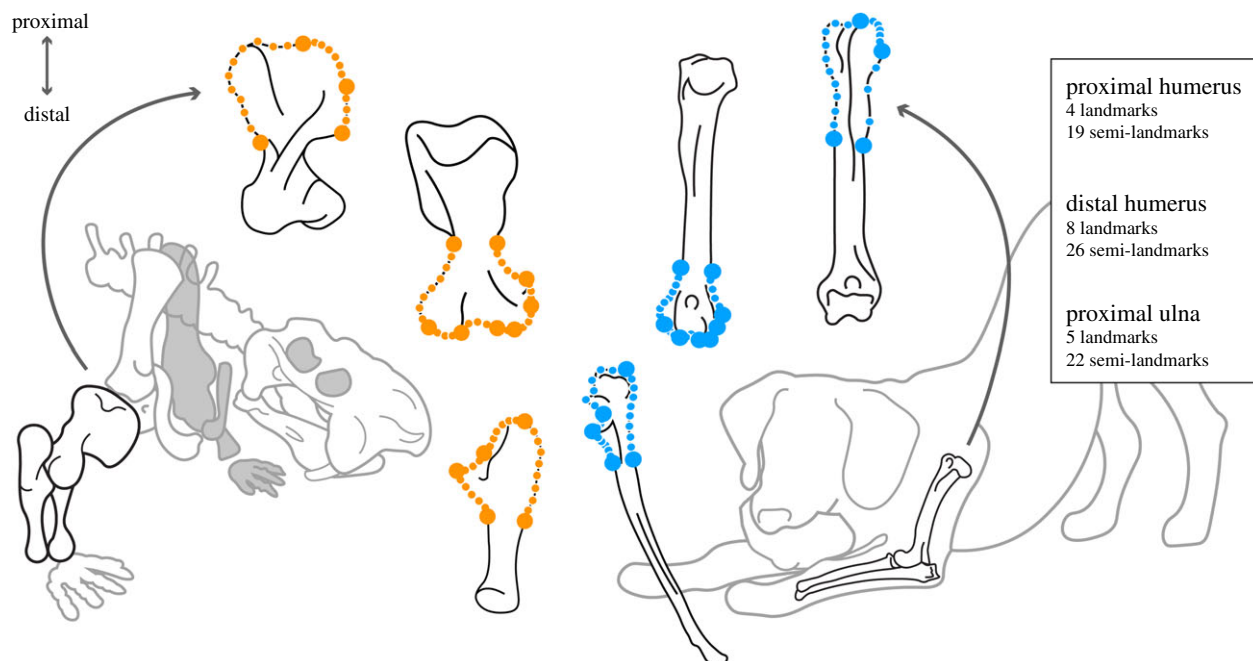


Figure 1. Schematic of landmark configurations shown on the forelimb elements of a representative fossil synapsid (the therapsid *Sinokannemeyeria*; left) and an extant mammal (*Canis*; right). Proximal humeri were analysed from a perspective that allowed the delto-pectoral crest (deltoid tuberosity in mammals) to be digitized. Due to posture changes across Synapsida, this is posteroventral view for the fossil sample and anterior view for the mammals. More detailed figures of landmark placement can be viewed in electronic supplementary material, S1. (Online version in colour.)

configurations are shown in figure 1, and more detailed information on landmark placements is presented in the electronic supplementary material.

We processed the coordinate data and conducted geometric morphometric analyses with the Geomorph R package [31]. Our analysis used the mean shapes for each genus. We averaged all specimen shapes for a given genus using the function 'mshape' in Geomorph [32], which uses the previously aligned coordinates to estimate a mean shape. For singletons, the single specimen itself represented the mean shape of that genus. We subjected the set of genus means to an additional general Procrustes alignment for all subsequent statistical analyses.

(c) Phylogenetic trees

We analysed each functional unit (proximal humerus, distal humerus, proximal ulna) in a phylogenetic framework. We constructed a composite phylogeny for each functional unit that encompassed the unit's taxonomic sample (full trees can be viewed in electronic supplementary material, S1). Because there is no single phylogeny that includes all of the taxa in this study, our composite trees are based on published phylogenetic analyses (electronic supplementary material, S1). We time scaled the trees using the first and last occurrence dates from the Paleobiology Database [33] and the Claddis package in R [34]. The first occurrence dates for extant taxa were based on [35], with the last occurrence dates set to zero to represent the present.

(d) Procrustes and patristic distances

Our primary method for comparing shape disparity among taxa was Procrustes distance [36,37]. We calculated Procrustes distance between each fossil genus and the mean of all extant mammalian shapes for each functional unit to quantify how far a given fossil genus was from the average of extant mammalian morphospace (i.e. its degree of shape divergence from the 'average' mammal). We measured phylogenetic signal using the ' K_{mult} ' statistic, which is a multivariate version of Blomberg's K [38]. K_{mult} is well suited for comparing across datasets because

the metric is a proportion wherein a value of 1 indicates that morphological divergence is proportional to branch lengths, as expected under a Brownian motion model of evolution. Values less than or greater than 1 represent less or more phylogenetic signal than expected under a Brownian motion model, respectively. Our results found that phylogenetic signal influences taxonomic groups and all functional units to differing degrees. To address how strongly similarity in shape is dictated by phylogenetic relatedness, we regressed Procrustes distance against patristic distance for each functional unit, quantifying the relationship between the phylogenetic position and morphospace location. We calculated patristic distance as the sum of branch lengths in units of time to the node of the first-diverging member of Theria in our sample, providing a measure of the phylogenetic proximity of each fossil genus to Theria. We estimated confidence intervals using a general linear model and conducted correlation tests in R [39] (electronic supplementary material, S1).

3. Results

(a) Morphospace occupation

Proximal humerus: The first five PCs capture nearly 90% of the variance in proximal morphology (PC1—58.45%; PC2—12.00%; PC3—9.42%; PC4—5.3%; PC5—4.4%). The group-level morphospace occupation for proximal morphology is differentiated, with more distantly related groups being farther apart. For example, extant Mammalia has a clearly defined morphospace (figure 2, top row, dark blue; additional PC plots in electronic supplementary material, S1), and with the exception of a few noteworthy taxa (*Tachyglossus*, members of the family Talpidae; figure 4), it does not overlap with the morphospace of its most distant relatives, the pelycosaurs (red). Therapsids (orange) occupy a large area of morphospace, and overlap every other group to at least to some degree. Cynodonts (yellow) and mammaliaforms (light blue) take

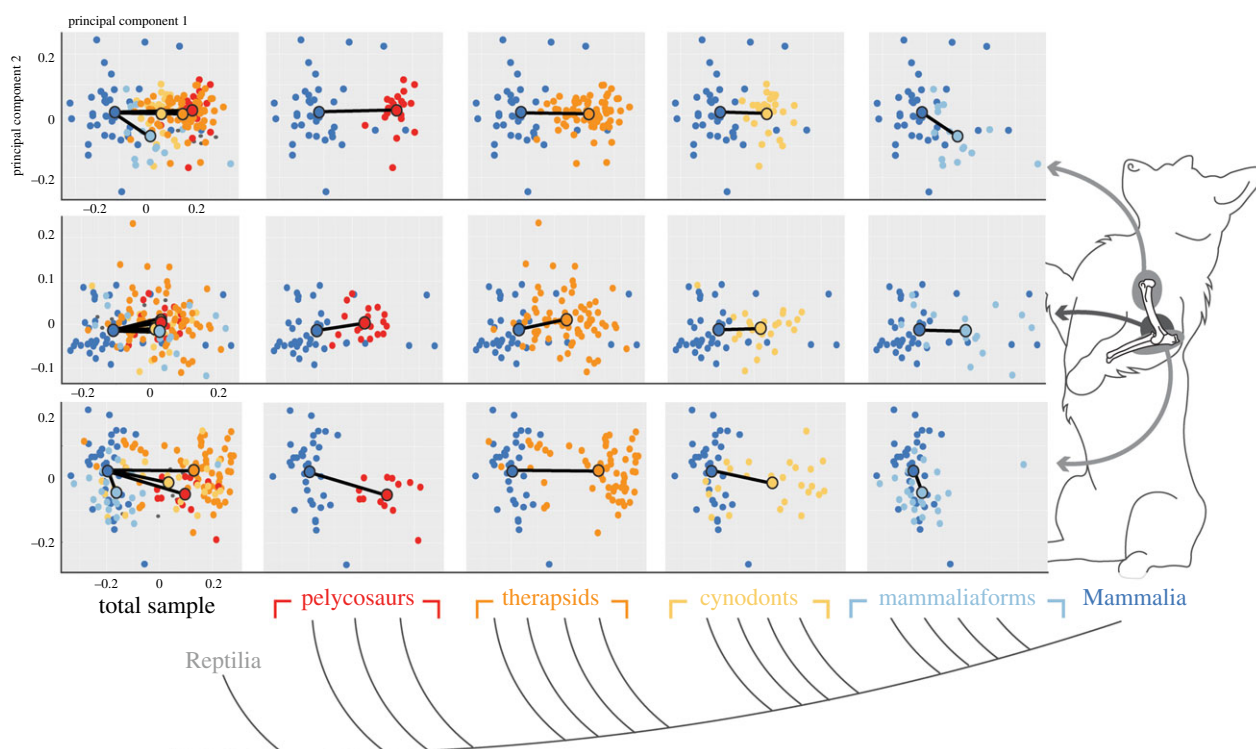


Figure 2. PC plots of shape data for the proximal humerus (top row), distal humerus (middle) and proximal ulna (bottom). The full dataset (far left column) is followed by plots highlighting comparisons between mammals and each of the major synsaur radiations. Larger dots represent the mean position of a group's morphospace. Black lines visualize the magnitude and direction of differences between mean shapes. (Online version in colour.)

Table 1. Measured values for each group by divided by functional unit. K_{mult} values represent phylogenetic signal and are reported with their respective adjusted p -value.

functional unit	K_{mult} by functional unit	K_{mult} by group				Procrustes distance	patristic distance
			n	K_{mult}	p -value		
proximal	$K = 0.622$ $p = 0.001$	outgroup	8	0.520	0.027	0.3835	552.55
		pelycosaur	21	0.540	0.898	0.3724	361.1095
		therapsid	68	0.639	0.001	0.3314	334.2062
		cynodont	27	0.681	0.174	0.2521	281.8526
		mammaliaform	14	0.420	0.273	0.2524	211.864
distal	$K = 0.288$ $p = 0.001$	outgroup	8	1.116	0.003	0.12498	548.55
		pelycosaur	19	0.641	0.775	0.1794	362.5437
		therapsid	73	0.671	0.001	0.1865	324.2812
		cynodont	27	0.622	0.432	0.1606	281.0444
		mammaliaform	15	0.506	0.409	0.1983	194.8573
ulna	$K = 0.421$ $p = 0.001$	outgroup	7	0.552	0.106	0.2865	447.9
		pelycosaur	13	0.877	0.025	0.3230	363.3654
		therapsid	63	0.692	0.001	0.3580	322.4351
		cynodont	24	0.924	0.022	0.2857	288.4625
		mammaliaform	22	0.272	0.961	0.1827	201.2909

smaller areas of morphospace along PC1 and PC2, but their mean positions are closer to extant mammalian morphospace. The two genera in Talpidae both fall far outside of the rest of mammalian morphospace, near the outer edges of morphospace in general. The mammaliaform genus *Fruitafossor* falls in a unique and otherwise completely unoccupied region (figure 4), and dramatically increases the dimensions

of mammaliaform morphospace. Shape differences captured by the PC axes are described in electronic supplementary material, S1, Morphospace Descriptions and figure S5.

Distal humerus: The first five principal components (PCs) capture over 80% of the variance in the dataset (PC1—50.84%; PC2—11.71%; PC3—9.48%; PC4—67.27%; PC5—4.84%). There is a significant overlap among all the fossil and extant groups

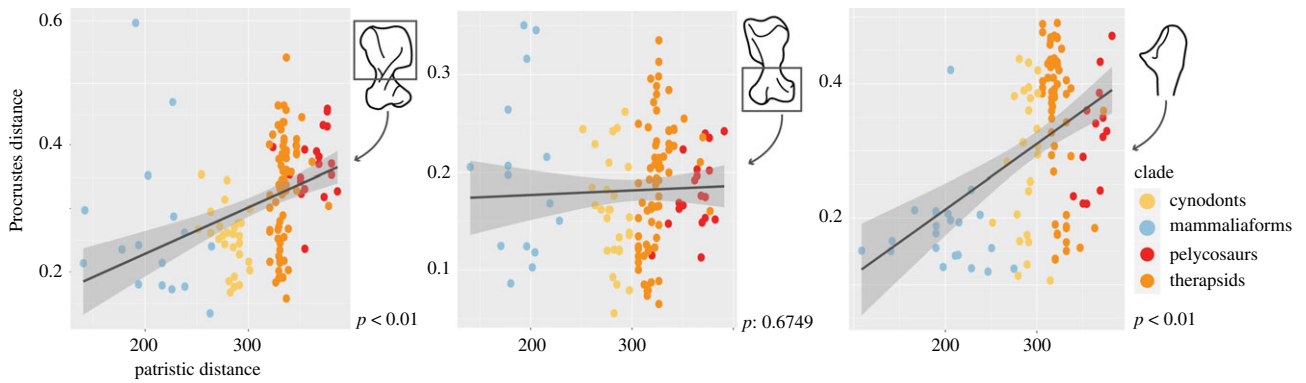


Figure 3. Linear regressions of Procrustes distance against patristic distance. Regressions are significant for the proximal humerus (left) and the proximal ulna (right). Shaded area represents 95% confidence interval. Range along the y-axis can be conceptualized as the disparity of shapes within the group. When compared with phylogenetic distance, instances can be observed where a fossil genus is more similar in shape to mammals than would be expected, given its phylogenetic relatedness (Procrustes distance below the regression line) and vice versa. (Online version in colour.)

on PC1 and PC2, providing no obvious means by which to differentiate group-specific areas of morphospace or classify areas of morphospace based on a given extant mammalian morphology (figure 2, middle row). Shape differences captured by the PC axes are described in electronic supplementary material, S1, Morphospace Descriptions and figure S6.

Ulna: The first five PC axes capture over 90% of the variance in ulnar morphology (PC1—67.09%; PC2—13.93%; PC3—5.12%; PC4—4.32; PC5—2.38%). Some group-level distinctions are present in ulnar morphospace (figure 2, bottom row), but an additional level of differentiation occurs as a strong demarcation between two primary ulnar morphologies that transcend taxonomic identification. Pelycosaurs (red) and out-group (reptile and amphibian; grey) taxa have high PC1 scores, whereas all extant mammals (dark blue) and mammaliaforms (light blue) excluding *Agilodocodon* are characterized by low PC1 scores. Therapsids (orange) and cynodonts (yellow) are spread across PC1, with some possessing more phylogenetically ‘basal’ shapes (high PC1 scores), whereas others fall closer to extant mammalian shape space (low PC1 scores). For therapsids, this differentiation is driven by the presence of enlarged olecranon processes in small burrowing dicynodonts and large Triassic dicynodonts, such as *Kawingasaurus* or *Ischigualastia*, respectively. Additional shape differences captured by the PC axes are described in electronic supplementary material, S1, Morphospace Descriptions and figure S7.

(b) Phylogenetic signal, Procrustes distance and patristic distance

The measured K_{mult} was less than 1.0 for each functional region, signalling lower phylogenetic signal than expected under a Brownian motion model and high within-group variability, regardless of whether it was calculated for our full phylogenies or for portions of the tree corresponding to our taxonomic subgroups (table 1). Despite its relatively low values, permutation tests showed that K_{mult} was always significantly greater than zero at the scale of the whole phylogeny. However, only the K_{mult} values for therapsids were significantly different than zero for all three functional regions. Values for the other subgroups typically were not significantly different from zero except for the ulna dataset.

Of the three functional areas, distal humerus Procrustes distance is the most similar across the groups (figure 3 and table 1). The plot of Procrustes distance versus patristic

distance provides additional evidence that there is little group-specific differentiation of the distal end, with most groups occupying similar ranges of Procrustes distance values. Procrustes distances for the proximal humerus conform to a more predictable phylogenetic pattern. The outgroup has the highest values and is farthest away from extant mammalian morphospace (table 1; electronic supplementary material, S1). Each subsequent phylogenetic group expresses a lower average Procrustes distance to the base of extant Mammalia, reflecting greater similarity to the mean shape of the extant mammals in our dataset. As for the distal humerus, therapsids and mammaliaforms have the highest ranges of distances. Therapsids have relatively even occupation of their full range, but the wide range in mammaliaforms is primarily driven by *Fruitafossor*, which has a unique, highly derived morphology relative to other mammaliaforms.

Ulnar Procrustes distances show a pattern in which there is a more abrupt constriction of morphologies near the cynodont–mammaliaform transition (figure 3), with a few noteworthy taxa providing individual exceptions (*Agilodocodon*, mammaliaform; *Heleosaurus*, pelycosaur). In general, the groups that are the most phylogenetically distant from extant Mammalia have the highest Procrustes distances to the mean extant mammalian shape, but therapsids and cynodonts include a mixture of both morphologically disparate and extant mammal-like morphologies (defined here by proximity to mammalian morphospace and characterized by features such as a more narrow proximal humerus with a delto-pectoral crest/tuberosity that is expanded proximal-distally instead of ventrolaterally (as is the case in most fossil synapsids)). Warp grids associated with shape change along the PC axes can be viewed in electronic supplementary material, figures S5–S7. Most of the large range of Procrustes distance values expressed in the other fossil synapsid groups is lost in mammaliaforms, which have a smaller range of distance values and thus are much more uniform in their possession of mammal-like shapes and in their overall proximity to extant mammalian morphospace.

The correlations between Procrustes distances and patristic distance are consistent across the various correlation tests (electronic supplementary material, S1). For distal humerus morphology, there is no correlation between patristic distance and Procrustes distance. This supports the interpretation of the morphospace plots in which there were no meaningful

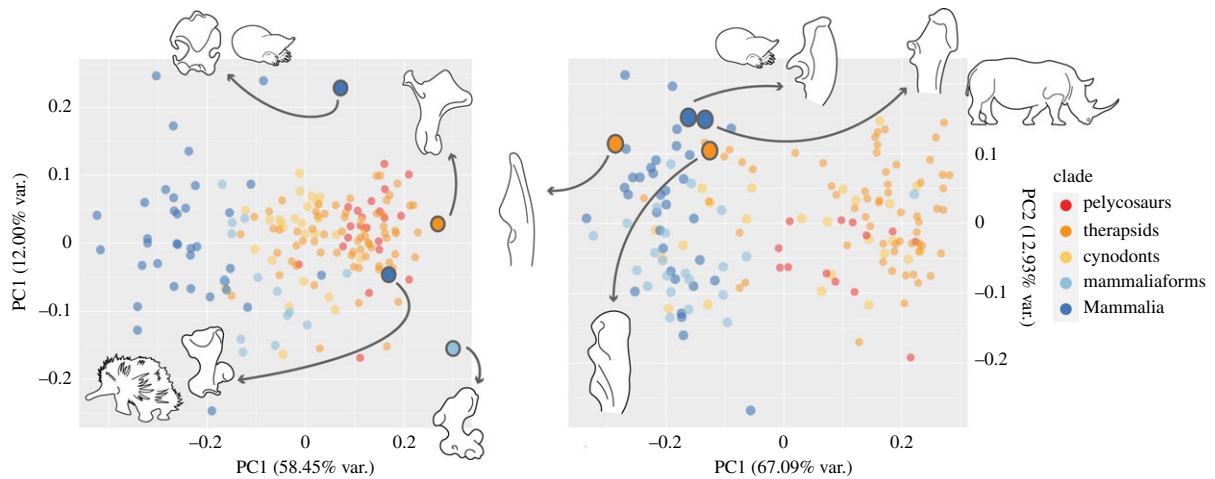


Figure 4. Plot of PCs 1 and 2 for the proximal humerus (left) and ulna (right) with highlighted examples of ecological convergence and shape convergence. For the proximal humerus, the fossil genera *Kawingasaurus* (therapsid) and *Fruitafossor* (mammaliaform) converge with the mammals *Tachyglossus* and *Scalopus*, supporting the hypothesis that these taxa were powerful substrate movers. The ulna plot shows an example where shape is convergent despite incongruence in ecology. The burrowers *Scalopus* (Mammalia) and *Kawingasaurus* (Therapsida) group with the large terrestrial Rhinocerotidae (Mammalia) and *Ischigualastia* (Therapsida). (Online version in colour.)

groupings or trends towards extant mammalian morphospace for the distal end. The proximal humerus shows a much stronger correlation than the distal end, and is highly significant. The ulnar results are similar to the proximal humerus and are also highly significant.

4. Discussion

It is tempting to view synapsid forelimb evolution as a simple trend towards increasingly mammal-like morphologies, particularly because discussions of the topic often focus on a relatively small number of exemplar taxa [40–42]. However, the distribution of synapsid taxa in morphospace is more consistent with the major synapsid groups exploring their own individual regions of morphospace than with a continuous shift towards more mammal-like shapes. This finding is corroborated when morphological similarity to extant mammals is considered alongside the phylogenetic context of patristic distance. Although there is a significant correlation between Procrustes distance and patristic distance for the proximal humerus and ulna, consideration of the plots in figures 2 and 3 reveals the complexity underlying this apparent trend. In both cases, the earliest synapsids (the pelycosaurs) are both morphologically disparate from extant mammals and relatively conservative in their morphology. With the origin of therapsids, morphological disparity expands both towards and away from more mammalian morphologies (expressed as an increase in the range of Procrustes distance values). For the ulna, the high range of shapes is initially maintained early in cynodont history, but this disparity is culled in more crownward cynodonts (e.g. prozostrodonts such as *Brasilodon* or *Bienotheroides*; full patristic distance and Procrustes distances for taxa can be viewed in electronic supplementary material, S2 dataset under the tabs titled Proximal_Correlation statistics, Distal_Correlation statistics and Ulna_Correlation statistics) such that only relatively mammal-like shapes remain in these taxa and in mammaliaforms. For the proximal humerus, this truncation occurs earlier, with the cynodont–mammaliaform range of variation being established at the base of cynodonts. The

pattern for the distal humerus is similar in having an initial increase in disparity going from pelycosaurs to therapsids, but lacks a subsequent contraction. Instead, a relatively constant range of variation is maintained from therapsids onwards. Therefore, instead of a simple trend towards more mammal-like forelimb shapes across synapsid history, forelimb evolution may be better characterized as an initial diversification into a broad array of shapes that was then winnowed in subsequent radiations in the cases of the proximal humerus and ulna.

These observations may also help to explain the pattern of phylogenetic signal in our data. The interpretation of phylogenetic signal is complex because a variety of evolutionary processes can result in high or low values [43,44]. However, stochastic peak shifts, in which stable selection is disrupted by occasional small to moderate shifts in fitness peak location, are known to produce values of Blomberg's K similar to our K_{mult} values [43]. Previous researchers have suggested that a number of significant shifts in the musculo-skeletal organization of the forelimb occurred over the course of synapsid evolutionary history, typically hypothesizing that these changes occurred near the base of therapsids, cynodonts and mammals [7,45–47]. These reorganizations could relocate fitness peaks, thus accounting for both the low phylogenetic signal in some groups and the expansions and contractions of morphological disparity observed in our dataset. However, further investigation of the functional disparity of the proposed grades of organization and the topographies of their adaptive landscapes is necessary to fully test this hypothesis (see [48,49] for examples of such tests involving early tetrapod humeri and synapsid vertebral columns, respectively).

(a) Are extant synapsids analogues for fossil synapsids?

In order for extant mammals to be appropriate analogues for fossil synapsids, fossil and extant species must overlap in morphospace in a relatively precise, ecologically and functionally structured way. Given the range of functions encapsulated by a complex structure like the forelimb, and the fact that different synapsid grades appear to explore their own regions of morphospace, it is reasonable to expect the evolution of distinct

morphofunctional solutions to common ecological problems in fossil synapsids and extant mammals (i.e. many-to-one functional mapping *sensu* [50]). However, the converse also may be true: similar morphologies can arise from simple biomechanical pressures, such as increasing mechanical advantage across a joint, while not signalling an accurate similarity in ecological usage (see *Functional convergence versus morphological convergence*). Therefore, not only must fossil and extant taxa overlap in morphospace, specific areas of morphospace must correspond to a narrow range of ecological functions. The results of our analyses demonstrate that these assumptions break down when making comparisons between fossil non-mammalian synapsids and extant mammals.

For example, there is relatively little overlap in proximal humerus morphology between our fossil and extant taxa. Although each successive synapsid group more closely approaches extant mammalian morphospace, even the mammaliaforms are located at the periphery of the core region occupied by extant mammals (figure 2). Because of this, extant mammals are likely to be imprecise functional analogues for synapsid shoulder function in general, let alone for identifying specific ecological functions. The opposite problem exists for the distal humerus, where the non-mammalian synapsid groups extensively overlap each other and extant mammals in morphospace. This pattern suggests that distal humerus function has been relatively conserved through synapsid history, and such conservatism implies that ecologically specific morphotypes are less likely to repeatedly evolve. Further research applying three-dimensional geometric morphometric techniques to aspects of morphology that are not well captured by our dataset, such as the shapes of the distal joint surfaces, will be important to test this hypothesis of conservatism and elucidate how it relates to stance and locomotion. The ulna dataset shows perhaps the greatest promise for identifying specific ecological analogues, given that select therapsids and cynodonts, and many mammaliaforms, fall well within the core of extant mammalian morphospace. However, the overall distribution of taxa suggests that the restriction of ulna morphologies to a consistently mammal-like form (and by extension function) was exclusive to mammaliaforms. Taken together, our results indicate that therian forelimb skeletal morphologies are unlikely to be good functional or ecological analogues for non-mammalian synapsid forelimb skeletons, even for taxa that are closely related to extant mammals.

(b) Functional convergence versus morphological convergence

Although the results of our analysis suggest that the extant mammals in our dataset have humeral and ulnar shapes that are very different from the majority of non-mammalian synapsids, there are some instances where ecomorphological convergence is evident. For example, fossorial therians have some of the highest proximal humerus PC1 scores for extant mammals (proximal humerus; figure 4) and fossil synapsids for which we have *a priori* evidence for fossoriality [51,52] also have high PC1 scores for their groups. The broad and square proximal humeri of the Permian therapsid genera *Kawingasaurus* and *Cistecephalus*, and the Jurassic mammaliaform *Fruitafossor* (figure 4), resemble those of the extant lipotyphlan moles *Scalopus* and *Condylura*. Interestingly, these fossil taxa also show considerable similarity to the

extant mammalian genus *Tachyglossus*, which is the mammal with the highest PC1 score in our dataset. *Tachyglossus* possesses a powerfully built shoulder girdle and forelimb used for digging as well as breaking open fallen logs and anthills when foraging for insects [53–55], raising the possibility of a similarly mixed functional ecology in cistecephalids and *Fruitafossor*.

There are also cases where convergence in shape and some aspects of function do not reflect shared ecologies. *Tachyglossus* also is an informative example in this context because it has an abducted (sprawling) limb posture, and functional characteristics of the shoulder joint that it shares with pelycosaurs have been hypothesized reflect similarities in stance and limb motions during locomotion. The position of *Tachyglossus* within pelycosaur proximal humerus morphospace corroborates this hypothesis, and, therefore, is not necessarily strong evidence for digging habits in the majority of pelycosaurs. Likewise, an elongate olecranon process of the ulna with a small, tightly defined semi-lunar notch is characteristic of large cursorial mammals and several large-bodied anomodonts such as the Triassic *Lisowicia* and *Sinokanmeyeria* (figure 4). However, because our analysis considers shape independent of size, animals like rhinos, hippos and bison also group with burrowing mammals and the hypothesized burrowing therapsids. All of these animals are under strong selective pressure for highly muscular, tightly integrated articulations at the elbow that emphasize movement along a single plane to prevent joint dislocation, but for different ecological reasons (resisting strong forces associated with digging versus large body size). This results in a noteworthy similarity in shape driven by the mechanics of the skeleton without ecological convergence, and emphasizes the breakdown that can happen when attempting to reconstruct fossil ecology without the addition of data such as body size. Though these structures follow predictable patterns of physical function, extending those to an organism's ecology can result in incorrect ecomorphological comparisons.

(c) Diversity of functional solutions in Synapsida

Given the highly predictable ways in which shape changes in response to mechanical demands, we might assume that common selective pressures associated with a capacity for burrowing, running or other highly derived locomotor ecologies will drive a similarity in morphological responses. However, this assumption fails to consider the way in which an organism's phylogenetic placement restricts the functional solutions available to it [50]. The more distantly related two organisms are, the more difficult it will be for them to evolve precisely matching solutions to shared ecological pressures because their evolutionary starting points are likely to be morphologically disparate.

Our study supports this hypothesis because fossil synapsid groups occupy and explore mostly independent regions of morphospace (figure 2). This implies that each of the main radiations derived its own solutions to functional problems, reflecting their different ancestral forelimb morphologies. For example, therapsids occupy a wide range of morphospace, including areas that are unexplored by other groups (e.g. ulna shape in figure 2). As part of this diversification, they arrived at functional solutions that do not have direct counterparts among extant mammals. The specialized digging dicynodont *Kawingasaurus* shows some similarities to modern diggers,

but its combination of humeral and ulnar morphologies is unique and related to its derivation from a more generalized therapsid ancestor (figures 2 and 4). Therefore, although some broad functional comparisons are possible (e.g. a large in-lever will be present when strength at the elbow is necessary), exact functional convergence between fossil synapsids and extant mammals should not be expected.

5. Conclusion

In this study, we investigated three complementary questions: (i) whether extant mammals are ecomorphological analogues for their fossil ancestors; (ii) if there are examples of ecomorphological convergence among the various synapsid radiations; and (iii) whether functional solutions are influenced by phylogenetic relatedness. We found that members of past synapsid radiations tend to occupy distinct areas of morphospace that are separated from modern mammals. The Mesozoic mammaliaforms approach crown mammals most closely, but even there the similarity is imperfect, especially when considering isolated skeletal elements. Therefore, modern mammals are unlikely to be accurate ecomorphological analogues for most non-mammalian synapsids. There is a limited degree of convergence associated with extreme ecologies such as burrowing, but the effects of physical constraints also lead to morphological

convergence in ecologically disparate taxa. Moreover, the functional solutions arrived at by the different radiations reflected their particular ancestral morphologies. This work counters the narrative of synapsid forelimb evolution as a linear progression towards more mammalian morphologies. Instead, an initial wide diversification of humerus and ulna shapes subsequently contracted towards mammal-like shapes to varying degrees.

Data accessibility. All data are included in the electronic supplementary material and are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9cnp5h9g0> [56].

Authors' contributions. J.K.L. and K.D.A. conceptualized the research project and wrote the manuscript. J.K.L. collected the data, analysed the data and made the figures.

Competing interests. We declare we have no competing interests.

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