The Carnian Pluvial Episode and the origin of dinosaurs

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Abstract: We present new evidence for a major inflection point in the history of tetrapods on land, a jump in the diversification of archosauromorphs, primarily dinosaurs, at 232–230 Ma. This corresponds to a long-noted changeover in Triassic terrestrial tetrapod faunas from those dominated by synapsids, many of them holdovers from the Permian, to those dominated by dinosaurs. The dinosaur explosion is shown here to correspond in timing to the Carnian Pluvial Episode (CPE), dated at 232 Ma, a time of increased rainfall and perturbation of oceans and atmospheres, followed by substantial aridification. The rock record through the CPE confirms that this event shared many characters with other mass extinctions driven by eruption of large igneous provinces, in this case the Wrangellia flood basalts of the west coast of North America. If this was a catastrophic extinction event, then the environmental perturbations of the CPE explain the sharp disappearance of various terrestrial tetrapods, and the subsequent sharp rise of dinosaurs and perhaps other clades too, especially those that constitute much of the modern terrestrial faunas, such as lissamphibians, turtles, crocodiles, lizards and mammals.

Dinosaurs famously dominated Mesozoic landscapes, and they (perhaps ironically) are identified as being part of a 'modern' fauna that included also lissamphibians (frogs, salamanders), turtles, lizards, crocodiles and mammals, all of which originated in the Triassic. How did this modern terrestrial vertebrate fauna rise to dominance, and what was the role of deep ecosystem turnovers in triggering it? Here we focus on the rise of dinosaurs, but future work should explore these wider questions.

There have been many opinions about the origin of the dinosaurs, with models involving competition, environmental triggers, or a mixture of both. The traditional view had been that dinosaurs emerged triumphant in the Late Triassic at the end of a series of replacement events throughout the Triassic (e.g. Colbert 1966; Romer 1970). Early Triassic faunas of synapsids were supplanted in the Middle Triassic by rhynchosaurs as herbivores, and basal archosaurs as carnivores, and then these two groups were replaced in turn by dinosaurs as both herbivores and carnivores in the Late Triassic. The rise to dominance of dinosaurs was seen as an ecological relay that was mediated in some way by competition, and is hence termed the competitive model, and the success of dinosaurs was explained in terms of their upright posture, predatory skills or warm-bloodedness (e.g. Bakker 1972; Charig 1972).

Benton (1983, 1986, 1991) opposed this viewpoint with an opportunistic model, in which dinosaurs emerged in the late Carnian or early Norian, and then diversified explosively. This is recorded best in the Ischigualasto Formation of Argentina, and stratigraphic equivalents in Brazil, India, Zimbabwe, Morocco, the southwestern USA, Poland and Scotland. The opportunistic model focused on rapid expansion, and Benton attributed this to the extinction of the formerly dominant herbivores, most notably dicynodonts and rhynchosaurs, triggered by a major worldwide floral change, during which floras dominated by the seed-fern *Dicroidium* were replaced by conifer floras. This was then tied to the rapid dry–humid–dry climate change event worldwide associated with the

Carnian pluvial episode of Simms & Ruffell (1989, 1990), renamed the Carnian Humid Episode by Ruffell *et al.* (2015), but we use the original term, Carnian Pluvial Episode (CPE), as given by Dal Corso *et al.* (2018).

Since 1990, there have been remarkable advances in five areas that have renewed focus on the CPE as the possible trigger that enabled dinosaurs, and possibly the other members of the modern terrestrial fauna, to diversify and dominate the land. First, our knowledge of Triassic vertebrate faunas has expanded substantially, and especially new evidence that dinosaurs did not originate in the late Carnian, 230 Ma, but at least in the Anisian or even Olenekian, 248–245 Ma (Brusatte *et al.* 2011; Nesbitt *et al.*, 2012). Second, the CPE, which had been debated in a few papers but had mainly been ignored, attracted renewed interest when Dal Corso *et al.* (2012) provided geochemical and stratigraphic evidence for a link to the Wrangellia flood basalt eruptions in western North America, and Dal Corso *et al.* (2015) and Ruffell *et al.* (2015) identified the CPE as a worldwide phenomenon. Third, improved chronostratigraphy, involving new radioisotopic dating, improved correlations of magnetostratigraphic models and improved biostratigraphy, has contributed to an order-of-magnitude enhancement in precision of dating and correlation (e.g. Furin *et al.* 2006; Bernardi *et al.* 2018a). Fourth, new computational techniques have allowed palaeontologists to explore macroevolution and macroecology in new ways, identifying changing rates of trait evolution, interactions between clades and models of diversification, and shedding new light on the patterns and processes behind the origin and later explosive diversification of dinosaurs (e.g. Brusatte *et al.* 2008; Sookias *et al.* 2012; Benton *et al.* 2014). Fifth, new fossil discoveries and new cladistic analyses are expanding our knowledge of the early evolution of dinosaurs and their nearest relatives, but also highlighting some contentious points about fundamental branching points in the early evolution of clade Dinosauria and its closest relatives (e.g. Baron *et al.* 2017; Langer *et al.* 2017; Nesbitt *et al.* 2017).

These advances have encouraged palaeontologists to look again at the origin of the dinosaurs in an ecological sense. The current view contains some aspects of both the classic competition model and the Benton (1983) opportunistic model, that crurotarsan-dominated faunas were replaced by a gradual process (Irmis *et al.* 2007; Brusatte *et al.* 2010; Nesbitt *et al.* 2010; Martínez *et al.* 2011; Benton *et al.* 2014) that was probably accelerated by the ecological perturbation of the CPE (Bernardi *et al.* 2018*a*). The CPE caused widespread extinction, and this was followed by the first substantial diversification of dinosaurs. The diversification of dinosaurs in the Triassic can in fact be divided into three phases: (1) a possible origin in the Olenekian–Anisian, 248–245 Ma (Nesbitt *et al.* 2010, 2012; Brusatte *et al.* 2011), related to the turmoil of recovering life in the aftermath of the devastating Permian–Triassic mass extinction (PTME); (2) a distinctive and rapid diversification of saurischians, primarily sauropodomorphs and possible theropods, termed the dinosaur diversification event (DDE) by Bernardi *et al.* (2018*a*) some 13–16 myr later in the late Carnian, following the CPE, at 232 Ma; (3) a further diversification of theropods and especially ornithischians after the end-Triassic mass extinction, 201 Ma.

Here, we explore new data on the relative abundances of archosauromorphs and early dinosaurs, based on both skeletal and footprint data through the Triassic, and especially through the DDE, where we find evidence of a substantial macroevolutionary jump in ecosystem composition. We then explore the dating of the CPE and DDE, to establish whether they did or did not occur at the same time. Finally, we consider possible causal links: how could a dry–humid–dry climatic shift have triggered the rise to ecological dominance of the dinosaurs?

Macroecology of Triassic tetrapod faunas: methods

Benton (1983) presented a summary of the relative abundances of tetrapod taxa in all major terrestrial faunas worldwide through the Triassic and Early Jurassic, and used this to provide evidence that the massive diversification of dinosaurs in the late Carnian followed, but did not cause, the extinction of dominant herbivores, including rhynchosaurs and dicynodonts. He distinguished (Benton 1986, 1991) two episodes in the dinosaurian takeover of the world: the expansion of sauropodomorph dinosaurs as herbivores through the Norian, and then the diversification of theropods, sauropods and ornithischians after further extinctions some 30 myr later, as part of the end-Triassic mass extinction (ETME). The purpose of exploring the data on fossil abundances was to determine what was happening at an ecological level; the extraordinary dominance by particular taxa at particular times is not so evident from simple taxon counts (numbers of species, genera or families). At an extreme, for example, many older faunas were ecologically dominated by rhynchosaurs, which could form 50–90% of all specimens collected (Benton 1983) but might be represented by just a single species in the diversity counts.

Here, we update the ecological database. We took the data appendix of Benton (1983) as a basis, and checked and updated every figure from literature sources and from correspondence with current experts on each of the faunas. In doing so, we increased the number of faunas from 31 as given by Benton (1983) to 47 in this study (supplementary material, Table S1), and from a total of 3575 specimens as given by Benton (1983) to 7773 here. We checked formation ages and species lists from the Early Tetrapod Database (Benton *et al.* 2013), followed by an exhaustive literature search of over 200 publications, which provided new discoveries and revisions. The Paleobiology Database was used to resolve queries. Faunas and formations were dated using current literature, summarized by Benton *et al.* (2013), as well as later revisions (Ezcurra *et al.* 2017; Bernardi *et al.* 2018*a*; Langer *et al.* 2018), and subdivided to epoch level, with the epochs having a mean duration

of 3.7 myr, according to information in the latest International Chronostratigraphic Chart (http://www.stratigraphy.org). We prefer this fine timescale division (supplementary material, Table S2) over the more generally used stage-level time bins or 10–11 myr time bins, because these can mask a great deal of macroevolution, even though there is a greater risk of mis-assignment of formations to our smaller time bins (Benton *et al.* 2013). In particular, we note that the Carnian Pluvial Event, occurring as it does in the middle of the Carnian Stage, has not been identified in previous analyses because the wrong, all-encompassing time bins were used. We present only limited results from this revision exercise, and will develop the new ecological database and its significance in another paper.

By expanding the database of Bernardi *et al.* (2018*b*) to include the Late Triassic we also calculated the relative abundance of dinosaurian ichnotaxa in the ichnoassociations spanning the whole Triassic, providing an independent source of data (supplementary material, Table S3). We used published sources only, and for dinosaur-produced footprints we considered only those confidently assigned to dinosaurian ichnotaxa (e.g. Olsen *et al.* 1998, and the criteria outlined by Bernardi *et al.* 2018*a*). We used the proportion of dinosaur ichnotaxa to tetrapod ichnotaxa (DT/TT) to avoid uncertainties on track–trackmaker attributions among non-dinosaurian tetrapods. However, given that with very few exceptions (e.g. *Rhynchosauroides* and some synapsid-related ichnogenera) the most common Triassic footprints are those of archosaurs, we highlight that the DT/TT ratio is in fact a good indicator of the relative proportion of dinosaurs versus non-dinosaurian archosaurs.

Macroecology of Triassic tetrapod faunas: results

There is a significant positive correlation between specimen count and generic richness among the formations used in this study, which is evidence that sample size has a direct effect on the counts of generic richness. Therefore, we show plots of relative abundance of the key clades through the Triassic and Early Jurassic. In the summary diagram (Fig. 1), the diapsids consist primarily of archosauromorphs (red line), and the rise and the fall of synapsids (black line) is clear. Breaks in the curves indicate low sampling in those time bins.

Looking at the rise of dinosaurs in more detail, as derived from a literal reading of the relative abundance data (Fig. 2, red line), the proportion represented by specimens (= relative abundance) rises from 0% in the early Carnian to 95% in the late Norian, then falls across the ETME, and rises again in the Early Jurassic. The proportions of dinosaurian genera (Fig. 2, blue line) show a similar pattern through this time interval, but slightly more muted, with other taxa such as synapsids, parareptiles and temnospondyls providing substantial numbers of genera, but evidently rather rare as individuals in faunas. Measured either way, these data document the DDE, the rise of the dinosaurs, from negligible numbers up to the late Carnian to 60–100% of specimens and 40–60% of genera by the mid- to late Norian, over a span of 20 myr.

There are many problems with analyses of this kind. For example, although these relative abundance plots (Figs 1 and 2) summarize the data in an ecologically relevant way, focusing on relative abundances in well-sampled faunas rather than on summary lists of species, however rare, as in traditional palaeodiversity plots, they are still enormously variable through time, presumably documenting facies variations and regional effects as much as evolution. For example, temnospondyl amphibians are diverse and abundant in Early Triassic faunas from Russia and Australia, but rare in coeval faunas in South Africa, which could reflect some biogeographical or climate-related effects, or simply sampling from different sedimentary environments. Further, even though the time bin sizes we used vary from 1.4 to 10.9 myr (mean 3.7 myr), some of them, especially the long early Norian bin (10.9 myr), presumably still
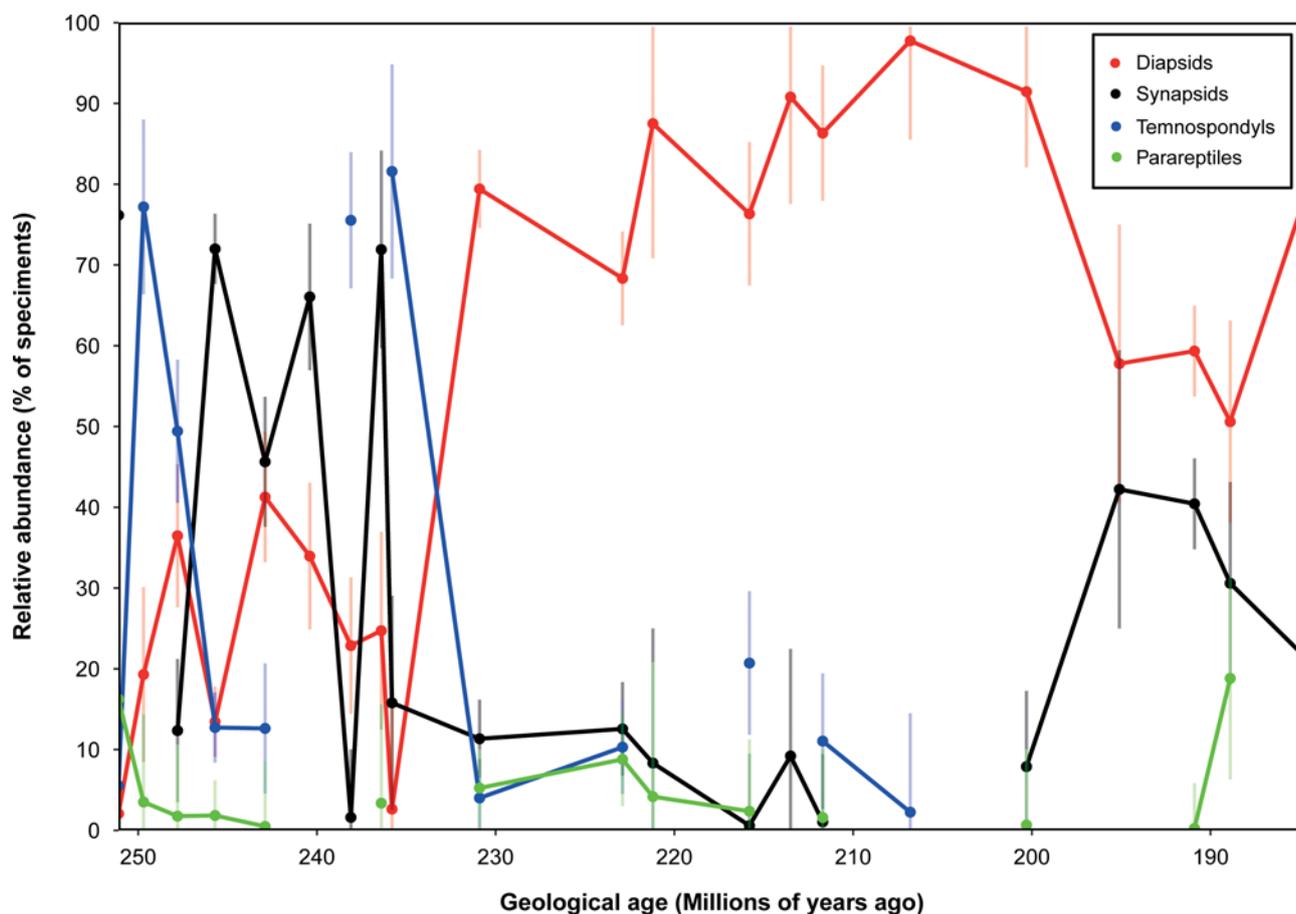
Fig. 1. Relative abundances of key tetrapod clades through the Triassic, based on counts of individual, rich faunal assemblages. The curves show spiky patterns because these are not averaged totals from multiple faunas within a time bin; therefore, they show some rapid switches up and down, reflecting regional and facies differences, as well as macroevolutionary change. Parareptiles (green) show low relative abundances throughout, rarely exceeding 10%, and often falling below the sampling threshold. Temnospondyls (blue) were highly abundant in some regions in the Early Triassic, and occasionally thereafter, but they generally declined to the end of the Triassic. Synapsids (black) show some high peaks in the Middle Triassic, but decline towards the end of the Triassic, being represented then and in the Jurassic by the first mammals and by tritylodonts. Archosauromorphs (red) also show a zig-zag pattern, but remained at levels generally below 30–40% in the Early and Middle Triassic, and then stepped up to levels from 60 to 100% from the mid-Carnian (c. 230 Ma) onwards. Based on data in Table S1.

mask a great deal of detail. Greater stratigraphic precision is required to determine exactly how and when the DDE occurred, and what might have driven it.

Seeking a change in macroevolutionary regime

The generic and specimen count data can be summarized differently, focusing on the changes through time, but also the relative proportions. In recent macroevolutionary works, several researchers have focused on the long-term rise of archosauromorphs and decline of synapsids through the Triassic (e.g. Sookias et al. 2012; Benton et al. 2014; Button et al. 2017), and we document this here, in terms of proportions of genera (Fig. 3a) and of specimens (Fig. 3b) per fauna. Both plots highlight the widely variable total size of the faunas, in terms of total genera or total specimens (indicated by bubble size), but that the ratio of archosauromorphs to the total of all tetrapods starts low at the beginning of the Triassic, rises and then reaches a plateau around 230 Ma. Plots are similar for dinosaurs alone, shown as proportions of genera (Fig. 3c) and of specimens (Fig. 3d), but with values of zero through the Early and Middle Triassic, and high values after the mid-Carnian, but more erratic because of greater differences in faunal composition between faunas, perhaps reflecting regional, environmental and taphonomic differences in faunas. For example, Norian faunas from Germany and South America may have 80–90% dinosaurs, whereas some

coeval faunas from North America and China have only 20–50% dinosaurs, in terms of proportions of specimens to all tetrapod specimens.

Rather than impose a break point in the best-fitting curve, we sought to identify one or more break points statistically and without *a priori* assumptions. We used the software 'segmented' in R (Muggeo 2008), which identifies segmented or broken-line models to fit bivariate data. These are regression models where the relationships between the response and one or more explanatory variables are piecewise linear, meaning that they can be represented by two or more straight lines that connect at so-called break points. The assumption is that a threshold is reached where the linear relationship shifts, and the method seeks the break point without pre-conditions, other than simply the best fit that can be achieved with two or more distinct linear models, each of which explains a range of the data.

Our analysis of the archosauromorph generic proportions plot (Fig. 3a) identified two straight lines that best fit the data with a substantial jump (Fig. 4a) located in the time range 231.1–230.9 Ma ($R^2 = 0.807$). This corresponds to the break point identified when the two best-fitting lines, before and after the break point, are plotted (Fig. 4b). The method independently identified the break point at 231 Ma as the time when the values shifted substantially, and the 'effect of the midpoint' jumps from 0.3 to >0.7 (Fig. 4a). This corresponds to the end of the CPE, the time at which climates shifted
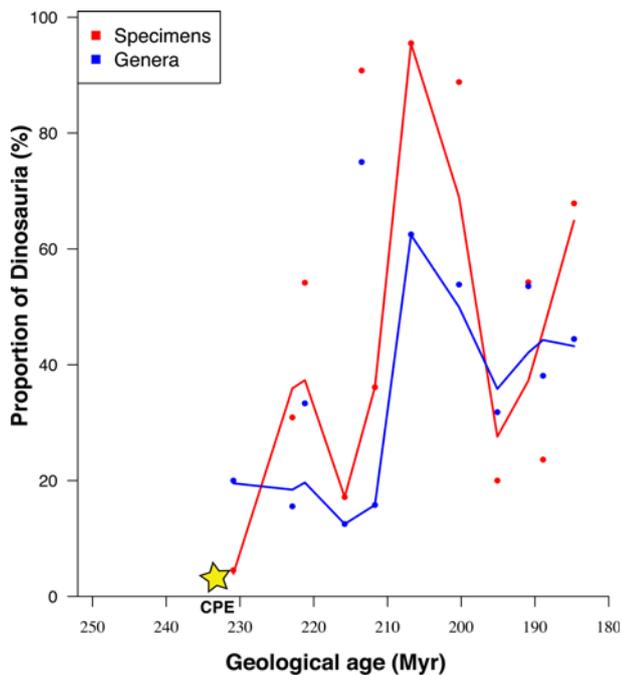
Fig. 2. Proportions of early dinosaurs through the Triassic, showing the rapid rise in the late Carnian and early to middle Norian. Two metrics are shown, numbers of specimens and numbers of genera in 12 sampled faunas, in proportion to all tetrapods; the linking line is a moving average. Specimen counts perhaps exaggerate the trend when compared with generic counts, or at least both show different aspects of the same rise in ecological impact of the dinosaurs in the Late Triassic. (Based on data in supplementary material Table S1.)

from pluvial to arid. When repeated for specimens (Fig. 4c and d), the algorithm focuses on the dip in values in the latest Triassic (Fig. 3b), and is perhaps swamped by the huge specimen count in the *Lystrosaurus* Assemblage Zone, and so fails to pick up this break point, but identifies break points at either 229.0 and 209.1 Ma ($R^2 = 0.644$) or 204.0 and 195.2 Ma ($R^2 = 0.648$), using the lm method and depending on the initial specified constraints, or 220.1 and 236.9 Ma using the glm method. This statistical method has, remarkably, identified the step-change in archosauromorph generic relative proportions, from 0–40% to 60–95%, visible in Fig. 3a, and identified to 1 myr after the CPE, dated at 232 Ma.

The segmented method did not work well for dinosaurs on their own, finding a variety of dates (e.g. 190 and 240 Ma for genera, and 191 and 237 Ma for specimens), probably because of the smaller sample sizes and heterogeneity of individual faunal counts; as noted above, proportions of dinosaurs in Late Triassic and Early Jurassic tetrapod faunas range from 0 to 90%, depending on palaeogeographical, environmental and taphonomic factors. Whereas all of these faunas have good representation of archosauromorphs, some of those that lack dinosaurs yield abundant crurotarsans. In any case, the counts appear to be too inconstant to reveal clearcut results.

The footprint record (Fig. 5a) shows a sharp change in the composition of tetrapod ichnoassociations from the late Carnian, when dinosaurs become abundant-to-dominant at most sites. Furthermore, when the ratio between dinosaur ichnotaxa and tetrapod ichnotaxa (DT/TT) is calculated for each site, a step-change in dinosaur relative proportion is seen at the early–late Carnian boundary, when the percentage shifts from 0 to 48% (Fig. 5b). The relative abundance of dinosaur ichnotaxa is then maintained throughout the Norian (56%), as recorded by the North American (Newark Supergroup, upper Chinle Formation and Dockum
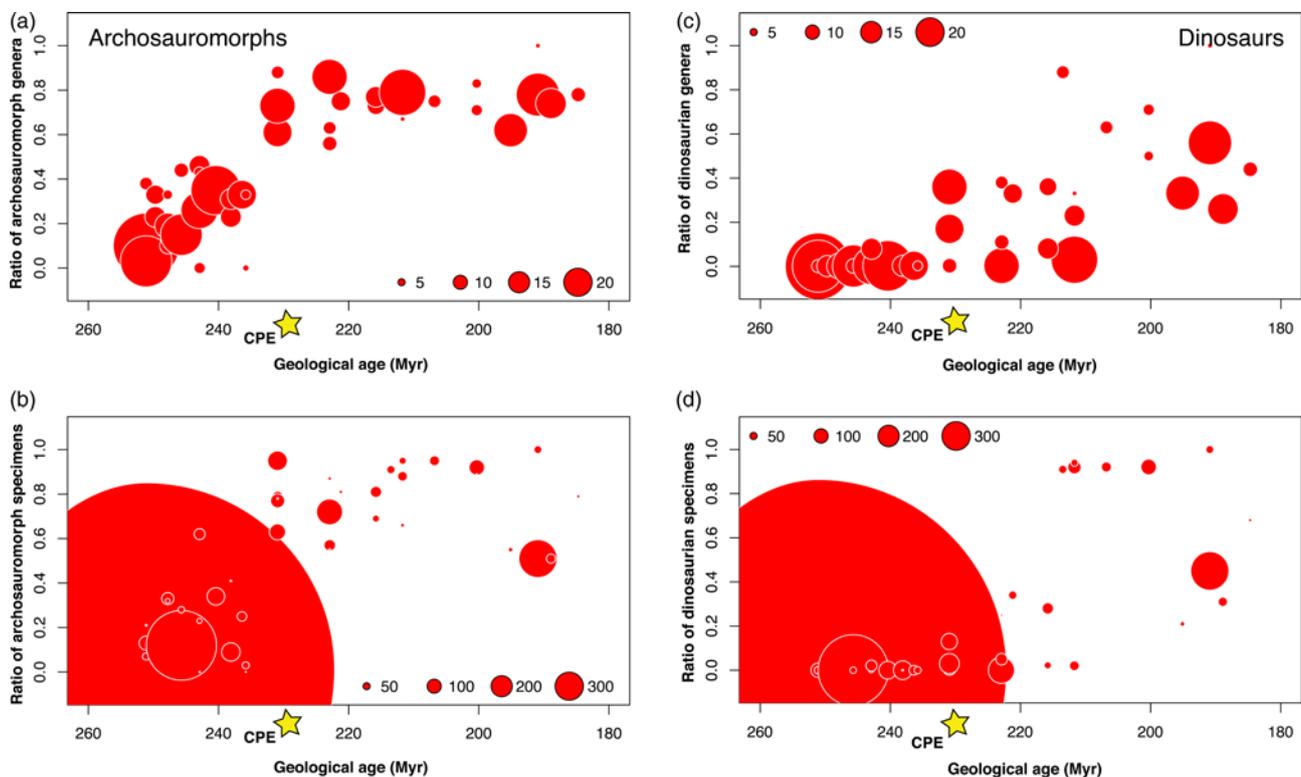

Fig. 3. Bubble plots of archosauromorph genera (**a**) and specimens (**b**), and dinosaur genera (**c**) and specimens (**d**), measured as proportions of all tetrapod taxa, in 47 faunas through the Triassic. Bubble size indicates sample size of each fauna, according to the keys in each portion of the figure. For archosauromorphs (**a**, **b**), the seeming regularity of positioning of values despite hugely varying sample sizes should be noted; the trend from low values (<0.4) in the Early and Middle Triassic to high values (>0.6) in the Late Triassic is clear. For dinosaurs (**c**, **d**), the initial values of zero in the Early and Middle Triassic, and then higher values, but irregular, because of small sample sizes and regional and taphonomic effects in the Late Triassic and Early Jurassic, should be noted.
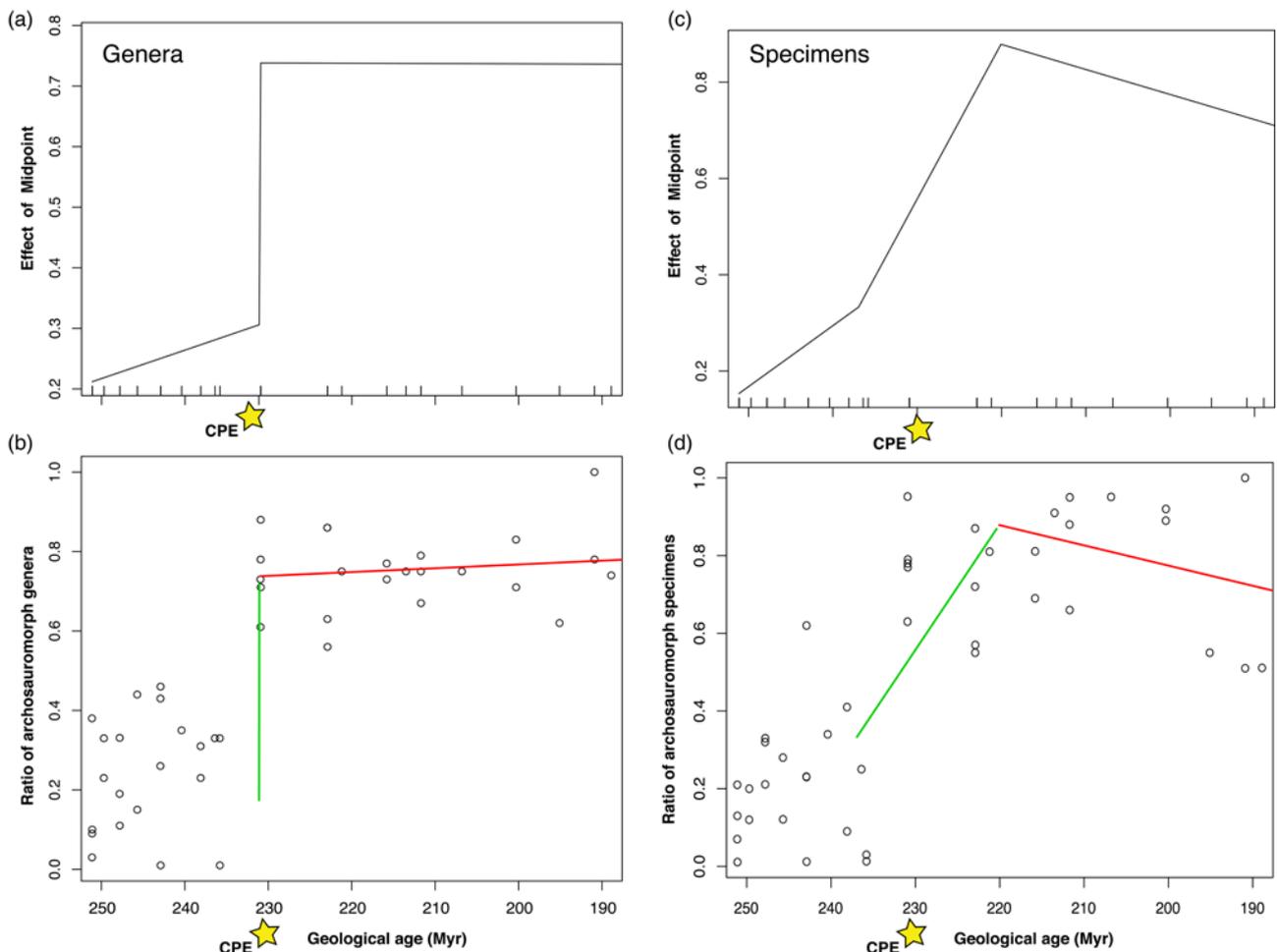
Fig. 4. Identifying break points in tetrapod faunal proportions throughout the Triassic, showing the effect of age (midpoint) for archosauromorph genera (**a**) and specimens (**c**), and the best-fitting lines before and after the break point for archosauromorph genera (**b**) and specimens (**d**). The result is most marked for archosauromorph genera (**a, b**), where a sharp state shift occurs at 231 Ma, but is less clear for archosauromorph specimens (**c, d**), where the values peak at 220 Ma, but with a gradual slope up from 237 Ma. Calculated using software 'segmented' in R (Muggeo 2008), this method uses no *a priori* assumptions, and identifies the break points to ensure best fit. The plots in (**a**) and (**c**) show the midpoints of time bins on the *x*-axis, and the effect of these values of the midpoints (*y*-axis).

Group), European (Löwenstein and Trossingen formations of the German Basin, the Dolomia Principale–Hauptdolomit of the Alps) and South African faunas (Bernardi *et al.* 2018*a*) and rises slightly in the Rhaetian (70%).

We could not identify break points using 'segmented' in R: the lm method gave break points at 225.3 and 248.2 Ma ($R^2 = 0.319$); the glm method gave break points at 222.7 and 223.6 Ma. The lack of resolution (low R^2; differing results with different linear modelling techniques) probably arises from the great variation in DD/TT ratios in the Late Triassic, from 0 to 100% (Fig. 5a), reflecting some ichnofaunas dominated by dinosaurian tracks, and others with none, perhaps as a result of different depositional regimes.

Dating the dinosaur diversification event

Attempts to establish the precise timing of key steps in the early history of dinosaurs have been hampered by the difficulty of precise temporal calibration for most dinosaur-bearing formations. Fossil footprints discovered in the reasonably well-dated Holy Cross Mountains sites (Brusatte *et al.* 2011) provided evidence for dinosauromorphs in the Olenekian of Poland, and the poorly age-constrained Middle Triassic Manda Formation of Tanzania has yielded remains of the possible oldest dinosaur, *Nyasasaurus parringtoni* (Nesbitt *et al.* 2012). Even if this is not a dinosaur, *Asilisaurus*, a member of Silesauridae, sister group of Dinosauria, is

also from the Manda Formation (Nesbitt *et al.* 2010), and so confirms the origin of dinosaurs by at least this date. Footprint evidence from Italy, France, Germany and Argentina (Lockley & Meyer 2000) confirms the presence of dinosauromorphs and possibly dinosaurs in the Middle Triassic of both Laurasia and Gondwana. But the oldest, well-dated, undisputed members of Dinosauria come from South America. These include taxa from the lower Ischigualasto Formation (late Carnian) of Argentina, whose age is radiometrically constrained between 231.4 ± 0.3 and 225.9 ± 0.9 Ma (Martínez *et al.* 2011). Similar ages are reported for horizons bearing early dinosaurs from the Santa Maria and Caturrita formations of Brazil, respectively 233.2 ± 0.7 and 225.4 ± 0.4 Ma (Langer *et al.* 2018). Other early dinosaur-bearing formations, such as the Lower (and Upper) Maleri Formation of India (Novas *et al.* 2011) and the Pebbly Arkose Formation of Zimbabwe (Langer *et al.* 2010), are poorly constrained in age, and are thought to be Carnian by loose biostratigraphic correlation (e.g. with the *Hyperodapedon* Assemblage Zone; Langer *et al.* 2010).

All these early records are largely of small to medium-sized (<6 m long; Benton 1983; Brusatte *et al.* 2010) and sparse dinosaurs, numerically not abundant, forming typically <5% of specimens in their faunas (Benton 1991). Larger body sizes (>10 m long), at least in some forms, and dramatically increased relative faunal abundances (up to 90% in mid- and late Norian faunas of Europe, South America and southern Africa at least) are seen after
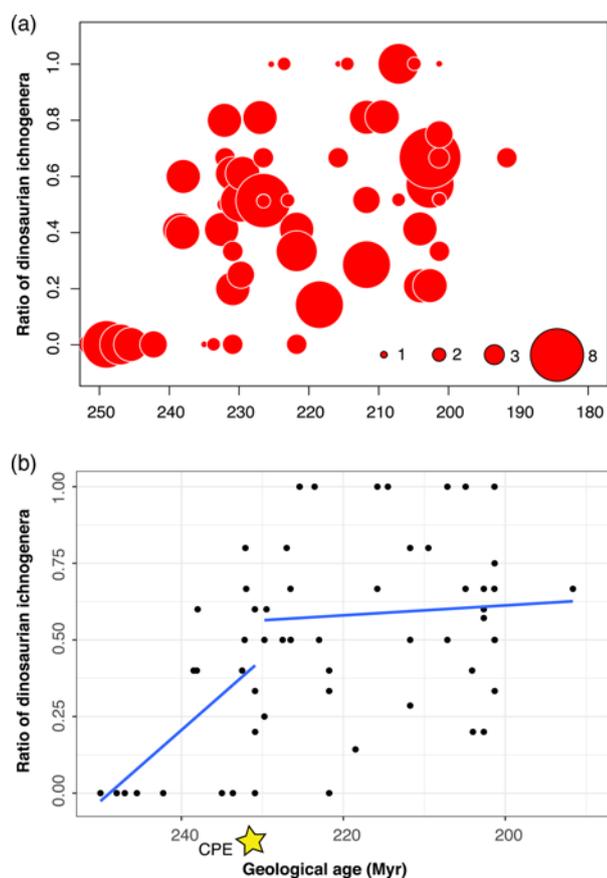
Fig. 5. Relative proportions of dinosaur to other archosaur footprints through the Triassic, focusing on Late Triassic ichnoassociations, shown as a bubble plot of ichnofaunas and their sizes (**a**), and as dated points with suggested break point indicated (**b**). Values jump from essentially no, or very rare, dinosaurs before 232 Ma, corresponding to the CPE, and then mean values of 48% in the late Carnian, 56% in the Norian and 70% in the Rhaetian. Formula for pre-CPE line is $y = 0.0179x + 4.4718$ ($R^2 = 0.27$), and for post-CPE is $y = 0.0033x + 1.291$ ($R^2 = 0.02$). (Based on data in supplementary material Table S3.)

the late Carnian, when dinosaurs became common components of terrestrial faunas (Bernardi *et al.* 2018*a*). This happened during the DDE (Bernardi *et al.* 2018*a*) as documented by the abundant tetrapod footprint faunas in the Dolomites region of Italy (Bernardi *et al.* 2018*a*,*b*) and the probably synchronous appearance of dinosaurs all over Pangaea, as in the Stuttgart Formation of the Germanic Basin, the Ipswich Coal Measures of Australia (Thulborn 1998), the Molteno Formation of South Africa (Raath *et al.* 1990), the Timezgadiouine Formation of Morocco (Lagnaoui *et al.* 2012), and the earliest dinosaur in the Los Rastros Formation (Marsicano *et al.* 2007) and the slightly younger skeletal remains in the Ischigualasto Formation (Martínez *et al.* 2011).

Recent dating provided by magnetostratigraphy, radioisotopic exact ages and non-tetrapod-based biostratigraphy has allowed reliable correlation of the well-dated European and Argentinian successions, leading to an order-of-magnitude improvement in our dating of the DDE (Bernardi *et al.* 2018*a*). When, for example, Benton (1983) posited a rather rapid DDE, he dated it as early Norian, based on the then-prevalent view of the age of the Ischigualasto Formation and its correlatives worldwide. The event is now shifted back in time to the mid-Carnian, from 228 to 232 Ma.

Dating the CPE

The CPE is thought to have been a global event (Ogg 2015; Ruffell *et al.* 2015) but to date it is best known from the Italian Dolomites

(Roghi *et al.* 2010; Dal Corso *et al.* 2015), the SW UK (Simms & Ruffell 1989; Miller *et al.* 2017), the Northern Calcareous Alps (Hornung *et al.* 2007; Roghi *et al.* 2010), the Trans-Danubian Range (Dal Corso *et al.* 2015) and the Germanic basin (Franz *et al.* 2014). Here a temporal constraint has been provided in recent years, especially taking advantage of the great bio-chrono-stratigraphic control available in some sections, and in particular in the Italian Dolomites. The CPE has always been dated as Carnian in age, and probably mid-Carnian (Simms & Ruffell 1989, 1990), but in the Italian Dolomites it has been shown to occur between the *Aonoides–Austriacum* boundary interval (about Julian) and the base of the *Subbullatus* Zone (Tuvalian), an interval that can be dated at 234–232 Ma (Roghi *et al.* 2010; Dal Corso *et al.* 2015). Recently, further constraint has been provided by astronomical correlation of the wide carbon isotope excursions documented in borehole successions of the SW UK, which indicate a maximum duration of 1.09 myr (Miller *et al.* 2017).

The CPE as trigger of the DDE

Despite some early suggestions (e.g. Benton 1986) that the Carnian might have witnessed as profound a mass extinction as the ETME, the event has been largely ignored in discussions of mass extinctions. However, in their review of the current understanding of mass extinctions, Bond & Grasby (2017) recognized the CPE as one of the most severe biotic crises in the history of life, even if not on the scale of the 'big five'. They noted the major environmental changes of the CPE, associated with global warming of up to 7°C, widespread ocean anoxia, $\delta^{13}C$ fluctuations, cessation of Western Tethyan carbonate platform productivity and the dry–humid–dry climate changes on land. In addition, they summarized associated extinctions among corals, crinoids and scallops, and turnovers of conodonts and ammonoids in the oceans, as well as the turnovers among plants, and among tetrapods, as noted in this paper. The physical driver of these catastrophic changes is linked to the emplacement of the Wrangellia large igneous province and other silicic and basaltic eruptive activity in the Huglu–Pindos, Kare Dere and South Taimyr complexes (Dal Corso *et al.* 2012). The model seems to replicate the PTME and ETME killing models, in which volcanic eruptions generate acid rain and greenhouse gases, which in turn lead to extinctions by shock warming, stripping of vegetation and soils on land, and ocean anoxia and acidification.

Our dating of the DDE suggests that it is coincident with the CPE, or at least the time immediately after, when climates recovered from humid to dry conditions again. In the wake of wide extinctions of plants and key herbivores on land, the dinosaurs were seemingly the main beneficiaries in the time of recovery, expanding rapidly in diversity, ecological impact (relative abundance) and regional distribution, from South America initially, to all continents.

The new dating and the new understanding of the CPE does not reconcile all steps of the DDE. Benton (1983, 1991) had argued that the extinctions of rhynchosaurs and dicynodonts were precursor to the explosion of dinosaurs, especially of the medium- to large-sized sauropodomorphs, and yet current views on dating show some discrepancies. The key is to date the *Hyperodapedon* Assemblage Zone (HAZ) correctly; this is characterized by the rhynchosaur *Hyperodapedon*, a herbivore that specialized on tough vegetation, and often occurs in great abundance, in the Santa Maria Formation of Brazil, the lower part of the Ischigualasto Formation of Argentina, the Lossiemouth Sandstone Formation of Scotland and the Lower Maleri Formation of India (Langer *et al.* 2010). The HAZ is dated as late Carnian to early Norian, perhaps 228–224 Ma by some researchers (e.g. Brusatte *et al.* 2010; Ezcurra *et al.* 2017), in line with earlier suggestions (e.g. Benton 1983, 1991), some 4–8 myr after the CPE. However, new dates and faunal analysis split the tetrapods of the Ischigualasto Formation into a lower and upper

fauna, the lower with rhynchosaurs and dicynodonts, the upper with dicynodonts (Langer *et al.* 2018). This places the extinction of rhynchosaurs as coincident with the CPE in Argentina and Brazil at least, and Langer *et al.* (2018, fig. 3) dated the HAZ as around 233 Ma, and hence coincident with the CPE. There is no independent age evidence for other members of the HAZ, such as the Lossiemouth Sandstone Formation and the Lower Maleri Formation, so they too could be older than generally assumed, dating to around the time of the CPE, or rhynchosaur extinction might be disconformable from continent to continent.

Benton (1983, 1991) was wrong to suggest that extinction of dicynodonts occurred at the same time as extinction of rhynchosaurs, as kannemeyeriid dicynodonts were important herbivores until at least 219 Ma, some 13 myr after the CPE. For example, they occur in the upper Ischigualasto Formation of Argentina (*c.* 226–224 Ma; Langer *et al.* 2018) and Caturrita Formation of Brazil (225.4 Ma; Langer *et al.* 2018), and are well known in North America up to the level of the *Placerias* Quarry in Arizona (Chinle Formation, lower Sonsela Member), dated at 220–219 Ma (Ramezani *et al.* 2014; Langer *et al.* 2018), and other survivors are known from post-Carnian strata in Poland and Morocco.

Therefore, the DDE probably occurred in steps, as suggested by Langer *et al.* (2010, 2018), with a first burst of dinosaurian diversity in the late Carnian, represented by the upper Ischigualasto Formation and coeval units; here, the dinosaurs were small to medium-sized, and mostly carnivorous, and diverse, but not abundant. Perhaps this followed the CPE and possible extinction of rhynchosaurs in most, or all, parts of the world. Then followed the long span of the early Norian, from 228.5 to 218 Ma, during which dicynodonts and sauropodomorph dinosaurs were the major herbivores, but often either one or the other in particular faunas. Finally, with the disappearance of dicynodonts, sauropodomorph dinosaurs became truly large in the middle and late Norian, from 218 Ma. This was followed by the extinction of such key basal archosaur groups as rauisuchians, phytosaurs and aetosaurs during the end-Triassic mass extinction, 201 Ma, and the diversification of sauropods, larger theropods, ornithopods and armoured dinosaurs subsequently, in the Jurassic.

Conclusions

We present statistical evidence that the Carnian Pluvial Episode (CPE) marks a major macroecological shift in faunas. We focus on the long-recognized major burst in dinosaurian diversity, the dinosaur diversification event, which corresponds in age to the CPE. The diversity and abundance of tetrapods through the Triassic indicate a major disjunction at exactly the CPE. This is shown by both skeletal and footprint data, and can be detected by use of novel computational means that seek to identify statistically significant breaks in lines of best fit. If this is confirmed as a rapid event, then it may have been one of the most important in the history of life in terms of its role in allowing not only the 'age of dinosaurs', but also the origins of most key clades that form the modern fauna of terrestrial tetrapods, namely the lissamphibians, turtles, crocodiles, lizards and mammals.

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