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Superiority, Competition, and Opportunism in the Evolutionary Radiation of Dinosaurs

Stephen L. Brusatte*, Michael J. Benton, Marcello Ruta, Graeme T. Lloyd
Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK.
*To whom correspondence should be addressed. E-mail: brusatte@uchicago.edu

ABSTRACT—The rise and diversification of the dinosaurs in the Late Triassic, from 230-200 Ma, is a classic example of an evolutionary radiation with supposed competitive replacement. Comparison of evolutionary rates and morphological disparity of basal dinosaurs and their chief "competitors," the crurotarsan archosaurs, shows that dinosaurs exhibited lower disparity and an indistinguishable rate of character evolution. The radiation of Triassic archosaurs as a whole is characterized by declining evolutionary rates and increasing disparity, suggesting a decoupling of character evolution from body plan variety. The results strongly suggest that historical contingency, rather than prolonged competition or general "superiority," was the primary factor in the rise of dinosaurs.

The rise of the dinosaurs in the Late Triassic and Early Jurassic (230-190 Ma) is a classic example of an evolutionary radiation. During that time, the clade Dinosauria expanded from a single lineage to many dozens of lineages, and from one ecological and morphological type to many, and the range of body sizes expanded to include truly gigantic forms (*1*, *2*). Through this expansion in diversity and disparity, dinosaurs became the pre-eminent vertebrates on land, occupying many ecological roles in terrestrial ecosystems worldwide, especially those at medium to large size.

The expansion of Dinosauria has long been seen as an example of a 'competitive adaptive radiation' in which one group supplants another (*3, 4*). The dinosaurs were said to have out-competed other terrestrial tetrapods (notably basal archosaurs, rhynchosaurs, and non-mammalian synapsids) by virtue of their upright or erect posture, which gave them advantages of speed and manoeuvrability (*5*), or because they were endothermic (possessing fully warm-blooded physiology) (*6*). The alternative, opportunistic model (*3*) proposes that dinosaurs diversified in the Norian, following a Carnian-Norian extinction event 228 Ma (CNEE) that saw the demise of rhynchosaurs, dicynodonts, and chiniquodontids, and dinosaurian clades were added through the Late Triassic and Early Jurassic until they reached their full diversity.

Most previous studies have treated the rise of the dinosaurs as a single event, whether competitive or opportunistic (*3, 5, 6, 7, 8*). However, phylogenies and diversity trends suggest it was a two-step process, with the diversification of herbivorous sauropodomorphs in the Norian, following the CNEE, and then larger theropods and armored herbivore groups in the Early Jurassic, following extinction of carnivorous crurotarsans at or near the Triassic-Jurassic boundary (TJEE). This two-step model has been supported by recent study of theropods, which became larger and more common after the TJEE (*7*), and ornithischians, which are now known to have been rare in the Late Triassic after the reassignment of many supposed ornithischian fossils to nondinosaurian groups (*9*).

The critical interval to consider is the Late Triassic, especially the Norian and Rhaetian (Fig. 1), a 28-myr span between the CNEE and TJEE. The key "competitors" of the early dinosaurs were the crurotarsans, the "crocodile-line" archosaurs, which show a range of morphologies and adaptations during this time: long-snouted fish-and-flesh-eating phytosaurs, armored herbivorous aetosaurs, and large to giant carnivorous "rauisuchians". The crurotarsans

even replicated many dinosaurian body plans (large terrestrial predators; small swift predators; mid-to-large-bodied low-browsing herbivores; agile bipedal herbivores). Several new discoveries show striking convergences between crurotarsans and dinosaurs (*10*), and many Triassic crurotarsans were previously erroneously identified either as dinosaur ancestors (*11*) or even true dinosaurs (*12*). Such morphological convergence suggests that dinosaurs and crurotarsans were exploiting similar resources in the Late Triassic. In some Norian faunas, crurotarsans were even numerically more abundant than dinosaurs (*3*), and seem to have exploited a wider range of body plans. However, by the end of the Triassic all crurotarsans were extinct, save a few lineages of crocodylomorphs.

The key question is why the major dinosaur lineages survived the TJEE, ushering in the 135-million-year "Age of Dinosaurs," while most crurotarsan groups went extinct. One common explanation is that dinosaurs "outcompeted" crurotarsans in the Late Triassic, and notions of general dinosaurian "superiority" have long pervaded the literature (*5*, *6*). Hypotheses of competition between major clades are often vague, difficult to test conclusively, and prone to oversimplification (*4*). Rather than focusing on such imprecise terms, it is illuminating to examine macroevolutionary patterns. Here, we compare evolutionary rates and relative morphospace occupation in dinosaurs and crurotarsans, which may shed light on their evolutionary dynamics and help assess long-standing perceptions such as "superiority."

We use a new phylogeny of Triassic archosaurs (Fig. 1) and a dataset consisting of 64 taxa and 437 discrete skeletal characters (*13*) to calculate numerical measures of evolutionary rates (patristic dissimilarity per branch and patristic dissimilarity divided by branch duration, *17*) and disparity (morphospace occupation) (*13*). It is important to note that rates analysis approximates the amount of morphologic evolution separating species, whereas disparity

approximates the amount of morphologic difference between species (*15*, *17*). These are related but separate measures of morphological evolution that together give insights into patterns of macroevolutionary change within and between clades. Disparity analysis does not depend on a specific phylogenetic hypothesis, but evolutionary rates analysis does.

There is no clear evidence for differences in overall evolutionary rates between dinosaurs and crurotarsans during the Triassic as a whole. Dinosaurs exhibit higher mean rates than crurotarsans for all measures (Fig. 2A-B, S2A-B)—as does the entire dinosaur "total group", Ornithodira (sister taxon to Crurotarsi)—but these differences are generally not significant (table S1, S28). A pruned analysis of equal sample sizes for the two clades returns the same result (table S2), as does an analysis restricted to Norian taxa (table S3). There is limited evidence for significantly higher rates in Carnian dinosaurs, but this may be due to small sample size (table S3). Temporal trends do not show a coupled increase in dinosaur rates and decrease in crurotarsan rates, as might be expected under some models of "competition" (Fig. 2E-F, S2E-F). Dinosaurs exhibit a significantly higher rate of evolution of the appendicular skeleton than crurotarsans, but not of the cranial or axial skeleton (table S9). However, there are no significant differences between rates for different regions of the dinosaur skeleton (tables S16-17).

Perhaps counterintuitively, the disparity study shows that crurotarsans occupied a larger amount of morphospace than dinosaurs and ornithodirans as a whole (Fig. 3A-B, S3 A-B; table S21, S29). Rarefaction curves show that these results are not biased by sample size (fig. S4). The same pattern holds within the Carnian and Norian (table S22), and there are no coupled temporal trends (Fig. 3E-F, S3E-F). Dinosaurs and crurotarsans occupy adjacent areas of morphospace (Fig. 1), which is expected because the analysis is based on cladistic characters. Importantly, crurotarsans convergent with dinosaurs (poposauroids, "rauisuchids," basal crocodylomorphs)

occupy an intermediate area between the majority of crurotarsans and dinosaurs. Higher disparity of crurotarsans is borne out by visual examination of Figure 1, which shows a much larger morphospace than that for dinosaurs. Unexpectedly, this larger crurotarsan morphospace is associated with significantly higher rates of homoplasy (table S18), suggesting that character oscillation is an important factor in body plan evolution.

Archosaurs radiated during the Triassic in the aftermath of the end-Permian mass extinction. Our analysis shows that this radiation was associated with declining evolutionary rates per lineage and increasing morphological disparity throughout the Triassic. One rate metric, dissimilarity calibrated by time interval duration, shows a general decrease through the Triassic, with significantly high rates in the Anisian and low rates in the Norian (Fig. 2D, S2D; tables S4-S5). Patterns within Crurotarsi and Dinosauria mirror those of Archosauria as a whole, as both subclades are characterized by decreasing rates (Fig. 2F, S2F; tables S6-S8). Similarly, decreasing rates are also seen in cranial, axial, and appendicular character partitions (tables S10-S15). The significantly high rates of character evolution in early archosaur history are consistent with the hypothesis of elevated rates during major morphological radiations ([17], [18], [20], [21]).

In contrast, archosaurs show increasing disparity throughout the Triassic, with a significant high peak in the Norian (Fig. 3C-D; tables S23-24). Both crurotarsans and dinosaurs show a general increase in disparity across the Triassic, except for a Ladinian drop for crurotarsans that may be due to small sample size, but the differences between time bins are not significant. (tables S25-26). This pattern differs from several paleontological studies, which have shown that disparity often peaks early in the history of major clades ([14], [15], [16], [21]).

Unexpectedly, these results indicate a decoupling of character evolution and morphological disparity in Triassic archosaurs ([22], [23]). The inverse relationship indicates that,

apparently, the burst of character evolution in early archosaur history did not translate into a wide range of body plans. Only later, when evolutionary rates decreased and homoplasy increased (tables S19-20), did a slower rate of character change result in the development of several new body plans (phytosaurs, aetosaurs, crocodylomorphs, pterosaurs, dinosaurs), all of which are first known from the Carnian or Norian. Decoupling of lineage diversification and disparity has been noted before, but only in the context of within-subclade disparity among extant lizards (*24*). Further work is needed to determine what, if any, broad generalizations characterize evolutionary radiations across a wide range of organisms, timescales, and clade dimensions.

For the first 30 million years of their history dinosaurs lived alongside and shared niches with another major clade (Crurotarsi) that occupied more morphospace and evolved at indistinguishable rates. These patterns seriously contrast with general notions of dinosaurian "superiority" and the long-standing view that dinosaurs were preordained for success (*5*, *6*). It is difficult to explain why crurotarsans and not dinosaurs went extinct at the TJEE, which may have been a catastrophic event (*7*) or an ecologically drawn-out affair triggered by eruption and elevated CO_2 levels (*25*). Either way, as in most mass extinction events, the death of species is often more random than ecologically selective (*26*), and so the relative proportions or success of two groups during normal times may reverse during a sudden crisis. Nonetheless, the results of our rates and disparity study are consistent with at least two explanations: i) crurotarsans died out by chance, despite their larger range of morphospace and similar evolutionary rates to dinosaurs; ii) dinosaurs prevailed because of one or several key adaptations. The second suggestion is difficult to entertain because dinosaurs and crurotarsans lived side by side for 30 million years, and crurotarsans occupied more morphospace and were often more abundant and

diverse than dinosaurs. It is likely that dinosaurs were the beneficiaries of two mass extinction events, and some good luck.

References and Notes

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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S4

Tables S1 to S29

References

Figure Captions

Fig. 1. Phylogenetic relationships and morphospace occupation for Triassic archosaurs.
A: Framework phylogeny for Triassic crurotarsans (*13*) scaled to the Triassic time scale
(*13*). Numbers on the time scale refer to millions of years before present; gray bars
represent the observed durations of major lineages; vertical dotted lines denote two
hypothesized extinction events (CNEE, TJEE); arrowheads indicate lineages that
survived the TJEE. **B**: Empirical morphospace for Triassic archosaurs, based on the first
two principal coordinates (see SOM). Symbols: large open circles=dinosaurs;
ovals=pterosaurs; squares=poposauroids; hexagons=phytosaurs; stars=aetosaurs;
x=crocodylomorphs; small circles= "rauisuchids"; large closed circles=non-dinosaurian
dinosauromorphs, *Scleromochlus*.

Fig. 2. Plots of rate of morphological character evolution for archosaurs based on two metrics
(patristic dissimilarity per branch, dissimilarity/time, see SOM). Rates are based on
ACCTRAN character optimization, but DELTRAN gives nearly identical results (fig. S2).
Boxes represent the distribution of real data, with boxes encompassing 25-75 percentiles and
the whiskers representing 5-95 percentiles. Plots **A-B** express the evolutionary rates of
crurotarsans and dinosaurs (All C=all Triassic crurotarsans; All D=all Triassic dinosaurs;
CC, CD, NC, ND=crurotarsans and dinosaurs subdivided into Carnian and Norian taxa).
Plots **C-D** show disparity against time for all crown group archosaurs, and plots **E-F** show
disparity against time for both crurotarsans and dinosaurs. Dinosaurs exhibit higher

evolutionary rates than crurotarsans, but these are not significant (table S1). Rates for all archosaurs are either approximately constant (dissimilarity metric) or decrease from an Anisian high to a Norian low (dissimilarity/time metric, table S4-S5). Patterns within Crurotarsi and Dinosauria mirror the general pattern (table S6-S9).

Fig 3. Plots of archosaur morphological disparity based on two metrics (sums of ranges and variances, see SOM). Squares represent mean values and error bars denote 95% confidence intervals based on bootstrapping. Plots **A-B** express disparity of crurotarsans and dinosaurs (abbreviations as in Fig. 2). Plots **C-D** show disparity against time for all crown group archosaurs, and plots **E-F** show disparity against time for both crurotarsans and dinosaurs. Crurotarsans exhibit a significantly higher disparity than dinosaurs when all Triassic taxa (NPMANOVA: F=29.89, p<0.0001) and Carnian (F=13.36, p=0.0003) and Norian (F=20.59, p<0.0001) subdivisions are analyzed. Archosaur disparity increases over time and reaches a statistically-significant peak in the Norian (tables S23-24). Crurotarsan and dinosaur disparity generally increase over time but differences between individual time bins are not significant (tables S25-26).