The first 50 Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity

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The evolutionary radiation of dinosaurs in the Late Triassic and Early Jurassic was a pivotal event in the Earth's history but is poorly understood, as previous studies have focused on vague driving mechanisms and have not untangled different macroevolutionary components (origination, diversity, abundance and disparity). We calculate the morphological disparity (morphospace occupation) of dinosaurs throughout the Late Triassic and Early Jurassic and present new measures of taxonomic diversity. Crurotarsan archosaurs, the primary dinosaur 'competitors', were significantly more disparate than dinosaurs throughout the Triassic, but underwent a devastating extinction at the Triassic–Jurassic boundary. However, dinosaur disparity showed only a slight non-significant increase after this event, arguing against the hypothesis of ecological release-driven morphospace expansion in the Early Jurassic. Instead, the main jump in dinosaur disparity occurred between the Carnian and Norian stages of the Triassic. Conversely, dinosaur diversity shows a steady increase over this time, and measures of diversification and faunal abundance indicate that the Early Jurassic was a key episode in dinosaur evolution. Thus, different aspects of the dinosaur radiation (diversity, disparity and abundance) were decoupled, and the overall macroevolutionary pattern of the first 50 Myr of dinosaur evolution is more complex than often considered.

Keywords: Crurotarsi; Dinosauria; disparity; diversity; evolutionary radiation

1. INTRODUCTION

The evolutionary radiation of dinosaurs in the Late Triassic and Early Jurassic (230–175 Ma) was a keystone event in the Earth's history. During this time, dinosaurs originated from a small, carnivorous archosaur ancestor and diversified into many dozens of lineages and body types (Benton 2004), setting the stage for 110 Myr of subsequent dominance in terrestrial ecosystems. However, much about the tempo and macroevolutionary pattern of this radiation remains poorly known (Irmis *et al.* 2007;

Brusatte *et al.* 2008). Most previous studies have treated the rise of dinosaurs as a single event, driven by either competition with other vertebrate groups (Bakker 1971; Charig 1984) or opportunistic expansion after mass extinction events (Benton 1983; Olsen *et al.* 2002). In particular, extinctions at the Carnian–Norian and Triassic–Jurassic (TJ) boundaries may have opened new niches for dinosaurs to exploit (Benton 2004), but the detailed patterns of these events have yet to be investigated. Was one event more important than the other in shaping the dinosaur radiation? Were different events characterized by different macroevolutionary responses, such as increases in absolute faunal abundance, taxonomic diversity or morphological body plan variety? We investigate these questions by examining trends in diversity and disparity through the Triassic and Early Jurassic.

2. MATERIAL AND METHODS

Disparity quantifies morphological diversity (as opposed to taxonomic diversity), and generally measures the extent of morphospace occupation. We used a new dataset consisting of 76 taxa and 470 discrete skeletal characters to calculate numerical measures of disparity. The dataset is based on the previous database of Brusatte *et al.* (2008), and is expanded to include 17 new taxa (15 Early Jurassic and two Triassic) and 33 new characters. Measures of disparity were calculated across time for three large clades: Dinosauria; Crurotarsi; and Avemetatarsalia. Crurotarsan archosaurs, which include crocodylomorphs and extinct relatives such as phytosaurs, aetosaurs and 'rauisuchians', were heavily convergent with dinosaurs, occupied many of the same general ecological niches and are hypothesized to have been the main 'competitors' to dinosaurs (Nesbitt 2007; Brusatte *et al.* 2008). As dinosaurs and crurotarsans are not sister taxa, disparity was also calculated for the entire clade Avemetatarsalia (the 'stem bird' clade, which is the sister taxon to Crurotarsi and includes dinosaurs, pterosaurs and several close dinosaur relatives) in an effort to remove temporal and taxonomic biases. All taxa were binned into four intervals of the Middle Triassic–Early Jurassic based on observed occurrences. The choice of these intervals best follows Foote's (1994, p. 323) recommendation to choose divisions that 'represent a compromise between resolution and sample size…(and are) sufficiently coarse that nearly all generic first and last occurrences can be unambiguously assigned'. More specific details of sampling strategy can be found in the electronic supplementary material.

The dataset was used to derive a Euclidean distance matrix, which was then subjected to principal coordinates analysis (PCO). The PCO analysis produced a single taxon-defined empirical morphospace (figure 1), and distilled the original matrix into a smaller and more manageable number of variables (76 axes). Disparity metrics were calculated using the first 65 PCO axes, which encompass 90 per cent of the cumulative variance. Four disparity metrics were calculated: the sum and product of the ranges and variances on the 65 axes (Wills *et al.* 1994) using the software program RARE (Wills 1998). Range measures indicate the entire spread of morphological variation (morphospace size), whereas variance measures denote average dissimilarity among forms (spread of taxa in morphospace). Statistical significance was assessed with non-parametric multivariate analysis of variance (NPMANOVA), which tests for significant differences in the distribution of groups in morphospace, and by the overlap or non-overlap of 95% bootstrap confidence intervals (calculated by RARE, 1000 replicates).

Taxonomic diversity estimates, both observed and corrected by phylogeny, were compiled based on a reference to a supertree of dinosaurs (Lloyd *et al.* 2008).

3. RESULTS

We report one disparity metric, sum of ranges, as our favoured measure (following Wills *et al.* 1994; Wills 1998). However, the same pattern is recovered with the three additional measures (see the electronic supplementary material). Disparity of crurotarsans, dinosaurs and avemetatarsalians as a whole increased
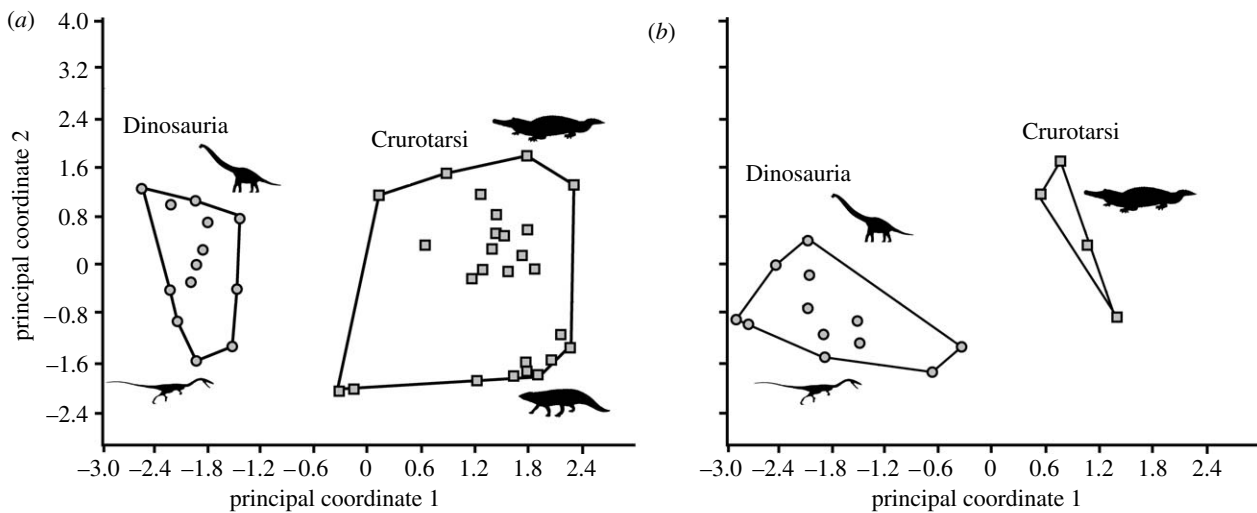
Figure 1. Morphospace occupation for dinosaurs and crurotarsans. (*a*) Late Triassic (Carnian–Norian) and (*b*) Early Jurassic (Hettangian–Toarcian). Triassic and Jurassic taxa are mapped onto a single two-dimensional morphospace, based on the first two principal coordinate axes recovered by the PCO analysis of the entire dataset. Dinosaur morphospace slightly increased in the Early Jurassic, whereas crurotarsan morphospace crashed after the TJ extinction. Note that dinosaur and crurotarsan morphospaces do not overlap: this is an artefact of the discrete character set, which has a phylogenetic structure. Importantly, those crurotarsans heavily convergent with dinosaurs (e.g. poposauroids, 'rauisuchids') are intermediate in morphospace between dinosaurs and the bulk of crurotarsans.

throughout the Triassic (figure 2). However, crurotarsan disparity crashed significantly in the Early Jurassic, after the near extinction of this clade (table 1*a*). Dinosaurs and avemetatarsalians, on the other hand, showed a large increase in disparity in the Norian but a small and non-significant increase in disparity in the Early Jurassic (table 1*a*). Crurotarsans were significantly more disparate than dinosaurs in the Late Triassic (Carnian–Norian), but dinosaurs were significantly more disparate than crurotarsans in the Early Jurassic (table 1*b*). Rarefaction curves show that these results are not heavily biased by sample size (see the electronic supplementary material). Visually, dinosaur morphospace shows only a slight expansion in the Early Jurassic whereas crurotarsan morphospace was greatly reduced (figure 1), in agreement with the quantitative metrics. Dinosaur diversity, both observed and implied, showed a steady increase from the Carnian to the Early Jurassic (figure 2*c*; table 2).

4. DISCUSSION

The most striking result of the disparity analysis is that dinosaur disparity remained essentially unchanged across the TJ boundary, despite the near total extinction of a crurotarsan clade that was hitherto significantly more morphologically diverse than dinosaurs. In other words, despite the heavy extinction of supposed competitors that shared many of the same niches and body plans, dinosaurs did not expand their morphospace in response. This finding contrasts with the suggestion of Olsen *et al.* (2002), who hypothesized that the TJ extinction of crurotarsans created a drop in competitive pressure that allowed Early Jurassic dinosaurs to radiate in a classical ecological release pattern. This hypothesis may hold true in a restricted sense, as Olsen *et al.* (2002) found evidence for an increase in theropod body size immediately after the TJ boundary within one formation, but there is no evidence for a

significant expansion in general dinosaur morphospace. Indeed, most major dinosaur body plans (theropods, 'prosauropods', true sauropods and ornithischians) are already known from the Late Triassic, albeit at varying levels of diversity and abundance.

Taxonomic diversity and morphological disparity, two different measures of biodiversity, did not follow the same trend early in dinosaur history. Although both measures were highest in the Early Jurassic, diversity increased steadily over time while disparity exhibited a major jump between the Carnian and the Norian. This is not unexpected, as several palaeontological studies have found disparity to peak early in the history of major clades, before peak diversity and out of step with overall diversity trends (Erwin 2007). Importantly, diversity and disparity do not show a simultaneous significant jump, as was the case in the mammalian radiation after the Cretaceous–Tertiary extinction (Alroy 1999).

Both the Carnian–Norian and TJ transitions appear to have played an important role in the dinosaur radiation, but each was characterized by different macroevolutionary changes. The Carnian–Norian transition was the major 'disparity event' in early dinosaur evolution, as morphospace greatly expanded across this boundary (figure 1*a*). The TJ transition, on the other hand, witnessed the major 'diversity event' and 'abundance event' in the radiation of dinosaurs. Not only was dinosaur diversity higher in the Early Jurassic than in the Late Triassic, but quantitative analyses of diversification have identified the Early Jurassic as the single most important time period for lineage diversification in this clade (Lloyd *et al.* 2008). In the same vein, compilations of faunal abundance show that dinosaur abundance varied greatly by formation and palaeolatitude in the Late Triassic, but, by the Early Jurassic, dinosaurs were the pre-eminent terrestrial vertebrates worldwide (Benton 1983). Coarse time bins, which are necessary
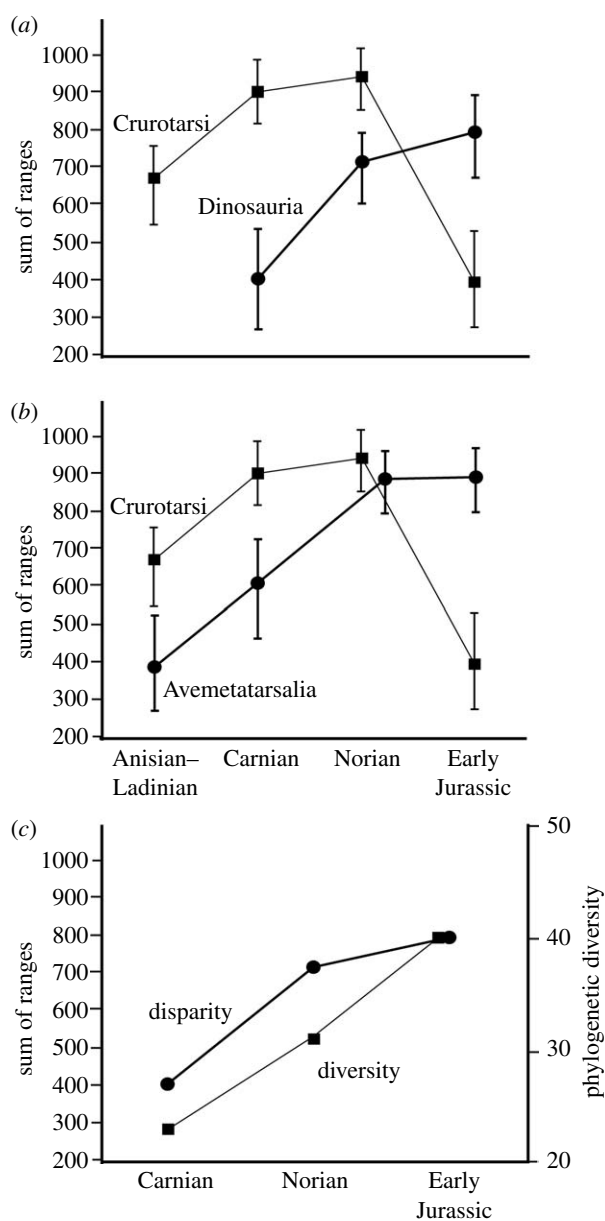
Figure 2. Morphological disparity for crurotarsans, dinosaurs and avemetatarsalians across the Triassic and the Early Jurassic. (*a*) Crurotarsans and dinosaurs, (*b*) crurotarsans and their sister clade, Avemetatarsalia, (*c*) disparity and diversity for dinosaurs. Error bars denote 95% bootstrap confidence intervals. Norian measures in (*b*) are shown offset to prevent the loss of information beneath overlapping error bars. Diversity count in (*c*) is a phylogenetic estimate based on total observed fossils plus implied ghost ranges.

to alleviate small sample sizes, make it difficult to ascribe these shifts as responses to mass extinctions. Nevertheless, it is probably not coincidental that major changes in dinosaur diversity, disparity and abundance followed two major extinctions of other vertebrate groups that probably shared niches with early dinosaurs (Benton 2004; Nesbitt 2007; Brusatte *et al.* 2008).

The dinosaur radiation is often treated—either explicitly or implicitly—as a single event, and is frequently explained by generalized mechanisms such as 'competition' or 'opportunism' (although see Butler *et al.* 2007 for an alternative view of

Table 1. Disparity statistical tests. (Disparity values compared by groups. Statistical test is NPMANOVA (10 000 replications), with test statistic F and probability p. First two numerical columns denote sample size for each group. (*a*) Disparity measures for crurotarsans and dinosaurs in the Late Triassic and Early Jurassic, with NPMANOVA testing whether there is a significant difference in disparity across the interval within each clade. (*b*) Comparison of crurotarsan and dinosaur disparity in the Late Triassic and Early Jurassic, with NPMANOVA testing whether one group is significantly more disparate than the other in each time bin. Asterisks denote significant results.)

clade	Carnian–Norian	Early Jurassic	F	p-value
(a) changes in disparity across the Triassic–Jurassic boundary by clade				
Crurotarsi	26	4	2.687	0.026[*]
Dinosauria	12	11	0.9309	0.4309
time	Crurotarsi	Dinosauria	F	p-value
(b) comparison of disparity between Crurotarsi and Dinosauria by time				
Late Triassic	26	13	11.72	<0.0001[*]
Early Jurassic	4	12	7.191	0.0005[*]

Table 2. Dinosaur diversity by time. (Taxonomic diversity measures: 'fossil' indicates observed fossil occurrences calculated from Weishampel *et al.* (2004); 'ghost' denotes ghost lineages implied by the supertree of Lloyd *et al.* (2008); and 'total' is a summation of observed and implied.)

	Carnian	Norian	Early Jurassic[a]	Early Jurassic[b]
fossil	9	22	26	27
ghost	14	9	8	13
total	23	31	34	40

[a] Early Jurassic estimates are calculated without inclusion of *Eshanosaurus*, a controversial derived theropod that, if correctly identified, drags several lineages into the Early Jurassic.
[b] Early Jurassic estimates are calculated with inclusion of *Eshanosaurus*, a controversial derived theropod that, if correctly identified, drags several lineages into the Early Jurassic.

ornithischian dinosaur evolution). Although these terms serve a broad descriptive purpose, the reality of the first 50 Myr of dinosaur history cannot be explained so easily. Evolutionary radiations have many components: lineage origination (mere presence or absence of groups); clade diversification (taxonomic diversity of groups); faunal abundance (numerical dominance of groups); and morphological disparity (morphospace occupation and body plan variety). These different components—each of which has been used in isolation to describe the dinosaur radiation—are clearly decoupled in this case. The evolutionary radiation of dinosaurs did not follow a simple pattern, but by the close of the Early Jurassic the age of dinosaur dominance was in full swing.

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