

Models for the Rise of the Dinosaurs

Review

Michael J. Benton^{1,*}, Jonathan Forth¹, and Max C. Langer²

Dinosaurs arose in the early Triassic in the aftermath of the greatest mass extinction ever and became hugely successful in the Mesozoic. Their initial diversification is a classic example of a large-scale macroevolutionary change. Diversifications at such deep-time scales can now be dissected, modelled and tested. New fossils suggest that dinosaurs originated early in the Middle Triassic, during the recovery of life from the devastating Permo-Triassic mass extinction. Improvements in stratigraphic dating and a new suite of morphometric and comparative evolutionary numerical methods now allow a forensic dissection of one of the greatest turnovers in the history of life. Such studies mark a move from the narrative to the analytical in macroevolutionary research, and they allow us to begin to answer the proposal of George Gaylord Simpson, to explore adaptive radiations using numerical methods.

Introduction

It may seem unusual to select dinosaurs as an exemplar group upon which to test numerical models in macroevolution. Dinosaurs dominated terrestrial environments for over 170 million years, in terms of their range of body sizes, their overall biomass within ecosystems, and their diversity of adaptations. Dinosaur phylogeny is relatively well understood from numerous cladistic analyses, and current intense study of the nearly 1000 species of dinosaurs has shed considerable light on the morphology and adaptation of all major subgroups. Sometimes — as with the remarkable specimens from the Jurassic and Cretaceous of China — fossils may preserve substantial anatomical detail, including the entire skeleton, as well as feathers and even some internal organs. Our purpose here is to seek to understand the nature of adaptive radiation in an intensively studied fossil example.

Ever since George Gaylord Simpson introduced a Darwinian approach to macroevolution in 1944, in his classic book *Tempo and Mode of Evolution* [1], researchers have sought to understand how clades diversify. Simpson stressed that diversifications, or ‘adaptive radiations’, were important times in the evolution of clades, when their morphological characteristics were acquired and their ecological roles established. When considering modern biodiversity, it is evident that some clades are ‘successful’, or at least rich in species, and others are not. For example, birds and crocodylians shared a common ancestor some 250 million years ago (Ma), in the Early Triassic, and yet there are 10,000 species of birds today, but only 23 species of crocodylians. Why the difference?

Simpson [1] stressed the importance of ‘key adaptations’ — morphological, physiological, or behavioral features that were instrumental in the early diversification of a clade. For example, the current species richness of birds might be explained by key adaptations such as feathers, powered flight, warm-bloodedness, or enhanced sensory ability [2]. Other diverse clades might have benefited from surviving a mass extinction, and then diversifying in the aftermath. This is the case for modern mammals, which diversified after the mass extinction of dinosaurs 66 Ma, and yet key adaptations, such as warm-bloodedness, intelligence, care for offspring, and adaptable dentitions were doubtless important drivers of their evolution [3]. In studying adaptive radiations, both species richness (number of species) and morphological variation are considered. In terms of species richness, the rate of diversification of a clade is the difference between speciation (origination) rate and extinction rate. Palaeontologists commonly call species richness and morphological variation ‘diversity’ and ‘disparity’, respectively (Box 1) [4,5].

Most models of adaptive radiations are built on the assumption that diversification and expansion of morphological variety occur in tandem, or are coupled [1,6,7]. And yet, there is no fundamental reason for such an assumption. It is perfectly possible for diversity and disparity to be decoupled, and for species numbers to expand independently of morphological variability (Figure 1). This might resolve a dilemma exposed in a recent study [8] of adaptive radiations. Whereas the classic model of an adaptive radiation [1] would imply an ‘early burst’ model, meaning a rapid expansion in species numbers soon after the origin of the clade, and a steady state thereafter, a comparison of many phylogenetic trees based on living taxa only [8] established that early burst models were rare. On the other hand, synoptic studies of palaeontological examples [6,7] have found that most diversifications show disparity first. This suggests that the classic Simpsonian early burst in clade origins [1] may be expressed through expansion of disparity first, and diversity second. Clades may commonly expand by divergence of lineages to the furthest limits of achievable morphology, and then new species emerge within these morphological bounds, effectively filling gaps in morphological space.

These new studies [6–8] have been enabled by improvements in data and methods. In terms of data, there are now many more fossils, of dinosaurs, and of most other groups, and they are much more precisely dated than ten or twenty years ago (Box 2). New fossils fill gaps in knowledge, and improved dating allows more accurate estimation of evolutionary rates. New numerical methods have also been developed that allow biologists and palaeontologists to construct large phylogenetic trees and assess their robustness, to explore morphometrics (shape measures), and to combine these in phylogenetic comparative analyses that do not treat species as independent entities, but as parts of phylogenetic lineages and trees [9,10].

When major clades diversify, this has often been after their precursors had died out, such as when mammals diversified after the demise of dinosaurs. Other biotic replacements, however, such as the diversification of the dinosaurs some 170 million years earlier in the Triassic, have occasionally been interpreted as examples of the competitive replacement of one clade by another and cited as evidence for progress in

¹School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, UK. ²Departamento de Biologia, FFCLRP, Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto-SP, Brazil.

*E-mail: mike.benton@bristol.ac.uk

This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.



Box 1

Glossary.

Amniota: the clade of tetrapods that lay shelled, amniotic eggs, including groups traditionally called reptiles, birds, and mammals.

Archosauria: the major amniote clade that includes dinosaurs, crocodiles and birds, and their ancestors.

Avemetatarsalia: the clade that includes largely small and medium-sized bipedal archosaurs in the Triassic, leading to pterosaurs, dinosaurs, and birds; sometimes called the 'bird line', or Ornithodira.

Cope's rule: the suggestion that animals evolve from small to large size, and more specifically, a driven one-way trend of increasing mean body mass within a clade.

Crurotarsi: the clade that includes various fish-eating, carnivorous, and herbivorous archosaurs in the Triassic, as well as crocodiles and their ancestors; sometimes called the 'crocodile line', or Pseudosuchia.

Digitigrade posture: standing up on the toes (digits), as in dogs, cattle and birds.

Dinosauromorpha: the larger clade including Dinosauria and its outgroups, Lagerpetidae and Silesauridae.

Disaster species: a species that survives and diversifies in post-extinction conditions, but disappears without giving rise to major components of the longer-term ecosystem.

Disparity: morphological variability, which can be measured from continuously varying or discrete characters.

Ecospace: a broad set of diets and other ecological parameters located within a habitat. Unlike a niche, ecospace can be empty (e.g. following a mass extinction) and can be circumscribed by the role of a single species or of many.

Gondwana: the southern supercontinent, part of Pangaea in the Triassic.

Laurasia: the northern supercontinent, part of Pangaea in the Triassic.

Lissamphibian: member of one of the living amphibian groups (frogs, salamanders, caecilians).

Macroevolution: evolution above the species level; large-scale patterns and processes in the history of life.

Ornithischia: one of two major clades of dinosaurs, including bipedal herbivores (ornithomorphs), and quadrupeds with horns (ceratopsians) or armour (stegosaurs, ankylosaurs).

Pangaea: 'all world', the global supercontinent that existed through the Permian and Triassic, comprising Gondwana and Laurasia.

Plantigrade posture: standing with the sole of the foot completely on the ground, as in basal tetrapods, humans, and bears.

Saurischia: one of two major clades of dinosaurs, including the primarily carnivorous theropods and herbivorous, long-necked sauropodomorphs.

Synapsida: the major amniote clade comprising mammals and their stem forms back to the Carboniferous, sometimes termed 'mammal-like reptiles'.

Ultrametric tree: a phylogenetic tree subtended from living taxa only; all branches in the tree terminate at a single time line, the present day.

evolution [11–13]. Such views are not widely accepted now [14,15], but deserve close examination to determine whether species and clades may have been interacting in some way. Here we choose the origin of the clade Dinosauria — the monophyletic group that includes all dinosaurs — as an exemplar of an adaptive radiation that has been explored using numerical tools. The data show rapid early evolution into empty ecospace (Box 1), but here diversification and expansion of morphospace were decoupled, with expansion in morphological range occurring first. What was once thought to be an evolutionary relay, in which inferior competitors gave way to the superior, fast-moving and toothy dinosaurs, appears to have been a more long-term, and perhaps passive process of replacement mediated by dramatic changes in the external environment.

Rise of the Dinosaurs in the Aftermath of the Permo-Triassic Mass Extinction

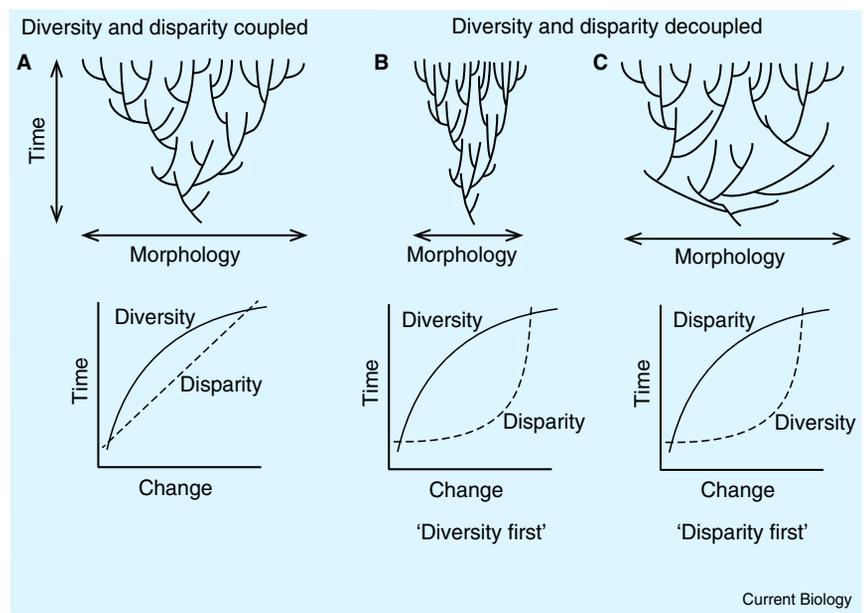
The origin of the dinosaurs began with the Permo-Triassic mass extinction event (PTME), 252 Ma. The PTME saw the demise of 80–90% of species [16], the highest level of loss in Earth's history. This crisis marked the beginning of the Triassic period, not simply the time when dinosaurs arose, but also the time when the roots of modern ecosystems were laid down on land and in the sea, with the origins of lissamphibians and turtles, as well as the emergence of early relatives of crocodiles, lizards, and mammals (Figure 2). The Triassic terminated with the end-Triassic mass extinction (ETME) 201 Ma, a much more modest affair in which perhaps <50% of species died out.

Recovery from a mass extinction might be controlled partly by the severity of the extinction, by the nature of species interaction during ecosystem rebuilding [17], and by the post-extinction physical environment [18]. For example, following a profound event such as the PTME, recovery would take a long time [17]. When small numbers of species are lost, their role in the ecosystem will affect recovery. Furthermore, the net effects of widespread species loss are not linear: a reduction of 10% might require only a short time to refill niches. However, after the PTME, reefs disappeared for up to 10 million years, and forests were much reduced for a similar time span; such profound destruction of major ecosystems required an extended period for the reef-builder and tree body plans to re-emerge [18].

Added to the depth of the extinction, the first 5 million years of the Triassic was a time of continuing harsh environmental conditions. The PTME was likely a consequence of massive volcanic eruption and consequent sharp global warming, acid rain, and ocean anoxia [16,19]. Carbon isotopes show that shock warming was repeated three or four times through the Early Triassic [19–21], causing repeated stress to life in the sea and on land [22]. Disaster species (Box 1) emerged for a short time, flourished, and died out. Some groups like foraminifera and ammonites in the oceans and temnospondyl amphibians on land recovered in diversity within the first 1–2 million years [18], but full ecosystem rebuilding took much longer, perhaps 10–15 million years for vertebrates on land [23,24]. It was

Figure 1. Models for evolution of diversity (species richness) and disparity (morphological variability).

These two modes of diversification may be either coupled (A), evolving at similar rates, or decoupled (B,C), evolving at different rates. In cases where the two are decoupled, either diversity can lead (B) or disparity expands first (C). The disparity-first model (C) appears to be the commonest case.



into this grim, recovering world that the first dinosaurs emerged.

The geological age of these first dinosaurs has been substantially revised. Until recently, the oldest dinosaurs (Figure 2) were late Carnian (232–228 Ma), occurring long after the recovery from the PTME: these include *Herrerasaurus* and *Eoraptor* from the Ischigualasto formation of Argentina and *Staurikosaurus* and *Saturnalia* from the upper Santa Maria Formation of Brazil [25]. New fossils now place the origin of dinosaurs 10–15 million years earlier. For some time, certain slender, three-toed footprints from the Early and Middle Triassic of central Europe had been ascribed to dinosaurs, or at least dinosauriforms, the wider clade that includes Dinosauria and some close relatives, and further examples have been described from Poland [26]. Then, the dinosauriform *Asilisaurus* was reported [27] from the Anisian (247–242 Ma) Manda beds of Tanzania. Finally, the world's oldest putative dinosaur, *Nyasasaurus* was announced from the Manda beds, based on a humerus and some vertebrae [28]. *Nyasasaurus* could be a dinosaur: it has a long deltopectoral crest on the humerus, with a deflected tip, elongate neck vertebrae with hollowed-out sides, and possibly three sacral vertebrae. The last two characters remain uncertain, however, because the vertebrae assigned to *Nyasasaurus* may not belong with the holotype humerus. Even if *Nyasasaurus* is not a dinosaur, it and *Asilisaurus* are close outgroups of Dinosauria [29,30], and so the lineage very close to dinosaurs, if not dinosaurs themselves, arose within 5–10 million years of the PTME.

Dinosaurs' Closest Relatives

Dinosaurs are a clade within Archosauria ('ruling reptiles'), the group that includes crocodiles and birds today. Tracking the forebears of crocodiles and birds back in time points to a common ancestor in the Early Triassic [31,32], and close relatives in the latest Permian, represented by *Archosaurus* from Russia. The archosaur stem-lineage survived the PTME, and radiated steadily through the Triassic, giving rise to numerous groups of largely carnivorous animals (Figure 3). These Triassic archosaurs have been the subject of much recent study based on new finds, restudy of older materials [28,33], and ambitious, large-scale cladistic analyses [29,32,34].

Within Archosauria, the bird line, Avemetatarsalia (Box 1), includes two subclades, Pterosauria (the flying reptiles) and Dinosauromorpha [27–34]. Within Dinosauromorpha, a series of small, bipedal animals delineate progressively less inclusive clades, Dinosauriformes, and then Dinosauria

itself [30,32]. All avemetatarsalians have elongate hindlimbs (suggesting bipedal posture), elongate tibiae (suggesting adaptations to fast running), and three or four slender, elongate metatarsals in a tightly bound bundle, so these animals all stood high on their tip-toes (digitigrade posture). Dinosauriforms had all these characters, as well as further elongation of the metatarsals and reduction of the fifth toe to a short single element. Dinosauriformes added to these specializations of the hindlimb some further modification of the pelvis and femur for speedy and efficient movement on two legs (Figure 2). Among these, the astragalus, the main ankle bone, sends a thin plate of bone up the front of the tibia, so linking the ankle firmly to the shin as a single functional unit. Many of these characters were once seen as exclusive to Dinosauria, but they are now known to exist in larger clades. Dinosaurs are characterized by some skull features, an elongate deltopectoral crest on the humerus (a major muscle attachment of the forearm), and an expanded articulation for the tibia on the astragalus [32,34].

A key recent discovery has been the new clade Silesauridae [25,27,30,35], the immediate sister group to Dinosauria; *Asilisaurus* from the Manda beds is a silesaurid, but see [36]. In that case, an Anisian silesaurid indicates that dinosaurs, or their immediate precursors, must have existed at the same time (Figure 3). Silesaurids were slender herbivores or omnivores, 1–3 meters in length, with long hindlimbs, and slender arms (Figure 3E), known from the Anisian to Norian of South America, North America, Africa, and Europe [25,27,30,35,37].

Macroevolution of the Basal Dinosaurs

Dinosaurs diversified in a step-wise fashion. Silesaurids and basal dinosaurs were minor elements in their faunas. Even in the Ischigualasto Formation, where diversity was highest, seven dinosaur species make up 11% of tetrapod specimens, hardly ecologically 'dominant' [25]. As in the Santa Maria Formation, there are for every dinosaur many skulls and skeletons of medium-sized, bulky herbivores (including rhynchosaurs, archosaur-relatives with hooked snouts, and cynodonts and dicynodonts, both of them synapsid

Box 2

Triassic time scales.

Dating Triassic terrestrial tetrapods is difficult. The fossils generally occur in redbeds — successions of red- or yellow-colored sandstones and siltstones deposited by rivers, lakes, and even deserts — and these generally lack all biostratigraphically useful fossils. On the other hand, such fossils are abundant in marine sediments: fast-evolving organisms such as foraminifers, graptolites or ammonites, whose species change every million years or less, and can be recognized worldwide. This is particularly the case for the Triassic, the subdivisions of which were mostly based on marine deposits of the Alps [65]. Therefore, until the 1980s, stratigraphic precision for Triassic terrestrial tetrapods was often no better than assigning them to the Lower, Middle, or Upper divisions of the period, each covering a time span of 50 million years!

The situation began to improve in the 1980s, with more detailed comparisons of tetrapod faunas on a global scale, and especially by attempts to correlate faunas back to the Germanic Basin [14,66]. The German terrestrial beds interfinger with the marine Alpine Triassic, and comparisons of long borehole sequences with oil-bearing North Sea sediments provided a reliable stratigraphic scheme. More recently, geologists have applied two independent dating methods, magnetostratigraphy and radioisotopic dating. Magnetostratigraphy uses the repeated, but irregular reversals of the Earth's magnetism to identify events, times of reversal, that match marine or terrestrial rock successions. Particularly in the North American Atlantic coast, the 'Newark Supergroup Astronomically-Calibrated Geomagnetic Polarity Time Scale' [67] provides precision of about 20,000 years or less. Moreover, a global magnetostratigraphic standard for the Triassic [68] allowed substantial revision especially of the Late Triassic time scale [69,70]. Radioisotopic dating now allows precision on Triassic dates down to hundreds of thousands of years, rather than 10 million years, as used to be the case. Practitioners concentrate on isotopic time series, generally U-Pb and Ar⁴⁰-Ar³⁹. Further, individual zircons from ash layers, or even from sandstones, can now be dated, and if these are interlayered with bone-bearing sediments can provide rather accurate dates against which the time scale can be fixed.

Spot dates constrain the timing of origin of dinosaurs. One from an ash layer near the base of the Ischigualasto Formation has given an Ar⁴⁰-Ar³⁹ age of 231.4 ± 0.3 Ma and a date of 225.9 ± 0.9 Ma was found near the top, constraining the dinosaur-bearing layer to 231–229 Ma [71]. U-Pb dating of detrital zircon crystals from the Chinle Formation [72,73] provides dates from 225 to 208 Ma.

subgroups with crushing teeth and slicing jaw margins, respectively). Dinosaurs then radiated substantially through the remaining 30 million years of the Triassic, in terms of numbers of taxa, numbers of locations worldwide, and range of body sizes.

In an early application of comparative phylogenetic methods to a fossil-based tree, a supertree of 420 dinosaurs [38] provided the opportunity to test for diversification shifts (Box 1) — times when the rate of evolution was unusually high or low (departing statistically from a random-walk assumption). In this case, of more than 400 branching points in the phylogenetic tree, only 11 showed significant asymmetry, or imbalance, indicating that one clade expanded much faster than its sister. Interestingly, most of these bursts of evolution happened in the Late Triassic and Early Jurassic, suggesting that, although overall diversity was low, key macroevolutionary differentiation between clades was being established during these times.

A key physiological character is body size. Dinosaurs famously grew large and very large, and they have been cited as classic examples of Cope's rule (Box 1), although a true driven trend to large size — the real meaning of Cope's rule — is hard to detect in dinosaurs, or indeed any other group [39,40]. New comparative phylogenetic methods allow biologists to explore whether evolution in any particular case follows one of a variety of different models. For example, in a study of body size increase in archosaurs through the Triassic [40], maximum-likelihood analyses indicated that Cope's rule was extremely rare, despite substantial changes in body size. In comparisons of archosauromorphs and synapsids (Figure 4A), passive evolutionary models (models in which variance in a character expands) dominated, whereas for smaller subclades, punctuated evolution (evolution occurring largely at the time of lineage splitting) was common. The timing of body-size increases seemed to depend on prior extinctions, so archosaurs, including dinosaurs, showed body-size increases within particular subclades

only after a synapsid clade had died out. Indeed, the demise of the medium- to large-sized herbivorous dicynodonts in the early Norian (Figure 2) predated the rise of sauropodomorph dinosaurs [14,25]. In an independent study [41], a variety of evolutionary models, including Brownian motion (models in which rates of evolution do not exceed those expected at random), was fit to data on body size increase among early dinosaurs, but no evidence was found for step changes in body size, nor for such size increases corresponding to any intrinsic or extrinsic factor. These studies confirm that the clade Dinosauria expanded substantially in its initial stages, but evidence that this was faster than random, or that body size increased according to an active trend, is missing.

Disparity-First Models of Diversification

As noted earlier, disparity-first models, in which morphospace occupation increases before diversity, predominated in examples of adaptive radiations from the fossil record [4]. This was confirmed in a comparative phylogenetic analysis of 98 metazoan clades [5]: clades that did not suffer a sudden ending at a mass extinction were three times as likely to be 'bottom heavy' than 'top heavy' in terms of disparity, meaning that morphospace occupation expanded early, rather than late, in clade history. If disparity-first models of clade diversification are common, this is remarkable for two reasons: first, it shows that diversity and disparity are commonly decoupled, and second substantial morphological steps take place before lineage multiplication.

The Triassic, marking the time when life recovered following the PTME, is a good time to explore diversity and disparity for different clades that were diversifying at the same time. Unusually, ammonoids, extinct coiled cephalopods, show a diversity-first model [42,43], with rapid diversification of these fast-evolving potential disaster taxa, but with little innovation in morphology. On the other hand, most tetrapod groups show a disparity-first model, whether

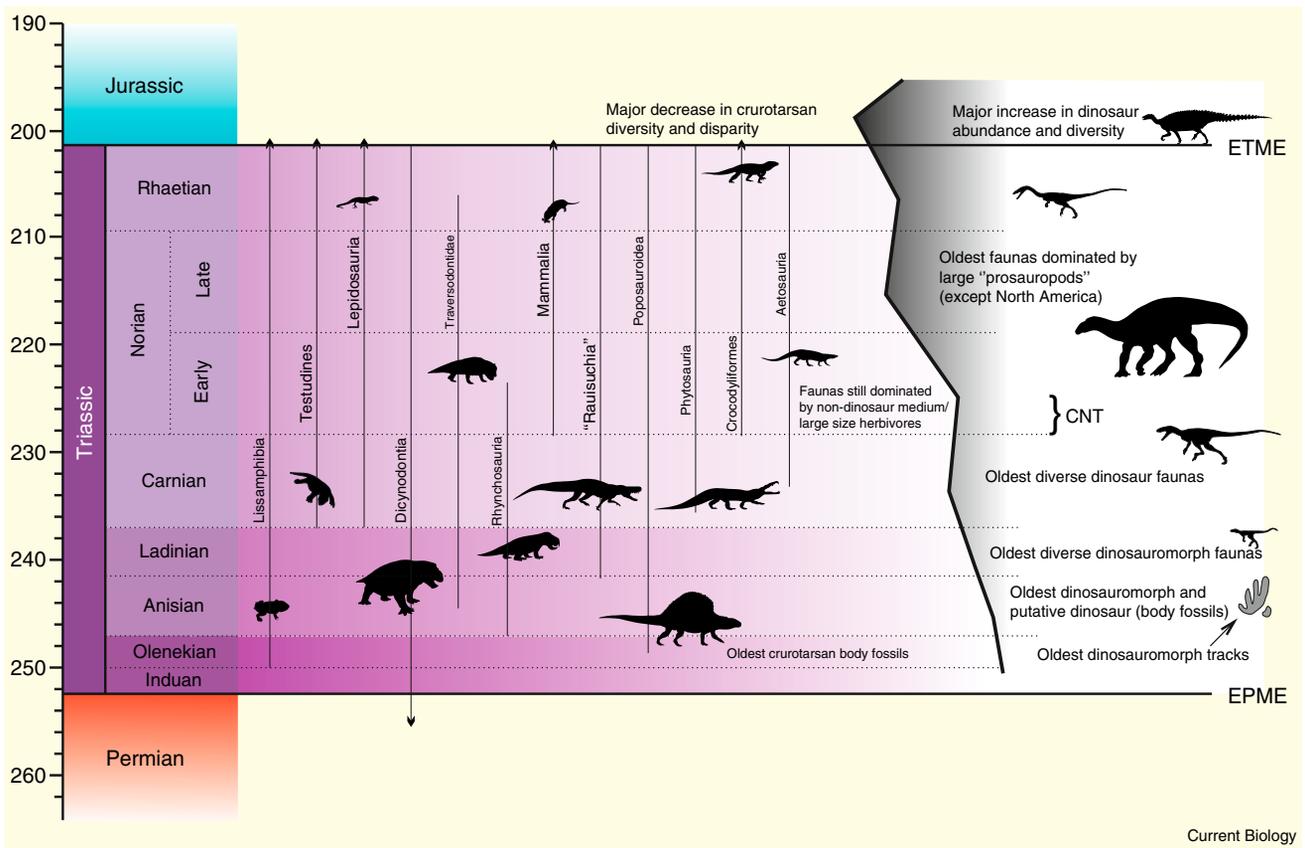


Figure 2. Macroevolutionary trends among terrestrial Triassic tetrapods.

The figure is showing major events leading to the diversification of dinosaurs. Timescale based on [65]. Lines indicate chronological distribution of various non-avemetatarsalian terrestrial tetrapods. Graph to the right depicts diversity curve for Dinosauria from [49]. Abbreviations: CNT, Carnian-Norian turnover; PTME, end-Permian mass extinction; ETME, end-Triassic mass extinction. Based on various sources, including [26,50]. Silhouettes not at the same scale.

temnospondyl amphibians [44], archosaurs [45,46], anomodonts [47], or cynodonts [48]. These four tetrapod clades had been major (anomodonts) or minor (amphibians, cynodonts, archosaurs) components of Late Permian ecosystems, and all suffered substantial losses through the PTME. Anomodonts in particular had been major herbivores worldwide, were reduced to three or four lineages that passed through the crisis and then recovered. However, for them the PTME crisis represented a macroevolutionary bottleneck, and, although diversity eventually recovered, disparity expanded, but then stalled, suggesting some loss of potential range of morphology [47].

Fossil-based studies thus suggest that clades commonly expand by an early burst in morphological variation (disparity), and that models of diversification may be similar whether they follow the acquisition of a key adaptation or occur into vacated ecospace.

Biotic Replacement

The classic story of the origin of the dinosaurs was that they had diversified in the Late Triassic at the expense of the crurotarsans, the clade comprising most other Triassic archosaurs, as a result of superior adaptations such as greater running speed or larger teeth [12,13]. This viewpoint has been refuted [14,49], and numerical studies tend to reject such a 'competitive' replacement model. In one analysis

[45,46], the aim was to assess whether the rise of dinosaurs had an impact on the crurotarsans. The data comprised 500 features of the skull and skeleton that varied among species. Evolutionary rates were calculated by mapping characters onto the phylogenetic tree, which was converted into a time tree by using the geological age of each species. This meant that the amount of change in the ensemble of characters could be assessed from one time bin to the next, so providing a measure of the rate of evolution. Perhaps surprisingly, dinosaurs and crurotarsans were evolving at nearly identical rates during the Late Triassic (Figure 4B). Neither group was outperforming the other, and they kept pace over their 30 million years of shared history.

The linked study of disparity also showed surprising results [45,46]. In this case, disparity based on cladistic characters provides a measure of the overall variety of morphological features, so the breadth of morphologies seen in different subclades can be compared. Crurotarsans were twice as disparate as dinosaurs in the Late Triassic (Figure 4C), which suggests that, far from the new dinosaurs competitively displacing crurotarsans, the latter group continued to experiment in evolutionary terms with many different morphologies [45]. Even after the extinction of major crurotarsan clades at the end of the Triassic, dinosaurs did not expand their morphological variability substantially

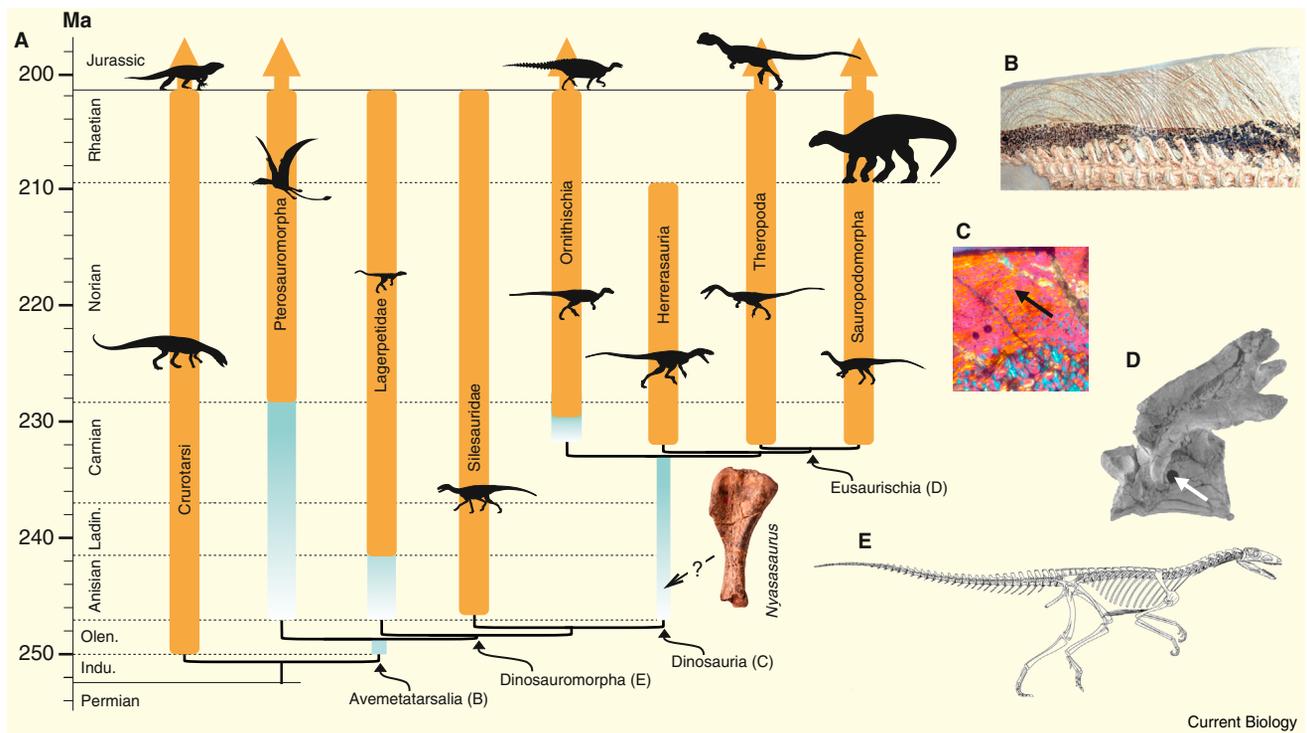


Figure 3. Time-calibrated phylogeny of the first dinosaurs and their closest relatives.

The figure also shows some key evolutionary acquisitions. Orange depicts known range of fossil records for each clade; ghost lineages (missing fossil record implied by sister group) in blue. (A) Phylogeny of basal dinosaurs and their nearest relatives, plotted against geological time. (B–E) ‘Typical’ dinosaur or dinosauromorph traits: (B) filamentous integumentary cover in the tail of the ornithischian *Psittacosaurus* [74]; (C) fibrolamellar cortical bone (arrow) in the femur of *Saturnalia* [75], indicative of rapid growth; (D) pneumatic foramen for air sac diverticuli (arrow) in a vertebra of the theropod *Majungasaurus* [76]; (E) *Silesaurus* reconstructed in bipedal stance [77], although this posture is debated. Positions in the cladogram where those features first appear are tentatively indicated, but the conditions in surrounding taxa are mostly ambiguous. Based on phylogenies of basal dinosaurs [34], where herrerasaurids are placed as basal saurischians rather than basal theropods, as sometimes suggested [32].

or rapidly (Figure 4D): it was more a slow step-wise acquisition of new morphologies [46].

Random and passive models of evolution — in which diversification rate does not exceed that expected at random or where variance increases but not according to an active trend, respectively — are ubiquitous in early dinosaur evolution. But that does not mean that dinosaurs became successful through the Triassic by accident and without any particular adaptation to their environments. It is much more likely that, even though active competitive replacement models have been rejected [14,40], dinosaurs had a range of adaptations that provided them with advantages over other taxa in post-crisis ecosystems [49]. It seems that dinosaurs owed their rise to three extinctions (Figure 1): first, the massive PTME 252 Ma, when synapsids were devastated, and the first dinosauromorphs emerged at least by the early Middle Triassic, 247–242 Ma; second, a time of turmoil and turnover on land associated with a switch from damp to arid climates in the Carnian–Norian transition, some 225 Ma, when sauropodomorphs replaced dicynodonts and rhynchosaurs; and third the substantial ETME 201 Ma, when all crurotarsans except for crocodylomorphs disappeared and theropods and ornithischians diversified [14,45,46,50,51].

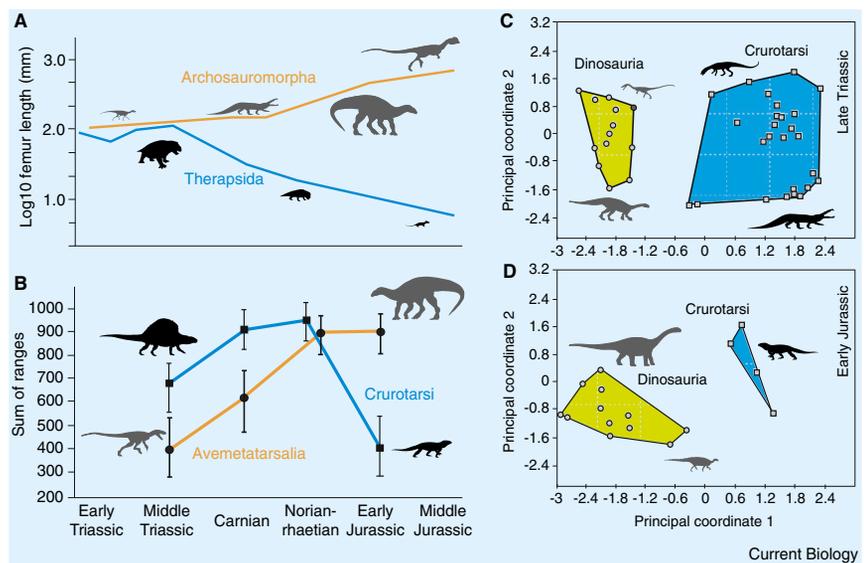
What were the characters that enabled dinosaurs, and indeed archosaurs more widely, to profit from these ecological crises? Two key attributes are their exceptional growth rates and efficient respiration systems [40,52]. Recent work

on dinosaurs shows, by measuring the age at death (from counting lines of arrested growth, essentially growth rings) and the estimated body mass (from femur lengths), that even giant dinosaurs reached adult size in 20–25 years and showed rates of growth in line (Figure 3C) with modern mammals rather than modern reptiles [52–54]. Dinosaurs almost certainly possessed the unidirectional respiratory system of birds, and apparently crocodiles [55], which is more efficient than the tidal system in mammals, and this might have characterized all archosaurs. Nearly all saurischian dinosaurs show pneumatization of at least parts of the vertebral column (Figure 3D), and sometimes other bones [56–58]. As in birds, these pneumatic cavities are interpreted as evidence for air sacs, auxiliary structures that allow the animal to take in large amounts of air, and perhaps at the same time to achieve larger size by weight saving [52]. Study of the internal structure of vertebrae [59] has shown unequivocal pneumatization only in dinosaurs and pterosaurs, whereas claimed pneumatic structures in crurotarsans and other basal archosaurs are less certain.

Earlier studies had identified other possible adaptive advantages of dinosaurs, and perhaps of most early archosaurs — their supposed mammalian-like endothermy [12] and their upright, bipedal posture [13]. Dinosaurian thermoregulation is somewhat speculative, but the majority of evidence now supports a high metabolic rate, especially in the small- and medium-sized feathered dinosaurs.

Figure 4. Macroevolution of tetrapods and the origin of the dinosaurs, associated with long-term size increase and extinctions of synapsid and crurotarsan groups.

(A) The relative fates of therapsids (derived synapsids) and archosauromorphs (archosaurs and close relatives) through the Triassic and the early part of the Jurassic, showing a long-term diminution of mean body size (indicated by femur lengths) of therapsids and increase in mean body size of archosauromorphs. Model fitting indicates these trends were not driven by active selection for larger body sizes within evolutionary lineages, based on [40]. (B) Changing fates of Avemetatarsalia (dinosaurs and immediate relatives) and Crurotarsi (crocodile-line archosaurs) through the Middle Triassic to Early Jurassic, showing parallel changes in disparity (measured by sum of ranges) in the Triassic, and the crash in crurotarsan disparity through the ETME, based on [45]. (C,D) Changing relative morphospace occupation by Dinosauria and Crurotarsi in the Late Triassic and Early Jurassic, suggesting a lack of impact of early dinosaurian evolution on crurotarsan morphospace in the Late Triassic, and a modest response by Dinosauria following substantial extinction of Crurotarsi through the ETME, based on [46].



Considering that these include members of both the saurischian [60] and ornithischian [61] branches, phylogenetic bracketing implies that the first dinosaurs might have had a high thermal inertia [62], given the insulation provided by the coverage of filamentous integumentary structures (Figure 2b), as well as fast growth and avian-like breathing.

In contrast to earlier opinion [13], all archosaurs may have adopted upright posture. Footprints [63] show that the PTME was associated with a switch from sprawling to parasagittal (upright) posture in all surviving lineages, perhaps a resetting of the arms race between predators and prey, in which synapsids and archosaurs in concert switched posture. Indeed, dinosauromorphs were digitigrade and bipedal since the end of the Early Triassic, and they remained so through a long span of ecological insignificance from 247 to 225 Ma. Accordingly, if the typical thermoregulation and posture of dinosaurs played a role in their diversification, it was not as long-term drivers, but triggered by Late Triassic events. Further, the common occurrence of parasagittal gait in all archosaurs, and bipedalism in avemetatarsalians and some crurotarsans indicate that posture was probably not a factor in crurotarsan extinctions at the end of the Triassic [49].

Conclusions

The origin of the dinosaurs has always been fascinating because of the power and majesty of these ancient animals, but also because they seemed to have been successful in replacing a broad diversity of precursors. This is one of the most discussed examples of biotic replacement, and it has been cited repeatedly as evidence for or against ideas such as evolutionary progress and competitive displacement of clades.

The current picture for the global ecological rise of dinosaurs in the Triassic suggests that they possessed many key adaptations, but that these were not the cause of their rise. In the post-PTME recovery, any one of several tetrapod clades — synapsids, crurotarsans, or dinosaurs — could

have risen to high diversity and abundance. The dinosaurs took that position, and this must reflect adaptations and competitive advantage of dinosaurian species in feeding, locomotion, thermoregulation, and other attributes. However, the evidence that these attributes drove the decline of the other two major terrestrial tetrapod clades is weak; indeed, body size change through the Triassic cannot be distinguished from a Brownian motion model (passive change), and diversity and disparity plots show no evidence that one clade supplanted another, nor even that dinosaurs were quick to occupy ecospace emptied by preceding extinction events.

Macroevolution research has moved from an older, narrative tradition to historical [64] hypothesis-testing numerical approaches. This would have been inconceivable a few years ago: after all, how can you hope to answer scientific questions about singular, historical events that cannot be repeated? This has been made possible by orders-of-magnitude improvements in the numbers of fossils and in their anatomical description and systematics, coupled with massively improved rock dating. The most important change, however, has been the application of rigorous cladistic methods to discover, and test, phylogenetic hypotheses, and these have opened the way to macroevolutionary testing that is equally powerful whether applied to ultrametric trees (Box1) of living taxa or to deep-time trees of extinct taxa.

This revolution is only just gaining traction [9], but it opens up extensive possibilities for testing best-fitting models of evolution, determining rates of trait evolution, exploring most plausible evolutionary drivers, and determining whether one clade interacts ecologically with another. Doubtless, evolutionary biologists and palaeobiologists will continue to quibble over the models and the algorithms, whether they have the statistical power to do what is claimed, but the opportunity to transcend narratives is a heady prospect for all evolutionary biologists interested in macroevolution and the origins of modern biodiversity.

Acknowledgements

M.J.B. is grateful for grant support from Natural Environment Research Council (NE/C518973/1), and M.C.L. thanks the Brazilian agency FAPESP for the financial support. We thank Steve Brusatte and other referees for their very helpful advice.

References

1. Simpson, G.G. (1944). *Tempo and Mode in Evolution* (Columbia University Press).
2. Dececchi, T.A., and Larson, H.C.E. (2013). Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution* 67, 2741–2752.
3. O’Leary, M., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.-X., Meng, J., et al. (2013). The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339, 662–667.
4. Erwin, D.H. (2007). Disparity: morphological pattern and developmental context. *Palaeontology* 50, 57–73.
5. Hughes, M., Gerber, S., and Wills, M.A. (2013). Clades reach highest morphological disparity early in their evolution. *Proc. Nat. Acad. USA* 110, 13875–13879.
6. Darwin, C. (1859). *On the Origin of Species* (John Murray).
7. Schluter, D. (2000). *The Ecology of Adaptive Radiation* (Oxford Univ. Press).
8. Harmon, L.J., et al. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64, 2385–2396.
9. Quental, T.B., and Marshall, C.R. (2010). Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* 25, 434–441.
10. Slater, G.J., Price, S.A., Santini, F., and Alfaro, M.E. (2010). Diversity versus disparity and the radiation of modern cetaceans. *Proc. R. Soc. Lond., Ser. B* 277, 3097–3104.
11. Provine, W.B. (1988). *Evolutionary Progress* (Chicago: Univ).
12. Bakker, R.T. (1972). Anatomical and ecological evidence of endothermy in dinosaurs. *Nature* 238, 81–85.
13. Charig, A.J. (1984). Competition between therapsids and archosaurs during the Triassic period: a review and synthesis of current theories. *Symp. Zool. Soc. Lond.* 52, 597–628.
14. Benton, M.J. (1983). Dinosaur success in the Triassic: a noncompetitive ecological model. *Q. Rev. Biol.* 58, 29–55.
15. Benton, M.J. (1987). Progress and competition in macroevolution. *Biol. Rev.* 62, 305–338.
16. Benton, M.J., and Twitchett, R.J. (2003). How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol.* 18, 358–365.
17. Solé, R., et al. (2010). Simple model of recovery dynamics after mass extinction. *J. Theor. Biol.* 267, 193–200.
18. Chen, Z.-Q., and Benton, M.J. (2012). The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat. Geosci.* 5, 375–383.
19. Payne, J.L., and Clapham, M.E. (2012). End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? *Annu. Rev. Earth Planet. Sci.* 40, 89–111.
20. Payne, J.L., et al. (2004). Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* 305, 506–509.
21. Sun, Y., et al. (2012). Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338, 366–370.
22. Benton, M.J., and Newell, A.J. (2013). Impacts of global warming on Permian-Triassic terrestrial ecosystems. *Gondwana Res.* <http://dx.doi.org/10.1016/j.gr.2012.12.010>, online ahead of print.
23. Benton, M.J., et al. (2004). Ecosystem remodelling among vertebrates at the Permian-Triassic boundary in Russia. *Nature* 432, 97–100.
24. Irmis, R.B., and Whiteside, J.H. (2012). Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. *Proc. R. Soc. Lond. B. Biol. Sci.* 279, 1310–1318.
25. Langer, M.C., Ezcurra, M.D., Bittencourt, J.S., and Novas, F.E. (2010). The origin and early evolution of dinosaurs. *Biol. Rev.* 85, 55–110.
26. Brusatte, S.L., Niedzwiedzki, G., and Butler, R.J. (2011). Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. *Proc. R. Soc. Lond. B. Biol. Sci.* 278, 1107–1113.
27. Nesbitt, S.J., Sidor, C.A., Irmis, R.B., Angielczyk, K.D., Smith, R.M.H., and Tsuji, L.A. (2010). Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature* 464, 95–98.
28. Nesbitt, S.J., Barrett, P.M., Werning, S., Sidor, C.A., and Charig, A.J. (2012). The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. *Biol. Lett.* 9, 20120949.
29. Brusatte, S.L., Benton, M.J., Desojo, J.B., and Langer, M.C. (2010). The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *J. Syst. Palaeontol.* 8, 3–47.
30. Langer, M.C., Nesbitt, S.J., Bittencourt, J.S., and Irmis, R.B. (2013). Non-dinosaurian Dinosauriforms. *Geol. Soc. Lond., Spec. Publ.* 379, 157–186.
31. Butler, R.J., Brusatte, S.L., Reich, M., Nesbitt, S.J., Schoch, R.R., and Hornung, J.J. (2011). The sail-backed reptile *Ctenosauriscus* from the latest Early Triassic of Germany and the timing and biogeography of the early archosaur radiation. *PLoS ONE* 6, e25693.
32. Nesbitt, S.J. (2011). The early evolution of archosaurs: relationships and the origin of major clades. *Bull. Am. Mus. Nat. Hist.* 352, 1–292.
33. Benton, M.J. (1999). *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* 354, 1423–1446.
34. Langer, M.C., and Benton, M.J. (2006). Early dinosaurs: A phylogenetic study. *J. Syst. Palaeontol.* 4, 309–358.
35. Dzik, J. (2003). A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *J. Vertebr. Paleontol.* 23, 556–574.
36. Langer, M.C. and Ferigolo, J. The Late Triassic dinosauriform *Sacisaurus agudoensis* (Caturrita Formation; Rio Grande do Sul, Brazil): anatomy and affinities. *Geol. Soc. Lond. Spec. Publ.* 379, 353–392.
37. Irmis, R.B., Nesbitt, S.J., Padian, K., Smith, N.D., Turner, A.H., Woody, D., and Downs, A. (2007). A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science* 317, 358–361.
38. Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W.E., Jennings, R., and Benton, M.J. (2008). Dinosaurs and the Cretaceous Terrestrial Revolution. *Proc. R. Soc. Lond. B. Biol. Sci.* 275, 2483–2490.
39. Hone, D.W.E., and Benton, M.J. (2005). The evolution of large size: how does Cope’s rule work? *Trends Ecol. Evol.* 20, 4–6.
40. Sookias, R.B., Butler, R.J., and Benson, R.B.J. (2012). Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. *Proc. R. Soc. Lond. B. Biol. Sci.* 279, 2180–2187.
41. Turner, A.H., and Nesbitt, S.J. (2013). Body size evolution during the Triassic archosauriform radiation. *Geol. Soc. Lond. Spec. Publ.* 379, 573–597.
42. McGowan, A.J. (2007). Ammonoid taxonomic and morphologic recovery patterns after the Permian-Triassic. *Geology* 32, 665–668.
43. Brosse, M., Brayard, A., Fara, E., and Neige, P. (2013). Ammonoid recovery after the Permian-Triassic mass extinction: a re-exploration of morphological and phylogenetic diversity patterns. *J. Geol. Soc.* 170, 225–236.
44. Ruta, M., Wagner, P.J., and Coates, M.I. (2006). Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proc. R. Soc. B.* 273, 2107–2111.
45. Brusatte, S.L., Benton, M.J., Ruta, M., and Lloyd, G.T. (2008). Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* 321, 1485–1488.
46. Brusatte, S.L., Benton, M.J., Ruta, M., and Lloyd, G.T. (2008). The first 50 million years of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biol. Lett.* 4, 733–736.
47. Ruta, M., Angielczyk, K.D., Fröbisch, J., and Benton, M.J. (2013). Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anodontid therapsids. *Proc. R. Soc. B* 280, 20131071.
48. Ruta, M., Botha-Brink, J., Mitchell, S.A., and Benton, M.J. (2013). The radiation of cynodonts and the ground plan of mammalian morphological diversity. *Proc. R. Soc. B* 280, 20131865.
49. Irmis, R.B. (2011). Evaluating hypotheses for the early diversification of dinosaurs. *Earth Envr. Sci. Trans. R. Soc. Edinburgh* 101, 397–426.
50. Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J., and Norell, M.A. (2010). The origin and early radiation of dinosaurs. *Earth Sci. Rev.* 101, 68–100.
51. Brusatte, S.L., Benton, M.J., Lloyd, G.T., Ruta, M., and Wang, S.C. (2011). Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). *Earth Envr. Sci. Trans. R. Soc. Edinburgh* 101, 367–382.
52. Sander, P.M., Christian, A., Clauss, M., Fehner, R., Gee, C.T., Griebeler, E.-M., Gunga, H.-C., Hummel, J., Mallison, H., Perry, S.F., et al. (2010). Biology of the sauropod dinosaurs: the evolution of gigantism. *Biol. Rev.* 86, 117–155.
53. Erickson, G.M. (2005). Assessing dinosaur growth patterns: a microscopic revolution. *Trends Ecol. Evol.* 20, 677–684.
54. de Ricqlès, A., Padian, K., Knoll, F., and Horner, J.R. (2008). On the origin of high growth rates in archosaurs and their ancient relatives: Complementary histological studies on Triassic archosauriforms and the problem of a “phylogenetic signal” in bone histology. *Ann. Paleontol.* 94, 57–76.
55. Farmer, C.G., and Sanders, K. (2010). Unidirectional airflow in the lungs of alligators. *Science* 327, 338–340.
56. O’Connor, P.M., and Claessens, L.P.A.M. (2005). Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436, 253–256.
57. Wedel, M.J. (2009). Evidence for bird-like air sacs in saurischian dinosaurs. *J. Exp. Zool.* 311, 611–628.
58. Benson, R.B.J., Butler, R.J., Carrano, M.Y., and O’Connor, P.M. (2011). Air-filled postcranial bones in theropod dinosaurs: physiological implications and the “reptile-to-bird” transition. *Biol. Rev.* 87, 168–193.
59. Butler, R.J., Barrett, P.M., and Gower, D.J. (2012). Reassessment of the evidence for postcranial skeletal pneumaticity in Triassic archosaurs, and the early evolution of the avian respiratory system. *PLoS ONE* 7, e34094.

60. Ji, Q.A., Currie, P.J., Norell, M.A., and Ji, S.A. (1998). Two feathered dinosaurs from northeastern China. *Nature* 393, 753–761.
61. Zheng, X.T., You, H.L., Xu, X., and Dong, Z.M. (2009). An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature* 458, 333–336.
62. Wu, P., Hou, L., Plikus, M., Hughes, M., Scehnet, J., Suksaweang, S., Widelitz, R., Jiang, T.X., and Chuong, C.M. (2004). Evo-devo of amniote integuments and appendages. *Int. J. Dev. Biol.* 48, 249–270.
63. Kubo, T., and Benton, M.J. (2009). Tetrapod postural shift estimated from Permian and Triassic trackways. *Palaeontology* 52, 1029–1037.
64. Cleland, C.E. (2002). Methodological and epistemic differences between historical science and experimental science. *Philos. Sci.* 69, 447–451.
65. Gradstein, F.M., Ogg, J.M., Schmitz, M.D., and Ogg, G.M., eds. (2012). *The Geologic Time Scale* (Elsevier).
66. Benton, M.J. (1994). Late Triassic terrestrial vertebrate extinctions: stratigraphic aspects and the record of the Germanic Basin. *Palaeontologia Lombarda* 2, 19–38.
67. Olsen, P.E., Kent, D.V., and Whiteside, J.H. (2011). Implications of the Newark Supergroup-based astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. *Earth Environ. Sci. Trans. R. Soc. Edinburgh* 101, 201–229.
68. Hounslow, M.W., and Muttoni, G. (2010). The geomagnetic polarity timescale, for the Triassic: linkage to stage boundary definitions. *Geol. Soc. London, Spec. Publ.* 334, 61–102.
69. Muttoni, G., Kent, D.V., Olsen, P.E., Di Stefano, P., Lowrie, W., Bernasconi, S.M., and Hernandez, F.M. (2004). Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and correlation to the Late Triassic Newark astrochronological polarity time scale. *Geol. Soc. Am. Bull.* 116, 1043.
70. Muttoni, G., Kent, D.V., Jadoul, F., Olsen, P.E., Rigo, M., Galli, M.T., and Nicora, A. (2010). Rhaetian magneto-biostratigraphy from the Southern Alps (Italy): Constraints on Triassic chronology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 285, 1–16.
71. Martinez, R.N., Sereno, P.C., Alcober, O.A., Colombi, C.E., Renne, P.R., Montañez, I.P., and Currie, B.S. (2011). A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* 331, 206–210.
72. Irmis, R.B., Mundil, R., Martz, J.W., and Parker, W.G. (2011). High-resolution U–Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. *Earth Planet. Sci. Lett.* 309, 258–267.
73. Ramezani, J., Hoke, J.D., Fastovsky, D.E., Bowering, S.A., Therrien, F., Dworkin, S.I., Atchley, S.C., and Nordt, L.C. (2011). High-precision UPb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): Temporal constraints on the early evolution of dinosaurs. *Bull. Geol. Soc. Am.* 123, 2142–2159.
74. Mayr, G., Peters, D.S., Plodowski, G., and Vogel, O. (2002). Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* 89, 361–365.
75. Stein, K., and Langer, M.C. (2009). The long bone histology of the stem-sauropodomorph *Saturnalia tupiniquim*, implications for the early evolution of dinosaur bone microstructure. *J. Vertebr. Paleontol.* 29, 185A.
76. O'Connor, P.M. (2007). The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* 27, 127–163.
77. Piechowski, R., and Dzik, J. (2010). The axial skeleton of *Silesaurus opolensis*. *J. Vertebr. Paleontol.* 30, 1127–1141.