

Developmental strategies underlying gigantism and miniaturization in non-avian theropod dinosaurs

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In amniotes, the predominant developmental strategy underlying body size evolution is thought to be adjustments to the rate of growth rather than its duration. However, most theoretical and experimental studies supporting this axiom focus on pairwise comparisons and/or lack an explicit phylogenetic framework. We present the first large-scale phylogenetic comparative analysis examining developmental strategies underlying the evolution of body size, focusing on non-avian theropod dinosaurs. We reconstruct ancestral states of growth rate and body mass in a taxonomically rich dataset, finding that contrary to expectations, changes in the rate and duration of growth played nearly equal roles in the evolution of the vast body size disparity present in non-avian theropods—and perhaps that of amniotes in general.

The concept of heterochrony—changes in the relative rate and/or timing of developmental events—was formalized by Alberch *et al.* (1) and has been used to explain the evolution of morphology and body size disparity in a variety of vertebrate clades for more than a century. Heterochrony is often invoked in studies of body size evolution, but most hypotheses rest on pairwise comparisons of sister taxa (implied or assumed to be ancestor-descendent pairs) or very few species of a given clade (2–18), most often examined outside of an explicit phylogenetic context. Vertebrate postnatal or post-hatching growth can generally be divided into three phases bounded by the onset and offset of a period of rapid growth (1, 3). Over the past two decades, acceleration or deceleration of the rapid growth phase has been inferred to be the predominant mechanism influencing body size evolution in most amniotes, including several clades of non-avian dinosaurs (2, 3, 5–10) and mammals (12–17). Much less commonly inferred mechanisms include changes in the duration of the rapid growth phase (prolongation or truncation through a change in the onset and/or offset timepoint of the phase of rapid growth), which have been used to explain body size change in a limited

few groups [e.g., some lizards (18), crocodile-line archosaurs (19), and synapsids (17, 20)]. Evidence for changes in rate versus timing is mixed or wanting in birds (2, 21–23). Metabolic theory predicts that changes in growth rates are the predominant mechanism underlying body size evolution; most somatic cells are body size-invariant (24) indicating that the evolution of body size largely involves changes in the number of cells rather than their size. A larger number of cells translates to higher metabolic and mitotic activity per unit body mass and thus accelerated growth (25). The overwhelming inference of changes in developmental rate over duration leading to body size evolution is axiomatic in review articles (26), broad comparative studies of extant taxa (27, 28), and the popular scientific literature (29).

However, no study to date has analyzed the evolution of developmental rate and duration in an explicit phylogenetic comparative framework, in part because there are few abundantly sampled, long-lived clades containing a diversity of body sizes with which to test the frequency of distinct heterochronic mechanisms. We assembled a comprehensive dataset of body size and growth data for non-avian theropod dinosaurs, established reliable protocols and proxies for estimating missing data in osteohistological cross sections, and developed a novel, standardized framework for analyzing the relative contribution of changes to growth rate and duration over the evolutionary span of a clade. Femora and tibiae were used to infer individual ages and body masses over ontogeny for each specimen in our dataset, because these elements scale tightly with one another and have a strongly predictive relationship with body mass (fig. S1). Dorsal ribs and fibulae, which often undergo less of the dense remodeling that obscures the cortical growth record, were used to ensure that the rapid (i.e., maximum annual) phase of growth was recorded in a given individual (i.e., the phase of growth preserving the most widely

spaced cortical growth marks). Some specimens were unavailable for thin sectioning, but histological features could be sufficiently resolved in computed tomographic data.

Our dataset includes measurements of ~500 annually deposited cortical growth marks (CGM) from more than 80 skeletal elements of 42 non-avian theropod dinosaur species of disparate body sizes (<0.5 m to >12 m body length) and ecologies (data S1). This dataset is derived from a cosmopolitan taxon sample and ranges from some of the geologically oldest non-avian theropods (e.g., *Herrerasaurus*, ca. 230 Ma) to those immediately preceding the K–Pg extinction event (e.g., *Tyrannosaurus*, *Majungasaurus*, ca. 66–68 Ma). We estimate maximum annual growth rates for 36 of these 42 taxa, plot them on a time-calibrated phylogeny (Fig. 1), and provide novel detailed histological descriptions for 10 previously unsampled taxa. We performed ancestral state reconstructions of body mass and annual growth rate using maximum likelihood to estimate the relative contribution of acceleration or prolongation for lineage-specific body size increases, and deceleration or truncation for lineage-specific body size decreases, in the evolution of dinosaurs on the line to birds.

This greatly expanded histological dataset reveals a wide range of growth records and tissue types indicative of a diversity of growth strategies, broader than the range found in smaller theropod datasets (e.g., 2, 30). Even small derived clades within Theropoda exhibit cortical bone histology corresponding to a high diversity of growth rates. For example, *Ceratosaurus* grew rapidly with plexiform neurovascular canal organization densely permeating a cortex of woven to parallel-fibered bone that is interspersed with few growth marks. By contrast, the similarly sized ceratosaurian *Majungasaurus* grew much more slowly (slower than extant *Alligator*; data S1), with longitudinal to circumferential neurovascular canal organization surrounding parallel-fibered to lamellar tissue that is interrupted by many closely spaced lines of arrested growth.

Although developmental plasticity has been inferred for several early dinosaurs and their relatives (4), about three-quarters of the species in our dataset belong to the clade Avetheropoda, a group inferred to have relatively low intraspecific variation in growth (31), an inference further confirmed by our expanded sampling. We find low intraspecific variation in several of the avetheropods in our dataset (when excluding data from young juveniles or old adults whose bones do not preserve the explosive phase of growth), including: *Acrocanthosaurus* (maximum annual growth rate 46 to 60%), *Aniksosaurus* (103 to 113%), *Gorgosaurus* (40 to 75%), *Sinornithomimus* (182 to 214%), and *Troodon* (77 to 79%). A notable exception in our dataset is *Allosaurus*, a

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Fig. 1. Evolution of maximum annual growth rate and body mass in non-avian theropods. Ancestral states reconstructed through maximum likelihood are shown as colors on lineages that are scaled to geologic time, whereas black circle size indicates estimated adult body mass. Yellow and/or orange colors and larger circles indicate faster-growing and larger individuals, respectively. Silhouettes from PhyloPic (see acknowledgments and data S1).

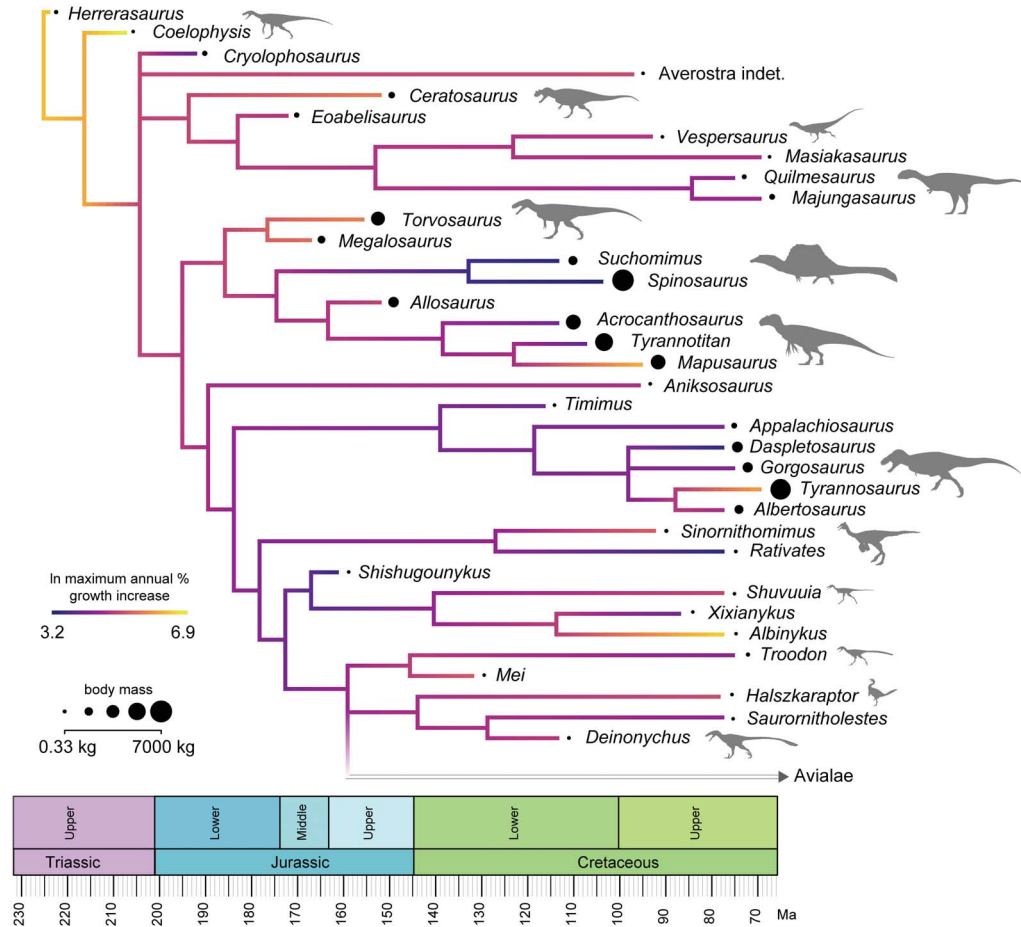


Fig. 2. Phylomorphospace plot of non-avian theropod maximum annual growth rate and body mass evolution. Concentric circles at each corner of the morphospace schematically represent cortical growth marks within diaphyseal cross sections as shown in the illustrated theropod femur; these indicate idealized “end members” in growth and body size. The branches represent evolutionary paths in body size and growth rate. Silhouettes from PhyloPic (see acknowledgments and data S1).

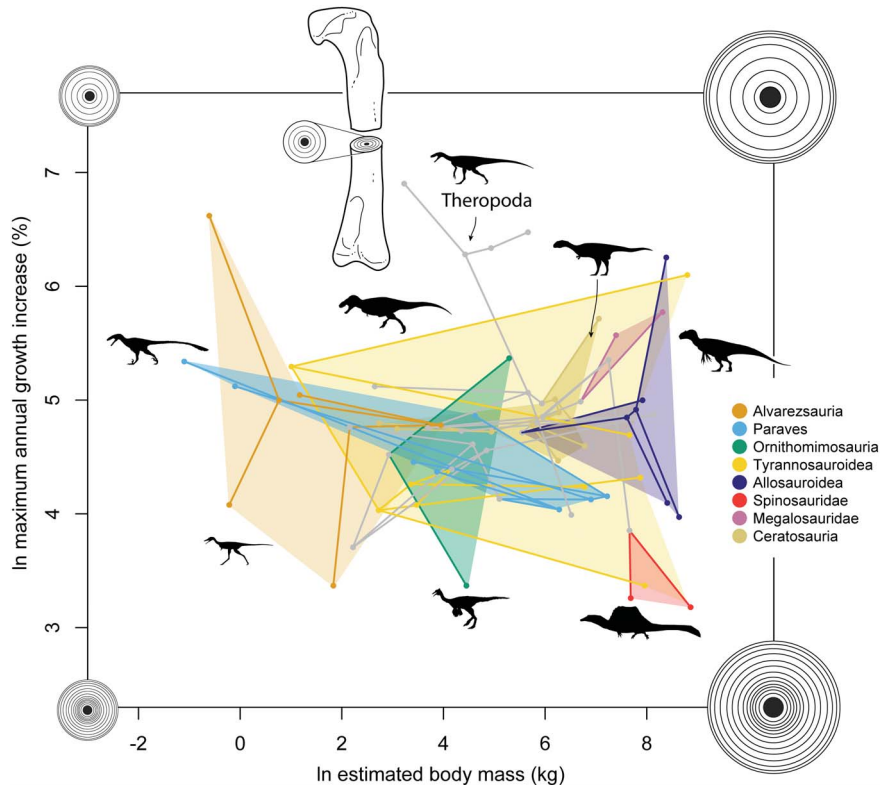
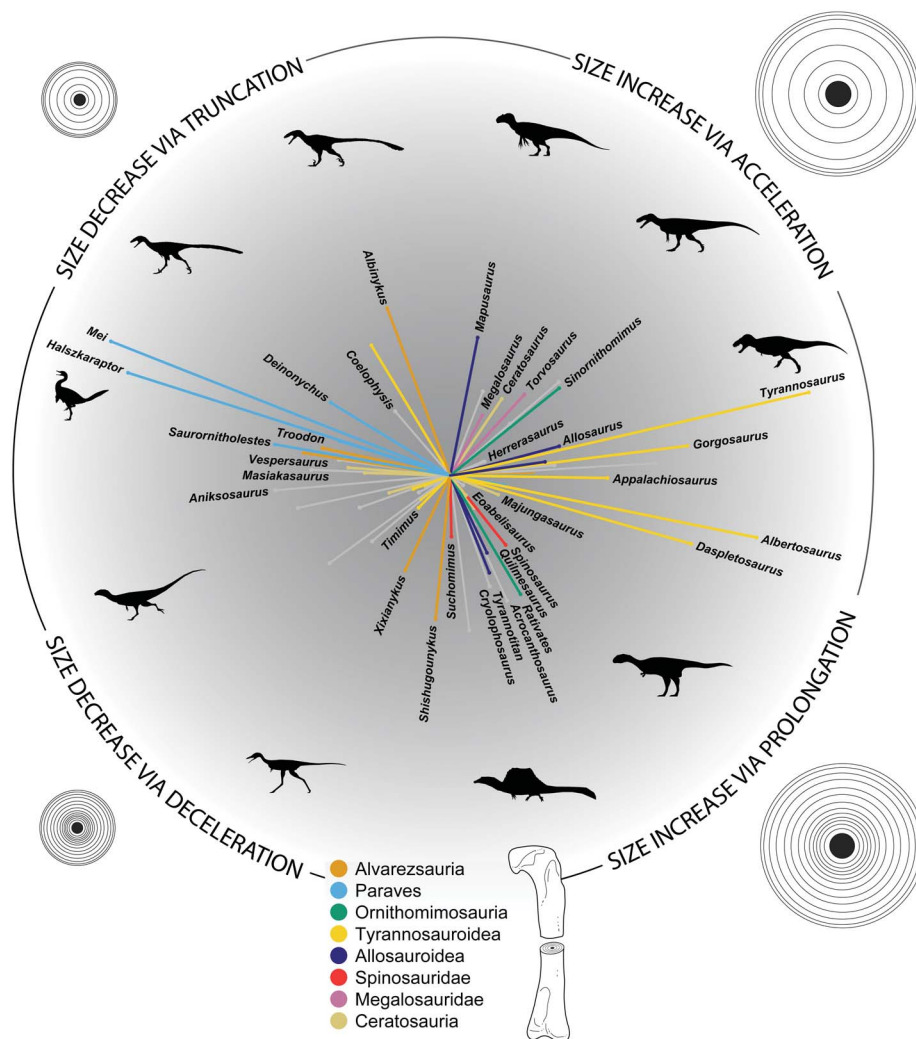


Fig. 3. Evolutionary mechanisms underlying body size evolution in non-avian theropods.

Each vector represents a reconstructed ancestor-descendent transition, with the length indicating the magnitude of change on that branch (on a natural log scale as in Fig. 2). The direction of each vector indicates the predominant mechanism underlying the evolution of body size in that lineage. Line colors pertain to members of the eight highlighted clades listed at the bottom of the figure. Concentric circles at each corner of the plot indicate schematic bone cross sections showing cortical growth marks as in Fig. 2. Silhouettes from PhyloPic (see acknowledgments and data S1).



taxon that is inferred to have sex-based or cryptic taxonomic differences that require a larger dataset to untangle.

We reconstruct the ancestral theropod condition as having high maximum annual growth rates (Fig. 1), consistent with both independently derived estimates of ancestrally high daily growth rates (2, 32) and the inference of endothermy in early dinosaurs and their relatives (33). The distribution of non-avian theropod maximum annual growth rates is strongly positively skewed (median maximum growth rate per year = 114%; Shapiro-Wilk test $W \sim 0.71$; $P \sim 1 \times 10^{-7}$; fig. S2). Non-avian theropods exhibit no significant trend in maximum annual growth rate through their evolution ($r = 0.3$; $P = 0.07$; fig. S3). However, there is a consistent decrease in maximum annual growth rate along the stem of the phylogeny on the line toward birds (Fig. 1), wherein the ancestral averostran, coelurosaurian, and maniraptoriform maximum annual growth rate fell from ~150 to ~110 to ~75%, respectively. This steady decrease parallels the trend of sustained miniaturization along the stem to birds (34). How-

ever, paravians decouple these trends, growing more quickly at even smaller body sizes (maximum annual growth rate increase ~100%). Substantial decreases in maximum annual growth rate evolved independently in spinosaurids, tyrannosauroids, and early maniraptorans, whereas increases evolved independently in derived allosauroids, alvarezsauroids, and paravians (Fig. 1). There is no relationship between body mass and maximum annual growth rate (fig. S4; $r = 0.02$; $P = 0.38$). This pattern is underscored by the marked range of variation in the growth rates of the largest theropods, such as some derived allosauroids and spinosaurids, groups that increased body mass by at most ~60% per year. By contrast, derived megalosaurids, ceratosaurians, some tyrannosauroids, and some allosauroids increased their mass more than 200% per year (Figs. 1 and 2). Similar disparity is exhibited by the smallest theropods, with ornithomimosaurids, alvarezsauroids, and smaller tyrannosauroids exhibiting a wide range of rates (Figs. 1 and 2).

Plotting each lineage as a vector in a phylo-morphospace of body mass versus maximum

annual growth rate, with the absolute value of its ancestral state at the center of a circle, reveals both the relative frequency of body size changes and the mechanisms underlying them (Fig. 3). Within our sample, ~60% of branches record an increase in size, compared with ~40% that record a decrease. Changes in the rate of the rapid growth phase occur on 50.7% of branches, whereas changes in its duration occur on 49.3%. The most common evolutionary change is size increase through acceleration of the explosive growth phase (31.3% of branches), followed closely by size increase through its prolongation (28.4%), size decrease through its truncation (20.9%; Fig. 3), and size decrease through its deceleration (19.4%). Analyzing theropod growth evolution as a percentage increase per year (i.e., relative growth rather than the typically compared absolute growth) (e.g., 2, 3), and analyzing it in a phylogenetic framework (i.e., comparing explicitly hypothesized ancestor-descendent values) contradicts the results of some previous studies. For example, we find that gigantism in allosauroids evolved through a range of growth strategies, not just

prolongation (30) or acceleration (5). We find support for some previous evolutionary hypotheses, including truncation of rapid growth characterizing the close relatives of birds (2, 21), and exceptionally high variability in alvarezsauroid growth rates (35). Our results generally align with clade-specific morphological studies of heterochrony in several theropod clades, including peramorphosis in carcharodontosaurids with prolonged, slow development (36) and paedomorphosis in paravians with truncated, rapid development (37). We find that many non-avian theropods grew proportionally slower than extant crocodylians (data S1), and changes in developmental duration were found to be similar in frequency to changes in developmental rate. Once quantified and analyzed in a phylogenetic framework, we predict that diverse growth strategies will be recognized in other clades, such as those currently thought to evolve in body size primarily through changes in developmental duration [e.g., crocodile-line archosaurs and lizards (18, 19)]. Just as broad, phylogenetic comparative studies have repeatedly failed to find support for directional evolution in body size [i.e., Cope's Rule (38)], with increased scrutiny the developmental mechanisms underlying body size evolution may be found to be equally prevalent across Amniota as a whole.

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SUPPLEMENTARY MATERIALS

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Histological Descriptions
Figs. S1 to S5
Data S1 and S2
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MDAR Reproducibility Checklist

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How to get big

Over evolutionary history, many different taxa have evolved very large body sizes. The general consensus has been that an animal grows to a large size based on an increase in growth rate. However, very few studies have explored this question across many species within a comparative phylogenetic framework. D'Emic *et al.* looked across a large dataset of non-avian theropod dinosaurs, which had an array of body sizes. They found evidence supporting changes in growth rate contributing to body size change, but also found that changes in the duration of growth played a large role. —SNV

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