

Evaluating hypotheses for the early diversification of dinosaurs

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ABSTRACT: Many hypotheses have been proposed for the rise of dinosaurs, but their early diversification remains poorly understood. This paper examines the occurrences, species diversity and abundance of early dinosaurs at both regional and global scales to determine patterns of their early evolutionary history. Four main patterns are clear: (1) sauropodomorph dinosaurs became abundant during the late Norian–Rhaetian of Gondwana and Europe; (2) Triassic dinosaurs of North America have low species diversity and abundance until the beginning of the Jurassic; (3) sauropodomorphs and ornithischians are absent in the Triassic of North America; and (4) ornithischian dinosaurs maintain low species diversity, relative abundance and small body size until the Early Jurassic. No one hypothesis fully explains these data. There is no evidence for a Carnian–Norian extinction event, but sauropodomorphs did become abundant during the Norian in some assemblages. No clear connection exists between palaeoenvironment and early dinosaur diversity, but environmental stress at the Triassic–Jurassic boundary is consistent with changes in North American dinosaur assemblages. Elevated growth rates in dinosaurs are consistent with the gradual phyletic increase in body size. This study demonstrates that early dinosaur diversification was a complex process that was geographically diachronous and probably had several causes.



KEY WORDS: Dinosauromorpha, Early Jurassic, Late Triassic, Ornithischia, Sauropodomorpha, Theropoda

“Although many pages have been written discussing the mystery of the extinction of the dinosaurs, almost as much uncertainty surrounds their origin. . .” (Cox 1976)

Dinosaurs were one of the most diverse terrestrial vertebrate clades of the Mesozoic Era, and they remain extremely successful today as the most speciose tetrapod clade (birds). The origin and early diversification of dinosaurs remains poorly understood. Though the past 30 years have seen a renewed interest in the early evolutionary history of dinosaurs, little consensus has emerged on the tempo and mode of early dinosaur diversification. The basic question remains: among the terrestrial tetrapod clades present in the Triassic, why was it dinosaurs that diversified and became so successful during the Mesozoic, relative to other contemporary groups? In addition, what was the pace of this diversification, and how does it relate to several possible mass extinctions during and at the end of the Late Triassic?

The modern study of dinosaur origins largely begins with Romer’s (1966, 1970) recognition that Triassic terrestrial vertebrate assemblages could be divided into three main time intervals: zone A, Early Triassic assemblages dominated by carnivorous cynodonts; zone B, Middle Triassic assemblages dominated by ‘gomphodont’ cynodonts; and a Late Triassic zone C dominated by dinosaurs and other archosaurs. Romer considered the Upper Triassic Ischigualasto Formation to be part of zone B, in which early dinosaurs are present but rare, and many of his zone C assemblages have since been reassigned to the Early Jurassic (e.g., Olsen & Galton 1977, 1984). Nonetheless, Romer’s divisions still largely hold up to our knowledge of Triassic faunas, and they were important in recognising that by the end of the Late Triassic, dinosaurs were

an important and abundant component of many vertebrate faunas.

This apparent decline in synapsids and concurrent diversification of dinosaurs led Bakker (1968, 1971, 1972, 1975) to propose that dinosaurs had outcompeted basal synapsids over longer timescales (>10 million years). He postulated that the dinosaurs had a competitive advantage over synapsids because they had an erect stance, parasagittal gait and high body temperatures. Bakker hypothesised that these features made dinosaurs more biomechanically and energetically efficient, and allowed them to evolve larger body size than their basal synapsid competitors (Bakker 1971, 1975). In contrast, Benton (Tucker & Benton 1982; Benton 1983, 1986a, b) argued that dinosaurs only became dominant components of their respective faunas after the extinction of several basal synapsid groups and rhynchosaurs at the Carnian–Norian boundary. He thus proposed that these groups were not in competition, and that dinosaurs radiated opportunistically after the extinction event.

Bonaparte (1982) reviewed the faunal succession of the South American Triassic and concluded that herbivorous synapsids went extinct during the Late Triassic because of the evolution of archosaur lineages that were herbivorous and/or had a ‘superior’ locomotory apparatus. He also proposed that increasing aridity played a role in the extinction of the synapsid groups, and that Triassic floral turnover generated significant new selective pressures among synapsids and archosaurs. Bonaparte (1984) reinforced these conclusions in his study of archosaur locomotion by noting the success (this was vaguely defined; presumably referencing taxonomic diversity in some way) of an upright stance in ‘rauisuchians’ and early dinosaurs.

Charig (1984) reviewed hypotheses about the origin and early diversification of dinosaurs. Although he was sceptical of

Bakker's claims of endothermy in dinosaurs, Charig agreed that dinosaurs outcompeted basal synapsids during the Late Triassic, principally as a result of their locomotor specialisations. In contrast to Bakker (1968, 1971, 1975), Charig (1984) viewed the success of dinosaurs as only one part of a larger competitive scenario between archosaurs and therapsid synapsids during the Triassic. Although he agreed there was probably little direct competition between dinosaurs and synapsids, Charig (1984) rejected Benton's hypothesis because he felt there was ample evidence that archosaurs and therapsids co-existed in the same places and times throughout the Triassic, and that these two groups therefore at least indirectly competed with each other. Thus, by re-casting the argument as an archosaur *vs.* therapsid comparison rather than a dinosaur *vs.* therapsid comparison, Charig was able to discard Benton's argument that dinosaurs and therapsids rarely, if ever, co-existed in space and time.

In the 1960s and 1970s, new discoveries from the Ischigualasto Formation of northwestern Argentina demonstrated that both ornithischian and saurischian dinosaurs had evolved by the early Late Triassic, and that they probably formed a monophyletic group (e.g., Reig 1963; Casamiquela 1967; Bonaparte 1976). Bonaparte (1976) further proposed that the evolution of herbivory and an upright stance in ornithischian dinosaurs allowed them to exploit previously un-filled ecological space in the Late Triassic. Further discoveries in the 1990s confirmed the importance of these taxa for understanding early dinosaur evolution (Serenó & Novas 1992; Sereno *et al.* 1993), and new radioisotopic data confirmed the Ischigualasto Formation as the oldest known dinosaur-bearing formation in the world (Rogers *et al.* 1993). These discoveries suggested that dinosaur diversification began well before they were species-rich or abundant in individual vertebrate assemblages (Serenó & Novas 1992). Largely on the basis of this evidence, Sereno (1997) concluded that an opportunistic model (cf. Benton 1983) best fitted the available data because there was such a long delay between the initial diversification and the rise of dinosaurs as a dominant component of their ecosystems. More recently, using evidence from the Newark Supergroup of eastern North America, Olsen *et al.* (2002) proposed that this delay lasted until the Triassic–Jurassic boundary. On the basis of footprint assemblages, Olsen and colleagues demonstrated a sudden increase in dinosaur body size and abundance immediately after the end-Triassic extinction. At the Triassic–Jurassic boundary, they documented evidence of an iridium anomaly and fern pollen spike, suggesting that an impact may have caused the end-Triassic extinction, which subsequently allowed dinosaurs to opportunistically diversify during the Early Jurassic (Olsen *et al.* 2002). There is new compelling evidence that the end-Triassic extinction was related to flood volcanism of the Central Atlantic Magmatic Province (CAMP) (Schoene *et al.* 2010; Whiteside *et al.* 2010), but this does not alter the patterns observed by Olsen *et al.* (2002).

Recent attention has also focused back on dinosaur physiology. Padian *et al.* (2001, 2004; de Ricqlès *et al.* 2003) documented that dinosaur growth rates are consistently higher than their crocodile-line archosaur counterparts. Padian *et al.* (2004) proposed that this potential for elevated growth rates allowed dinosaurs to quickly achieve a larger body size during ontogeny, and that it may have played a role in the success of early dinosaurs during the Late Triassic and Early Jurassic. These authors also documented high growth rates in pterosaurs, so this trait could be a synapomorphy of bird-line archosaurs (i.e., ornithodirans) or may have evolved separately in these two clades (Padian *et al.* 2001, 2004).

A renewed interest in early dinosaur macroevolutionary patterns has led to investigations of archosaur and early dinosaur diversity, disparity and morphological evolutionary rates (Brusatte *et al.* 2008a, b, 2011). These studies have recast the test of competitive hypotheses as a comparison between dinosaurs and their relatives (ornithodirans, or bird-line archosaurs) and crocodylomorphs and their relatives (pseudosuchians/crurotarsans, or crocodile-line archosaurs). Brusatte *et al.* (2008a, b, 2011) conclude that Triassic dinosaurs did not overlap the morphospace of contemporaneous pseudosuchians, and were not special in terms of rate of diversification or morphological change. They observed that diversity and disparity of pseudosuchians decreased across the Triassic–Jurassic boundary, suggesting that differential survival during the end-Triassic extinction was a factor in early dinosaur success (Brusatte *et al.* 2008a, b). These and other authors (Ezcurra 2010b; Langer *et al.* 2010) have proposed a two-step model for dinosaur origins, with an initial diversification and increase in species richness during the late Carnian and/or early Norian, and a later diversification and increase in abundance after the end-Triassic extinction.

New fossil discoveries continue to change our understanding of dinosaur origins. It is now known that basal dinosauromorphs persisted well into the Late Triassic (Dzik 2003; Irmis *et al.* 2007a) and coexisted with dinosaurs for an extended interval of 15–20 million years (Irmis *et al.* 2007a; Nesbitt *et al.* 2009a). Dzik *et al.* (2008) documented the unexpected co-occurrence of dicynodont synapsids and dinosaurs in the latest Triassic of Poland; previously, Benton had hypothesised (e.g., Benton 1983, 1986a, 1994) that dicynodonts became extinct at the Carnian–Norian boundary. These recent studies have stressed the importance of local and regional studies of faunal assemblages; it is now clear that contemporaneous Late Triassic terrestrial vertebrate assemblages vary significantly in taxonomic composition, diversity and abundance (Irmis *et al.* 2007a; Irmis 2008; Dzik *et al.* 2008; Nesbitt *et al.* 2009b; Ezcurra 2010a).

The goal of the present study is to evaluate proposed hypotheses for the early diversification of dinosaurs using a variety of methods with the newest available data. New discoveries have substantially changed our understanding of many early Mesozoic terrestrial vertebrate assemblages (e.g., Irmis *et al.* 2007a; Dzik *et al.* 2008; Nesbitt *et al.* 2009b), and new geochronologic data have also changed our understanding of the ages of these records (e.g., Muttoni *et al.* 2004; Furin *et al.* 2006; Irmis & Mundil 2008, 2010). A variety of detailed phylogenetic studies have focused on basal dinosaurs, clarifying understanding of the early evolutionary history of these groups (Smith *et al.* 2007; Yates 2007a, b; Butler *et al.* 2008; Irmis 2008; Nesbitt *et al.* 2009b, 2010). Recent work on the origin and early diversification of dinosaurs has not fully incorporated these new data in terms of possible taxon sampling (e.g., Benton 2004, 2006; Brusatte *et al.* 2008a, b); This is the aim of the present paper. In addition, hypotheses will be evaluated explicitly in regional contexts to avoid conflating biogeographic, palaeoecological and biostratigraphic patterns.

1. Materials and methods

1.1. Phylogeny

The phylogeny used in this study (Figs 1, 2) is based on recent phylogenetic hypotheses for basal dinosauromorphs (Irmis 2008; Nesbitt *et al.* 2010), basal ornithischians (Butler *et al.* 2008), basal sauropodomorphs (Smith & Pol 2007; Yates 2007a, b; Yates *et al.* 2010) and basal theropods (Smith *et al.* 2007; Nesbitt *et al.* 2009b; Benson 2010). Where these

studies overlapped, they were in nearly unanimous agreement, so formal supertree methods to combine the trees were not necessary. *Euparkeria*, *Smilosuchus*, *Revueltosaurus*, *Riojasuchus*, *Effigia*, *Postosuchus* and *Hesperosuchus* were used as outgroups for the comparative analyses (i.e., body size evolution). Because the analyses in this present study required a fully resolved tree (i.e., no hard polytomies), coelophysid interrelationships were resolved using data from Tykoski (2005a; Tykoski & Rowe 2004), and the polytomy of Eusauropoda in Yates (2007a, b) was resolved with data from Wilson (2002). A variety of Middle and Upper Jurassic taxa were included to ensure that the phylogeny captured all ghost lineages that extended back to the Early Jurassic.

Several taxa (e.g., Kutty *et al.* 2007; Martínez 2009; Barrett 2009) were not included in the phylogeny because either their phylogenetic position is poorly understood, they have not been included in a phylogenetic analysis, or were included in phylogenetic analyses whose results differ significantly from the consensus of more recent results. So as not to bias the analyses, these taxa were also left out of taxonomic diversity estimates (see below).

1.2. Age assignments

Branch lengths of the phylogeny were calculated using the geologic ages of the tips of the tree (i.e., the individual terminal taxa). Because the ages of most Triassic terrestrial vertebrate assemblages are poorly constrained (e.g., Irmis *et al.* 2010), the age of each taxon was only estimated to stage level, with the exception of the Norian, which was split into two 10 million-year bins. The placement of taxa in a particular stage was based on available age data in the literature. Stratigraphic consistency was a guiding factor. For example, the lower Elliot Formation of southern Africa is typically assigned to the Norian stage (e.g., Knoll 2004) based on broad vertebrate biostratigraphic correlation to Europe and South America. However, the Triassic–Jurassic boundary is placed in the middle of the Elliot Formation, so it seemed most parsimonious to assign the lower Elliot taxa to the Rhaetian and the upper Elliot taxa to the Hettangian, because these two stages are immediately before and after the Triassic–Jurassic boundary. The Los Colorados Formation taxa were assigned to the late Norian because the top of the underlying Ischigualasto Formation is clearly early Norian in age (Shipman 2004; Irmis & Mundil 2008, 2010), and the Los Colorados vertebrate assemblage is from the top third of the formation (i.e., it does not come from strata that directly overlie the Ischigualasto Formation).

Because precision is rarely available below the stage level, taxa were placed at the midpoint of each stage (one exception is *Lophostropheus*, which is placed at the Triassic–Jurassic boundary; see Ezcurra & Cuny 2007). For the few taxa that have precise radioisotopic ages, this midpoint placement was consistent with the available data. For example, *Eoraptor* and *Herrerasaurus* are placed at 230.5 Ma, and come from sediments that overly a layer dated at 231.4 Ma (Rogers *et al.* 1993; Furin *et al.* 2006); *Chindesaurus* and *Dromomeron romeri* are placed at 213 Ma, nearly identical to their radioisotopic age constraints (Riggs *et al.* 2003; Mundil *et al.* 2008; Irmis & Mundil 2010). Stage durations were converted to a numerical scale using the geologic timescale of Gradstein *et al.* (2004) including the important modifications of Muttoni *et al.* (2004), Furin *et al.* (2006) and Schaltegger *et al.* (2008); this yields stage ages and durations similar to those values presented by Walker & Geismann (2009).

Two approaches were used to time-calibrate the phylogeny. Because the fossil record is incomplete, yielding significant ghost lineages, not all nodes are constrained by a minimum age

from a terminal taxon of one of the branches, so there can be significant temporal uncertainty in assigning an age to these nodes and associated branches. One phylogeny (Fig. 1) was internally calibrated so that the time represented in a particular ghost lineage was evenly spread across unconstrained nodes and branches, following the method of other recent studies (Ruta *et al.* 2006; Brusatte *et al.* 2008a; Nesbitt *et al.* 2009b). For this calibration, the age of Suchia was set to the Olenekian, following new data on the age of this clade (Nesbitt *et al.* 2011). A second time-calibrated phylogeny (Fig. 2) took a more literal approach to the fossil record, by assigning a minimal branch length of 0.1 Ma to unconstrained internodes of ghost lineages.

1.3. Calculating diversity

These time-calibrated phylogenies were used to estimate taxonomic and phylogenetic diversity metrics for basal dinosauro-morphs, ornithischians, sauropodomorphs, theropods, all dinosauro-morphs and all dinosaurs (Figs 3, 4). Phylogenetic diversity is useful because it corrects for ghost lineages (Norell 1992; Fara 2004), and this metric was calculated for both the smoothed and strict temporally-calibrated phylogenies. Because only three taxa (*Heterodontosaurus*, *Plateosaurus engelhardti* and *Massospondylus carinatus*) cross time bin boundaries, methods using only boundary-crossing taxa were impractical. Graphs of diversity through time were scaled to the relative duration of each stage interval. Taxonomic diversity was calculated from the same dataset as phylogenetic diversity, meaning that taxa not included in the phylogeny were completely absent from both diversity estimates. The benefit of this decision is that the taxonomic and phylogenetic diversity estimates are directly comparable in that they derive from exactly the same taxa. The limitation is that the analysis obviously does not include all early dinosaur diversity, and could be substantially biogeographically biased for regions where most taxa are very poorly known and have not been revised or included in modern phylogenetic studies (e.g., India).

The geologic record clearly influences the observed diversity of dinosaurs (e.g., Upchurch & Barrett 2005; Barrett *et al.* 2009); therefore, diversity estimates were compared to the number of dinosauro-morph-bearing geologic formations in the taxon dataset for each time bin (Fig. 3). Because these analyses were restricted to taxa that could be placed in the phylogeny, it would be overly conservative to include geologic dinosauro-morph-bearing formations whose taxa were not in the taxonomic dataset, and this would also assume that the lack of certain groups in certain areas was strictly a sampling problem. Thus, the number of dinosauro-morph-bearing formations pertains directly to those formations sampled by the taxa in the phylogeny. Diversity values were then normalised (i.e., divided) by the number of formations as a first-order correction for geologic bias in the dataset (Fig. 4). This method is less refined than measuring outcrop area (e.g., Smith & McGowan 2007) or packages of continuous stratigraphic sequences (e.g., Peters 2005), but it is a clear first step in correcting diversity estimates for biases in the geologic record that will undoubtedly be refined in future iterations.

1.4. Reconstructing body size

Body size was estimated using femur length as a proxy measurement. Although femur allometry scales differently across dinosaur clades (e.g., Bybee *et al.* 2006), it remains a good proxy for overall body size (Anderson *et al.* 1985; Christiansen & Fariña 2004). Most importantly, it avoids the large uncertainties associated with estimating extinct dinosaur

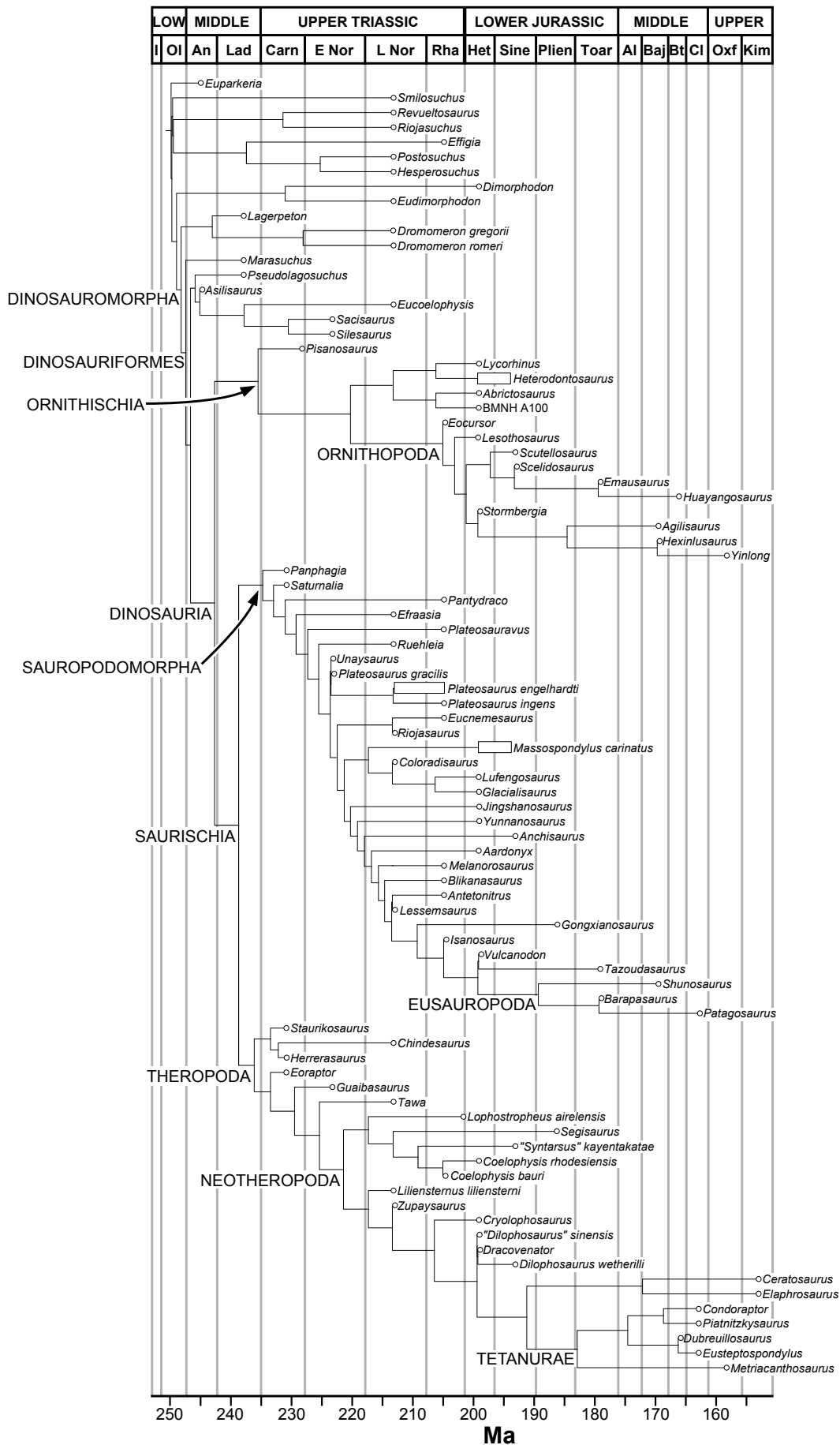


Figure 1 Time-calibrated phylogeny of Dinosauria used in this study. Branch length values are smoothed across unconstrained nodes. See text for phylogeny sources. Abbreviations: Al=Aalenian; An=Anisian; Baj=Bajocian; Bt=Bathonian; Carn=Carnian; Cl=Callovian; E Nor=early Norian, Het=Hettangian; I=Induan; Kim=Kimmeridgian; L Nor=late Norian; Lad=Ladinian; OI=Olenekian; Oxf=Oxfordian; Plien=Pliensbachian; Rha=Rhaetian; Sine=Sinemurian; Toar=Toarcian.

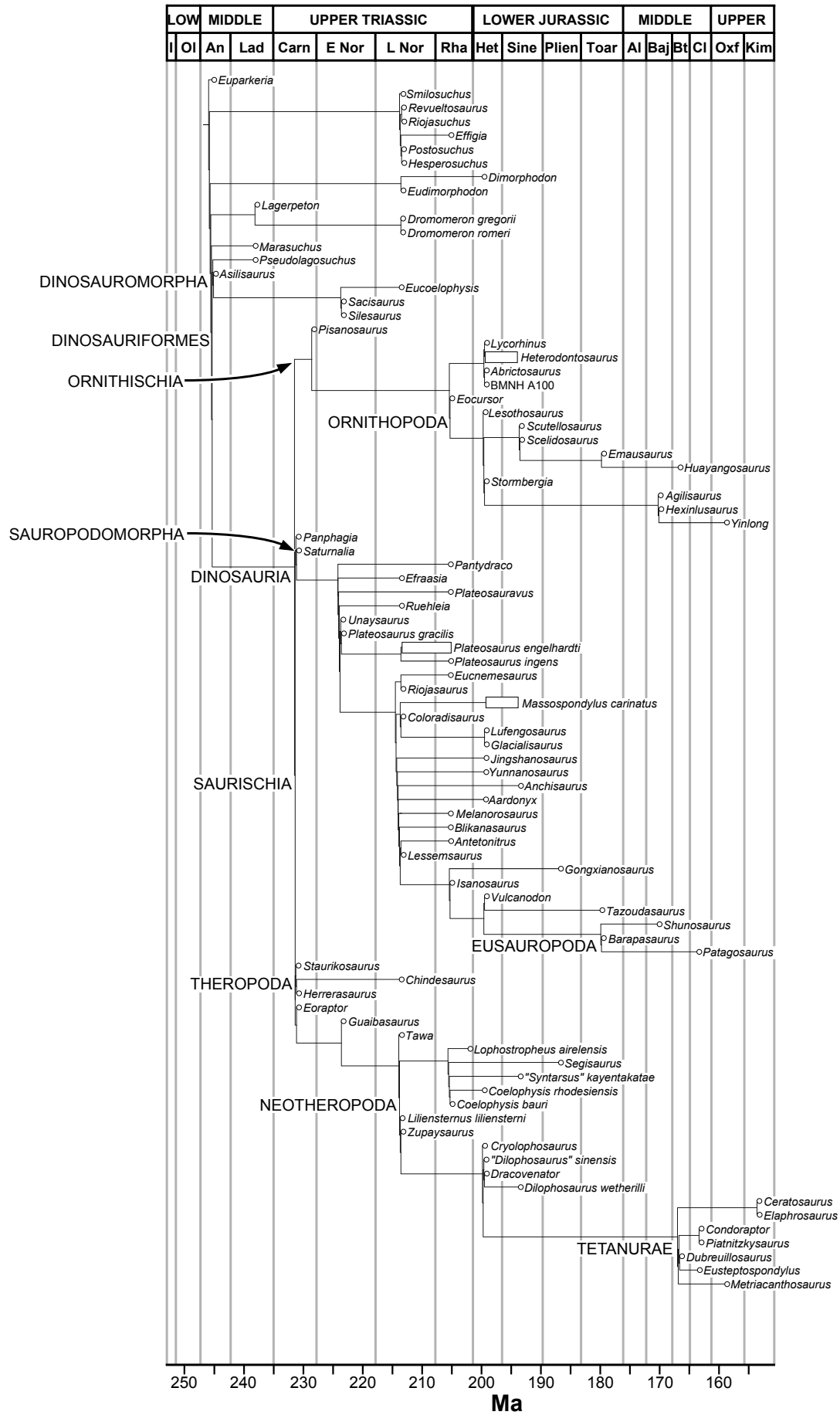


Figure 2 Strict time-calibrated phylogeny of Dinosauria where unconstrained branches are set to minimal length (0.1 Ma). Abbreviations: Al=Aalenian; An=Anisian; Baj=Bajocian; Bt=Bathonian; Carn=Carnian; Cl=Calloviaian; E Nor=early Norian; Het=Hettangian; I=Induan; Kim=Kimmeridgian; L Nor=late Norian; Lad=Ladinian; OI=Olenekian; Oxf=Oxfordian; Plien=Pliensbachian; Rha=Rhaetian; Sine=Sinemurian; Toar=Toarcian.

body mass (e.g. Seebacher 2001; Alexander 2006). Because the raw values did not conform to a normal distribution, all data were log-transformed prior to analysis.

Body size was reconstructed across both the smoothed and strict time-calibrated phylogenies using phylogenetic generalised least-squares (pGLS) regression (Pagel 1997; Garland & Ives 2000). Nodal reconstructions of ancestral states were calculated using a maximum likelihood model in COMPARE v4.6b (Martins 2004). Because pGLS can be implemented using maximum likelihood, it allows the testing of explicit models of evolution and the estimation of error associated with individual ancestral state values. For each phylogeny, the likelihood of a directional evolution two parameter model *vs.* a one parameter Brownian motion model was tested using BayesTraits v1.0 (Pagel 2006). This software also allows the variance of several parameters related to changes of the trait(s) along individual branches, which can help test hypotheses about trait evolution (e.g., stasis *vs.* gradualism, impact of phylogenetic history) across the tree (Pagel 1999). Models were evaluated using a likelihood ratio test. Each analysis was run using ten maximum likelihood attempts per tree.

2. The shape of early dinosaur diversity

2.1. Global species diversity

The global diversity of early dinosaurs has essentially the same shape as for all dinosauromorphs (Fig. 3). Diversity increases steadily from the Ladinian (late Middle Triassic) through the late Norian. There is a substantial decrease in diversity beginning in the Sinemurian (middle Early Jurassic) that continues through the end of the Early Jurassic. Taxonomic and phylogenetically corrected diversity indices both show essentially the same pattern; the only difference is that the absolute values of phylogenetic diversity are higher because this metric accounts for ghost lineages. The most notable pattern in the presented data is the lack of a change in origination rate across the Carnian–Norian and Triassic–Jurassic boundaries, with a possible decrease across the latter. These data suggest a linear increase in dinosauromorph diversity through the late Norian rather than a sudden radiation after the Carnian–Norian or Triassic–Jurassic boundaries. Correcting for number of formations (Fig. 4) shows a more complicated trend, where normalised diversity was at its highest early in the history of Dinosauromorphs and Dinosauria, and then generally declining through time. One exception is a clear spike in diversity for all indices across the Triassic–Jurassic boundary, but the steep drop in diversity across the Hettangian–Sinemurian boundary is still present.

Examination of the diversity of individual groups reveals similar trends. The peak diversity of non-dinosaur dinosauromorphs (Fig. 3) occurred during the Anisian–Ladinian, though they maintained a significant phylogenetic and taxonomic diversity through the late Norian. In terms of raw species diversity, sauropodomorph dinosaurs have the highest diversity of any clade during the Late Triassic (Figs 3, 4). The overall shape of their diversity curve mirrors that for all dinosaurs even when normalising by number of formations (Figs 3, 4), but one difference for sauropodomorphs is that normalised diversity does not spike across the Triassic–Jurassic boundary. Theropod dinosaurs show an initial peak of diversity in the Carnian that represents herrerasaurs. Their overall diversity peaks in the late Norian, spikes slightly across the Triassic–Jurassic boundary, and then decreases in the middle Early Jurassic (Fig. 3). Normalised diversity shifts the overall peak to the early Norian, and shows a modest spike across the Triassic–Jurassic boundary. Ornithischian dinosaurs

possess a significantly different pattern. Their species diversity during the Late Triassic is low and flat; diversity peaks sharply in the Hettangian, and then decreases in the later Early Jurassic like other groups (Fig. 3); this pattern is even starker for normalised diversity (Fig. 4). The Hettangian peak of Ornithischia largely reflects the relative high diversity of ornithischians in the upper Elliot Formation, which contains at least six taxa (Butler 2005; Irmis & Knoll 2008, table 1).

In all of the diversity plots, there is a clear decrease in diversity starting in the Sinemurian (middle Early Jurassic) even when accounting for number of formations (Fig. 4), and a similar trend is also apparent in other recent studies of dinosaur diversity (Upchurch & Barrett 2005; Lloyd *et al.* 2008; Barrett *et al.* 2009; Butler *et al.* 2011). This seems unusual, given that dinosaurs were quite diverse and abundant throughout the Jurassic and Cretaceous (e.g., Lloyd *et al.* 2008). Given that the Hettangian, Sinemurian and Pliensbachian bins all have a shorter duration than the Ladinian, Carnian, early Norian and late Norian bins, a reasonable hypothesis would be that the lowered diversity estimates are a result of shorter time bins (a temporal equivalent of the species-area effect). However, regressions of diversity versus bin duration reveal an insignificant relationship ($r^2 < 0.01$). Taxon sampling can also be ruled out, because care was taken to sample all Middle and Late Jurassic lineages in recent phylogenies (Smith *et al.* 2007; Yates 2007a, b; Butler *et al.* 2008; Benson 2010; Yates *et al.* 2010) that might extend back into the Early Jurassic.

The most likely explanation is a combination of poorly sampled formations, taphonomic bias, and rock outcrop area/volume. During the Early Jurassic, increasingly arid conditions in some areas created unfavourable conditions for dinosaur body fossil preservation. For example, the Pliensbachian Navajo Sandstone in the southwestern US preserves a meagre body fossil record (e.g. Irmis 2005b), because it is dominated by thick aeolian deposits. A similar situation is found in the Sinemurian Clarendon Formation (e.g. Bordy & Catuneanu 2002). Rock outcrop area and volume also have a large effect on palaeodiversity estimates (e.g. Peters 2005; Smith & McGowan 2005, 2007), and these values do not scale directly with number of geologic formations. A variety of factors substantially reduced available dinosaur-bearing outcrop beginning in the Pliensbachian. In southern Africa, the sedimentary record was terminated by the extrusion of the Drakensberg volcanics during the Pliensbachian (Jourdan *et al.* 2005). Available terrestrial sedimentary rocks are scarcer in general because of the beginning of a long-term global transgression that lasted through the Middle Jurassic (Miller *et al.* 2005). Those fossiliferous formations that date to the Pliensbachian–Toarcian are poorly sampled; many of them have only recently been systematically prospected for vertebrates (e.g., Allain & Aquesbi 2008). Thus, the drop in diversity that began in the Sinemurian (Fig. 3) is unlikely to be a palaeoecological pattern; rather, in agreement with previous studies (e.g., Upchurch & Barrett 2005; Lloyd *et al.* 2008; Barrett *et al.* 2009; Butler *et al.* 2011), it is a combination of taphonomic biases and reduced outcrop area.

A general factor complicating the interpretation of these global diversity estimates is that diversity is not equally spread across Pangaea for each time bin. Separating diversity values into regional groups demonstrates that diversity levels from the Carnian and Norian are largely driven by the South American record, and Rhaetian, Hettangian and Sinemurian taxa are mainly from southern Africa (Fig. 5). The late Norian and Rhaetian are the only time bins where diversity values are comprised of taxa from at least three regions (Fig. 5).

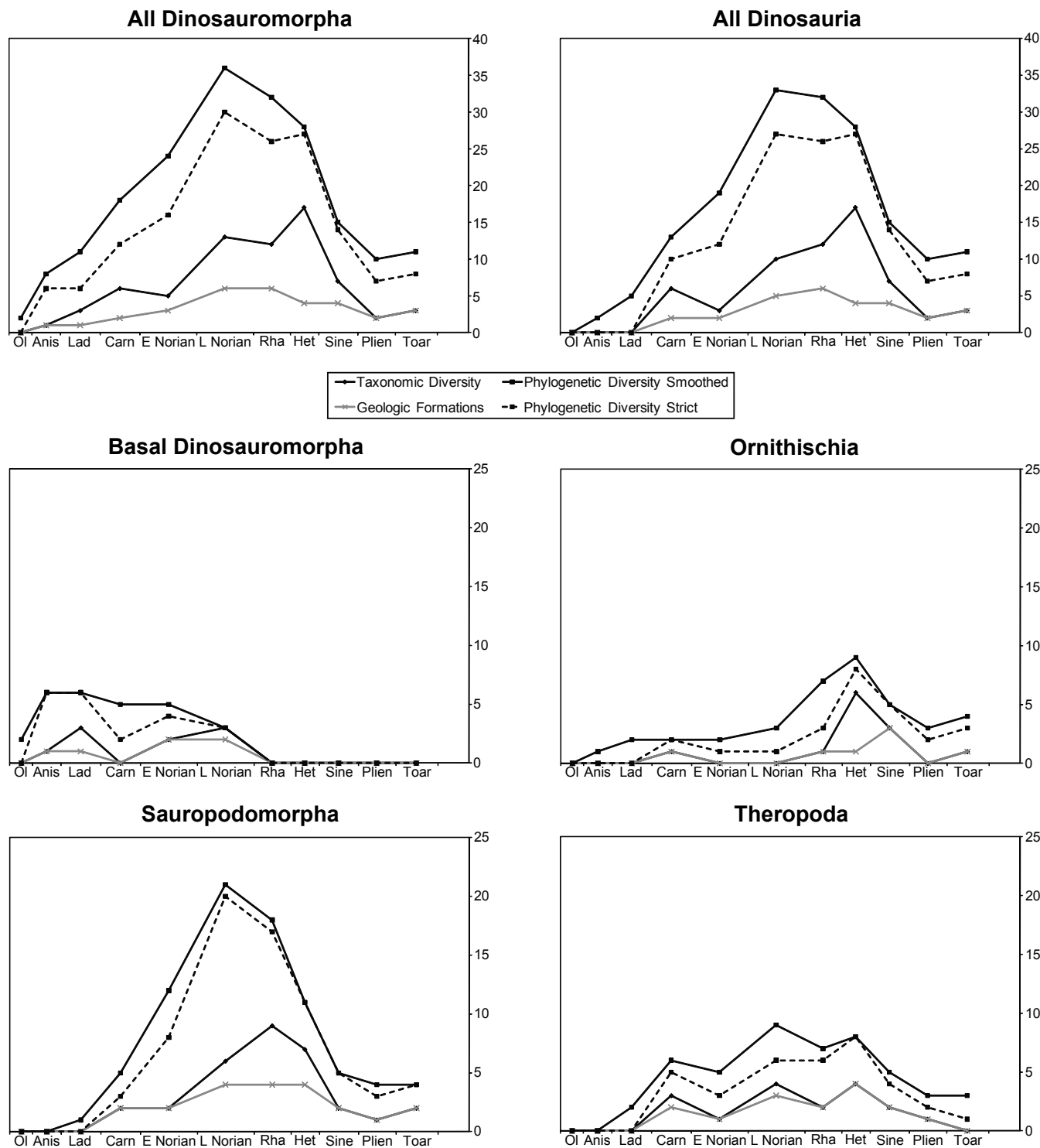


Figure 3 Early Mesozoic species diversity patterns for all dinosauromorphs, all dinosaurs, basal dinosauromorphs, Ornithischia, Sauropodomorpha and Theropoda, based on the phylogenies in Figures 1 and 2. Abbreviations: Anis=Anisian; Carn=Carnian; E Norian=early Norian; Het=Hettangian; L Norian=late Norian; Lad=Ladinian; Ol=Olenekian; Plien=Pliensbachian; Rha=Rhaetian; Sine=Sinemurian; Toar=Toarcian.

2.2. Regional diversity

Even though most landmass was concentrated in the supercontinent Pangaea during the early Mesozoic, many Late Triassic and Early Jurassic terrestrial vertebrate assemblages were biogeographically distinct (Romer 1970; Shubin & Sues 1991; Ezcurra 2010a). New discoveries (e.g., Irmis *et al.* 2007a; Dzik *et al.* 2008; Nesbitt *et al.* 2009b) and new radioisotopic age data (e.g., Irmis & Mundil 2008, 2010) have only reinforced this conclusion, and emphasise the importance of evaluating faunal change on a regional scale (e.g., Rogers *et al.* 1993;

Irmis 2008). This section reviews the early dinosauromorph and dinosaur record for a variety of early Mesozoic assemblages on a region-by-region basis. Both species diversity and relative abundance data are presented where possible, because both metrics are important for understanding early dinosaur diversification (e.g., Benton 1983, 1986b).

2.2.1. Argentina. The Triassic record of the Ischigualasto–Villa Unión Basin in northwestern Argentina is one of the main sources of data for understanding the origin and early diversification of dinosaurs. The Lower–Middle Triassic

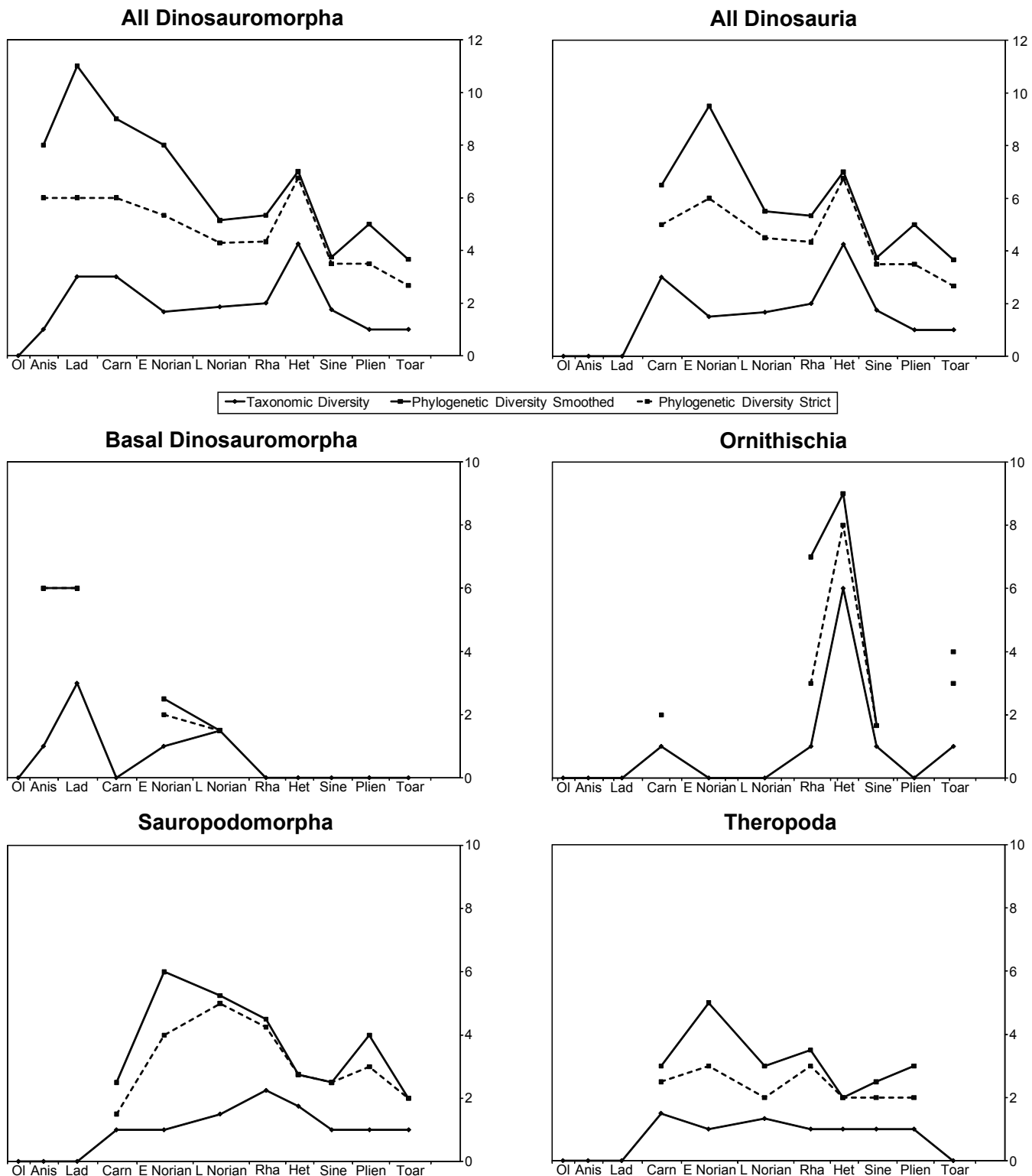


Figure 4 Early Mesozoic dinosauriform species diversity patterns normalised by number of dinosauriform-bearing formations. Abbreviations: Anis=Anisian; Carn=Carnian; E Norian=early Norian; Het=Hettangian; L Norian=late Norian; Lad=Ladinian; Ol=Olenekian; Plien=Pliensbachian; Rha=Rhaetian; Sine=Sinemurian; Toar=Toarcian.

Talampaya and Tarjados formations are unfossiliferous, but the Middle Triassic (Ladinian) Los Chañares Formation preserves a spectacular small tetrapod assemblage (Bonaparte 1997; Rogers *et al.* 2001). This assemblage includes several basal dinosauriforms, including the lagerpetid *Lagerpeton chanarensis* (Arcucci 1986; Sereno & Arcucci 1994a), the basal dinosauriform *Marasuchus lilloensis* (Sereno & Arcucci 1994b), and the silesaurid taxa *Pseudolagosuchus* and *Lewisuchus*, which may be synonymous (Arcucci 1987, 1997, 1998, 2005;

Nesbitt *et al.* 2007, 2009a, 2010; Irmis 2008). Although the Los Chañares assemblage is species rich, the early dinosauriform component is still relatively rare; cynodonts are by far the most common taxa, and basal archosauriforms are also common (Rogers *et al.* 2001, table 2).

The overlying Los Rastros Formation is traditionally assigned to the Ladinian (e.g. Bonaparte 1997; Rogers *et al.* 2001; Marsicano *et al.* 2007), but an early Carnian age is possible given that the overlying Ischigualasto Formation is

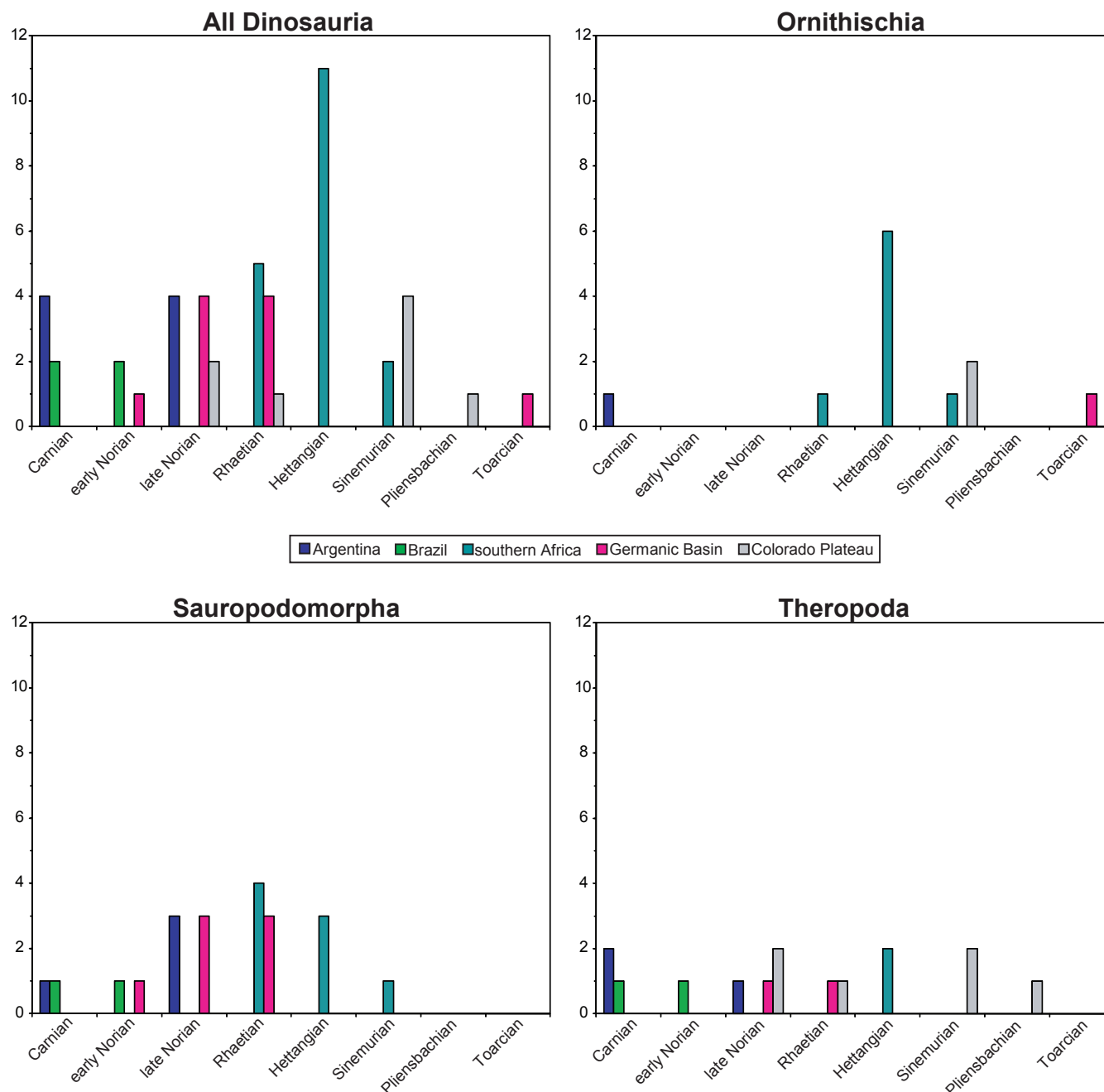


Figure 5 Early Mesozoic species diversity for major dinosaur-bearing regions.

now considered late Carnian–early Norian in age (Furin *et al.* 2006; Irmis & Mundil 2008, 2010). Although it does not preserve tetrapod body fossils, the Los Rastros Formation does preserve important lake-margin footprint assemblages (Marsicano *et al.* 2004, 2007; Mancuso & Marsicano 2008). These footprint horizons include abundant tridactyl prints (Marsicano *et al.* 2004, 2007), that traditionally would be assigned to Dinosauria. Unfortunately, this morphotype cannot be assigned to dinosaurs using apomorphy-based identifications, as at least some silesaurids possess a functionally tridactyl pes (Carrano & Wilson 2001; Dzik 2003; Marsicano *et al.* 2007; Nesbitt *et al.* 2007), but the Los Rastros assemblages are still important because they document the presence of abundant dinosauriforms during the late Middle or early Late Triassic.

The Ischigualasto Formation unconformably overlies the Los Rastros Formation (Stipanovic & Bonaparte 1972; Rogers *et al.* 1993, 2001; Currie *et al.* 2009). This unit is the oldest well-dated dinosaur-bearing formation in the world. Although

traditionally assigned to the early Carnian (e.g. Rogers *et al.* 1993, Gradstein *et al.* 2004), the re-calibration of an existing radioisotopic age from near the base of the Ischigualasto Formation (Rogers *et al.* 1993; Furin *et al.* 2006) and new ages from the top of the formation (Shipman 2004; Tabor *et al.* 2006) indicate that the strata are late Carnian–early Norian in age (~231–225 Ma). Most vertebrate fossils are from the lower third of the formation (Rogers *et al.* 1993; Currie *et al.* 2009), and the assemblage contains at least two basal theropod dinosaurs, *Eoraptor* and *Herrerasaurus* (Serenó & Novas 1992; Sereno *et al.* 1993; Irmis 2008) and two sauropodomorphs, *Panphagia* (Martinez & Alcober 2009) and *Chromogisaurus* (Ezcurra 2008, 2010b). The earliest known ornithischian dinosaur, *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976; Irmis *et al.* 2007b), is also from the Ischigualasto Formation, but it is younger than the theropods because it is found in the middle of the formation (Rogers *et al.* 1993). A new theropod dinosaur has recently been reported from the Ischigualasto Formation (Martinez *et al.* 2008), but has not been formally

described. Although the Ischigualasto dinosaur assemblage is species rich, it is a minority component in relative abundance. The lower Ischigualasto Formation is dominated by rhynchosaurs, whereas traversodont cynodonts are the most common clade in the middle portion of the formation (Rogers *et al.* 1993).

The conformably overlying Los Colorados Formation contains a diverse tetrapod assemblage from the top third of the formation (Bonaparte 1971, 1997; Arcucci *et al.* 2004). This assemblage is probably late Norian in age because the top of the Ischigualasto Formation is ~223–225 Ma (Shipman 2004; Tabor *et al.* 2006) and there is a thick sequence of strata between this boundary and the vertebrate-bearing sequences (Arcucci *et al.* 2004). Dinosaur taxa from the Los Colorados include the theropod dinosaur *Zupaysaurus* (Arcucci & Coria 2003; Ezcurra 2007; Ezcurra & Novas 2007) and at least three sauropodomorph dinosaurs: *Riojasaurus*, *Coloradisaurus*, and *Lessemisaurus* (Bonaparte 1971, 1978, 1999; Bonaparte & Pumares 1995, Pol & Powell 2007a). Although the vertebrate assemblage also includes synapsids, turtles, and pseudosuchian archosaurs, it is dominated by sauropodomorph dinosaurs in number of specimens and occurrences (Bonaparte 1971, Arcucci *et al.* 2004).

Other Late Triassic terrestrial vertebrate assemblages from Argentina are not as well known as the Ischigualasto–Villa Unión Basin. The Laguna Colorada Formation in the El Tranquilo Basin is probably Norian–Rhaetian in age, because it is underlain by Ladinian–Carnian sediments and cross-cut by granitoid intrusions that are dated to 203 ± 2 Ma (Pankhurst *et al.* 1993; Báez & Marsicano 2001). This vertebrate assemblage includes abundant specimens of the basal sauropodomorph *Mussaurus patagonicus* (Bonaparte & Vince 1979; Pol & Powell 2007b), and a single fragmentary specimen of a heterodontosaurid ornithischian dinosaur (Báez & Marsicano 2001; Irmis *et al.* 2007b). Marsicano & Barredo (2004) reported a footprint assemblage from the Portezuelo Formation in San Juan Province. Trackmakers included synapsids, pseudosuchian archosaurs, dinosauriforms and possibly sauropodomorphs (Marsicano & Barredo 2004; Wilson 2005). Domnanovich and colleagues (Domnanovich & Marsicano 2006; Domnanovich *et al.* 2008) described a footprint assemblage from the lower Vera Formation (Carnian) of Patagonia. In this assemblage, dinosauriforms (and other archosaurs) are conspicuously absent; most footprints are assignable to synapsids (Domnanovich & Marsicano 2006; Domnanovich *et al.* 2008). Finally, Martínez (2009) described multiple skeletons of a new basal sauropodomorph, *Adeopapposaurus mognai*, from the Lower Jurassic Cañón del Colorado Formation in San Juan Province.

2.2.2. Brazil. The Upper Triassic strata in Rio Grande do Sul of southern Brazil preserve a rich assemblage of terrestrial vertebrates (Langer *et al.* 2007a; Schultz & Langer 2007). The lower Santa Maria Formation is generally considered Ladinian in age; it is dominated by cynodonts and dicynodonts and no dinosauriforms are known (Bonaparte 1982; Azevedo *et al.* 1990; Langer *et al.* 2007a). The upper Santa Maria Formation is assigned to the Carnian, and is often correlated with the Ischigualasto Formation in Argentina (Langer 2005; Langer *et al.* 2007a). It contains two dinosaurs: the herrerasaurid theropod *Staurikosaurus* (Colbert 1970; Bittencourt & Kellner 2009) and the basal sauropodomorph *Saturnalia tupiniquim* (Langer *et al.* 1999, 2007b; Langer 2003). Dinosaurs are rare in this assemblage; these two taxa comprise four known dinosaur specimens. There are a few other indeterminate dinosaur specimens (e.g., Kischlat 1999), but the upper Santa Maria vertebrate assemblage is largely composed of rhynchosaurs (Langer *et al.* 2007a), which have a very high relative abun-

dance (Azevedo *et al.* 1990), and cynodonts are also common in some levels (Abdala *et al.* 2001). The overlying Caturrita Formation is generally considered early Norian in age (Langer 2005; Langer *et al.* 2007a). Dinosauriforms include the silesaurid dinosauriform *Sacisaurus* (Ferigolo & Langer 2007; Irmis 2008; Nesbitt *et al.* 2010), the theropod *Guaibasaurus* (Bonaparte *et al.* 1999, 2007; Langer *et al.* 2011; though see Ezcurra 2010b for an alternate phylogenetic placement), and the plateosaurid sauropodomorph *Unaysaurus* (Leal *et al.* 2004). Although many specimens of *Sacisaurus* were found at the type locality (Ferigolo & Langer 2007), dinosauriforms are rare in comparison to cynodonts and dicynodonts (rhynchosaurs are also present in the lower Caturrita Formation) (Langer *et al.* 2007a).

2.2.3. Southern Africa. The Karoo Supergroup in southern Africa contains an extensive Late Triassic and Early Jurassic record of terrestrial vertebrates. The Molteno Formation preserves an extensive plant and insect record, but no diagnostic vertebrates (Olsen & Galton 1984; Anderson *et al.* 1998) except for a few tridactyl dinosauriform footprints (Raath *et al.* 1990). This unit is overlain by the Elliot Formation, which is divided into upper and lower units. The lower Elliot Formation is traditionally assigned to the Norian (e.g., Olsen & Galton 1984; Anderson *et al.* 1998), but it seems likely that this unit is at least partly Rhaetian in age or younger, given that it is overlain by Early Jurassic sediments and there is no apparent major unconformity. The lower Elliot has a species rich assemblage of sauropodomorph dinosaurs, including *Plateosaurus*, *Euclimaceras*, *Blikanasaurus* and *Antetonitrus* (van Hoepen 1920; Houghton 1924; Galton & van Heerden 1985, 1998; Yates & Kitching 2003; Yates 2007a). Butler *et al.* (2007) reported the first ornithischian dinosaur from these strata, *Eocursor parvus*. Sauropodomorphs are by far the most common vertebrate body fossils based on number of occurrences, followed by temnospondyls and cynodonts (Anderson *et al.* 1998). Paradoxically, tridactyl dinosauriform and pseudosuchian archosaur footprints are the most common tracks in the lower Elliot Formation, whereas sauropodomorph tracks are rare and temnospondyl and cynodont tracks are unknown (Olsen & Galton 1984; Anderson *et al.* 1998).

The Triassic–Jurassic boundary is typically placed in the middle of the Elliot Formation (Olsen & Galton 1984; but see Smith *et al.* 2009) and it is directly overlain by a thin intraformational conglomerate called the *Tritylodon* Acme Zone, which is interpreted as a period of environmental stress during the earliest Jurassic (Smith & Kitching 1997). This zone is dominated by the tritylodontid cynodont *Tritylodon*, and dinosaurs are also common (Smith & Kitching 1997, fig. 4). Overall, the dinosaur assemblage of the upper Elliot Formation is composed of the sauropodomorphs *Massospondylus* (e.g., Cooper 1981; Gow *et al.* 1990; Sues *et al.* 2004; Barrett 2009), *Aardonyx* (Yates *et al.* 2010) and *Ignavusaurus* (Knoll 2010), the theropod dinosaurs *Coelophysis rhodesiensis* (Raath 1969, 1977, 1980; Bristowe & Raath 2004) and *Dracovenator* (Yates 2005) and the ornithischians *Lesothosaurus* (e.g., Sereno 1991), *Stormbergia* (Butler 2005), and at least four heterodontosaurids (Butler *et al.* 2008; Porro *et al.* 2011). Yates *et al.* (2007) reported additional unnamed sauropodomorphs from the upper Elliot Formation, and the early sauropod *Vulcanodon* is known from correlative sediments in Zimbabwe (Raath 1972). *Massospondylus* is by far the most common vertebrate fossil in the upper Elliot Formation, followed by *Tritylodon*, ornithischian dinosaurs, and other cynodonts; tridactyl dinosauriform and other dinosaur footprints are also very common (Anderson *et al.* 1998). The overlying aeolian Clarens Formation contains the upper Elliot taxa

Massospondylus and *Heterodontosaurus* (Crompton & Charig 1962; Gow *et al.* 1990; Sues *et al.* 2004). A minimum age constraint for the Clarens Formation is the extrusion of the Drakensberg volcanics, which was initiated during the mid-Pliensbachian (Jourdan *et al.* 2005).

2.2.4. Madagascar. Flynn *et al.* (1999) announced the discovery of a diverse Late Triassic vertebrate assemblage from Madagascar. This record is dominated by cynodonts and rhynchosaurs, but Flynn *et al.* (1999) also reported the presence of *Azendohsaurus*-like sauropodomorph dinosaurs, which they considered the oldest members of that clade. Subsequent discoveries have demonstrated that this 'sauropodomorph' material actually belongs to a bizarre basal archosauromorph (Flynn *et al.* 2008, 2010), and no confirmed dinosaur material is known from this assemblage. The Jurassic assemblages from Madagascar are very poorly dated; dinosaurs are surprisingly rare in small vertebrate assemblages (Burmeister *et al.* 2006; Flynn *et al.* 2006), but sauropodomorph dinosaurs are definitely present (Buffetaut 2005; Lang & Goussard 2007).

2.2.5. India. The Pranhita–Godavari Valley in India contains an extensive early Mesozoic stratigraphic record with abundant terrestrial vertebrate fossils. The Maleri Formation is Carnian or Norian in age and contains temnospondyl amphibians, pseudosuchian archosaurs and some synapsids (Kutty *et al.* 1987, 2007; Kutty & Sengupta 1989; Bandyopadhyay & Sengupta 2006). Chatterjee (1987) described the theropod dinosaur *Alwalkeria* from this unit. Recent re-study of the specimen suggests that it may be a chimaera, but that at least part of the hypodigm is dinosaurian (Remes & Rauhut 2005). Kutty *et al.* (2007) also listed a *Guaibasaurus*-like taxon from the upper Maleri Formation. Further study of this and other saurischian material from the Late Triassic of India should greatly improve our knowledge of these early dinosaur assemblages (Novas *et al.* 2011). The overlying Dharmaram Formation appears to straddle the Triassic–Jurassic boundary; there are no confirmed dinosaur specimens from the Triassic lower Dharmaram, but the basal sauropodomorph dinosaurs *Lamplughsaura* and *Pradhania* are known from the Early Jurassic upper Dharmaram Formation (Kutty *et al.* 2007). The Dharmaram Formation is itself overlain by the late Early Jurassic Kota Formation (Kutty *et al.* 1989; Bandyopadhyay & Roy Chowdhury 1996; Bandyopadhyay & Sengupta 2006). This unit contains at least two early sauropods, *Kotasaurus* and *Barapasaurus* (Jain *et al.* 1975; Bandyopadhyay & Roy Chowdhury 1996; Yadagiri 2001; Gillette 2003; Bandyopadhyay *et al.* 2010), but there is also an extremely diverse mammaliaform assemblage (Bandyopadhyay & Sengupta 2006). Unfortunately, there are no relative abundance data available for these Indian strata.

2.2.6. China. The Lower Jurassic Lufeng Formation of Yunnan, China and its correlative units contain an extremely abundant and diverse terrestrial tetrapod assemblage (Sun *et al.* 1985; Sun & Cui 1986; Luo & Wu 1994). Like many other Early Jurassic assemblages, sauropodomorphs of the Lufeng are very species-rich, including *Lufengosaurus*, *Yunnanosaurus*, *Jingshanosaurus* (Young 1951; Zhang & Yang 1994; He *et al.* 1998; Barrett *et al.* 2005, 2007), and also *Gongxianosaurus* and *Chinshakiangosaurus* from correlative formations (He *et al.* 1998; Upchurch *et al.* 2007). The only diagnostic theropod material is '*Dilophosaurus*' *sinensis* (Hu 1993), which may form a clade with *Dilophosaurus wetherilli* and *Dracovenator* (Smith *et al.* 2007; though see alternate phylogenetic hypotheses of Nesbitt *et al.* 2009b and Brusatte *et al.* 2010). At least two thyreophoran ornithischian dinosaurs are present, but ornithischian material is very rare in the Lufeng Formation, and none of it can be diagnosed as a valid species (Norman *et al.* 2007; Irmis & Knoll 2008). Among non-dinosaur vertebrates,

tritylodont and mammaliaform synapsids and crocodylomorphs are equally as species-rich as sauropodomorphs (Sun *et al.* 1985; Sun & Cui 1986; Luo & Wu 1994; Barrett & Xu 2005). Based on number of occurrences, sauropodomorphs are the most abundant clade, followed by tritylodont synapsids (Simmons 1965; Luo & Wu 1994, table 14.2). These data are largely similar to that for the upper Elliot Formation of southern Africa described above.

2.2.7. Morocco. The Atlas Mountains of Morocco preserve a fossiliferous Late Triassic–Jurassic terrestrial stratigraphic record. Although Dutuit (e.g. 1972a, 1977a, b, 1979, 1988) described an extensive vertebrate assemblage from the Upper Triassic Argana Formation (Jalil 1996, 1999), it does not contain any confirmed dinosaur remains. *Azendohsaurus* was initially described as an ornithischian dinosaur (Dutuit 1972b), and later as a sauropodomorph (Galton 1985; Gauffre 1993), but the discovery of closely related material from Madagascar indicates it is actually a basal archosauromorph (Flynn *et al.* 2008, 2010). Recent work in the Toarcian (late Early Jurassic) of Morocco has revealed an important dinosaur assemblage that includes the basal sauropod *Tazoudasaurus* (Allain *et al.* 2004; Allain & Aquesbi 2008), the possible ceratosaur theropod *Berberosaurus* (Allain *et al.* 2007; but see Xu *et al.* 2009), and an undescribed small theropod dinosaur (Taquet 1985).

2.2.8. Eastern North America. Both the Moroccan and eastern North American early Mesozoic stratigraphic records represent rift basins from the initial separation of Pangaea (Olsen 1997). In eastern North America, outcrops of these rift basin sediments extend from Nova Scotia to North Carolina (Olsen 1997), and preserve a variety of terrestrial vertebrate assemblages as both footprints and body fossils. Carnian age strata from North Carolina preserve a footprint assemblage in which pseudosuchian tracks are most common, but tridactyl dinosauriform tracks are also present (Olsen & Huber 1998). The body fossil record from these sediments includes dicynodonts, traversodontid cynodonts, phytosaurs, aetosaurs, and crocodylomorphs, but no confirmed dinosaurs (Huber *et al.* 1993; Lucas 1998; Green *et al.* 2005; Schneider *et al.* 2008; Sues & Hopson 2008). Dinosaurs are absent and cynodonts are common in similar aged strata in Virginia (Sues & Olsen 1990; Sues *et al.* 1994a).

Norian body fossils from the Newark Supergroup are best known from the Durham Basin of North Carolina (Sues *et al.* 2003a). A recently discovered assemblage includes dicynodonts, cynodonts, aetosaurs, 'rauisuchian' archosaurs, and crocodylomorphs, but again, no dinosaurs (Sues *et al.* 1999, 2003a, b; Peyer *et al.* 2008). In contrast, a high-resolution record of footprints from the Norian–Hettangian strata of the Newark Supergroup shows an intriguing pattern: although the Triassic assemblages include occurrences of dinosauriform tracks (e.g. *Grallator* and *Atreipus*), they are relatively rare in comparison with Early Jurassic assemblages of the Newark (Olsen *et al.* 2002). Only after the Triassic–Jurassic boundary do dinosauriform footprints become common and sauropodomorph footprints appear; in addition, the maximum dinosaur footprint size increases abruptly at the boundary (Olsen *et al.* 2002). The best Early Jurassic Newark body fossil record comes from the lowermost Jurassic McCoy Brook Formation in Nova Scotia (Shubin *et al.* 1994). Although records include a number of undescribed sauropodomorph dinosaurs (e.g., Shubin *et al.* 1994; Fedak 2001), they are relatively rare compared to the diverse assemblage of cynodonts, crocodylomorphs, and other non-dinosaurian reptiles (Olsen *et al.* 1987; Shubin *et al.* 1991, 1994; Sues *et al.* 1992, 1994c, 1996). The sauropodomorph *Anchisaurus* from the Portland Formation in the Hartford Basin (Galton 1976; Yates 2004; Fedak & Galton

2007) is significantly younger, most likely from the Sinemurian (Olsen *et al.* 2005). This formation also produced a single theropod, the type of *Podokesaurus holyokensis* (Talbot 1911).

2.2.9. Western North America. Recent re-evaluation has significantly changed our understanding of the western North American Triassic dinosaur record (Parker *et al.* 2005; Irmis *et al.* 2007b; Nesbitt *et al.* 2007). Some previous authors had suggested that dinosaurs were quite common (e.g., Hunt & Lucas 1994; Hunt *et al.* 1998), but a revision of the record suggests dinosaurs are not diverse, are rare in abundance, and that no sauropodomorphs or ornithischians were present during the Triassic (Nesbitt *et al.* 2007; Irmis *et al.* 2007b). Recent discovery of non-dinosaur dinosauromorphs coexisting with dinosaurs during the Late Triassic have further modified our understanding of the Late Triassic western North American record (Irmis *et al.* 2007a; Nesbitt *et al.* 2010).

The Upper Triassic Chinle Formation of Arizona and northern New Mexico has been the primary source for examining early dinosaur diversity in western North America (e.g., Hunt *et al.* 1998; Nesbitt *et al.* 2007). New age constraints suggest that all or nearly all of the Chinle Formation is Norian in age (Irmis & Mundil 2008, 2010), although some of the uppermost units might be Rhaetian (Zeigler 2008; Zeigler & Geissman 2008). The best-known assemblage from near the base of the Chinle Formation is the *Placerias* Quarry in northern Arizona (Camp & Welles 1956; Long & Murry 1995; Fiorillo *et al.* 2000). Here, dinosauromorphs include a specimen of *Dromomeron* (Irmis *et al.* 2007a, supplemental information; Nesbitt *et al.* 2009a), indeterminate dinosauriform material and a coelophysoid theropod dinosaur (Hunt *et al.* 1998; Nesbitt *et al.* 2007). Nonetheless, dinosaurs are very rare in the quarry, even when factoring out the anomalous abundance of the dicynodont *Placerias* (Fiorillo *et al.* 2000, fig. 9). Although *Placerias* is very common in the quarry, it is extremely rare at other localities within the Chinle Formation (Long & Murry 1995; Irmis 2005a; Parker & Martz 2011); the remaining *Placerias* Quarry assemblage is dominated by pseudosuchian archosaurs (Fiorillo *et al.* 2000). Only a few indeterminate dinosaur specimens and a single silesaurid femur are known from elsewhere in the lower Chinle Formation (Nesbitt *et al.* 2007).

The Petrified Forest Member of the upper Chinle Formation in Arizona contains the basal theropod *Chindesaurus bryansmalli* (Long & Murry 1995; Parker & Irmis 2005) and a *Coelophysis*-like coelophysoid (Padian 1986; Nesbitt *et al.* 2007). These remains are rather rare; the assemblage is dominated by the pseudosuchians *Revueltosaurus*, phytosaurs and aetosaurs (Irmis 2008). The Owl Rock Member overlies the Petrified Forest Member in northern Arizona; this unit contains abundant phytosaurs and aetosaurs, but no confirmed dinosaur specimens (the specimen described by Spielmann *et al.* 2007 is a shuvosaurid). The Petrified Forest Member in northern New Mexico has a higher species diversity of dinosauromorphs; the assemblage includes the lagerpetid *Dromomeron romeri*, the silesaurid *Eucoelophysis*, *Chindesaurus bryansmalli*, the basal theropod *Tawa hallae* and at least one coelophysoid theropod (Irmis *et al.* 2007a; Irmis 2008; Nesbitt *et al.* 2009b). Despite this high diversity, dinosaurs are not abundant in comparison to pseudosuchian archosaurs (Irmis 2008). The overlying 'upper siltstone' member vertebrate assemblage is largely known from a single locality, the famous *Coelophysis* Quarry (e.g. Colbert 1989). *Coelophysis* is the only dinosaur described from this site, but it is extremely abundant (Irmis 2008). Unfortunately, it appears that this is more of a taphonomic anomaly than a representation of true abundance in the ecosystem (Schwartz & Gillette 1994; Irmis 2008).

The Chinle Formation is overlain by the Glen Canyon Group, a series of Lower Jurassic fluvial and aeolian strata (Clark & Fastovsky 1986). The lowermost strata of this unit are the Moenave Formation and Wingate Sandstone; there is evidence that at least the bases of these strata are Late Triassic in age (Morales & Ash 1993; Lucas & Tanner 2007). The Triassic section of the Moenave Formation has produced vertebrate tracks, which include both pseudosuchian (*Brachychirotherium*) and tridactyl dinosauriform prints (Lucas & Tanner 2007). The Jurassic portion of the Moenave Formation includes abundant tridactyl dinosauriform tracks (e.g., Kirkland & Milner 2006; Milner *et al.* 2006). Body fossils are scarce; most specimens are of the crocodyliform *Protosuchus* (Colbert & Mook 1951), but also include two coelophysoid theropod specimens (Lucas & Heckert 2001). The overlying (?Sinemurian–?Pliensbachian) Kayenta Formation is much better sampled (e.g., Sues *et al.* 1994b; Tykoski 2005b). Dinosaurs are species rich, including the theropods *Dilophosaurus wetherilli*, 'Syntarsus' *kayentakatae*, the 'shake-n-bake' theropod, the thyreophoran ornithischian *Scutellosaurus lawleri*, possible osteoderms of *Scelidosaurus*, an unnamed heterodontosaurid, and a sauropodomorph previously assigned to *Massospondylus* (Attridge *et al.* 1985; Padian 1989; Sues *et al.* 1994b; Tykoski 2005b) and recently renamed *Sarhsaurus* (Rowe *et al.* 2011). This species diversity is approximately equivalent to that of the synapsid assemblage, which includes tritylodonts and mammaliaforms (e.g., Sues 1986; Sues *et al.* 1994b). *Scutellosaurus* is very abundant and theropod specimens are not uncommon, but tritylodonts are probably the single most abundant clade based on number specimens (Sues *et al.* 1994b; Tykoski 2005b). The overlying Pliensbachian Navajo Sandstone preserves a very limited vertebrate body fossil record that includes three sauropodomorph specimens and one coelophysoid theropod, *Segisaurus halli* (Carrano *et al.* 2005; Irmis 2005b; Loewen *et al.* 2005; Sertich & Loewen 2010). The total number of vertebrate body fossils is too low to come to a conclusion regarding relative abundance (Irmis 2005b). In contrast, the Navajo preserves an abundant footprint assemblage that is dominated by tridactyl dinosauriform and synapsid tracks (Irmis 2005b).

Moving off the Colorado Plateau, the Dockum Group of eastern New Mexico and west Texas is time-equivalent with the Chinle Formation. The Otis Chalk quarries near the base of the unit contain the basal dinosauromorph *Dromomeron gregorii* (Nesbitt *et al.* 2009a), a silesaurid (Nesbitt *et al.* 2010) and the basal theropod *Chindesaurus* (Nesbitt *et al.* 2007). These specimens are a minor component of the assemblage when compared with the abundance of the archosauriform *Trilophosaurus*, phytosaurs and aetosaurs (Gregory 1945; Long & Murry 1995). The overlying Tecovas Formation has only produced a couple of isolated dinosaur specimens, most notably *Caseosaurus* (Hunt *et al.* 1998; Nesbitt *et al.* 2007). Nesbitt & Chatterjee (2008) demonstrate the presence of at least two theropods from the Cooper Canyon Formation in west Texas, but again, these taxa are a small part of the pseudosuchian-dominated assemblage (Long & Murry 1995; Martz 2008). This formation also includes *Dromomeron* and indeterminate dinosauriform material (Martz 2008). Rare dinosaurs from the Bull Canyon Formation of New Mexico include a coelophysoid theropod and indeterminate saurischian remains (Carpenter 1997; Nesbitt *et al.* 2007). The youngest Dockum Group unit, the Redonda Formation of eastern New Mexico, does not contain any dinosaur body fossils, but footprints include tridactyl dinosauriform tracks as a common, but not dominant, part of the assemblage (Klein *et al.* 2006).

2.2.10. Greenland. Jenkins *et al.* (1994) reported a diverse Norian assemblage of tetrapods from the Fleming Fjord

Formation of Greenland. This record includes specimens of a *Plateosaurus*-like sauropodomorph and a single undescribed theropod. Based on specimen lists, sauropodomorphs are the second most abundant taxon after the plagiosaurid temnospondyl *Gerrothorax* (Jenkins *et al.* 1994). The assemblage also includes abundant footprints; tridactyl dinosauriform tracks are the most common morphotype (Jenkins *et al.* 1994; Gatesy *et al.* 1999).

2.2.11. Western Europe fissure fills. The early Mesozoic fissure fills of Britain and France are very difficult to interpret because they are poorly dated (e.g., Whiteside & Marshall 2008) and their taphonomic mode biases them against larger vertebrates such as dinosaurs. Sauropodomorphs are present in Norian/Rhaetian British fissure fills (e.g., Fraser & Walkden 1983; Fraser 1994; Yates 2003a; Whiteside & Marshall 2008), but they can range from being totally absent to being extremely abundant (e.g., Galton 2007). Other dinosaur material is rare but present (Fraser *et al.* 2002). Although not preserved in fissure fills, the Norian vertebrate assemblage of Elgin, Scotland contains a possible dinosauriform, *Saltopus* (Benton & Walker 2011). The Late Triassic fissure fills of France and Belgium are overwhelmingly dominated by cynodont and mammaliaform teeth (e.g., Sigogneau-Russell & Hahn 1994; Godefroit & Battail 1997), and with the exception of some possible sauropodomorph teeth, confirmed dinosaur specimens are absent (Godefroit & Cuny 1997; Irmis *et al.* 2007b).

2.2.12. Germany. The Upper Triassic strata of the Germanic Basin are one of the longest-studied terrestrial Late Triassic records. Carnian units preserve terrestrial tetrapods, but no confirmed dinosaurs (Schoch & Wild 1999; Seegis 2005). The Norian lower and middle Löwenstein Formation contains the sauropodomorphs *Efraasia minor* and *Plateosaurus gracilis*, whereas the upper Löwenstein Formation, the overlying Rhaetian Trossingen Formation and lateral equivalents in France and Switzerland, contain *Plateosaurus engelhardti* (Schoch & Wild 1999; Moser 2003; Yates 2003b; Seegis 2005). These sauropodomorphs are the most abundant taxa in their assemblages using both number of specimens and number of occurrences as a metric (Benton 1986b; Sander 1992; Hungerbühler 1998; Moser 2003). Theropod material is restricted to the indeterminate specimens of *Halticosaurus longotarsus* and *Procompsognathus* from the Löwenstein Formation, and several individuals of *Liliensternus liliensterni* from the late Norian or Rhaetian of Thuringia (Rauhut & Hungerbühler 2000). The Germanic Basin also includes abundant dinosauriform footprint assemblages (e.g., Haubold & Klein 2000), but as previously discussed, assigning these to specific clades is difficult.

2.2.13. Poland. New discoveries have begun to illuminate distinct Late Triassic vertebrate assemblages in Poland. The locality of Krasiejow contains a very diverse tetrapod fauna, including the dinosauriform *Silesaurus*, but no dinosaurs (Dzik 2003; Dzik & Sulej 2007). Although *Silesaurus* specimens are not uncommon, the highest relative abundances are specimens of metoposaurid temnospondyls and phytosaurs (Dzik 2001; Dzik & Sulej 2007). Krasiejow was originally dated to the Carnian (Dzik 2001; Dzik & Sulej 2007) based on 'stage of evolution' biostratigraphic arguments, but an early Norian age is equally likely (Szulc 2005; Gruszka & Zieliński 2008), based on sedimentology and inferred lithostratigraphic correlation. In addition, Dzik *et al.* (2008) recently reported a latest Triassic vertebrate assemblage that includes temnospondyls, dicynodonts and theropod dinosaurs.

2.2.14. Summary. The regional species diversity and abundance data make apparent some striking patterns. Dinosaurs have moderate species diversity but are not abundant in

Carnian and early Norian assemblages that also contain rhynchosaurs and synapsids (i.e., Argentina and Brazil). By the late Norian, sauropodomorphs are species rich and abundant in South America, southern Africa, and Europe, but theropod dinosaurs are rare or absent in these same assemblages. Ornithischians are also rare or absent, but they become diverse after the Triassic–Jurassic boundary in southern Africa. Dinosaurs are not common in eastern or western North America and Morocco until after the Triassic–Jurassic boundary. In western North America, Early Jurassic dinosaurs are species rich and abundant, but they co-exist with a rich and common tritylodont fauna. This early Jurassic pattern is also present as a sauropodomorph-tritylodont association in southern Africa and China.

3. Hypotheses for early dinosaur diversification

Previous ideas about the rise of dinosaurs can generally be divided into two categories. Some are descriptive; that is, they describe a pattern of the early dinosaur record, but do not explicitly invoke a cause for the pattern. The second class of hypotheses explicitly describes a mechanism or cause for the rise of dinosaurs. The evidence for existing descriptive and mechanism-based hypotheses is reviewed below.

One of the difficulties with evaluating hypotheses for the rise of dinosaurs is that authors are not always explicit about cause and effect. For example, some authors have proposed that increasing aridity caused the extinction of synapsid groups and the rise of dinosaurs. But these authors do not explicitly explain *how* aridity had this effect. In these cases, the first step is to test the correlation, but it is difficult to evaluate causation when hypotheses are incompletely explained.

Previous authors have often treated each idea as a mutually exclusive hypothesis. In most cases this is incorrect. It is probably more realistic to assume that multiple factors were involved in the rise of dinosaurs, and that different mechanisms were important at different times and places. This view is reinforced by the diachronous nature of the early dinosaur record across Pangaea. Another notable logical fallacy in previous work is that if hypothesis A and B are incorrect, hypothesis C must be correct. Proving certain hypotheses to be incorrect does not necessarily confirm alternate hypotheses.

3.1. Descriptive hypotheses

3.1.1. Carnian–Norian extinction. Benton (1983, 1986a, b, 1991, 1994, 2004, 2006) proposed that an extinction of terrestrial tetrapods at or near the Carnian–Norian (C–N) boundary cleared the way for subsequent diversification of early dinosaurs. His hypothesis specifically focuses on the extinction of the rhynchosaurs, dicynodonts and 'gomphodont' cynodonts (e.g., Benton 2006, fig. 4). Although he provided one detailed example from the Germanic Basin (1986b), most of the data in support of this hypothesis come from a concatenated global taxic database (e.g., Benton 1986a, b, 1994). Benton's hypothesis makes two testable predictions: (1) rhynchosaurs, dicynodonts and 'gomphodont' cynodonts that are associated with early dinosaur-bearing assemblages became extinct at or near the C–N boundary; and (2) dinosaurs show an increase in diversification rate and abundance after the C–N boundary, and after rhynchosaurs, dicynodonts and 'gomphodont' cynodonts go extinct or decline dramatically in diversity.

One of the problems with the C–N hypothesis is that many previous 'late Carnian' terrestrial tetrapod assemblages are now recognised to be Norian in age (e.g., Muttoni *et al.* 2004; Furin *et al.* 2006; Irmis & Mundil 2008, 2010). Thus, the only well-understood assemblages that actually cross the

Table 1 Ancestral state reconstructions of body size (femur length in mm) for early dinosauromorph and dinosaur nodes in Figure 6.

Node	Smoothed phylogeny			Strict phylogeny		
	Femur length	Lower 95%	Upper 95%	Femur length	Lower 95%	Upper 95%
Ornithodira	102.33	99.62	105.03	102.33	71.27	133.39
Pterosauromorpha	69.18	63.53	74.84	41.69	22.53	60.84
Dinosauromorpha	104.71	101.88	107.55	107.15	66.20	148.10
Lagerpetidae	91.20	87.55	94.85	77.62	58.91	96.34
<i>Dromomeron</i>	104.71	99.79	109.64	109.65	99.82	119.47
Dinosauriformes	109.65	106.75	112.55	112.20	67.30	157.10
Silesauridae + Dinosauria	120.23	117.39	123.06	117.49	75.59	159.39
<i>Pseudolagosuchus</i> + all other silesaurids	128.82	126.12	131.53	125.89	95.54	156.25
Asilisaurus + all other silesaurids	138.04	135.84	140.24	131.83	115.52	148.13
<i>Eucoelophysis</i> + all other silesaurids	151.36	147.07	155.64	147.91	116.85	178.97
<i>Sacisaurus</i> + <i>Silesaurus</i>	147.91	144.09	151.73	147.91	138.09	157.73
Dinosauria	147.91	144.18	151.65	204.17	139.27	269.08
Ornithischia	109.65	104.49	114.80	109.65	63.70	155.59
Heterodontosauridae	102.33	97.52	107.14	93.33	74.61	112.04
<i>Eocursor</i> + all other ornithischians	109.65	107.45	111.85	109.65	91.36	127.94
<i>Lesothosaurus</i> + all other ornithischians	128.82	125.93	131.72	144.54	114.19	174.90
Thyreophora + all other ornithischians	165.96	162.99	168.93	162.18	135.74	188.62
<i>Scutelosaurus</i> + all other thyreophorans	194.98	191.81	198.16	213.80	195.08	232.51
<i>Scelidosaurus</i> + <i>Huayangosaurus</i>	398.11	395.91	400.31	295.12	280.92	309.32
<i>Stormbergia</i> + all other ornithischians	199.53	197.33	201.73	181.97	166.40	197.54
<i>Agilisaurus</i> + all other ornithischians	181.97	177.16	186.78	173.78	154.63	192.93
<i>Hexinlusaurus</i> + <i>Yinlong</i>	154.88	152.68	157.08	162.18	147.98	176.38
Saurischia	186.21	182.72	189.69	204.17	175.18	233.16
Sauropodomorpha	194.98	191.88	198.09	169.82	154.26	185.39
<i>Pantyraco</i> + all other sauropodomorphs	239.88	236.40	243.37	478.63	29.62	927.64
<i>Efraasia</i> + all other sauropodomorphs	316.23	312.66	319.79	489.78	186.21	793.35
<i>Plateosaurus</i> + all other sauropodomorphs	398.11	394.62	401.59	501.19	300.62	701.75
<i>Ruehleia</i> + all other sauropodomorphs	478.63	475.45	481.81	512.86	383.37	642.36
<i>Plateosaurus</i> + all other sauropodomorphs	537.03	534.62	539.44	524.81	446.78	602.84
<i>Plateosaurus</i>	537.03	534.83	539.23	537.03	518.74	555.32
<i>Riojasaurus</i> + all other sauropodomorphs	549.54	546.64	552.44	660.69	440.78	880.61
<i>Massospondylus</i> + all other sauropodomorphs	562.34	559.16	565.52	660.69	450.68	870.71
<i>Massospondylus</i> + <i>Lufengosaurus</i>	549.54	545.45	553.64	645.65	– 1879.31	3170.62
<i>Jingshanosaurus</i> + all other sauropodomorphs	575.44	572.11	578.77	676.08	480.08	872.08
<i>Yunnanosaurus</i> + all other sauropodomorphs	575.44	572.03	578.85	676.08	501.40	850.77
<i>Anchisaurus</i> + all other sauropodomorphs	588.84	585.44	592.25	691.83	539.69	843.98
<i>Ardonyx</i> + all other sauropodomorphs	630.96	627.63	634.29	691.83	570.98	812.68
<i>Melanorosaurus</i> + all other sauropodomorphs	660.69	657.51	663.87	707.95	616.27	799.62
<i>Antetonitrus</i> + all other sauropodomorphs	776.25	773.89	778.60	741.31	703.96	778.66
<i>Antetonitrus</i> + <i>Lessemsaurus</i>	776.25	774.05	778.45	758.58	741.11	776.05
<i>Gongxianosaurus</i> + all other sauropodomorphs	794.33	790.84	797.81	776.25	730.30	822.19
<i>Isanosaurus</i> + all other sauropodomorphs	758.58	756.38	760.78	758.58	739.86	777.30
<i>Vulcanodon</i> + all other sauropodomorphs	1096.48	1094.12	1098.83	1096.48	1050.53	1142.43
<i>Vulcanodon</i> + <i>Tazoudasaurus</i>	1096.48	1094.28	1098.68	1096.48	1077.76	1115.20
<i>Shunosaurus</i> + all other sauropodomorphs	1230.27	1225.88	1234.66	1348.96	1301.95	1395.98
<i>Barapasaurus</i> + <i>Patagosaurus</i>	1348.96	1346.76	1351.16	1348.96	1330.25	1367.68
Theropoda	213.80	210.54	217.05	223.87	205.58	242.16
Herrerasauridae	281.84	278.87	284.80	269.15	255.28	283.03
<i>Chindesaurus</i> + <i>Herrerasaurus</i>	363.08	360.24	365.91	363.08	350.13	376.03
<i>Eoraptor</i> + all other theropods	190.55	187.37	193.72	173.78	159.25	188.31
<i>Guaibasaurus</i> + all other theropods	208.93	205.36	212.50	213.80	195.08	232.51
<i>Tawa</i> + all other theropods	234.42	230.51	238.33	269.15	222.14	316.17
Neotheropoda	281.84	277.93	285.75	302.00	260.09	343.90
Coelophysidae	239.88	235.60	244.17	234.42	144.83	324.01
' <i>Syntarsus</i> ' <i>kayentakatae</i> + <i>Coelophysis</i>	239.88	236.15	243.62	234.42	189.52	279.32
<i>Coelophysis</i>	234.42	232.22	236.62	234.42	216.13	252.71
<i>Liliensternus</i> + all other theropods	371.54	367.89	375.18	338.84	307.78	369.91
<i>Cryolophosaurus</i> + all other theropods	575.44	571.62	579.26	660.69	612.58	708.81
' <i>Dilophosaurus</i> ' <i>sinensis</i> + all other theropods	588.84	586.43	591.25	645.65	602.77	688.53

Table 1 Continued.

Node	Smoothed phylogeny			Strict phylogeny		
	Femur length	Lower 95%	Upper 95%	Femur length	Lower 95%	Upper 95%
Ornithodira	102·33	99·62	105·03	102·33	71·27	133·39
' <i>Dilophosaurus</i> ' <i>sinensis</i> + <i>D. wetherilli</i>	588·84	586·49	591·20	616·60	585·53	647·66
Ceratosauria + Tetanurae	602·56	597·86	607·26	467·74	315·59	619·88
Ceratosauria	616·60	610·94	622·25	630·96	621·13	640·78
Tetanurae	602·56	597·64	607·48	467·74	384·13	551·34
<i>Condoraptor</i> + all other theropods	537·03	532·94	541·13	467·74	425·83	509·64
<i>Condoraptor</i> + <i>Piatnitzkysaurus</i>	562·34	558·69	565·99	575·44	565·62	585·26
<i>Dubreuillosaurus</i> + <i>Eustreptospondylus</i>	457·09	454·89	459·29	457·09	439·21	474·96

C–N boundary are the records in Argentina and Brazil. In Argentina, the highest occurrences of rhynchosaurs, dicynodonts, and 'gomphodont' cynodonts are in the middle of the Ischigualasto Formation (Rogers *et al.* 1993). Given that the top of the Ischigualasto Formation is approximately 225 Ma, and that the C–N boundary is now placed at 228–227 Ma (Furin *et al.* 2006), these youngest occurrences are likely to be within the Norian. Furthermore, rhynchosaurs and dicynodonts are also present in the early Norian Caturrita Formation of southern Brazil (Langer *et al.* 2007a). The record in North Carolina also crosses the Carnian–Norian boundary, and Norian assemblages possess 'gomphodont' cynodonts (e.g., Sues *et al.* 1999). Occurrences of *Placerias* in the Blue Mesa Member of the Chinle Formation in Arizona (Long & Murry 1995; Irmis 2005a; Parker & Martz 2011) are likely younger than 220 Ma (Irmis & Mundil 2008, 2010), and Dzik *et al.* (2008) recently reported abundant dicynodonts from the latest Triassic of Poland. 'Gomphodont' cynodonts are also present in the Norian–Rhaetian lower Elliot Formation of southern Africa (e.g. Abdala *et al.* 2007). Therefore, there is clear evidence that rhynchosaurs, dicynodonts and 'gomphodont' cynodonts did not become extinct at the C–N boundary.

A plausible question is whether the C–N extinction is a real event that has been moved into the early to mid Norian via re-dating of assemblages. Available data suggest this is incorrect, with different groups going extinct at different times, and in different places. For example, whereas no dicynodonts are found in North America beyond the mid-Norian (Parker & Martz 2011), they are found into the Rhaetian in Poland (Dzik *et al.* 2008). Similarly, there is no evidence for rhynchosaurs above the early Norian middle Ischigualasto Formation in Argentina (Rogers *et al.* 1993), but they extend well into younger aged strata in southern Brazil (Langer *et al.* 2007a). Furthermore, there's no evidence that, even at a regional level, any of these extirpations comprise related events. There is little evidence for synchronous dicynodont, rhynchosaur and/or 'gomphodont' cynodont extirpation in Argentina or Brazil (Rogers *et al.* 1993; Arcucci *et al.* 2004; Langer *et al.* 2007a), nor is it clear that the last appearance of dicynodonts in western North America is correlated to the last appearance of dicynodonts or 'gomphodont' cynodonts elsewhere in North America (Olsen *et al.* 2011; Parker & Martz 2011). Thus, it appears that the extirpation and eventual extinction of dicynodonts, 'gomphodont' cynodonts, and rhynchosaurs were not part of a single event; rather they occurred at different times throughout Pangaea. This of course does not preclude a regional importance of the decline of one or more of these groups for early dinosaur success.

Global diversity estimates in this study clearly indicate that there is no acceleration in diversification across the C–N boundary (Figs 3, 4). It is important to emphasise that the

global diversity data do show an increase in total richness throughout the Late Triassic, including across the C–N boundary, but that the *rate* of diversification does not increase across this interval. Based on the evidence outlined in the previous section, dinosaurs are abundant by the late Norian in Argentina, but they are no more species rich than in the underlying Ischigualasto Formation. This is the only stratigraphic section where dinosaurs become abundant after the disappearance of rhynchosaurs and dicynodonts. Sauropodomorphs are species rich and abundant in the late Norian–Rhaetian of southern Africa, but only one rhynchosaur specimen has been reported from this basin (Raath *et al.* 1992). Rhynchosaurs and dicynodonts are very rare (Lucas *et al.* 2002; Nesbitt & Whatley 2004; Irmis 2005a) and dinosaurs are never particularly abundant or species rich in the Triassic of western North America (Nesbitt *et al.* 2007; see section 2). Thus, there is little evidence for dinosaur diversification after a rhynchosaur, dicynodont or 'gomphodont' cynodont extinction or regional extirpation. In summary, a Carnian–Norian extinction and related dinosaur diversification is not supported by the current evidence.

3.1.2. Triassic–Jurassic body size increase. One of the most striking patterns in the data presented by Olsen *et al.* (2002) is the abrupt increase in maximum size of dinosaur footprints at the Triassic–Jurassic boundary in the Newark Supergroup of eastern North America. These authors hypothesised that dinosaurs became much more abundant directly after the Triassic–Jurassic boundary, and part of this expansion included a rapid increase in maximum body size, at least for theropods. Later authors have criticised this hypothesis because large tridactyl dinosauriform footprints in putative Triassic strata occur elsewhere in the world (Thulborn 2003; Lucas *et al.* 2006; Lucas & Tanner 2007). However, the ages of these records are poorly constrained by non-biostratigraphic data, and no one has explicitly tested the Olsen *et al.* (2002) hypothesis against the body fossil record.

To test this hypothesis, the evolution of body size in early dinosaurs was reconstructed using phylogenetic ancestral state reconstruction (see section 1 for details) (Table 1; Figs 6, 7). Given the data, a two-parameter directional model was not significantly more likely than a single parameter Brownian motion model based on the likelihood ratio test (Table 2). The values of the branch length scaling parameters (Table 2) indicate that body size did not change significantly more across longer branches, and that most significant body size change occurred early in the evolutionary history of the analysed phylogeny (Pagel 1999). 'Large body size' is defined here as a femur length greater than 500 mm, because the *Eubrontes* tracks in question from Olsen *et al.* (2002) would have been made by a theropod of that approximate size, assuming the hindlimb proportions of *Liliensternus* or *Dilophosaurus* (Lucas *et al.* 2006).

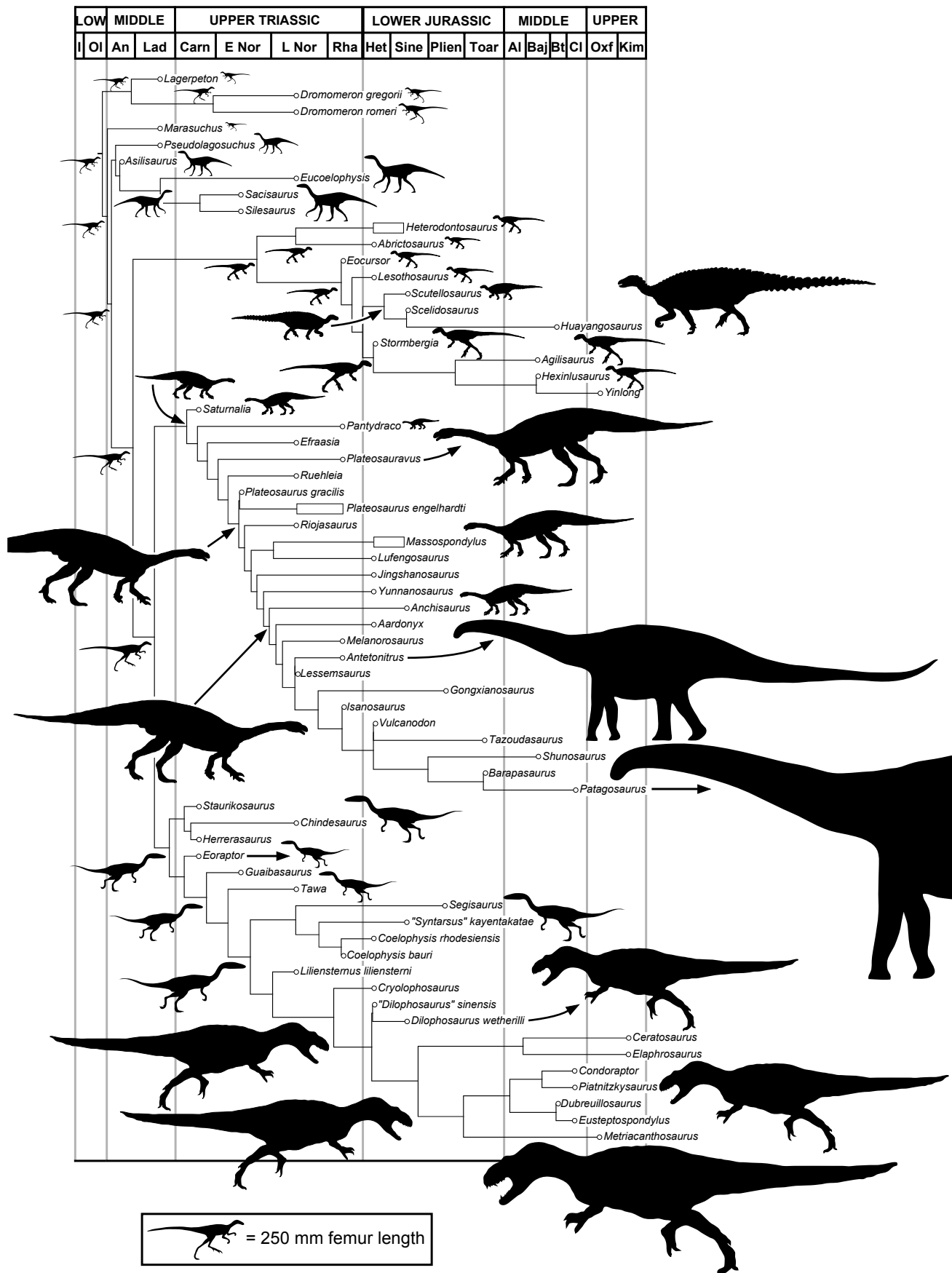


Figure 6 Smoothed time-calibrated phylogeny (see Fig. 1) showing the evolution of body size in early dinosauriforms and dinosaurs. Body size silhouettes are scaled to femur length data presented in Table 1 and Appendix. Left-facing silhouettes are observed values for terminal taxa. Right-facing silhouettes are ancestral-state reconstructions for the nodes (see text for details). Non-dinosauriform archosauriforms in Figure 1 were included in the analysis but are not shown here. Abbreviations: Al=Aalenian; An=Anisian; Baj=Bajocian; Bt=Bathonian; Carn=Carnian; Cl=Callovian; E Nor=early Norian, Het=Hettangian; I=Induan; Kim=Kimmeridgian; L Nor=late Norian; Lad=Ladinian; Ol=Olenekian; Oxf=Oxfordian; Plien=Pliensbachian; Rha=Rhaetian; Sine=Sinemurian; Toar=Toarcian.

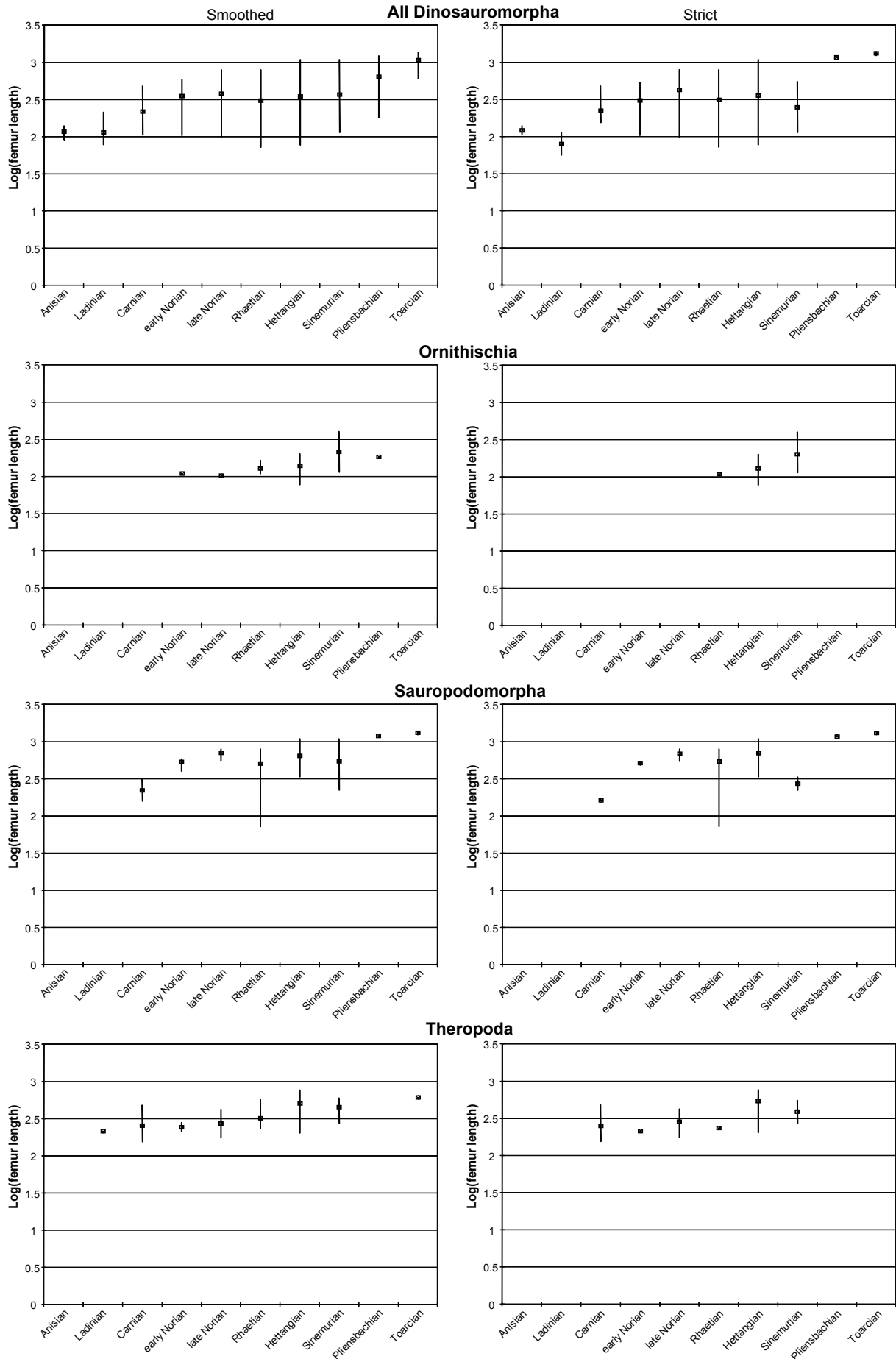


Figure 7 Early dinosaur body size evolution through time. Values are the \log_{10} of femur length (in mm). The black square represents the mean, and the vertical lines are the range for each temporal bin. Left column values are based on smoothed temporally-calibrated phylogeny, whereas those on the right are based on the strict temporally-calibrated phylogeny.

Table 2 Results of evolutionary model tests of body size for Dinosauromorpha. See text for discussion.

Phylogeny	Model	Rates of evolution	Likelihood	Scaling parameters		
				Kappa	Delta	Lambda
Smoothed	Random Walk	1	-0.393020	-	-	-
Smoothed	Random Walk	1	7.368328	0.450715	0.431820	1.000000
Smoothed	Directional	2	0.651891	-	-	-
Smoothed	Directional	2	10.069369	0.368240	0.439058	1.000000
Strict	Random Walk	1	-64.956172	-	-	-
Strict	Random Walk	1	2.827823	0.065451	0.367884	1.000000
Strict	Directional	2	-64.946993	-	-	-
Strict	Directional	2	5.735835	0.073311	0.377436	1.000000

The reconstructed results show strong patterns in body size evolution of early dinosaurs (Figs 6, 7) and results are congruent between the analyses using smoothed and strict time-calibrated phylogenies (Table 1). Dinosauromorph body size steadily increased through the Triassic and Early Jurassic. Maximal and mean body size of dinosaurs did increase across the Triassic–Jurassic boundary (Fig. 7), but this increase was no greater in magnitude than similar changes in the Late Triassic. Ornithischian dinosaurs were fairly small in the Late Triassic, and they stay small across the Triassic–Jurassic boundary. Only thyreophorans evolve large body size during the Early Jurassic. Sauropodomorphs evolve a large body size early in their evolutionary history, at least by the early Norian (Figs 6, 7), and continue to increase in size through the Middle Jurassic. The ancestral state reconstructions indicate that *Dilophosaurus*-sized large theropods had evolved during the Late Triassic (Fig. 6), and this reconstruction would be placed even earlier in the Late Triassic if *Zupaysaurus* was included (it is approximately the size of *Dilophosaurus*, but was not included because it does not preserve a femur). All these data strongly support the idea that large sauropodomorph and theropod (femur length > 500 mm) dinosaurs existed before the Triassic–Jurassic boundary, which conflicts with the general hypothesis of Olsen *et al.* (2002). However, the present data do not contradict a regional body size increase at the boundary for dinosaurs in the Newark Supergroup.

3.2. Mechanism-based hypotheses

3.2.1. Non-competition. The consequence of Benton's (1983, 1986a, b, 1991, 1994, 2004, 2006) Carnian–Norian extinction hypothesis was that dinosaurs became 'victors by accident'. He proposed that the C–N extinction cleared ecological space that dinosaurs were able to diversify into. Benton cited the lack of identifiable competition (see models in Benton 1996) as evidence for this opportunistic non-competitive model. Olsen *et al.* (2002) suggested that a similar event happened at the Triassic–Jurassic boundary, allowing dinosaurs to diversify further and increase in relative abundance. In support of these hypotheses, Brusatte *et al.* (2008a, b) demonstrated that dinosaur disparity, diversity and morphological evolution rates are similar to other archosaurs during the Late Triassic, and that pseudosuchian archosaurs drastically reduce in morphological disparity across the Triassic–Jurassic boundary.

As already demonstrated, the supposed C–N victims, rhynchosaurs, dicynodonts and 'gomphodont' cynodonts, actually extend into the Norian in South America, where they overlap with dinosaurs. Except in the Germanic Basin, where these groups are absent, other stratigraphic records preserving body fossils in Laurasia do not extend into the Carnian. Therefore, these data do not support an opportunistic radiation of

dinosaurs after the C–N boundary. Late Norian Gondwanan assemblages do have an increased abundance of sauropodomorphs and a lack of rhynchosaurs and dicynodonts, but there is not enough evidence to ascribe this to a replacement by sauropodomorphs. Global diversity of dinosaurs normalised by number of formations (Fig. 4) does show a substantial increase across the Triassic–Jurassic boundary. Furthermore, North American and north African assemblages do show an increase in dinosaur diversity and abundance across the Triassic–Jurassic boundary, but little change is seen in Gondwanan assemblages. This might provide support for a Laurasian radiation of dinosaurs after the Triassic–Jurassic boundary. The post-Triassic diversification of ornithischians (Fig. 3) is also consistent with this model. The early pseudosuchian disparity crash reported by Brusatte *et al.* (2008b) might be over estimated, because they did not include morphologically disparate crocodylomorphs such as *Calsoyasuchus* (Tykoski *et al.* 2002), the Kayenta *Edentosuchus* (Sues *et al.* 1994b) and thalattosuchians.

The wider problem with 'non-competition' or historically contingent opportunistic scenarios is that they are impossible to test directly. In effect, they propose that dinosaurs became dominant because of a coincidental event (i.e., an extinction). Responses to extinctions, however, are not coincidental. For example, the timing and location of a bolide impact may be unpredictable, but this only causes coincidental extinction for species whose entire range is in the direct path of the bolide. Other indirect effects of an impact (e.g., environmental stress) can cause differential extinction. Because these effects cause differential survival, and resulting extinction is not 'random', survival during a contingent event does relate to how well-adapted a particular species is to changes in its ecosystem. Therefore, there are explanations for the survival and diversification of certain clades after an extinction versus extinction of other groups, and invoking opportunism is not an ultimate explanation. Furthermore, just because competition is disproved as a hypothesis does not mean that it confirms opportunism as the mechanism. Dinosaurs may have diversified after the end-Triassic extinction, and this is certainly an important conclusion, but ascribing this success to opportunism ultimately does not explain why dinosaur lineages had such a high survival rate compared with pseudosuchian archosaurs or other groups.

3.2.2. Extraterrestrial impact. Olsen & Sues (1986) and Olsen *et al.* (1987) proposed that a bolide impact might have caused the end-Triassic extinction, and suggested that the Manicouagan Crater in Quebec, Canada might be a record of this impact. Subsequent radioisotopic dating using a variety of methods strongly support a mid-Norian (~215.5 Ma) age for the crater, long before the Triassic–Jurassic boundary (Hodych & Dunning 1992; Ramezani *et al.* 2005). Nonetheless, Olsen

et al. (2002) renewed interest in this hypothesis by documenting an iridium anomaly at the Triassic–Jurassic boundary in the Newark Supergroup of eastern North America.

The Triassic–Jurassic iridium anomaly in the Newark has been replicated at other localities, but its presence and intensity might be pedogenically controlled (Tanner & Kyte 2005; Tanner *et al.* 2008). There is no other strong evidence for an impact at the Triassic–Jurassic boundary, and recent evidence indicates that massive outgassing of CO₂ and other greenhouse gases from CAMP volcanism is directly coincident with end-Triassic marine and terrestrial extinctions (Whiteside *et al.* 2010). Although the Manicouagan impact did not occur during this end-Triassic interval, given its size and proximity to several Late Triassic vertebrate assemblages, it is worth asking whether the impact event had any biotic effects. For example, Walkden *et al.* (2002) documented an impact ejecta layer from Britain that was consistent with a Manicouagan source. Well-dated vertebrate records that span this time interval (215 Ma) do not show any major faunal change in eastern North America (Olsen *et al.* 2002), and only minor species turnover in western North America (Parker 2006; Parker & Martz 2011).

3.2.3. Locomotion. Bakker (1968, 1971, 1972, 1975), Bonaparte (1982, 1984) and Charig (1984) proposed that dinosaurs out-competed other reptiles because they had an erect posture (better split into erect stance and parasagittal gait; Padian *et al.* 2010). This hypothesis is not supported because a variety of pseudosuchian archosaurs had an erect stance (e.g. Bonaparte 1984; Parrish 1986; Nesbitt & Norell 2006), and a parasagittal gait may have in fact been plesiomorphic for Archosauria (Padian *et al.* 2010). Charig (1984) actually considered all archosaurs together in his analysis (including dinosaurs), but in this case locomotion would not explain why dinosaurs diversified and pseudosuchians with an erect stance became extinct.

3.2.4. Physiology. Bakker (1968, 1971, 1972, 1975) suggested that one reason dinosaurs became successful is that their endothermic physiology allowed them to achieve large body size faster than their competitors. More recently, Padian *et al.* (2001, 2004) documented elevated growth rates across dinosaurs and suggested that high growth rates were a synapomorphy of Dinosauria and that dinosaurs could achieve a large body size earlier in ontogeny than other Triassic reptiles. This presumably gave dinosaurs a survival advantage over other archosaurs and reptiles because they could reach a large body size earlier in ontogeny than their non-dinosaur predators/prey. If an elevated growth rate and ontogenetic increase in body mass increase were an advantage, it would also be consistent with a phyletic increase in overall body size.

The available data are consistent with this hypothesis, inasmuch as high growth rates are optimised at the base of Dinosauria. The abundance and large body size of sauropodomorphs during the Triassic is especially consistent with the idea that high growth rates conferred an advantage. If this hypothesis is correct, an interesting question is why North American Triassic dinosaurs do not increase in body size until after the Triassic–Jurassic boundary. Because these dinosaurs had a small body size, increased growth rates would not have conferred an advantage in getting to adult size ontogenetically earlier than their predators/prey. This could be a simple historical contingency, but it is odd that North American dinosaurs increase in size so abruptly at the Triassic–Jurassic boundary.

Unfortunately, short of demonstrating that high growth rates are not a dinosaur synapomorphy, it is unclear how one would disprove hypotheses that these growth rates conferred a survival advantage. Another limitation is that no non-dinosaur

dinosauromorphs have been sampled. If basal dinosauromorphs possess elevated growth rates, it is possible that this is an ornithodiran rather than dinosaurian character, because pterosaurs also had elevated growth rates (Padian *et al.* 2001, 2004).

3.2.5. Palaeoenvironmental change. A variety of authors link the early Mesozoic increase in aridity and decrease in atmospheric oxygen to the rise of dinosaurs (Tucker & Benton 1982; Ward 2006; Berner *et al.* 2007) and the end-Triassic extinction (McElwain *et al.* 1999; Marzoli *et al.* 2004; Berner *et al.* 2007). Unfortunately, these authors generally have not explained how the palaeoenvironmental changes would provide an advantage to dinosaurs over other tetrapods. Some studies have investigated the effect of hyperoxia on animals, but there are few data on how the trend toward a hypoxic atmosphere during the early Mesozoic would have affected reptiles (Berner *et al.* 2007), particularly if dinosaurs were endothermic. Oxygen levels may show a general inverse relationship with dinosaur global species diversity (Fig. 3; cf. Bergman *et al.* 2004; Berner 2006; Algeo & Ingall 2007), but this correlation does not provide evidence that falling oxygen levels are the cause of dinosaur diversification, especially in the absence of a direct mechanism that favours dinosaurs.

More importantly, many of the models utilised for the hypoxia hypothesis (e.g., Berner 2006; Berner *et al.* 2007; Algeo & Ingall 2007) are in serious doubt, because they fail to predict the extensive charcoal record during the early Mesozoic (Belcher & McElwain 2008). Belcher & McElwain (2008) provided empirical evidence that early Mesozoic atmospheric O₂ levels were at least 15%, the minimum for creating charcoal, and this rules out general hypoxic conditions. The COPSE model of Phanerozoic atmospheric O₂ (Bergman *et al.* 2004) does predict such levels, but it is still unclear how accurate this model is. Given that early Mesozoic atmospheric O₂ levels were relatively 'normal', the bird-like lungs of dinosaurs (e.g., O'Connor & Claessens 2005) were probably of little advantage because, on average, bird lungs extract no more O₂ from a breath than do mammals (Frappell *et al.* 2001). Even if there was some physiological advantage to a flow-through avian-style lung in hypoxic conditions, this feature may have been shared by all archosaurs (Farmer & Sanders 2010), which does not explain the differential success of dinosaurs.

There is evidence for increasing aridity through the Late Triassic in some areas (e.g. Dubiel *et al.* 1991; Dubiel 1994; Parrish 1993), which could be a result of global circulation patterns (Sellwood & Valdes 2006) and/or northward movement of Laurasia out of the tropics (Kent & Tauxe 2005). Tucker & Benton (1982) invoked this climate change as a cause of Late Triassic palaeofloral change and thus the rise of dinosaurs, but there is no documented evidence for the linkages among Late Triassic climate, floral composition and dinosaur diversification that they propose. The few stratigraphic records with well-understood vertebrate assemblages (e.g., Rogers *et al.* 1993; Irmis 2008) and palaeoenvironmental records (e.g., Cleveland *et al.* 2008a, b; Shipman 2004; Tabor *et al.* 2006; Colombi & Parrish 2008) do not show any clear correspondence between environmental change and vertebrate faunal change. There is clear evidence of severe environmental stress worldwide at the Triassic–Jurassic boundary that is linked to the extinction event (e.g., McElwain *et al.* 1999; Cohen & Coe 2007; Michalik *et al.* 2007; Hautmann *et al.* 2008; Whiteside *et al.* 2010). In North America, dinosaurs become significantly more abundant at the Triassic–Jurassic boundary, and there is a global spike in diversity (Fig. 4), but there is no specific hypothesis for why dinosaurs would benefit from environmental stress at this time.

4. Discussion and conclusions

“So the poor palaeontologist searching for answers is therefore, in the origin of the dinosaurs, confronted with complexity where he had hoped for simplicity. . .” (Cox 1976)

It is clear that there is currently little or no evidence to support the hypothesis that an upright stance or a bolide impact was the cause of early dinosaur diversification, but other hypotheses are more difficult to assess. There is no evidence for a Carnian–Norian extinction of rhynchosaurs, dicynodonts and ‘gomphodont’ cynodonts, but in Gondwana, the disappearance of these groups during the Norian and the subsequent Late Triassic radiation of sauropodomorphs could be linked. On the other hand, these groups are not known from the Late Triassic of Europe, but sauropodomorphs were still abundant there during the late Norian–Rhaetian.

The spike in dinosaur global diversity across the Triassic–Jurassic boundary, post-Triassic increase in dinosaur abundance in North America, diversification of ornithischians and change in archosaur disparity are consistent with a link to the end-Triassic extinction, but the ultimate cause for the dinosaurs’ success is not clear. The magnitude, accuracy and biotic effects of potentially falling atmospheric oxygen levels are too poorly understood to invoke as a cause at the moment, and detailed inspection of vertebrate assemblages indicates little correlation with increasing aridity. Elevated growth rates in dinosaurs are consistent with their phyletic increase in size and in abundance, but it is difficult to directly disprove the hypothesis that elevated growth rates were responsible for dinosaurian success. Furthermore, the discovery of elevated growth rates in currently unsampled basal dinosauriforms would indicate that this character evolved at the base of Ornithodira.

Ultimately, a combination of hypotheses for the early diversification of dinosaurs is necessary to explain five major patterns: (1) the diversification and increase of sauropodomorph dinosaurs during the Norian of Gondwana and Europe; (2) the low species diversity and low abundance of dinosaurs in the Triassic of North America, and their Early Jurassic expansion; (3) the complete lack of sauropodomorphs and ornithischians in the Triassic of North America; (4) the low diversity and relative rarity of ornithischians during the Triassic, their Early Jurassic diversification, and the maintenance of small body size through the Triassic–Jurassic boundary; and (5) a more general increase in global diversity of dinosaurs across the Triassic–Jurassic boundary. It seems apparent from these patterns that the end-Triassic mass extinction played a role in the eventual success of dinosaurs as the dominant players in Jurassic and Cretaceous ecosystems, but plausible causal linkages are unclear.

Traditionally, studies have investigated the early diversification of *dinosaurs*, because non-dinosaur dinosauriforms were largely restricted to the Middle Triassic of Argentina (e.g. Bonaparte 1997). It is now known that basal dinosauriforms include clades that were geographically widespread and extended well into the Late Triassic at least at lower palaeolatitudes (Irmis *et al.* 2007a; Nesbitt *et al.* 2007, 2009a; 2010). Given that many of these taxa are anatomically very similar to dinosaurs (e.g., Dzik 2003), it is worth considering them as part of a larger dinosauriform radiation that should be explained along with the diversification of dinosaurs. Alternatively, it is curious that these taxa did not survive into the Jurassic. Is this because they simply became extinct before the end of the Triassic, or because they were somehow different than early dinosaurs and succumbed to the end-Triassic mass

extinction that dinosaurs survived? Future studies need to consider early dinosauriforms when proposing hypotheses for the rise of dinosaurs, particularly when analysing physiology, palaeoecology and functional scenarios.

One of the main issues with any palaeobiological study is uneven sampling of the palaeontological record. The revised ages of many dinosaur-bearing sequences (e.g., Muttoni *et al.* 2004; Furin *et al.* 2006; Irmis & Mundil 2008, 2010) leaves us with very few true Carnian assemblages that document the initial evolution of dinosaurs. Several classic Late Triassic records only begin during the middle or late Norian (e.g. the Chinle Formation and the Karoo Basin), limiting the power of the available data for testing hypotheses. In contrast, the classic Germanic Basin does not preserve the Triassic–Jurassic boundary, so hypotheses related to this time interval in this region cannot be tested. Nonetheless, available data are promising because, as outlined above, there are clear early dinosaur patterns in Gondwana and North America.

A related issue is the available geochronologic framework for early Mesozoic terrestrial sequences. The Late Triassic timescale is very poorly constrained (Mundil 2007; Mundil *et al.* 2010). Many of the vertebrate assemblages discussed in this study are only dated using vertebrate biostratigraphy, which is imprecise and can sometimes be wildly inaccurate and circular (e.g., Irmis & Mundil 2008, 2010; Irmis *et al.* 2010). Better geochronologic constraints are needed to make sure that cross-continent comparisons of early dinosaur assemblages are accurate. Preferably, these constraints should use precise non-biostratigraphic methods such as radioisotopic ages and magnetostratigraphy. Only methods with sub-million-year accuracy are precise enough to make confident long-distance correlations.

The lack of precise geochronological constraints has confused biogeographic and biostratigraphic differences. Only after the analysis of new radioisotopic ages was it realised that sauropodomorphs were abundant in Argentina at the same time that all dinosaurs were rare in North America (Irmis & Mundil 2008, 2010). More attention needs to be paid to these biogeographic differences. Recent authors (Irmis *et al.* 2007a; Nesbitt *et al.* 2009b; Ezcurra 2010a) suggest that latitude may be structuring faunas; for example, the sauropodomorph-dominated vertebrate assemblages during the Late Triassic were located at moderate to high latitudes, whereas the assemblages where dinosaurs are rare are at low latitudes. But, not all tetrapod taxa uphold this division. Phytosaurs are found in low-latitude assemblages of North America and Morocco and in high-latitude assemblages of India and Europe, but not in the moderate-high latitude assemblages of Argentina and southern Africa. Therefore, a careful examination of Late Triassic biogeography is necessary to understand to what extent latitude and biogeographic barriers are structuring terrestrial vertebrate assemblages during the early Mesozoic.

The take-home message of this study is that a ‘one-size-fits-all’ hypothesis does not successfully explain patterns of early dinosaur diversification. It is critical to separate data categories to examine individual trends. For example, global analysis suggests a steady increase in species diversity through most of the Late Triassic (e.g. Fig 3), whereas regional analysis (e.g., Argentina) suggests that species diversity does not change very much within this specific assemblage. Hypotheses need to account separately for the global increase in diversity and the multiple events of relative abundance increase across Pangaea, during the Late Triassic and after the Triassic–Jurassic boundary. Similarly, not all dinosaur clades show the same diversity patterns (Figs 3, 4). Sauropodomorph diversity and abundance increased substantially earlier than in theropods or ornithischians, and ornithischian diversity and abundance only increases

at all after the Triassic–Jurassic boundary (Figs 3, 4). It is therefore imperative that analyses of early dinosaur diversification and palaeoecology parse out species diversity versus relative abundance, different geographic areas, separate dinosaur clades, and events that occurred before and after the Triassic–Jurassic boundary.

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6. Appendix. Body size data and geologic ages for taxa used in this study.

Taxon	Femur length	Source	Age
<i>Euparkeria</i>	61.6	Ewer 1965	Anisian
<i>Smilosuchus</i>	522	Colbert 1947	late Norian
<i>Revueltosaurus</i>	93	PEFO 34561	late Norian
<i>Riojasuchus</i>	163	PVL 3827	late Norian
<i>Effigia</i>	–	–	Rhaetian
<i>Postosuchus</i>	505	Chatterjee 1985	late Norian
<i>Hesperosuchus</i>	140	Colbert 1952	late Norian
<i>Dimorphodon</i>	86	BMNH R1034	Hettangian
<i>Eudimorphodon</i>	41	Wild 1978	late Norian
<i>Lagerpeton</i>	77.8	Sereno & Arcucci 1994a	Ladinian
<i>Dromomeron gregorii</i>	96	Nesbitt <i>et al.</i> 2009a	late Norian
<i>Dromomeron romeri</i>	127.6	GR 236	late Norian
<i>Marasuchus</i>	56.3	Carrano 2006	Ladinian
<i>Pseudolagosuchus</i>	115	Carrano 2006	Ladinian
<i>Asilisaurus</i>	140	NMT RB uncatalogued	Anisian
<i>Eucoelophysis</i>	210	Sullivan & Lucas 1999	late Norian
<i>Sacisaurus</i>	103	Ferigolo & Langer 2007	early Norian
<i>Silesaurus</i>	210	ZPAL Ab III 361/23	early Norian
<i>Pisanosaurus</i>	–	–	earliest Norian
<i>Lycorhinus</i>	–	–	Hettangian
<i>Heterodontosaurus</i>	113.2	Carrano 2006	Hettangian–Sinemurian
<i>Abriotosaurus</i>	77.1	Carrano 2006	Hettangian
BMNH A100	–	–	Hettangian
<i>Eocursor</i>	109	Butler <i>et al.</i> 2007	Rhaetian
<i>Lesothosaurus</i>	102	Carrano 2006	Hettangian
<i>Scutellosaurus</i>	114	Carrano 2006	Sinemurian
<i>Scelidosaurus</i>	403	Carrano 2006	Sinemurian
<i>Emausaurus</i>	–	–	Toarcian
<i>Huayangosaurus</i>	475	Carrano 2006	Bathonian
<i>Stormbergia</i>	202	Butler 2005	Hettangian
<i>Agilisaurus</i>	198.5	Carrano 2006	Bajocian
<i>Hexinlusaurus</i>	153.4	Carrano 2006	Bajocian
<i>Yinlong</i>	190	Xu <i>et al.</i> 2006	Oxfordian
<i>Panphagia</i>	–	–	Carnian
<i>Saturnalia</i>	157	Langer 2003	Carnian
<i>Pantydraco</i>	72	Yates 2003a	Rhaetian
<i>Efraasia</i>	551	Carrano 2006	late Norian
<i>Plateosauravus</i>	600	Haughton 1924	Rhaetian
<i>Ruehleia</i>	800	Galton 2001	late Norian
<i>Unaysaurus</i>	–	–	early Norian
<i>Plateosaurus gracilis</i>	543	SMNS 5715	early Norian
<i>Plateosaurus engelhardti</i>	750	Carrano 2006	late Norian–Rhaetian
<i>Plateosaurus ingens</i>	–	–	Rhaetian
<i>Eucnemesaurus</i>	–	–	Rhaetian
<i>Riojasaurus</i>	608	Carrano 2006	late Norian
<i>Massospondylus carinatus</i>	335	Carrano 2006	Hettangian–Sinemurian
<i>Coloradisaurus</i>	–	–	late Norian
<i>Lufengosaurus</i>	780	Carrano 2006	Hettangian
<i>Glacialisaurus</i>	–	–	Hettangian
<i>Jingshanosaurus</i>	845	Carrano 2006	Hettangian

Taxon	Femur length	Source	Age
<i>Yunnanosaurus</i>	435	Young 1942	Hettangian
<i>Anchisaurus</i>	221	Carrano 2006	Sinemurian
<i>Aardonyx</i>	681	Yates <i>et al.</i> 2010	Hettangian
<i>Melanorosaurus</i>	583·3	Carrano 2006	Rhaetian
<i>Blikanasaurus</i>	–	–	Rhaetian
<i>Antetonitrus</i>	794	Yates & Kitching 2003	Rhaetian
<i>Lessemsaurus</i>	780	Pol & Powell 2007a	late Norian
<i>Gongxianosaurus</i>	1164	Carrano 2006	Pliensbachian
<i>Isanosaurus</i>	760	Carrano 2006	Rhaetian
<i>Vulcanodon</i>	1100	Carrano 2006	Hettangian
<i>Tazoudasaurus</i>	1230	Allain & Aquesbi 2008	Toarcian
<i>Shunosaurus</i>	1250	Carrano 2006	Bajocian
<i>Barapasaurus</i>	1365	Carrano 2006	Toarcian
<i>Patagosaurus</i>	1542	Carrano 2006	Callovian
<i>Staurikosaurus</i>	220	Carrano 2006	Carnian
<i>Chindesaurus</i>	265	Long & Murry 1995	late Norian
<i>Herrerasaurus</i>	482	Carrano 2006	Carnian
<i>Eoraptor</i>	154	Carrano 2006	Carnian
<i>Guaibasaurus</i>	214	Carrano 2006	early Norian
<i>Tawa</i>	174	GR 244	late Norian
<i>Lophostropheus airelensis</i>	–	–	Rhaetian
<i>Segisaurus</i>	142·9	Carrano 2006	Pliensbachian
' <i>Syntarsus</i> ' <i>kayentakatae</i>	272	Carrano 2006	Sinemurian
<i>Coelophysis rhodesiensis</i>	203	Carrano 2006	Hettangian
<i>Coelophysis bauri</i>	233	GR 148	Rhaetian
<i>Liliensternus liliensterni</i>	424	Carrano 2006	late Norian
<i>Zupaysaurus</i>	–	–	late Norian
<i>Cryolophosaurus</i>	769	Smith <i>et al.</i> 2007	Hettangian
' <i>Dilophosaurus</i> ' <i>sinensis</i>	587	Carrano 2006	Hettangian
<i>Dracovenator</i>	–	–	Hettangian
<i>Dilophosaurus wetherilli</i>	552	Carrano 2006	Sinemurian
<i>Ceratosaurus</i>	759	Carrano 2006	Kimmeridgian
<i>Elaphrosaurus</i>	529	Carrano 2006	Kimmeridgian
<i>Condoraptor</i>	600	Rauhut 2005	Callovian
<i>Piatnitzkysaurus</i>	548	Carrano 2006	Callovian
<i>Dubreuillosaurus</i>	450	Allain 2005	Bathonian
<i>Eusteptospondylus</i>	510	Carrano 2006	Callovian
<i>Metriacanthosaurus</i>	849	Carrano 2006	Oxfordian

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