



Antiquity of forelimb ecomorphological diversity in the mammalian stem lineage (Synapsida)

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Mammals and their closest fossil relatives are unique among tetrapods in expressing a high degree of pectoral girdle and forelimb functional diversity associated with fully pelagic, cursorial, subterranean, volant, and other lifestyles. However, the earliest members of the mammalian stem lineage, the “pelycosaur”-grade synapsids, present a far more limited range of morphologies and inferred functions. The more crownward nonmammaliaform therapsids display novel forelimb morphologies that have been linked to expanded functional diversity, suggesting that the roots of this quintessentially mammalian phenotype can be traced to the pelycosaur–therapsid transition in the Permian period. We quantified morphological disparity of the humerus in pelycosaur-grade synapsids and therapsids using geometric morphometrics. We found that disparity begins to increase concurrently with the emergence of Therapsida, and that it continues to rise until the Permo-Triassic mass extinction. Further, therapsid exploration of new regions of morphospace is correlated with the evolution of novel ecomorphologies, some of which are characterized by changes to overall limb morphology. This evolutionary pattern confirms that nonmammaliaform therapsid forelimbs underwent ecomorphological diversification throughout the Permian, with functional elaboration initially being more strongly expressed in the proximal end of the humerus than the distal end. The role of the forelimbs in the functional diversification of therapsids foreshadows the deployment of forelimb morphofunctional diversity in the evolutionary radiation of mammals.

Therapsida | Mammalia | humerus | ecological diversity | morphological disparity

Modern mammals have modified their shoulders and forelimbs for an unparalleled variety of functions. In contrast to the rest of Amniota, mammals have evolved highly distinctive forelimb shapes and functional specialization associated with burrowing, climbing, running, brachiating, flying, and swimming (1, 2). An expansion in ecological diversity is well documented in the forelimbs of the fossil forerunners of mammals as far back as 164 Mya. This includes the discovery of swimming, gliding, and digging mammaliaforms in the Jurassic (3–5), demonstrating the presence of functionally derived ecological diversity outside of crown Mammalia.

However, Synapsida, the clade that includes all living mammals and their fossil relatives, has a history extending back to over 315 Mya (6). Within the very earliest members of Synapsida, the Pennsylvanian and early Permian “pelycosaur”-grade synapsids (hereafter referred to as pelycosaurs), groupwide ecomorphological diversity across the pectoral girdle and forelimbs qualitatively appears to be very low. Despite comprising one of the first major amniote radiations (7), including the earliest large-bodied terrestrial forms (8), some of the first instances of tetrapod herbivory (6, 9), and a substantial taxonomic diversity, the forelimb morphological disparity of pelycosaurs is surprisingly limited (10–12). Pelycosaurs are characterized by robust, widely sprawling (abducted) forelimbs, and all members of the grade possess a screw-shaped scapular glenoid and humeral head indicative of a

highly restricted range of motion (11, 13). This can be contrasted with the phenotype of the nonmammaliaform therapsids (hereafter therapsids), the more crownward synapsids that replaced pelycosaurs as the dominant tetrapods in the middle Permian (approximately 275 Mya). Permian therapsids include more gracile large- and small-bodied predators (14–16), highly specialized scratch-digging burrowers (17–19), and arboreal herbivores (20). Important shifts in therapsid limb morphology have been linked to inferred changes in locomotion, posture, and gait (21–23). Multiple hypotheses on the timing and staging of this morphological transition during the Permian period have been posited (6, 24), but questions remain on the magnitude of morphological change and how that may relate to ecological and phylogenetic diversification patterns within Synapsida.

Considering the importance of forelimb disparity to the evolutionary radiation of Mammalia, the juxtaposition between the extant representatives of Synapsida (mammals) and the very earliest synapsids is striking. However, little work has been done to pinpoint the temporal and phylogenetic first appearance of increased forelimb disparity in a quantitative framework, or to explore this characteristic’s role in synapsid macroevolution. Here, we quantified the morphological disparity of synapsid humeri in the two earliest evolutionary radiations of Synapsida, starting in the Pennsylvanian with pelycosaurs and continuing through the Permian and into the Triassic with therapsids. Because pelycosaurs and therapsids are temporally successive major synapsid radiations, they are well suited for comparisons of

Significance

Mammals and their closest fossil relatives use their shoulders and forelimbs for many functions, which is reflected by the great range of mammalian forelimb shapes. We found that forelimb shape diversity in the early mammalian lineage (Synapsida) began to increase about 270 million years ago, with the emergence of a group called Therapsida, and is accompanied by new forelimb functions. The functional diversification of therapsid forelimbs was curtailed by the Permo-Triassic mass extinction, but eventually continued as more mammal-like therapsids evolved new ecologies. Our analyses characterize the deep time origin of a quintessential part of the mammalian body plan: evolutionarily labile forelimbs that can be deployed in a wide range of functional and ecological roles.

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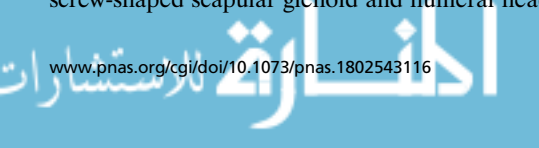
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ecomorphological disparity through time. Studies of other aspects of morphological disparity have been conducted on Permian synapsid groups (25–27), but little work has addressed the magnitude of morphological changes between pelycosaurs and therapsids in the context of the important functional and ecological transitions observed across this interval. Our analyses characterize the origin of a canonical aspect of the derived synapsid bauplan: evolutionarily labile forelimbs that can be deployed in a wide range of functional and ecological roles.

Results

Principal Components Analysis. Shape data were acquired through 2D landmark-based geometric morphometrics. Landmark placements are visualized in Fig. 1B, and detailed in *Methods* and *SI Appendix*. Landmarks and semilandmarks were collected separately for the distal and proximal ends of the humerus. Mean proximal and distal humeral shapes were calculated for each sampled genus and used in subsequent analyses. For singletons or genera that did not have multiple sampled representatives, the single sampled individual was used as the representative for the genus. The full sample list is presented in *Dataset S1*. A principal components analysis was conducted to compare pelycosaur and therapsid humeral shape spaces (Fig. 1B). For both the distal and proximal humerus, therapsids occupy a larger volume of morphospace than pelycosaurs; this is particularly pronounced for the proximal humerus. However, there is considerable overlap in the regions of morphospace occupied by pelycosaurs and therapsids. This implies that the evolution of therapsids was not accompanied by a wholesale change in humerus shape. Instead, some therapsids began to explore new areas on the periphery of synapsid morphospace that likely correspond to novel ecologies and locomotor modes.

Disparity. Procrustes variance across the entire humerus is low during the early stages of the pelycosaur-dominated Permian. Variance levels of the distal and proximal ends only vary slightly between 305 and 275 Mya, with proximal humerus disparity being notably low from 300 to 295 Mya (Fig. 2A). Pelycosaur

variance is highest during the later stages of their evolutionary history, specifically within the 275 Mya time bin for the proximal end (0.0065) and at 270 Mya for the distal end (0.0085). Although sampling does not correlate with the variance results through time (Fig. 2B and C and *SI Appendix*), the presence of unusual pelycosaur taxa played a role in the heightened variance values during the latest stages of pelycosaur sampling. Specifically, the taxonomic and morphological diversification of Caseidae, a derived and enigmatic clade of large-bodied herbivorous pelycosaurs, drives the pelycosaur disparity increase starting at 285 Mya.

Therapsids emerge in the sample during the 270- and 265-Mya time bins for the proximal and distal humerus, respectively. It is at this point in the time series that total disparity for both parts of the humerus begins to increase to variance levels that are higher than the range seen through the majority of the early synapsid sample. It is also during these time bins that the distal and proximal ends begin to express increasingly different values of disparity, though the overall pattern of increase continues to hold. Specifically, with the exception of the time bin representing the Permo-Triassic mass extinction, proximal disparity contains a disproportionate amount of the total humeral variance, and proximal values remain higher throughout the remainder of the sample.

Overall, therapsids have greater Procrustes variance than pelycosaurs in both the distal and proximal ends of the humerus, across the majority of sampled time bins. Within therapsids, the proximal end of the humerus displays more variance than the distal end across all sampled time bins, and the magnitude of the difference between the proximal and distal variance values fluctuates only slightly through time. Therapsid proximal humerus variance was highest in the time bin just after the Permo-Triassic mass extinction (placed at 252 Mya instead of 250 Mya, following the 252.24-Mya age of the Permo-Triassic boundary) (28) (proximal = 0.014). Excluding the time bins that have noteworthy departures from the overall pattern (300–295, and 252 Mya) pelycosaur proximal humeri account for 50.49% of humeral variance on average, whereas in therapsids the proximal humerus accounts for 61.55% of humeral variance on average.

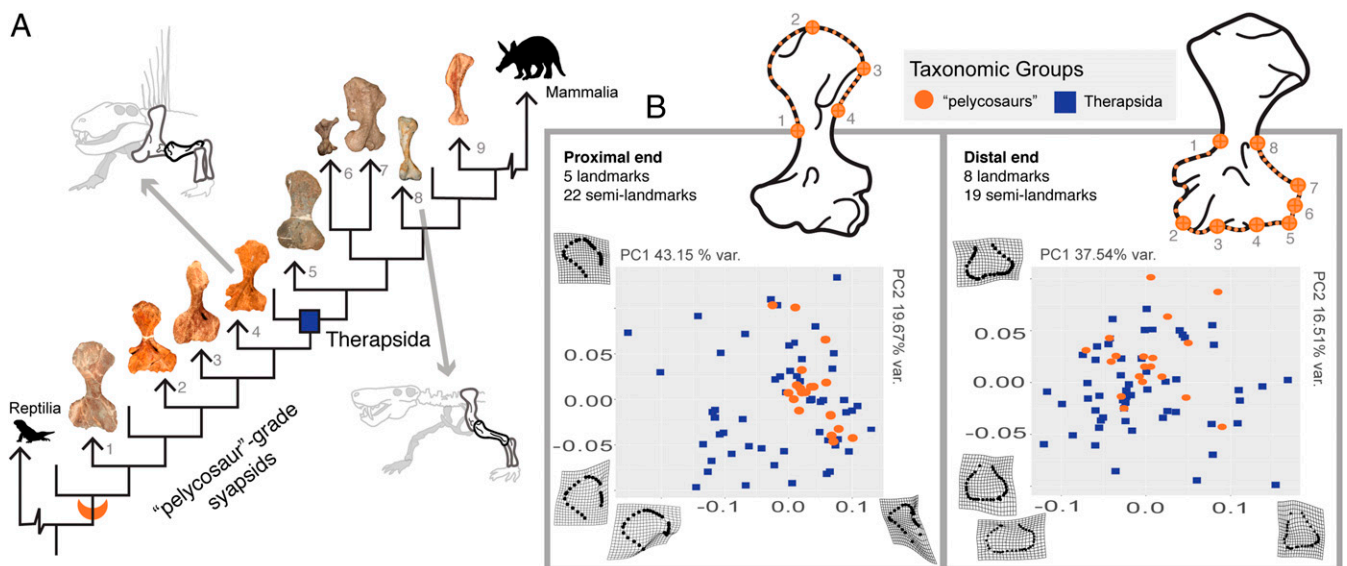


Fig. 1. Contrasting forelimb disparity in the rise of Therapsida. Simplified cladogram of Synapsida showing humeral diversity and morphospace distribution of major studied clades. (A) Pelycosaurs (orange semicircle) comprise the first major radiation following the split from Sauropsida. Sample humeri from four pelycosaur clades display morphological conservatism: (1) *Cotylorhynchus hancocki*, (2) *Ophiacodon retroversus*, (3) *Edaphosaurus* sp, and (4) *Dimetrodon limbatus*. Pelycosaurs were replaced by therapsids (blue square) in the middle Permian. Five sample humeri display the morphological disparity of therapsids: (5) *Jonkeria* sp, (6) *Cistecephalus microrhinus*, (7) *Ischigualastia jenseni*, (8) *Gorgonopsia*, and (9) *Massetognathus pascuali*. See *SI Appendix, Table S1* for specimen numbers. (B) Principal component plots of the humeral datasets, with percent variance captured by each axis and warp grids displaying morphological change along these axes. Landmark and semilandmark placement is shown above the associated morphospaces.

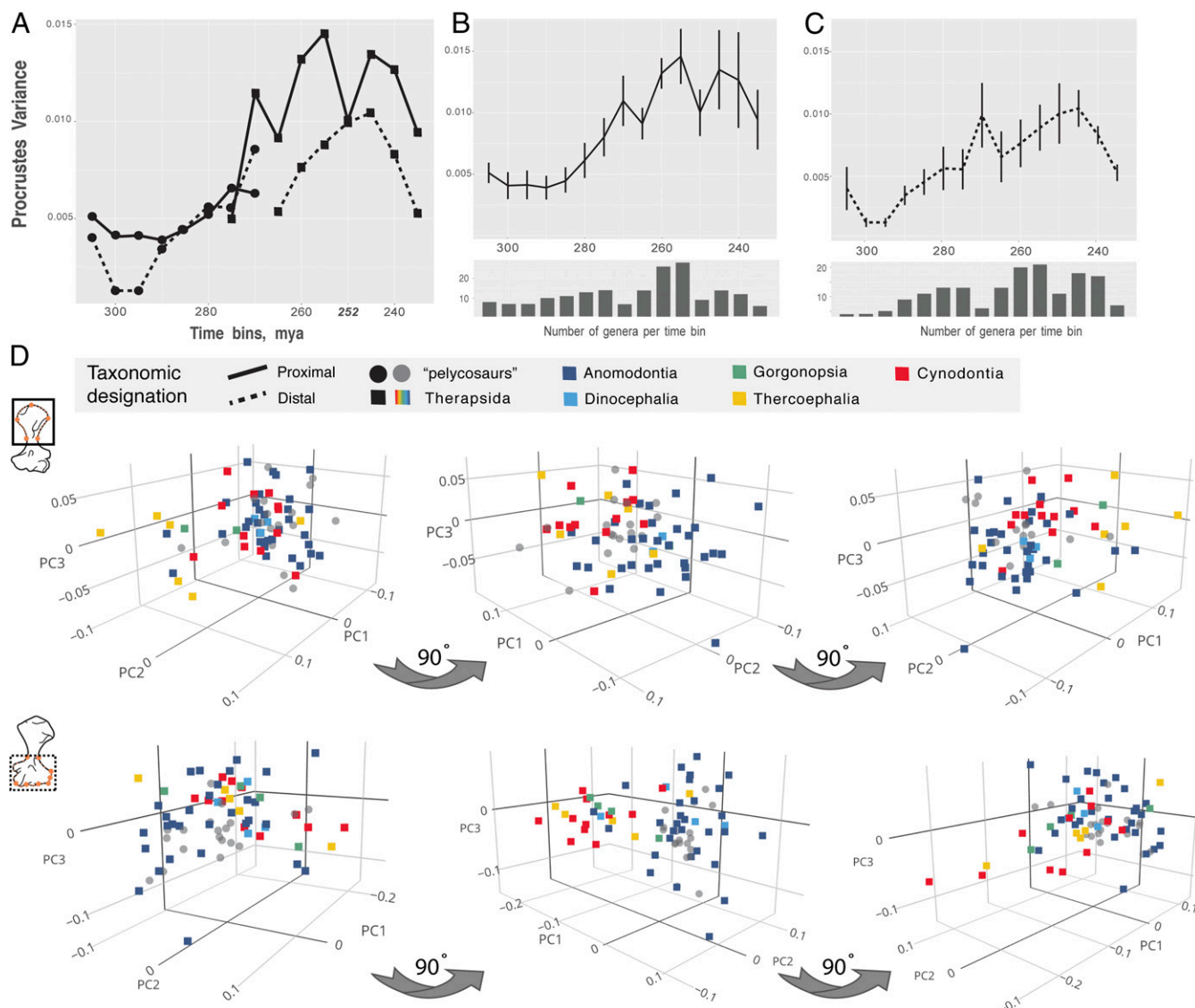


Fig. 2. Disparity of pelycosaurs and therapsids through time with associated therapsid morphospace distributions. (A) Total Procrustes variance through time split by synapsid radiation. The lines linked by circles represent pelycosaurs; therapsids are represented by squares. (B and C) The total-group disparity pattern through time including error bars for each sampled time bin. The histograms below show total genera sampled across each end of the humerus per time bin for the proximal end (B) and distal end (C). (D) Three dimensional morphospace (PC1vPC2vPC3) for the proximal end and the distal end. When viewed in three dimensions, therapsid exploration of previously unoccupied morphospace is evident. Colored squares represent therapsids; gray circles represent pelycosaurs. Each plot is rotated 90° counterclockwise from the one immediately *Left*. Areas of morphospace that are unoccupied by pelycosaur specimens are instead occupied by groups representing novel therapsid ecomorphologies, such as cynodonts (yellow) and anomodonts (blue).

Proximal variance remains high through the 240-Mya bin, but decreases following this maximum and returns to preextinction values in the Middle Triassic (235 Mya). Counter to the proximal trend, distal humeral disparity increases across the extinction interval. Analyses revealed that this disparity increase is caused by the removal of intermediate morphologies during the extinction; see *SI Appendix* for further discussion.

Discussion

Our results show that the rapid increase in humeral disparity beginning in the mid-Permian is coincident with the emergence of therapsids (Fig. 2A). Although the earliest therapsids are known from before 265 Mya (arguably as early as 275 Mya) (29–31), many of the oldest and phylogenetically most basal therapsids either have no known forelimb material or could not be sampled for this project due to rarity. As therapsids diversify

taxonomically through the Permian, disparity of both ends of the humerus continues to increase to levels much higher than those ever achieved by pelycosaurs. This result supports the distinctiveness of therapsid humeral morphology and variance relative to those of pelycosaurs.

Therapsida is hypothesized to have split from its pelycosaur sister group (Sphenacodontidae) in the Pennsylvanian (6). In the earliest time bins including therapsids (275–265 Mya), phylogenetically basal clades (primarily Dinocephalia) dominate the therapsid sample. The similar levels of disparity between pelycosaurs and therapsids in these bins, and the position of the dinocephalians in morphospace, reinforce the perspective of dinocephalians as morphologically “primitive” branches of Therapsida that had not diverged from the ancestral morphotype to the degree seen in later taxa. The low early therapsid variance levels in our sample could indicate a gradual accumulation of morphological

disparity during their earlier history, which is unsampled in the known fossil record. Alternatively, the therapsid bauplan, including heightened forelimb disparity, might have evolved rapidly in the middle Permian, as suggested by a more literal reading of our data, with dinocephalians simply preserving an early stage in this process. Variance increases continuously from the middle Permian onwards, corroborating the hypothesis that therapsids underwent morphological diversification throughout the remainder of the Permian. The finding that variance decreased in the 252-Mya time bin represents the effect of the Permo-Triassic mass extinction, the largest extinction in Earth history (32), although the details of this decline differed between the proximal and distal ends of the humerus.

The therapsid disparity-through-time pattern corresponds with their notably greater total morphospace occupation than pelycosaurs (Figs. 1B and 2D). Critically, some of this novel humeral morphospace is associated with the first experiments by therapsid clades with ecologies that have no counterparts among pelycosaurs. Fig. 2D shows that when considered in three dimensions the peripheral areas of morphospace uniquely occupied by therapsids correspond to taxa that have been hypothesized to represent the first occurrences of various ecotypes among nonmammalian synapsids. Examples include fossorial cistecephalid dicynodonts (represented by the color blue), small-bodied faunivores such as therocephalians and cynodonts (red and yellow, respectively), and the gracile, mid-sized predatory gorgonopsians (green).

Pelycosaur total group disparity varies less across the two ends of the humerus than in Therapsida. This association in values presumably reflects the functionally restrictive morphology of the humeral joint surfaces of pelycosaurs (13, 22), and the role the humerus played in stabilizing the pelycosaur body (10, 22). The complex and mechanically costly gait of pelycosaurs likely limited the morphofunctional diversification of the upper limb. In contrast, therapsid disparity is characterized by a separation of shape variance in the distal and the proximal ends of the humerus, with proximal humeral disparity disproportionately heightened in comparison with the distal humerus. Importantly, the pattern of increasing morphological disparity is most strongly expressed in the vicinity of the proximal articulation (glenohumeral joint). Pelycosaurs and therapsids possess distinctly different pectoral girdle morphotypes. Pelycosaur glenohumeral articulations are screw shaped, anteroposteriorly long but dorsoventrally narrow with a spiraling joint surface, and are characterized by a precise fit between the humeral and pectoral joint surfaces that limits range of motion (10, 12). In contrast, the therapsid glenohumeral joint is characterized by smooth, convex surfaces that present few bony limits on joint mobility (33–35).

Therefore, the therapsid rise in ecomorphological disparity is not accompanied by an increasingly complex humeral form but by simplification, in particular of the humeral head. Coupled with the simplification of the glenoid and scapulocoracoid complex in therapsids, the changes in humeral morphology facilitated innovation in forelimb function by increasing locomotor capabilities. Specifically, these findings support the hypothesis that the reorganization of the pectoral girdle and forelimb played a key role in the diversification of therapsids by increasing forelimb range of motion (17, 20, 21, 23, 36). Freeing the forelimb from the constraints of limited mobility was a critical first step that allowed therapsids to explore new ecologies, foreshadowing further simplification of the pectoral girdle and ecological diversification of the forelimb later in mammaliaform evolution. Mammalian evolution is characterized by the heightened functional diversity of the forelimb, and the earliest roots of this macroevolutionary pattern lie in the Middle Permian emergence of therapsids.

Methods

Temporal and Taxonomic Sampling. All specimens were categorized to the genus level. Pelycosaur and therapsid taxa were grouped for analysis using the current consensus view of pelycosaur and therapsid phylogeny (37–39).

The distal humerus sample comprised 284 specimens representing every major clade from the temporal range of this study except Biarmosuchia. Mean shapes were calculated for 73 genera (18 pelycosaurs, 55 therapsids). The proximal humerus sample comprised 309 specimens, with the same taxonomic sampling as the distal end analysis. Mean proximal shapes were calculated for 73 genera (19 pelycosaurs, 54 therapsids). The total time range of this study spanned from 305 Mya (Pennsylvanian) to 235 Mya (Middle Triassic), representing three separate geological periods and nearly all of pelycosaur and noneucynodontian therapsid history (6, 26, 32).

Genus stratigraphic ranges were compiled from the Paleobiology Database (PBDB) (www.paleobiology.org) and literature sources (time ranges can be viewed in [Dataset S1](#)), and occurrences were binned as presence/absence data across 5-My time intervals. We conducted a generalized distancing analysis in R (40) to check whether taxonomic sampling was correlated with measured trends in disparity and found no correlation between taxonomic sampling and disparity values across all of the analyzed time bins ([SI Appendix](#)). A detailed description of the sample, including specimen numbers and stratigraphic ranges, is presented in [Dataset S1](#).

Geometric Morphometrics and Disparity Analysis. Shape outline data were acquired through 2D landmark-based geometric morphometrics, using photographs taken by the authors and a small number of high-quality illustrations from the published literature ([SI Appendix, Table S5](#)). The geometric morphometric analysis of the humerus was split into distal and proximal end shapes. Because the proximal and distal ends of the humerus are offset in most pelycosaurs and many therapsids, and the degree of offset frequently is affected by taphonomic distortion, splitting the analysis into distal and proximal portions allows for the full 2D shape of both functional surfaces to be measured accurately. All analyses were conducted on left humeri; in cases where the only available element was a right humerus, the element was mirrored across its proximal–distal axis for analysis.

The landmarks and semilandmarks were digitized and scale recorded using tpsDIG2ws (41). Landmark and curve positions are shown in Fig. 1B, and descriptions of landmark placements are presented in [SI Appendix, Table S3](#). The landmarks represent consistently recognizable extrema on the outlines of the humerus because there are no usable internal landmarks on either end of the humerus across this evolutionary interval. The proximal humerus was analyzed in posteroventral view, emphasizing the perspective that maximized the total width of the proximal end. This view permits the posterior side of the humeral head to be viewed, as well as the entire deltopectoral crest in a way that captures the curvature of the deltopectoral crest along the long axis of the humerus. The distal humerus was analyzed in dorsal view, although all analyzed morphology is visible in either dorsal or ventral view.

The resulting data were processed in R, and all analyses were conducted with the Geomorph package (42). Data underwent a general Procrustes superimposition to reorient and scale all specimens (42–46) ([SI Appendix](#)). Sliding semilandmark position was based on minimizing Procrustes distances. The multivariate disparity analysis was conducted directly on the superimposed geometric morphometric data. Disparity was analyzed within a given time bin using the genera present during that time bin. Centroid size was treated as a covariate in the disparity analyses to remove the influence of shape on the disparity pattern. Therapsids and pelycosaurs overlapped in only two time bins, so those were the only bins for which the within-group designation was strictly necessary. Full disparity values can be viewed in [SI Appendix, Table S2](#). Variance of Procrustes values was the disparity metric used and was measured on the geometric morphometric data. Disparity was calculated from the within-group mean of genera present during a given time bin, grouped on the taxonomic level of pelycosaur or therapsid. Error bars for the disparity data are reported as the SDs of a dataset randomly resampled (with replacement) to the size of the sample in the given time bin, with 1,000 overall permutations. A phylogenetic least squared (PGLS) analysis was run to check for phylogenetic signal in the shape data, based on a composite phylogeny built off of published literature on sampled groups (full details in [SI Appendix](#)). Pagel's lambda (λ) was calculated from the covariance matrix produced by the PGLS. The results were not significant (proximal: $\lambda = 0.1753$, $P = 0.6305$; distal: $\lambda = 0.1761$, $P = 0.5095$) (see [SI Appendix](#) for details).

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