The roles of herbivory and omnivory in early dinosaur evolution

Paul M. Barrett[1], Richard J. Butler[2] and Sterling J. Nesbitt[3,4]

[1] Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK
    Email: p.barrett@nhm.ac.uk

[2] Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany
    Email: butler.richard.j@gmail.com

[3] Jackson School of Geosciences, The University of Texas at Austin, TX 78712, USA

[4] Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA
    Email: nesbitt@jsg.utexas.edu

ABSTRACT: Herbivorous and omnivorous dinosaurs were rare during the Carnian stage of the Late Triassic. By contrast, the succeeding Norian stage witnessed the rapid diversification of sauropodomorphs and the rise of the clade to ecological dominance. Ornithischians, by contrast, remained relatively rare components of dinosaur assemblages until much later in the Mesozoic. The causes underlying the differential success of ornithischians and sauropodomorphs remain unclear, but might be related to trophic specialisation. Sauropodomorphs replaced an established herbivore guild consisting of rhynchosaurs, aetosaurs and basal synapsids, but this faunal turnover appears to have been opportunistic and cannot be easily attributed to either competitive interactions or responses to floral change. Consideration of diversity patterns and relative abundance suggests that the ability to eat plants might have been a major factor promoting sauropodomorph success, but that it was less important in the early evolution of Ornithischia. On the basis of current evidence it is difficult to determine the diet of the ancestral dinosaur and scenarios in which omnivory or carnivory represent the basal condition appear equally likely.

KEY WORDS: Early Jurassic, Late Triassic, Ornithischia, Sauropodomorpha, Silesauridae

Non-avian dinosaurs were the dominant vertebrate herbivores in late Mesozoic terrestrial ecosystems (Weishampel & Norman 1989). Herbivorous dinosaurs were species-rich, accounting for approximately 54% of total known Mesozoic dinosaur diversity (based on data in Weishampel *et al.* 2004a), and numerically abundant, comprising between 50% and 95% of the individuals present in many dinosaur assemblages (e.g. Farlow 1976; Osmólska 1980; Russell *et al.* 1980; Galton 1985, 1986). Dinosaurs occupied the entire spectrum of herbivory, ranging from facultative omnivory through to obligate high-fibre herbivory (e.g. Galton 1986; Weishampel & Norman 1989; Norman & Weishampel 1991; Barrett 2000; Zanno *et al.* 2009) and the ability to eat plants is inferred to have been present in some of the earliest members of the clade (e.g. Bonaparte 1976; Langer *et al.* 1999; Butler *et al.* 2007; Martinez & Alcober 2009). A great deal of work has been carried out on the functional morphology and palaeoecology of dinosaur herbivory (see reviews in Weishampel & Norman 1989; King 1996; Fastovsky & Smith 2004), but most of these studies have concentrated on Late Jurassic and Cretaceous taxa (such as ornithopods, ceratopsians and sauropods) and relatively few have attempted to address the importance of herbivory in the origin and early evolution of dinosaurs in the Late Triassic–Early Jurassic (Crompton & Attridge 1986; Galton 1986; Weishampel & Norman 1989). This present paper reviews how herbivory (inclusive of habitual omnivory) might have impacted the early evolution and ecology of dinosaurs, focusing on when, and how many times, herbivory appeared, whether this diet played a role in promoting the early diversification of the clade, and on its possible palaeoecological and macroevolutionary implications.

1. Diet and dinosaur origins

The common ancestor of dinosaurs is generally assumed to have been a small, bipedal carnivore (Sereno 1997). Most scenarios of dinosaur evolution posit that theropods retained this primitive, faunivorous habit and that omnivory/herbivory appeared as a derived condition at the bases of Sauropodomorpha and Ornithischia, respectively, and within some theropod lineages (e.g. Bakker & Galton 1974; Paul 1984; Sereno 1997; Barrett 2000, 2005; Barrett & Rayfield 2006; Xu *et al.* 2009; Zanno *et al.* 2009). This hypothesis has been based on two main lines of evidence. First, dinosaur outgroups, such as pterosaurs and non-dinosaurian dinosauromorphs, were considered to be carnivorous on the basis of craniodental form and function (Bonaparte 1975; Wellnhofer 1991). Nevertheless, it should be noted that craniodental remains of non-dinosaurian dinosauromorphs are exceptionally rare. Indeed, the only strong evidence for carnivory in this grade of taxa has been the association of a maxilla containing recurved, finely serrated teeth with a partial skeleton of *Marasuchus* (Bonaparte 1975; Sereno & Arcucci 1994a). This single discovery has a major impact on the distribution of carnivory in Dinosauromorpha: until recently it provided the only strong evidence for dietary preferences among a plexus of taxa close to dinosaur origins. Unfortunately, cranial material is unknown for *Lagerpeton*, *Pseudolagosuchus* or *Dromomeron*

(Arcucci 1987; Sereno & Arcucci 1994b; Irmis *et al.* 2007a). Consequently, the dietary preferences of these taxa remain unknown and should be scored as ambiguous in any attempt to optimise diets onto the base of the dinosaur tree. Secondly, many of the early phylogenetic analyses of dinosaur interrelationships recovered the Late Triassic carnivorous taxa *Herrerasaurus* and *Staurikosaurus* as basal dinosaurs positioned outside the ornithischian/saurischian dichotomy (Gauthier 1986; Brinkman & Sues 1987; Benton 1990; Novas 1992). Optimisation of inferred dinosaur and non-dinosaurian dinosauriform diets onto these cladograms using MacClade 4.07 (Maddison & Maddison 2004) unambiguously supports carnivory as the ancestral dinosaur condition (Fig. 1A). However, it is important to note that the diets of the common ancestor of Saurischia and Ornithischia ('Eudinosauria': Novas 1992) and of the ancestral saurischian are unresolved, with omnivory/herbivory recovered as the ancestral state under ACCTRAN and carnivory following DELTRAN optimisation (see also Barrett & Rayfield 2006). This implies that carnivory was not necessarily the ancestral condition for the majority of dinosaurs, raising the possibility that omnivory/herbivory may have been more important in the initial diversification of the clade than has been usually suspected. This observation is reinforced by recent discoveries of new non-dinosaurian dinosauromorphs and other Late Triassic dinosaurs, as well as reinterpretations of early dinosaur phylogeny (see below; also Langer *et al.* 2010).

Subsequent work on *Herrerasaurus* and *Staurikosaurus* re-identified these taxa as early theropod dinosaurs, thereby removing them from their basal positions in the dinosaur tree (e.g. Sereno & Novas 1992, 1994; Sereno *et al.* 1993; Novas 1996; Sereno 1999; Rauhut 2003; Nesbitt *et al.* 2009a). This relatively minor adjustment to tree topology has a significant effect on dietary optimisations, rendering the diet of both the ancestral saurischian and the ancestral dinosaur ambiguous (Fig. 1B). The situation is complicated further by the inclusion of another Late Triassic dinosaur, *Eoraptor*, into phylogenies of early dinosaurs. *Eoraptor* was initially described as the basalmost theropod and possesses an unusual mixture of trophic characteristics (Sereno *et al.* 1993), including trenchant manual unguals (associated with predation) and a heterodont dentition (incorporating a number of sauropodomorph-like lanceolate teeth). Although regarded as a faunivore by some authors (Sereno *et al.* 1993; Sereno 1999), others have suggested that this character combination is suggestive of omnivory (Langer 2004; but see Langer *et al.* 2010). In particular, the presence of lanceolate teeth is strongly correlated with omnivory in other dinosaur taxa (e.g. basal sauropodomorphs, some coelurosaurian theropods: Paul 1984; Barrett 2000; Zanno *et al.* 2009; Nesbitt *et al.* 2010). If *Eoraptor* is interpreted as a faunivorous basal theropod, its inclusion in dinosaur phylogenies does nothing to alter the pattern of dietary evolution evinced by the inclusion of herrerasaurids in Theropoda: the ancestral diets for Saurischia and Dinosauria remain ambiguous. However, if *Eoraptor* is included as an omnivore, this, in combination with the establishment of omnivory/herbivory at the base of Sauropodomorpha and Ornithischia, gives a result that implies omnivory as the primitive dietary condition for theropods, saurischians and dinosaurs as a whole, regardless of the type of optimisation used.

Other recent treatments of dinosaur phylogeny have removed herrerasaurids and *Eoraptor* from Theropoda and placed them as successive outgroups to the clade Eusaurischia (Theropoda + Sauropodomorpha: e.g. Langer 2004; Langer & Benton 2006; Irmis *et al.* 2007a; Nesbitt *et al.* 2009b). If *Eoraptor* is a carnivore, this re-arrangement renders dinosaurs and saurischians primitively faunivorous and demonstrates

that omnivory/herbivory had two origins near the base of Dinosauria, in Ornithischia and Sauropodomorpha. Conversely, if *Eoraptor* is treated as an omnivore, ancestral saurischian and dinosaur diets are ambiguous, with carnivory or omnivory/herbivory equally likely at most of the basal nodes within the tree.

Silesaurus, from the Late Triassic of Poland, provided the first serious challenge to the view that all proximate dinosaur outgroups were faunivorous (Dzik 2003). *Silesaurus* is a non-dinosaurian dinosauriform represented by material from numerous associated individuals, including excellent cranial material, allowing for an almost complete skeletal reconstruction (Dzik 2003). Unlike other non-dinosaurian dinosauromorphs, which were bipedal saltators or cursors (Sereno & Arcucci 1994b), *Silesaurus* was a quadruped. Moreover, its jaws contain teeth with mesiodistally-expanded crowns that lack the fine marginal serrations and recurvature seen in carnivorous archosaurs (e.g. Abler 1992). These dental features, in combination with the hooked, beak-like structure of the anterior dentaries, strongly suggest that *Silesaurus* was an omnivore or herbivore (Dzik 2003). In addition, it was noted that *Silesaurus* shares a number of features with dinosaurs that are absent in other non-dinosaurian dinosauromorphs, implying that this omnivorous/herbivorous taxon was closer to the origin of dinosaurs than the carnivorous *Marasuchus* (Dzik 2003). This conclusion has been confirmed by several other analyses of ornithodiran interrelationships (Ezcurra 2006; Irmis *et al.* 2007a; Nesbitt *et al.* 2009a, b, 2010). The phylogenetic position of *Silesaurus*, in combination with its omnivorous/herbivorous habits, substantially changes dietary optimisations at the base of Dinosauria. If *Eoraptor* is considered to be carnivorous, *Silesaurus* renders basal dinosaur diets ambiguous, with carnivory and omnivory equally plausible (Fig. 1C). However, if *Eoraptor* is included as an omnivore, the inclusion of *Silesaurus* results in omnivory becoming the basal dinosaur condition, with the novel result that carnivory becomes a secondary reversion to a more primitive archosaurian trait (Fig. 1D).

Several other silesaurids have now been recognised, many of which possess craniodental features consistent with omnivory or herbivory, including *Sacisaurus* (Late Triassic, Brazil: Ferigolo & Langer 2007), *Asilisaurus* (Middle Triassic, Tanzania: Nesbitt *et al.* 2010) and an undescribed taxon from the Late Triassic of Arizona (Irmis *et al.* 2007a). If Silesauridae comprised only these taxa, this would provide strong support for recognising dinosaurs as a primitively omnivorous radiation. However, *Lewisuchus*, another non-dinosaurian dinosauromorph from the Middle Triassic of Argentina, has been identified as the basalmost member of this clade (Nesbitt *et al.* 2010). By contrast with other silesaurids, *Lewisuchus* appears to be a carnivore: the dentition consists of recurved, conical teeth (Romer 1972). Nevertheless, optimisation of diets onto the dinosauromorph tree presented by Nesbitt *et al.* (2010) cannot resolve ancestral diets along the dinosaur stem: optimisation reveals that diets of the ancestral saurischian, dinosaur and dinosaur + silesaurid clades should all be regarded as ambiguous (although carnivory and omnivory can be recovered at each of these nodes under DELTRAN and ACCTRAN optimisations, respectively). This is the result of the repositioning of the dinosaur taxa *Herrerasaurus* and *Eoraptor*, which are recovered as basal theropods (rather than basal saurischians) in the phylogenetic hypothesis of Nesbitt *et al.* (2009a, 2010; Fig. 1E). This ambiguity is compounded further if *Eoraptor* is regarded as an omnivore, which has the effect of spreading dietary ambiguity among the basal branches of theropod phylogeny (Fig. 1F). Moreover, some authors have proposed that the tooth-bearing bones of *Lewisuchus*
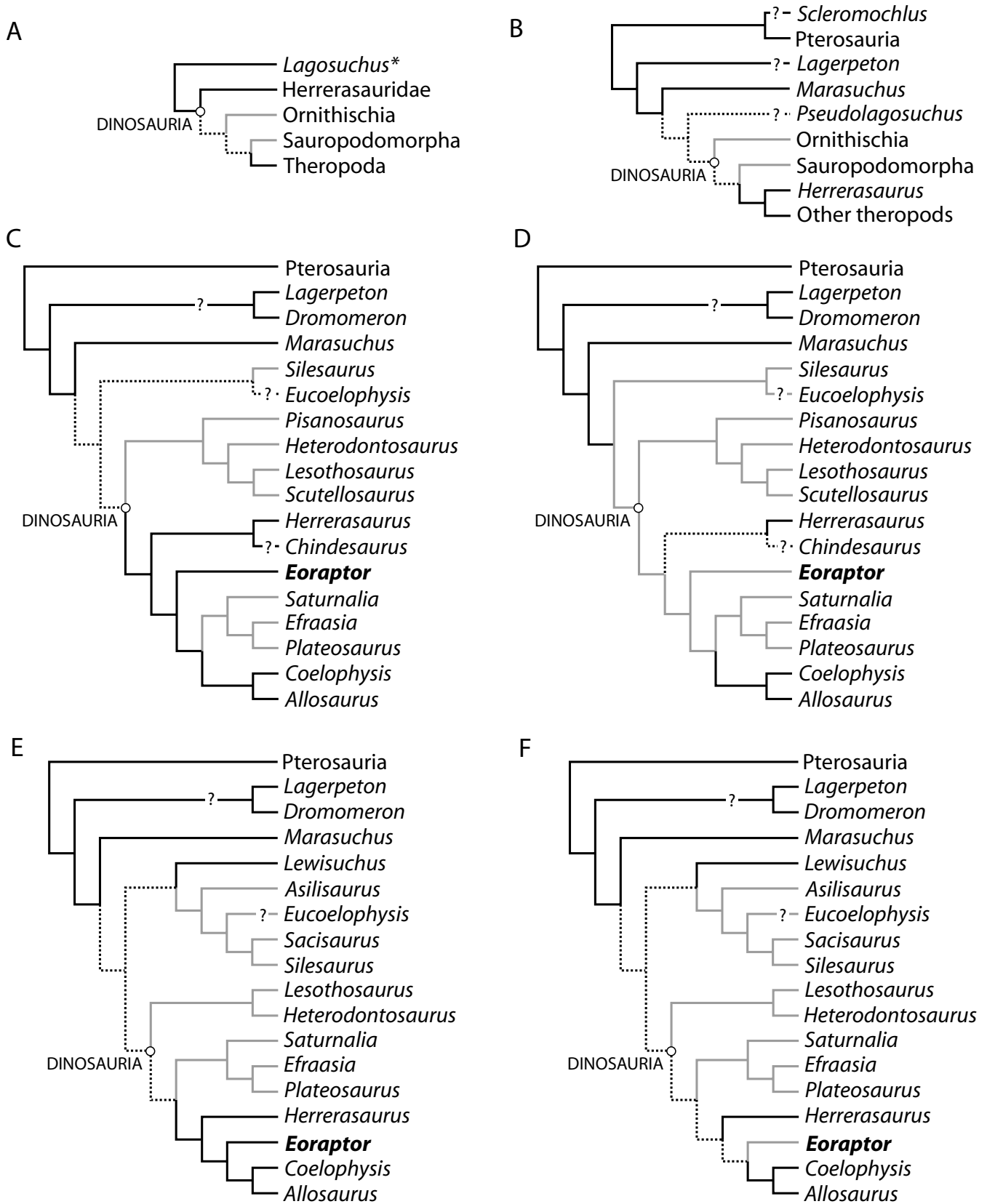
Figure 1 Optimisation of inferred diets on to dinosaur phylogenies. Dietary information is based on the sources cited in the text. All optimisations were carried out using MacClade 4.07 (Maddison & Maddison 2004). As the ability to eat plants is the innovation of interest, omnivores and herbivores are combined into a single dietary category for each set of optimisations: (A) based on the phylogeny of Gauthier (1986). Note that material included as *Lagosuchus* in this phylogeny is now referred to *Marasuchus* (Sereno & Arcucci 1994a); (B) based on Novas (1996). *Eoraptor* was excluded from this example to illustrate the effect of changing the phylogenetic position of herrerasaurids on dietary optimisations. If *Eoraptor* is included in this tree basal to other theropods (Novas 1996) and is regarded as a faunivore, the pattern of optimisations remains constant. If, however, *Eoraptor* was an omnivore, many of the basal lineages among dinosaurs would optimise as omnivorous; (C), (D) based on Nesbitt *et al*. (2009b) with *Eoraptor* as a faunivore (C) or omnivore (D); (E), (F) based on Nesbitt *et al*. (2010), with *Eoraptor* as a faunivore (E) or omnivore (F). Black lines indicate faunivory, grey lines omnivory or herbivory and dashed lines ambiguity. Question marks indicate taxa for which craniodental material is absent. Interpretations of these optimisations are given in the text.

might not be from the same individual as the other material in Romer's holotype, as this material was extracted from a nodule containing specimens of several different archosaur taxa and there may be a size discrepancy between the jaws and postcranial material (Langer *et al.* 2010). If this claim is substantiated, the diet of *Lewisuchus* should be regarded as ambiguous. This would have a major effect on all dietary optimisations, rendering all of the ancestors at the major basal nodes in Dinosauria + Silesauridae omnivorous. Finally, doubts have also been expressed regarding the diet of *Marasuchus*: Langer *et al.* (2010) contend that the teeth of the referred maxilla (Bonaparte 1975) are too poorly preserved to establish diet with confidence. This change would render the ancestral diet for Dinosauria + Silesauridae ambiguous, even if *Lewisuchus* were considered to be a carnivore.

Nesbitt *et al.* (2010) used concentrated changes tests (Maddison 1990) to determine if the distributions of craniodental character states recovered by their phylogenetic analysis of dinosauromorph interrelationships were correlated with inferred dietary preferences. These tests indicated that three dental character states (reduction in marginal denticle number/increase in relative denticle size; overlap of adjacent tooth crowns in the maxillary and dentary tooth rows; and presence of tooth crowns that are mesiodistally expanded with respect to the root) were all significantly correlated with omnivory/herbivory. Results of the concentrated changes tests also showed that each of these character states was gained on 3–4 independent occasions within Dinosauromorpha. This led Nesbitt *et al.* (2010) to conclude that omnivory/herbivory had appeared independently in silesaurids, sauropodomorphs and (possibly) ornithischians. Although the results of Nesbitt *et al.* (2010) appear contrary to the evidence gained from the foregoing dietary optimisations, it should be noted that these two approaches address slightly different questions. The optimisations presented in the present paper have considered omnivory/herbivory as a character complex or ecological trait, whereas the correlated changes tests of Nesbitt *et al.* (2010) are dealing with the distributions of particular character states, that each comprise only a portion of the total number of features that might be used to infer an omnivorous/herbivorous diet. Consequently, it might be expected that concentrated changes tests would have the potential to identify more examples of character state change (and thus the potential to identify more homoplasy) than the optimisation tests, as the latter rely on a broad suite of character evidence to identify dietary preferences that is less sensitive to changes in the distributions of single character states.

Consideration of dental morphology among ornithodirans highlights some of the difficulties associated with interpreting dietary evolution within the group. For example, some taxa, including *Silesaurus* (Dzik 2003), *Eoraptor* (Sereno *et al.* 1993), *Panphagia* (Martinez & Alcober 2009) and *Saturnalia* (Langer & Benton 2006) possess teeth that are intermediate in morphology between the recurved, finely serrated, unexpanded tooth crowns of herrerasaurids and neotheropods and the straighter, coarsely serrated (denticulate), mesiodistally expanded tooth crowns present in ornithischians and more derived sauropodomorphs (Crompton & Attridge 1986; Galton 1986; Barrett 2000). In addition, some of these animals are also heterodont and possess mixtures of teeth with 'carnivorous' and 'herbivorous' attributes. In the absence of other evidence (such as the presence/absence of trenchant ungulals, a rhampthotheca or gastric mill) dietary determinations based on such dentitions are problematic (Barrett 2000). In addition, dental morphology is either unknown or poorly characterised in several key genera (e.g. *Dromomeron*, *Eucoelophysis*, *Lagerpeton*, *Scleromochlus* and some basal theropods).

The foregoing discussion demonstrates that evidence for the dietary preferences of many non-dinosaurian dinosauromorphs and basal dinosaurs is equivocal (due either to a lack of appropriate craniodental material or to differing functional interpretations) and the phylogenetic interrelationships of these taxa remain labile (see above). As a consequence, minor changes in tree topology or re-assessment of the palaeobiology of a single taxon can have major influences on the inferred diets at the bases of many dinosauromorph clades. Until better craniodental material or direct evidence of diet is found for many of these taxa, the current consensus view that dinosaurs were primitively carnivorous (e.g. Sereno 1997; Barrett 2000; Nesbitt *et al.* 2010) should be viewed with caution, as an omnivorous origin for dinosaurs is certainly plausible on the basis of current data (see also Langer *et al.* 2010). Basal omnivory would imply that theropod carnivory was a homoplastic reversal, rather than a symplesiomorphy, but would still be consistent with multiple origins of obligate, high-fibre herbivory in more derived dinosaur clades (Barrett 2000, 2005; Barrett & Rayfield 2006; Zanno *et al.* 2009). Until more definitive data comes to light, it is suggested that the diet of the ancestral dinosaur should simply be regarded as ambiguous and that this factor should be taken into account in discussions of early dinosaur evolution and ecology.

2. Is herbivory a key evolutionary innovation for dinosaurs?

Herbivory is generally regarded as a 'major adaptive zone' (*sensu* Simpson 1953), and the ability to process and digest plant material has been viewed as one of the key events underpinning the diversification of terrestrial tetrapods (e.g. Hunter & Jernvall 1995; King 1996; Hotton *et al.* 1997; Hunter 1998; Sues & Reisz 1998; Reisz & Sues 2000). Many tetrapod lineages exhibit a wide variety of adaptations to a herbivorous or omnivorous diet, including changes to craniodental and postcranial anatomy, physiology, jaw mechanics and musculature, behaviour, and life history strategies, allowing them to exploit a spectrum of possible dietary niches ranging from occasional utilisation of plants to high-fibre folivory (Hotton *et al.* 1997). Indeed, some authors have proposed that herbivory, or characters associated with such a diet, might represent a key evolutionary innovation that promoted increased speciation rates within the clades that acquired them. For example, Moore & Brooks (1996) surveyed families of extant amniotes and found that herbivorous clades were, on average, 16 times more speciose than their carnivorous sister-clades. Similarly, Hunter & Jernvall (1995) argued that those herbivorous mammal clades possessing a hypocone were more diverse that those lacking this feature. This disparity in herbivore and carnivore species-richness is unsurprising: as primary consumers herbivores have direct access to the energy captured by plants, whereas less energy is available at higher trophic levels. The same patterns are also seen in other terrestrial groups: some herbivorous insect clades achieve levels of species-richness that are several orders of magnitude higher than those of their predatory sister-taxa (e.g. Mitter *et al.* 1988; Farrell 1998). Plant-eating non-avian dinosaurs are more diverse than carnivores and possess a wide variety of feeding mechanisms: moreover, herbivory/omnivory has generally been regarded as a derived feature for the group (see above). These observations led to the suggestion that the ability to exploit plants was an important factor, or even a key evolutionary innovation, that fuelled dinosaur diversification (e.g. Galton 1973, 1986; Crompton & Attridge 1986; Weishampel & Norman 1989; Norman & Weishampel 1991; Sereno 1997;

Barrett 1998; Fastovsky & Smith 2004; Barrett & Upchurch 2005). However, can this claim be justified?

Evolutionary biologists set two main criteria for the recognition of key evolutionary innovations and adaptive radiations (Heard & Hauser 1995; Schluter 2000; Brooks & McLennan 2002). First, tests of key innovations should be carried out within a phylogenetic framework to enable comparisons of speciation-rates and/or species-richness between monophyletic sister-groups (Heard & Hauser 1995; Schluter 2000; Brooks & McLennan 2002). As sister-groups originate at the same point in time, this criterion excludes the possibility that one group may have higher species-richness simply because it is has greater longevity. However, herbivorous dinosaurs do not form a monophyletic clade, but represent a polyphyletic assemblage incorporating ornithischians, sauropodomorphs and members of several disparate theropod lineages (Barrett & Rayfield 2006). In turn, carnivorous dinosaurs (all theropods) are paraphyletic with respect to various herbivorous theropod lineages (Barrett 2000, 2005; Zanno et al. 2009). Perhaps more importantly, birds should be included within Theropoda in order to render it monophyletic (Gauthier 1986). As a result, a simple comparison between species-richness dietary categories in non-avian dinosaurs does not take evolutionary history into account. Given the current consensus on dinosaur interrelationships (e.g. Sereno 1999; Pisani et al. 2002; Lloyd et al. 2008), a more rigorous approach would involve comparisons between ornithischians and saurischians (inclusive of birds), sauropodomorphs and theropods (inclusive of birds), and between a variety of theropod clades. However, this entails a number of problems when examining the potential role of herbivory as a key innovation, as all major dinosaur clades include at least some herbivorous members, preventing strict comparisons between sister-taxa that possess/lack the feature of interest. This becomes particularly difficult when considering birds as an integral part of Dinosauria, as herbivory appeared on numerous independent occasions within Aves (Storer 1971; see Brooks & McLennann 2002 for a discussion dealing with similar methodological problems in testing key innovation hypotheses for insect herbivory). Secondly, key innovation hypotheses are only deemed supportable in cases where the clade possessing the feature of interest exhibits a statistically significant increase in species-richness or net speciation rate in comparison with that recorded in its sister-clade (Heard & Hauser 1995; Schluter 2000; Brooks & McLennan 2002). Generally, the group with the key innovation should contain at least 90% of the total diversity of the two sister-groups under study (Guyer & Slowinski 1993). Unfortunately, the staggering diversity of Tertiary and extant birds (approximately 10 000 species of extant taxa alone: Pough et al. 1999) leads to strong asymmetry in the distribution of species-richness over the dinosaur tree. Consequently, it becomes exceptionally difficult to disentangle the effects that any new anatomical or behavioural features may have had on extinct dinosaur clades, as any potential signal is swamped by the addition of avian diversity.

Nevertheless, in spite of these objections, Hunter (1998) has argued that strict sister-group comparisons are not necessarily important in groups with a long fossil record, as the diversity dynamics of these clades are already set within a temporal context: by contrast, sister-group comparisons are more appropriate for extant clades without a good fossil record that lack information on the timing of speciation events. Hunter (1998) also argued that paraphyletic groups could be valid units to study if changes in taxon origination or extinction rate were considered rather than species-richness per se. Finally, comparisons between different ecological groupings of organisms are also potentially informative if their diversity changes can be observed over extended timescales (Hunter 1998).

Taking these caveats into account, comparisons between dietary guilds in dinosaurs can still yield some useful information. For illustrative purposes, if the non-avian dinosaur dataset provided by Weishampel et al. (2004a) is considered, herbivores/omnivores are, on average, 2·6 times more diverse than carnivores in any Mesozoic timeslice, with actual values varying from 1·2 to 10 times as speciose (Fig. 2A: see the figure legend for details of the procedures used to generate these diversity curves). The only exception to this pattern occurs during the Carnian when carnivores dominate. Addition of Mesozoic birds to this dataset leads to a reduction in this figure, with an average herbivore:carnivore ratio of 2·2 per timeslice (it should be noted that all of the Mesozoic birds included in this dataset were considered to be faunivores or insectivores (Padian 2004; Fig. 2A). Consequently, although herbivory/omnivory could be posited as an important evolutionary strategy for some Mesozoic dinosaur clades, due to the variety, abundance and disparity of these taxa, the ability to eat plants did not promote the elevated levels of species-richness achieved by other terrestrial herbivore clades (mammals and insects, above). This result might suggest that dinosaur herbivory/omnivory should not be regarded as a key evolutionary innovation per se. Indeed, this guild comprises approximately 54% of Mesozoic dinosaur genus-richness (based on data from Weishampel et al. 2004a), which is substantially lower than the 90% figure that would be regarded as a statistically significant difference (see above).

Comparisons between sister-clades, or slightly modified versions thereof, complicate this result. Although strict sister-group comparisons among dinosaur clades are difficult (for the reasons outlined above) insights can be gained by relaxing some of the strict criteria established for the recognition of key innovations (Hunter 1998). In the following discussion, Theropoda (inclusive of birds) is limited to Mesozoic taxa: as all non-avian dinosaur herbivores are restricted to the Mesozoic, the exclusion of Cenozoic avian diversity allows more meaningful comparisons between taxa that exist in the same ecological and temporal milieux. Moreover, as modern birds represent the only Cenozoic dinosaurs, they extend the duration of the theropod lineage 65 million years beyond the time at which all other non-avian dinosaurs became extinct. It could be argued, therefore, that the high diversity of modern avians (in comparison with extinct non-avian dinosaurs) simply reflects the longevity of this clade. Furthermore, in order to avoid comparisons between clades that include both herbivorous/omnivorous and carnivorous members, only predatory theropods are retained in the dataset. Similar modifications have been adopted in comparative analyses of insect adaptive radiations where, for example, herbivorous insect taxa occurring in clades otherwise dominated by saprophytic or faunivorous taxa were removed (Mitter et al. 1988; Brooks & McLennan 2002). This procedure partially accounts for the phenomenon whereby key innovations continue to evolve within a clade (Brooks & McLennan 2002), or where such innovations appear convergently, but with substantially different times of origin. (It should be noted that herbivorous/omnivorous theropods account for approximately 14% of Mesozoic theropod diversity on the basis of taxon lists provided by Weishampel et al. (2004a) and dietary determinations in Barrett (2005) and Zanno et al. (2009)). Sauropodomorpha represents the sister-group to this restricted version of Theropoda (Gauthier 1986); ornithischian diversity can also be contrasted with theropod diversity, though it should be remembered that this is not a true sister-group comparison (see above).
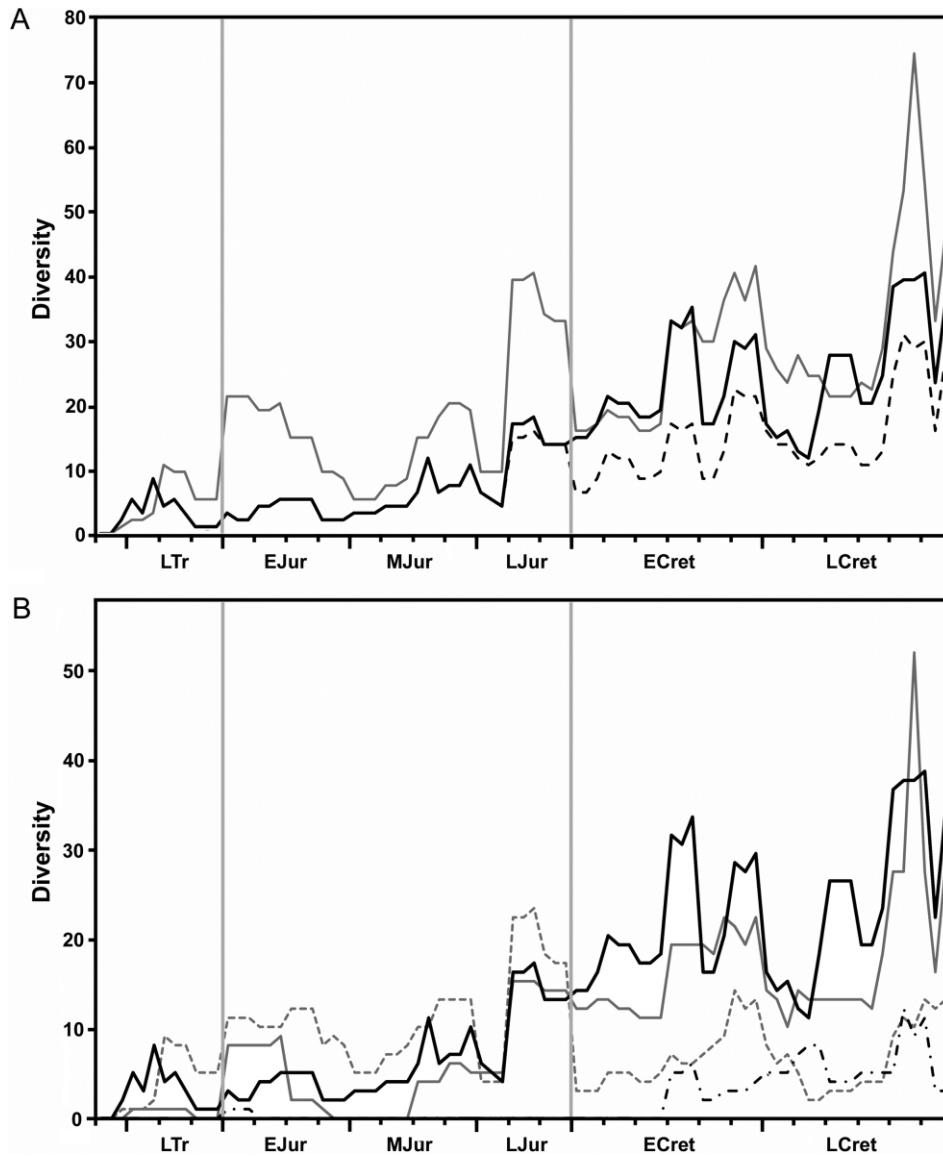
Figure 2 Raw patterns of dinosaur species-richness through time. These curves represent simple taxic diversity estimates (summation of species present in each time bin) based on the taxonomic, systematic and stratigraphical data compiled in Weishampel *et al.* (2004a). Time bins are Standard European Stages. Dietary inference is based on the information summarised by Barrett (2000, 2005), Barrett & Rayfield (2006), Weishampel *et al.* (2004a) and Zanno *et al.* (2009). All ornithischians, all sauropodomorphs and some theropods (therizinosauroids, ovirapto-rosaurians and ornithomimids with the exception of *Pelecanimimus*) are regarded as herbivores or omnivores; all remaining theropods (inclusive of Mesozoic birds) are considered to be faunivores. (A) comparisons of raw species-richness in herbivores/omnivores (grey line), carnivores including birds (black line) and carnivores excluding birds (dashed line: NB there are no birds prior to the Tithonian). (B) comparisons of raw species-richness in ornithischians (grey line), carnivorous theropods including birds (black line), sauropodo-morphs (grey dashed line) and herbivorous theropods (black dashed line). Abbreviations: ECret=Early Cretaceous; EJur=Early Jurassic; LCret=Late Cretaceous; LJur=Late Jurassic; LTr=Late Triassic; MJur=Middle Jurassic.

When these assumptions are taken into account, theropods are consistently more speciose than ornithischians in almost all Mesozoic timeslices (with the exception of the earliest Jurassic and the late Campanian: Fig. 2B). By contrast, sauropodo-morphs are generally more diverse than theropods in the Late Triassic to Jurassic (with the exception of the Carnian), but are substantially less species-rich in the Cretaceous (Fig. 2B). Consequently, it appears that omnivory/herbivory did not promote any substantial enhancement of ornithischian species-richness in comparison with theropod diversity. A similar argument could be made for sauropodomorphs if the Mesozoic is viewed as a whole; however, the early success of this group in comparison with theropods is noteworthy. In some Late Triassic and Early Jurassic timeslices, sauropodo-morphs are more than five times more diverse than theropods,

accounting for approximately 85% of saurischian diversity at these times (Fig. 2B). Moreover, sauropodomorphs were exceptionally abundant during this interval, accounting for up to 95% of the dinosaur individuals present in many faunas (Young 1951; Bonaparte 1972; Kitching & Raath 1984; Galton 1985, 1986, 2007; Sander 1992). Similarly, the numbers of first appearances of sauropodomorph taxa are also higher than those for theropods during this time interval (Fig. 3; see also Weishampel & Norman 1989). Finally, high sauropodomorph diversity in the Norian and late Early Jurassic diversity does seem to represent a genuine biological event as it is not an artefact of either the rock record or collector biases (Barrett *et al.* 2009; Mannion *et al.* 2011). These observations suggest that it is plausible to regard the inception of omnivory/ herbivory in early sauropodomorphs as an important factor,
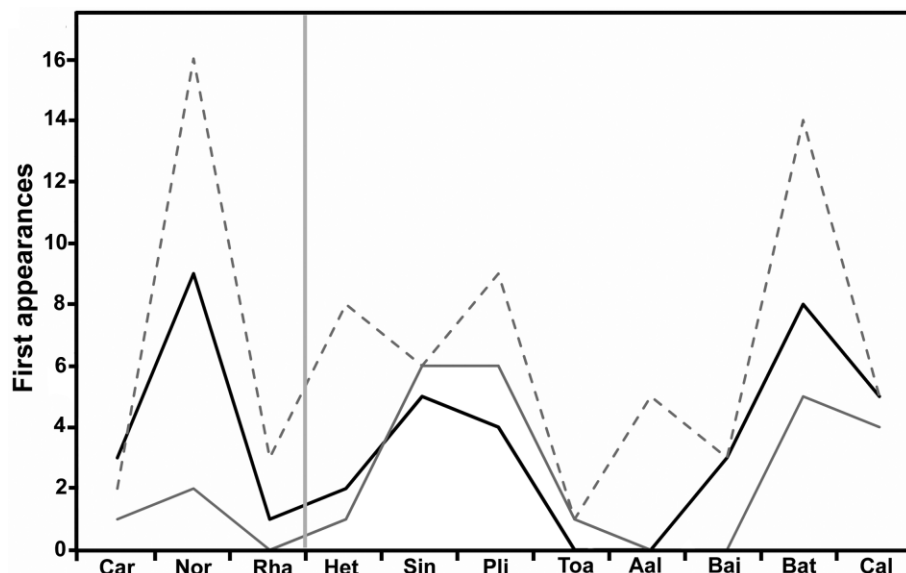
Figure 3 Numbers of first appearances of ornithischian (grey line), theropod (black line: all Late Triassic and Early Jurassic theropod taxa are faunivores, with the possible exception of *Eoraptor*) and sauropodomorph (dashed line) species in the Late Triassic and Early Jurassic. Taxa included and their first appearance dates are provided as Electronic Supplementary Material. Abbreviations: Aal=Aalenian; Baj=Bajocian; Bat=Bathonian; Cal=Callovian; Car=Carnian; Het=Hettangian; Nor=Norian; Pli=Pliensbachian; Rha=Rhaetian; Sin=Sinemurian; Toa=Toarcian.

possibly a candidate key evolutionary innovation, which allowed the group to diversify rapidly in comparison with its carnivorous sister-clade. This example demonstrates that it is necessary to view potential key innovations over extended temporal contexts, as well as within particular timeslices (as with analyses of extant clades), as it is possible that a number of factors can reduce the original effect of an innovation on diversification (de Queiroz 1999). These factors include the filling of available niches or the evolution of additional traits within the lineage that might obscure the impact of the key innovation (de Queiroz 1999). In this case, the ability to eat plants may have conferred an early increase in sauropodomorph dinosaur diversification rates, but failed to maintain its influence later in the history of the clade. Further work is necessary in order to determine if this might have been due to niche occupancy, the evolution of some character that constrained sauropodomorph diversity, or whether or the acquisition of a new trait among theropods allowed the latter group to diversify at a greater rate than previously (thereby negating or even reversing any comparative trends in species-richness between these sister-groups).

The foregoing discussion is based on the assumption that omnivory/herbivory represents a derived condition that appeared within Dinosauria. However, if it is hypothesised that plants formed a significant part of early dinosaur diets, as suggested by some dietary optimisations, then comparisons would have to be made between the species-richness of dinosaurs (excluding carnivores, for the reasons given above) and dinosaur outgroups. In this case dinosaur species-richness would clearly be substantially greater than that present in the faunivorous outgroups (which are represented by only a few species rather than substantial clades), and would certainly account for >90% of total diversity within the clades being examined (e.g. Dinosauromorpha). If herbivorous dinosaurs+silesaurids are compared with their faunivorous outgroup (*Marasuchus* and, for the sake of argument, other non-silesaurid, non-dinosaur dinosauromorphs, data on species-richness from Weishampel *et al.* (2004a) and Nesbitt *et al.* (2010)) herbivorous dinosaurs and silesaurids account for 422 species, whereas non-dinosaurian dinosauromorphs only

contribute four named species to total dinosauromorph diversity. Nevertheless, even if omnivory/herbivory can trace its origin to the base of the dinosaur+silesaurid clade, it should be remembered that other synapomorphies occur at this node that could account for the relative success of these animals relative to their outgroups (Irmis *et al.* 2007a; Nesbitt *et al.* 2010) and it may be these, rather than diet (or in combination with diet), that might be regarded as key innovations. (Similarly, additional synapomorphies occur at the base of Dinosauria and, as dinosaurs comprise the majority of the dinosaur+silesaurid clade, it could be these features that enable the clade as a whole to achieve high species-richness).

Numerous methodological problems frustrate attempts to identify key evolutionary innovations (Schluter 2000; Brooks & McLennan 2002). Although many key evolutionary innovation hypotheses have been proposed for many different animal and plant groups, few have withstood rigorous scrutiny (Heard & Hauser 1995; de Queiroz 1999; Schluter 2000; Brooks & McLennan 2002). These issues are especially pertinent when attempting to examine the role of key innovations in diverse, long-lived groups, such as dinosaurs (see above). Dinosaur species-richness, palaeoecology and phylogeny indicate that omnivory/herbivory was important in dinosaur evolutionary history (e.g. Weishampel & Norman 1989). However, whether it was a key evolutionary innovation in a strict sense is open to question, with the answer entirely dependent on the choices of groups (guilds, sister-groups or restricted sister-groups) and timescales being compared.

3. Herbivory, omnivory and early dinosaur ecology

Late Triassic vertebrates undergo a series of major taxonomic and ecological turnovers (e.g. Benton 1983a, 1986; Charig 1984; Olsen & Sues 1986; Olsen *et al.* 1987, 2002; Brusatte *et al.* 2008a, b). Early to early Late Triassic terrestrial communities are composed of various basal synapsid, pseudosuchian archosaur, basal archosauromorph and parareptile clades; by contrast, ornithodiran archosaurs, lepidosaurs and crocodylomorphs were either rare or absent at this time.

However, an extinction event (or series of events) during the late Carnian and/or early Norian led to a reversal of this pattern, with severe declines in the species-richness and abundance of 'typically' Triassic clades, such as non-mammalian synapsids, and the emergence of dinosaurs as the dominant ecological group. Although the cause(s), timing and exact pattern of the Late Triassic faunal turnover remains controversial (e.g. Benton 1994; Tanner *et al.* 2004; Irmis *et al.* 2007a; Dzik *et al.* 2008; Langer *et al.* 2010), all authors recognise a significant restructuring of the herbivore and omnivore guilds during this interval. Crompton & Attridge (1986), Galton (1986) and Weishampel & Norman (1989) noted that pre-Norian faunas were dominated by herbivorous taxa that possessed sophisticated masticatory apparatuses (such as propalinal grinding) or powerful bite forces, whereas later faunas were composed largely of dinosaurs (principally basal sauropodomorphs) that lacked well-developed chewing mechanisms and might have relied upon fermentative digestion and gastric mills in order to triturate plant food. In addition, pre-Norian herbivores were all habitual quadrupeds that browsed within the first 1–2 m above ground level. By contrast, basal sauropodomorphs were able to adopt bipedal stances and use their elongate necks to extend the vertical feeding range (1–4 m above ground level), marking the first occurrence of vertebrate high browsing (Bakker 1978). Several hypotheses were proposed to account for the paradoxical decline of oral processing, high-fibre herbivores and the subsequent radiation of sauropodomorph taxa that lacked extensive craniodental adaptations for dealing with vegetation. Some authors suggested that the combination of a gastric mill, fermentative digestion and fully upright gait (enabling foraging over wider ranges) might have facilitated the diversification of basal sauropodomorphs, allowing them to out-compete the sprawling, oral processing taxa that were prevalent in pre-Norian ecosystems (Charig 1984; Crompton & Attridge 1986; Galton 1986), a scenario that would imply a key role for herbivory or omnivory in promoting the early ecological success of dinosaurs to the detriment of other amniote groups. Other authors have posited alternative hypotheses that attribute the depletion of the pre-Norian herbivore guild to global climatic or vegetational changes, which might have caused selective extinctions among the earlier herbivores, thereby allowing dinosaurs to enter empty ecological space or to exploit new floral resources (Tucker & Benton 1982; Benton 1983a; Crompton & Attridge 1986; Zawiskie 1986; Weishampel & Norman 1989; Tiffney 1992; Wing *et al.* 1992). The latter scenarios suggest that dinosaur herbivory/omnivory might have been important in promoting dinosaur diversification immediately after the Late Triassic faunal replacement, but that it was not a causative factor in driving such replacements.

Both sets of hypotheses are difficult to test, due to the relatively small number of terrestrial formations and localities available for the Carnian–Norian, the incompleteness of many key sections, their uneven geographical distribution and persistent problems in stratigraphical correlation (Benton 1994; Padian 1994). Nevertheless, literal readings of the available record do allow partial evaluation of these scenarios. For example, the likelihood of 'candidate competitive replacements' (CCRs) between clades can be tested against a set of criteria (Benton 1996). The clades in question should share similar ecology (habitat, diet, body size), overlaps in geographical and stratigraphical ranges, and the 'successful' group should survive the 'unsuccessful' group (Benton 1996). In addition, relative abundance could be added as a fifth criterion, as it would be expected that individuals of the 'successful' group would increase in number at the expense of the 'unsuccessful' group. Application of these criteria to Late

Triassic herbivore groups suggests that competition was unlikely to have been a driving factor in these faunal replacements (see also Benton 1983a, 1986). First, although it could be argued that basal sauropodomorphs and other Late Triassic herbivore groups did overlap ecologically, a number of factors suggest that they employed distinctive modes of life that would have precluded direct competition. In terms of body size, aetosaurs could reach 4–5 m (Long & Murry 1995), most rhynchosaurs were between 1 m and 2 m in length (e.g. Benton 1983b) and the largest Late Triassic dicynodonts were up to 4·5 m long and could weigh in excess of 1000 kg (Reisz & Sues 2000; Dzik *et al.* 2008). These figures are comparable with those for some basal sauropodomorphs, which ranged from 2·5m to 10 m in adult body length (Galton & Upchurch 2004) and achieved body masses of up to three tonnes (Seebacher 2001). However, this body size overlap is misleading, as the majority of basal sauropodomorphs exceeded 3–4 m in length; also, high-browsing basal sauropodomorphs were able to access food from levels that were inaccessible to other Triassic herbivores. In addition, precise dietary information is unavailable for all of these animals (no Late Triassic herbivore/omnivore cololites or coprolites have been discovered to date), so it not possible to determine if they were utilising the same plant resources. Food was processed in fundamentally different ways (oral processing *vs* gut processing, see above) by these groups and it is also possible that at least some basal sauropodomorphs were omnivores rather than strict herbivores (Barrett 2000). Secondly, it has been suggested that the spatiotemporal distributions of Late Triassic herbivores offer little support for competitive interactions (Tucker & Benton 1982; Benton 1983a, 1986; Crompton & Attridge 1986). Global compilations of Triassic terrestrial faunas indicate that dicynodonts, some herbivorous cynodonts, rhynchosaurs and, to a lesser extent, aetosaurs either became extinct prior to the onset of the herbivorous dinosaur radiation or were rare at this time, implying that the taxonomic composition of the herbivore guild changed rapidly and possibly synchronously around the world at some point during the Norian, with limited overlap between the different clades (Tucker & Benton 1982; Benton 1983a, 1986). Abundance data are generally in accord with these diversity signals: aetosaurs, dicynodonts and rhynchosaurs are by far the most common taxa in Carnian herbivore faunas (e.g. Benton & Spencer 1995; Long & Murry 1995; Langer 2005; Dzik & Sulej 2007), whereas this situation is generally reversed in the Norian, when basal sauropodomorph dinosaurs are ecologically dominant (e.g. Sander 1992; Jenkins *et al.* 1994; Arcucci *et al.* 2004; Knoll 2004). Nevertheless, there are exceptions to these patterns, which suggest that the replacements may have occurred in a more complex sequence involving regional differences in the timings of dicynodont/rhynchosaur/aetosaur extinction and herbivorous dinosaur radiation. These include the Norian of western North America (e.g. Chinle, Bull Canyon and Cooper Canyon formations) and India (Maleri Formation) and the Norian/Rhaetian of Poland (Lisowice fauna), where basal sauropodomorph remains are currently absent and aetosaurs and/or dicynodonts remain the pre-eminent herbivore taxa (e.g. Long & Murry 1995; Kutty *et al.* 2007; Dzik *et al.* 2008; Vijaya *et al.* 2009). Finally, it has been shown that non-dinosaurian archosaurs occupied more morphospace than coeval dinosaurs and that these two groups had similar evolutionary rates, suggesting that it is unlikely that dinosaurs would have outcompeted other archosaur clades (Brusatte *et al.* 2008a). Consequently, competition was probably not a major factor in determining the pattern of faunal replacements in the Late Triassic, although further work is clearly needed to disentangle the diversity and abundance signals from different clades and

regions in order to gain a more accurate understanding of faunal dynamics at this time.

Changes in floral composition have been posited to impact Late Triassic herbivore communities (Tucker & Benton 1982; Benton 1983a; Tiffney 1992). Middle and early Late Triassic Gondwanan floras were composed largely of seed ferns, along with some cycadophytes, equisitealeans, various ferns and some conifers (collectively termed the *Dicroidium* flora); during the Norian seed ferns declined in importance, a change attributed to increasing aridity, and the *Dicroidium* flora was replaced by a conifer- and bennettitalean-dominated flora that had already become established in Laurasia sometime earlier (see summary in Wing *et al*. 1992). Tucker & Benton (1982: see also Benton 1983a) suggested that rhynchosaurs and synapsids were dependent upon the *Dicroidium* flora: the replacement of this flora by conifers and bennettitaleans was hypothesised to lead to the decline and extinction of these herbivores. Conversely, sauropodomorph dinosaurs were envisioned to have co-evolved with the Laurasian flora and thereby benefitted from its expansion into Gondwana during the Norian, leading to the global ascendancy of dinosaurs. However, as noted elsewhere, sauropodomorphs were already diverse and abundant in Gondwana prior to the floral change, so the latter cannot account for the success of these animals (Crompton & Attridge 1986; Barrett & Upchurch 2005). Nevertheless, there have been no quantitative studies of tetrapod–plant interactions in the Triassic, and rigorous comparisons between the plant and vertebrate fossil records would have the potential to yield interesting co-evolutionary or macroecological signals. The palaeobotanical record indicates that other floral changes occurred during the Triassic (including major differences in provinciality during the Late Triassic and decreases in diversity at the Triassic–Jurassic boundary: Wing *et al*. 1992; McElwain *et al*. 1999, 2009), which might have had an impact on the evolution or distribution of herbivorous vertebrates. Moreover, the advent of vertebrate high-browsing might have had significant effects on plant physiognomy, life histories and defences, which remain to be investigated. Geographical Information Systems could be used to investigate some of these data, by comparing the geographical and temporal ranges of particular plant and vertebrate taxa in order to establish whether interactions could have occurred between them and if these interactions persisted or changed through time (e.g. Butler *et al*. 2010), whereas detailed work on changes in plant morphology (such as the identification of mechanical defences) might yield information on possible responses to high-browsing. On the basis of current information, however, causes other than competition and floral change should be sought to account for the Late Triassic faunal replacements. These might include climate change, extraterrestrial impacts or other abiotic events (e.g. McElwain *et al*. 1999, 2009; Olsen *et al*. 2002). Current data suggest that the rise of basal sauropodomorphs should be regarded as opportunistic, with herbivory/omnivory (and potentially high browsing) driving their radiation.

Most discussions on Late Triassic dinosaur herbivory and its possible role in faunal replacement focus almost exclusively on basal sauropodomorphs, a bias that reflects their high abundance and species-richness at this time (e.g. Tucker & Benton 1982; Benton 1983a; Galton 1986; Wing *et al*. 1992), whereas ornithischians are seldom mentioned. Indeed, the only known Late Triassic ornithischians are from southern Africa (*Eocursor*: Butler *et al*. 2007) and Argentina (*Pisanosaurus* and an indeterminate heterodontosaurid: Bonaparte 1976; Baez & Marsicano 2001) and each of these taxa is currently known from only a single specimen. Other purported records of Triassic ornithischians have been re-dated as Early Jurassic (Olsen & Galton 1984) or shown to pertain to other archosaur groups (Parker *et al*. 2005; Butler *et al*. 2006; Irmis *et al*. 2007b; Nesbitt *et al*. 2007). Ornithischians become more conspicuous in the Early Jurassic and achieve a global distribution at this time (Weishampel *et al*. 2004b). However, they remain rare components in many basal Jurassic faunas. For example, the Lower Lufeng Formation of southern China has yielded numerous complete skeletons and hundreds of isolated elements of basal sauropodomorph taxa (e.g. Young 1951; Simmons 1965), whereas this same unit has produced only three confirmed ornithischian specimens (Irmis & Knoll 2008). Ornithischian abundance also remains lower than that of sauropodomorphs in other regions, even where they achieve levels of species-richness comparable to those of sympatric basal sauropodomorphs, as occurs in the upper Elliot and Clarens formations of southern Africa. The basal sauropodomorph *Massospondylus* is the most abundant taxon known from these units and is represented by well over 80 individuals (e.g. Cooper 1981; Kitching & Raath 1984; Galton & Upchurch 2004). This is probably a conservative estimate and the actual figure is likely to be far higher on the basis of the numerous specimens housed in European and southern African museums, as well as on the frequency with which basal sauropodomorph specimens are encountered in the field (PMB pers. obs.). The standing biomass of *Massospondylus* is likely to have been considerable (individuals reached an estimated body weight of 130–140 kg: Seebacher 2001) and other similarly sized, and larger, basal sauropodomorph taxa are also known from these units (e.g. Yates *et al*. 2004, 2007, 2010). Although ornithischians (including several heterodontosaurids, *Lesothosaurus* and *Stormbergia*) account for approximately 60 individuals from these units (Galton 1978; Knoll & Battail 2001; Knoll 2002; Butler 2005; Porro *et al*. 2011 (this volume)) these animals were all relatively small, with body masses of only a few kilogrammes (e.g. Seebacher 2001), and their contribution to total herbivore biomass would have been negligible. However, it should be noted that ornithischians are the most abundant dinosaurs in other Early Jurassic faunas, including those from southern England (Benton & Spencer 1995) and Arizona (Sues *et al*. 1994), in which sauropodomorphs are either absent or rare. Many basal ornithischians possessed sophisticated craniodental and postcranial adaptations to high-fibre herbivory, including rhampthothecae, dental occlusion (sometimes accompanied by complex jaw movements), cheeks, and retroverted pubes that permitted an elongate digestive tract (e.g. Crompton & Attridge 1986; Galton 1986; Weishampel & Norman 1989; Norman & Weishampel 1991; Barrett 2001; Porro 2007). This contrasts with the adaptations that were present in basal sauropodomorphs, which were relatively simple in comparison: for example, all basal sauropodomorphs lacked complex jaw movements and dental occlusion (Galton 1985, 1986; Crompton & Attridge 1986; Barrett & Upchurch 2007). Comparisons between the feeding mechanisms present in these clades might suggest that ornithischians were 'better' herbivores than basal sauropodomorphs. Consequently, it is surprising that ornithischians remained rare components of Late Triassic and many Early Jurassic ecosystems, while basal sauropodomorphs prospered (Crompton & Attridge 1986; Galton 1986). Indeed, ornithischians continued to be rare members of Mesozoic biomes until well into the Middle or Late Jurassic (Bakker 1978; Sereno 1997, 1999; Barrett & Willis 2001; Butler *et al*. 2007, 2008).

Competition is unlikely to have played a role in suppressing the early radiation of ornithischians. Basal sauropodomorphs and ornithischians co-occurred in many Late Triassic and Early Jurassic deposits (Weishampel *et al*. 2004b), but the

larger body size and increased browse height of sauropodo-morphs suggests that they would not have been in direct competition with ornithischians (Barrett & Upchurch 2005). All basal ornithischian taxa were relatively small animals, reaching only 1–2 m in body length and browsing within the first metre above ground level (Crompton & Attridge 1986; Galton 1986; Weishampel & Norman 1989; Norman & Weishampel 1991). Although juvenile sauropodomorphs would be feeding at these lower levels (as would adults at least some of the time), the strongly contrasting feeding mechanisms present in basal sauropodomorphs and ornithischians rein-forces their ecological separation and reduces the likelihood of competition between them. Moreover, the main ornithischian radiations in the Middle–Late Jurassic significantly post-date the late Early Jurassic extinctions of non-eusauropod sauro-podomorphs (Barrett & Upchurch 2005); a time lag that is inconsistent with either ecological release from competition or the opportunistic filling of the niches left vacant by these extinctions. With the exception of the Ischigualasto Formation in Argentina, which yields abundant remains of rhynchosaurs and aetosaurs alongside rare ornithischians (Bonaparte 1972; Rogers *et al.* 1993), all other faunas yielding early ornithis-chian remains either lack significant numbers of other low-browsing herbivores, or have herbivore faunas comprising taxa that are considerably smaller than ornithischians (such as tritylodontid synapsids) that are unlikely to have been direct competitors. These include the Laguna Colorada Formation of Argentina (Baez & Marsicano 2001), the lower Elliot Forma-tion (Kitching & Raath 1984; Knoll 2004) and upper Elliot and Clarens formations (Kitching & Raath 1984; Knoll 2005) of South Africa, the Kayenta Formation of the USA (Sues *et al.* 1994) and the Lower Lufeng Formation of China (Young 1951; Simmons 1965; Luo & Wu 1994). Silesauridae included several herbivorous or omnivorous taxa, and these animals did overlap with ornithischians in terms of body size, browse height and stratigraphical distribution (with silesaurids rang-ing from the late Anisian to the Norian: Nesbitt *et al.* 2010). However, herbivorous/omnivorous silesaurids (*Asilisaurus*, *Sacisaurus*, *Silesaurus*, *Technosaurus* (in part) and one un-named taxon) are known from the late Anisian of Tanzania (Nesbitt *et al.* 2010), the late Carnian of Poland (Dzik 2003), the late Carnian/early Norian of Brazil (Ferigolo & Langer 2007) and the Norian of North America (Cooper Canyon and Petrified Forest formations: Irmis *et al.* 2007a; Nesbitt *et al.* 2010) – ornithischians are currently unknown from these regions at these times, although other dinosaur groups may be present (e.g. Weishampel *et al.* 2004b). Conversely, silesaurids are absent from sites yielding Triassic ornithischians. It is not clear if these disjunct distributions have any evolutionary or ecological significance, or if the presence/absence of a particular group in a fauna is the result of sampling biases.

A considerable lag time exists between the Late Triassic acquisition of herbivory in ornithischians and their major taxonomic and ecological radiations, supporting the inference that herbivory *per se* was not a key innovation in these animals (see above; Butler *et al.* 2007). Indeed, it is conceivable that specialisation for herbivory might have been a constraint in early ornithischian evolution, which could account for the low diversity and abundance of the group at this time. The subsequent success of ornithischians in the Late Jurassic and Cretaceous would signal the end of such a constraint, as evidenced by the development of more advanced food process-ing mechanisms, such as the advent of pleurokinesis in orni-thopods (Norman 1984; Weishampel 1984) and of propaliny or specialised orthal slicing in ceratopsians (e.g. Sereno *et al.* 2010), and the rise of the group to ecological dominance (Weishampel & Norman 1989; Barrett & Willis 2001). Various

factors might have acted as a potential constraint on early ornithischian herbivores, although the effects of these are difficult to test on the basis of current data and remain highly speculative. For example, ornithischians might have evolved to exploit a relatively small number of potential food plants (or plant organs) in Triassic floras, and the availability of this resource might have limited ornithischians to small population sizes or restricted environments; while basal sauropodomorphs might have been able to access a broader range of fodder. Later changes in the compositions of Mesozoic floras, or to ornithischian feeding preferences, might have allowed escape from this constraint. One way to test these hypotheses would be to compare the spatiotemporal distributions of possible food plants and environmental indicators with those of dino-saur taxa, in order to determine if their ranges exhibited significant overlap or non-overlap. This information could be combined with relative abundance data from individual locali-ties to provide a more detailed overview of possible ecological changes. Alternatively, it is possible that physiology also played a role in the differing success of ornithischians and basal sauropodomorphs; for example, divergent responses to water stress, plant toxicity or some other environmental factor might have influenced the relative success of these groups during the Late Triassic and Early Jurassic. In this case, comparisons of bone histology might be helpful in identify-ing major physiological differences (Chinsamy-Turan 2005). Nevertheless, the causes underlying the differential success of sauropodomorphs and ornithischians remain unknown, but are clearly amenable to further investigation.

4. Conclusions

The ability to eat plants allowed dinosaurs to dominate Late Mesozoic ecosystems, but the influence of herbivory and omnivory was more nuanced in Late Triassic and Early Jurassic terrestrial communities. Dietary optimisations indi-cate that the diets of basal dinosaurs and saurischians are difficult to resolve, as they are sensitive to minor differences in tree topology and taxon inclusion. Until better dietary infor-mation is available for many basal dinosaurs and dinosauro-morphs, it might be advisable to regard the diet of the ancestral dinosaur as ambiguous in scenarios of early dinosaur evolution. Moreover, although herbivory is often regarded as a key evolutionary innovation for dinosaurs, evidence for this supposition is weak, as the observed species-richness of herbivorous/omnivorous taxa does not signal a statistically significant increase in the diversity of these clades. Neverthe-less, herbivory/omnivory might have been an important factor in the initial radiation and diversification of sauropodo-morphs. By contrast, early ornithischians appeared to gain little benefit from herbivory, which presents a paradox, given the presence of the many craniodental adaptations that would have permitted high-fibre folivory in these animals. The reason(s) for the differential success of these two groups remain unclear, although competitive interactions and responses to large-scale floral perturbations are unlikely. Many of the solutions to problems associated with the evolution of dinosaur herbivory will only be solved by serendipitous discov-eries of new dinosaur and basal dinosauromorph material from Triassic and Early Jurassic strata (for example, basal dinosaurs with well preserved skulls and teeth, or direct evidence of diet such as gut contents), but fine-grained comparisons between the faunal and floral records might provide some novel, rigorous insights into the patterns of ecological and evolutionary change that occurred during this critical interval in Earth history.

5. Acknowledgements

6. Supplementary material

A table of the taxa used to construct Figure 3, and their first appearance dates, is provided as Supplementary Material with the online version of this paper. This is hosted by the Cambridge Journals Online service and can be viewed at http://journals.cambridge.org/tre

7. References

Abler, W. L. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology* **18**, 161–83.

Arcucci, A. B. 1987. Un nuevo Lagosuchidae (Thecodontia–Pseudosuchia) de la fauna de los Chañares (edad reptile Chañarense, Triasico Medio), La Rioja, Argentina. *Ameghiniana* **24**, 89–94.

Arcucci, A. B., Marsicano, C. A. & Caselli, A. T. 2004. Tetrapod association and palaeoenvironment of the Los Colorados Formation (Argentina): a significant sample from western Gondwana at the end of the Triassic. *Geobios* **37**, 557–68.

Baez, A. M. & Marsicano, C. A. 2001. A heterodontosaurid ornithischian dinosaur from the Upper Triassic of Patagonia. *Ameghiniana* **38**, 271–78.

Bakker, R. T. 1978. Dinosaur feeding behaviour and the origin of flowering plants. *Nature* **274**, 661–63.

Bakker, R. T. & Galton, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature* **248**, 168–72.

Barrett, P. M. 1998. *Herbivory in the non-avian Dinosauria.* Unpublished PhD Dissertation, University of Cambridge. 308 pp.

Barrett, P. M. 2000. Prosauropods and iguanas: speculation on the diets of extinct reptiles. *In* Sues, H.-D. (ed.) *Evolution of Herbivory in Terrestrial Vertebrates: perspectives from the fossil record*, 42–78. Cambridge, UK: Cambridge University Press.

Barrett, P. M. 2001. Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyreophoran dinosaurs. *In* Carpenter, K. (ed.) *The Armored Dinosaurs*, 25–52. Bloomington and Indianapolis: Indiana University Press.

Barrett, P. M. 2005. The diets of ostrich dinosaurs (Theropoda: Ornithomimosauria). *Palaeontology* **48**, 347–58.

Barrett, P. M., McGowan, A. J. & Page, V. 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society B* **276**, 2667–74.

Barrett, P. M. & Rayfield, E. J. 2006. Dinosaur feeding: recent advances and evolutionary implications. *Trends in Ecology and Evolution* **21**, 217–24.

Barrett, P. M. & Upchurch, P. 2005. Sauropod diversity through time: possible macroevolutionary and palaeoecological implications. *In* Curry-Rogers, K. A. & Wilson, J. A. (eds) *The Sauropods: evolution and paleobiology*, 125–56. Berkeley: University of California Press.

Barrett, P. M. & Upchurch, P. 2007. The evolution of herbivory in sauropodomorph dinosaurs. *In* Barrett, P. M. & Batten, D. J. (eds) *Evolution and palaeobiology of early sauropodomorph dinosaurs. Special Papers in Palaeontology* **77**, 91–112.

Barrett, P. M. & Willis, K. J. 2001. Did dinosaurs invent flowers? Dinosaur–angiosperm coevolution revisited. *Biological Reviews* **76**, 411–47.

Benton, M. J. 1983a. Dinosaur success in the Triassic: a noncompetitive ecological model. *Quarterly Review of Biology* **58**, 29–55.

Benton, M. J. 1983b. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society B* **302**, 605–718.

Benton, M. J. 1986. The Late Triassic tetrapod extinction events. *In* Padian, K. (ed.) *The Beginning of the Age of the Dinosaurs*, 303–20. Cambridge, UK: Cambridge University Press.

Benton, M. J. 1990. Origin and interrelationships of dinosaurs. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (1st edn), 11–30. Berkeley: University of California Press.

Benton, M. J. 1994. Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern. *In* Fraser, N. C. & Sues, H.-D. (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 366–97. Cambridge, UK: Cambridge University Press.

Benton, M. J. 1996. On the nonprevalence of competitive replacement in the evolution of tetrapods. *In* Jablonski, D., Erwin, D. H. & Lipps, J. H. (eds) *Evolutionary Paleobiology*, 185–210. Chicago, Illinois: University of Chicago Press.

Benton, M. J. & Spencer, P. S. 1995. *Fossil Reptiles of Great Britain.* London: Chapman and Hall. 386 pp.

Bonaparte, J. F. 1972. Los tetrapodos del sector superior de la Formacion Los Colorados, La Rioja, Argentina (Triásico Superior). *Opera Lilloana* **22**, 1–183.

Bonaparte, J. F. 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia – Pseudosuchia) y su significado en el origen de los Saurischia. Chañarense inferior, Triásico Medio de Argentina. *Acta Geologica Lilloana* **13** (1), 5–89.

Bonaparte, J. F. 1976. *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. *Journal of Paleontology* **50**, 808–20.

Brinkman, D. B. & Sues, H.-D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. *Palaeontology* **30**, 493–503.

Brooks, D. R. & McLennan, D. A. 2002. *The Nature of Diversity: an evolutionary voyage of discovery.* Chicago, Illinois: University of Chicago Press. 668 pp.

Brusatte, S. L., Benton, M. J., Ruta, M. & Lloyd, G. T. 2008a. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* **321**, 1485–88.

Brusatte, S. L., Benton, M. J., Ruta, M. & Lloyd, G. T. 2008b. The first 50 mya of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters* **4**, 733–36.

Butler, R. J. 2005. The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. *Zoological Journal of the Linnean Society* **145**, 175–218.

Butler, R. J., Porro, L. B. & Heckert, A. B. 2006. A supposed heterodontosaurid tooth from the Rhaetian of Switzerland and reassessment of the European Late Triassic record of Ornithischia (Dinosauria). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2006**, 613–33.

Butler, R. J., Smith, R. M. H. & Norman, D. B. 2007. A primitive ornithischian dinosaur from the Late Triassic of South Africa, and the early evolution and diversification of Ornithischia. *Proceedings of the Royal Society of London, Series B* **274**, 2041–46.

Butler, R. J., Norman, D. B. & Upchurch, P. 2008. The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology* **6**, 1–40.

Butler, R. J., Barrett, P. M., Penn, M. G. & Kenrick, P. 2010. Testing coevolutionary hypotheses over geological timescales: interactions between Cretaceous dinosaurs and plants. *Biological Journal of the Linnean Society* **100**, 1–15.

Charig, A. J. 1984. Competition between therapsids and archosaurs during the Triassic Period: a review and synthesis of current theories. *Symposia of the Zoological Society of London* **52**, 597–628.

Chinsamy-Turan, A. 2005. *The Microstructure of Dinosaur Bone.* Baltimore, Maryland: The Johns Hopkins University Press. 216 pp.

Cooper, M. R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments Rhodesia, Series B, Natural Sciences* **6**, 689–840.

Crompton, A. W. & Attridge, J. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic time. *In* Padian, K. (ed.) *The Beginning of the Age of the Dinosaurs*, 223–36. Cambridge, UK: Cambridge University Press.

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* **23**, 556–74.

Dzik, J., Sulej, T. & Niedzwiedzki, G. 2008. A dicynodont-theropod association in the latest Triassic of Poland. *Acta Palaeontologica Polonica* **53**, 733–38.

Dzik, J. & Sulej, T. 2007. A review of the early Late Triassic Krasiejów Biota from Silesia, Poland. *Palaeontologia Polonica* **64**, 3–27.

Ezcurra, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* **28**, 649–84.

Farlow, J. O. 1976. A consideration of the trophic dynamics of a Late Cretaceous large-dinosaur community (Oldman Formation). *Ecology* **57**, 841–57.

Farrell, B. D. 1998. 'Inordinate fondness' explained: why are there so many beetles? *Science* **281**, 555–59.

Fastovsky, D. E. & Smith, J. B. 2004. Dinosaur paleoecology. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 614–26. Berkeley: University of California Press.

Ferigolo, J. & Langer, M. C. 2007. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone. *Historical Biology* **19**, 23–33.

Galton, P. M. 1973. The cheeks of ornithischian dinosaurs. *Lethaia* **6**, 67–89.

Galton, P. M. 1978. Fabrosauridae, the basal family of ornithischian dinosaurs (Reptilia: Ornithopoda). *Paläontologische Zeitschrift* **52**, 138–59.

Galton, P. M. 1985. Diet of prosauropod dinosaurs from the Late Triassic and Early Jurassic. *Lethaia* **18**, 105–23.

Galton, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. *In* Padian, K. (ed.) *The Beginning of the Age of the Dinosaurs*, 203–21. Cambridge, UK: Cambridge University Press.

Galton, P. M. 2007. Notes on the remains of archosaurian reptiles, mostly basal sauropodomorph dinosaurs, from the 1834 fissure fill (Rhaetian, Upper Triassic) at Clifton in Bristol, southwest England. *Revue de Paléobiologie* **26**, 505–91.

Galton, P. M. & Upchurch, P. 2004. Prosauropoda. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 232–58. Berkeley: University of California Press.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* **8**, 1–55.

Guyer, C. & Slowinski, J. B. 1993. Adaptive radiation and the topology of large phylogenies. *Evolution* **47**, 253–63.

Heard, S. B. & Hauser, D. L. 1995. Key evolutionary innovations and their ecological mechanisms. *Historical Biology* **10**, 151–73.

Hotton, N., Olson, E. C. & Beerbower, R. 1997. Amniote origins and the discovery of herbivory. *In* Sumida, S. S. & Martin, K. L. M. (eds) *Amniote Origins: Completing the Transition to Land*, 207–64. San Diego, California: Academic Press.

Hunter, J. P. 1998. Key innovations and the ecology of macroevolution. *Trends in Ecology and Evolution* **13**, 31–36.

Hunter, J. P. & Jernvall, J. 1995. The hypocone as a key innovation in mammalian evolution. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 10718–22.

Irmis, R. B., Nesbitt, S. J., Padian, K., Smith, N. D., Turner, A. H., Woody, D. & Downs, A. 2007a. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. *Science* **317**, 358–61.

Irmis, R. B., Parker, W. G., Nesbitt, S. J. & Lui, J. 2007b. Early ornithischian dinosaurs: the Triassic record. *Historical Biology* **19**, 3–22.

Irmis, R. B. & Knoll, F. 2008. New ornithischian dinosaur material from the Lower Jurassic Lufeng Formation of China. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **247**, 117–28.

Jenkins, F. A. Jr, Shubin, N. H., Amaral, W. W., Gatesy, S. M. Schaff, C. R., Clemmensen, L. B., Downs, W. R., Davidson, A. R., Bonde, N. & Osbæck, F. 1994. Late Triassic continental vertebrates of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser om Grønland, Geoscience* **32**, 1–25.

King, G. M. 1996. *Reptiles and Herbivory*. London: Chapman & Hall. 160 pp.

Kitching, J. W. & Raath, M. A. 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the north-eastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia Africana* **25**, 111–25.

Knoll, F. 2002. Nearly complete skull of *Lesothosaurus* (Dinosauria: Ornithischia) from the upper Elliot Formation (Lower Jurassic: Hettangian) of Lesotho. *Journal of Vertebrate Paleontology* **22**, 238–43.

Knoll, F. 2004. Review of the tetrapod fauna of the 'Lower Stormberg Group' of the main Karoo Basin (southern Africa): implication for the age of the Lower Elliot Formation. *Bulletin de la Société géologique de France* **175**, 73–83.

Knoll, F. 2005. The tetrapod fauna of the Upper Elliot and Clarens formations in the main Karoo Basin (South Africa and Lesotho). *Bulletin de la Société Géologique de France* **176**, 81–91.

Knoll, F. & Battail, B. 2001. New ornithischian remains from the Upper Elliot Formation (Lower Jurassic) of Lesotho and stratigraphical distribution of southern African fabrosaurids. *Geobios* **34**, 415–21.

Kutty, T. S., Chatterjee, S., Galton, P. M. & Upchurch, P. 2007. Basal sauropodomorphs (Dinosauria: Saurischia) from the Lower Jurassic of India: their anatomy and relationships. *Journal of Paleontology* **81**, 1218–40.

Langer, M. C. 2004. Basal Saurischia. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 25–46. Berkeley: University of California Press.

Langer, M. C. 2005. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences* **19**, 205–18.

Langer, M. C., Abdala, F., Richter, M. & Benton, M. J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Academie des Sciences Paris, Sciences de la Terre et des Planètes* **329**, 511–17.

Langer, M. C., Ezcurra, M. D., Bittencourt, J. S. & Novas, F. E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* **85**, 55–110.

Langer, M. C. & Benton, M. J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology* **4**, 309–58.

Lloyd, G. T., Davis, K. E., Pisani, D., Tarver, J. E., Ruta, M., Sakamoto, M., Hone, D. W. E., Jennings, R. & Benton, M. J. 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proceedings of the Royal Society of London, Series B* **275**, 2483–90.

Long, R. A. & Murry, P. A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *Bulletin of the New Mexico Museum of Natural History and Science* **4**, 1–254.

Luo, Z.-X. & Wu, X.-C. 1994. The small tetrapods of the Lower Lufeng Formation, Yunnan, China. *In* Fraser, N. C. & Sues, H.-D. (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 251–70. Cambridge, UK: Cambridge University Press.

Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–57.

Maddison, W. P. & Maddison, D. R. 2004. *MacClade: analysis of phylogeny and character evolution, Version 4.07*. Sunderland, Massachusetts: Sinauer Associates.

Mannion, P. D., Upchurch, P., Carrano, M. T. & Barrett, P. M. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* **86**, 157–81.

Martinez, R. N. & Alcober, O. A. 2009. A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS One* **4** (2), e4397 (doi:10.1371/journal.pone.0004397).

McElwain, J. C., Beerling, D. J. & Woodward, F. I. 1999. Fossil plants and global warming at the Triassic–Jurassic boundary. *Science* **285**, 1386–90.

McElwain, J. C., Wagner, P. J. & Hesselbo, S. P. 2009. Plant relative abundances indicate sudden loss of Late Triassic biodiversity in East Greenland. *Science* **324**, 1554–56.

Mitter, C., Farrell, B. & Weigmann, B. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist* **132**, 107–28.

Moore, B. R. & Brooks, D. R. 1996. A comparative analysis of herbivory and amniote diversification in recent terrestrial ecosystems. *Special Publications of the Palaeontological Society* **8**, 280.

Nesbitt, S. J., Irmis, R. B. & Parker, W. G. 2007. A critical evaluation of the Late Triassic dinosaur taxa of North America. *Journal of Systematic Palaeontology* **5**, 209–43.

Nesbitt, S. J., Smith, N. D., Irmis, R. B., Turner, A. H., Downs, A. & Norell, M. A. 2009a. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* **326**, 1530–33.

Nesbitt, S. J., Irmis, R. B., Parker, W. G., Smith, N. D., Turner, A. H. & Rowe, T. 2009b. Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. *Journal of Vertebrate Paleontology* **29**, 498–516.

Nesbitt, S. J., Sidor, C. A., Irmis, R. B., Angielczyk, K. D., Smith, R. M. H. & Tsuji, L. A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature* **464**, 95–98.

Norman, D. B. 1984. On the cranial morphology and evolution of ornithopod dinosaurs. *Symposia of the Zoological Society of London* **52**, 521–47.

Norman, D. B. & Weishampel, D. B. 1991. Feeding mechanisms in some small herbivorous dinosaurs: processes and patterns. *In* Rayner, J. M. V. & Wootton, R. J. (eds) *Biomechanics in Evolution*, 161–81. Cambridge, UK: Cambridge University Press.

Novas, F. E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* **35**, 51–62.

Novas, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**, 723–41.

Olsen, P. E., Shubin, N. H. & Anders, M. H. 1987. New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science* **237**, 1025–29.

Olsen, P. E., Kent, D. V., Sues, H.-D., Koeberl, C., Huber, H., Montanari, A., Rainforth, E. C., Fowell, S. J., Szajna, M. J. & Hartline, B. W. 2002. Ascent of dinosaurs linked to an iridium anomaly at the Triassic–Jurassic boundary. *Science* **296**, 1305–07.

Olsen, P. E. & Galton, P. M. 1984. A review of the reptile and amphibian assemblages from the Stormberg Group of southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* **25**, 87–110.

Olsen, P. E. & Sues, H.-D. 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic–Jurassic tetrapod transition. *In* Padian, K. (ed.) *The Beginning of the Age of the Dinosaurs*, 321–51. Cambridge, UK: Cambridge University Press.

Osmólska, H. 1980. The Late Cretaceous vertebrate assemblages of the Gobi Desert, Mongolia. *Mémoires de la Société géologique de la France, nouvelle série* **139**, 145–50.

Padian, K. 1994. What were the tempo and mode of evolutionary change in the Late Triassic to Middle Jurassic? *In* Fraser, N. C. & Sues, H.-D. (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 401–07. Cambridge, UK: Cambridge University Press.

Padian, K. 2004. Basal Avialae. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 210–31. Berkeley: University of California Press.

Parker, W. G., Irmis, R. B., Nesbitt, S. J., Martz, J. W. & Browne, L. S. 2005. The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. *Proceedings of the Royal Society B* **272**, 963–69.

Paul, G. S. 1984. The segnosaurian dinosaurs: relics of the prosauropod–ornithischian transition? *Journal of Vertebrate Paleontology* **4**, 507–15.

Pisani, D., Yates, A. M., Langer, M. C. & Benton, M. J. 2002. A genus-level supertree of the Dinosauria. *Proceedings of the Royal Society B* **269**, 915–21.

Porro, L. 2007. Feeding and jaw mechanism in *Heterodontosaurus tucki* using finite element analysis. *Journal of Vertebrate Paleontology* **27** (3-Suppl.), 131A.

Porro, L. B., Butler, R. J., Barrett, P. M., Moore-Fay, S. & Abel, R. 2011. New heterodontosaurid specimens from the Lower Jurassic of southern Africa and the early ornithischian dinosaur radiation. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101** (for 2010), 351–66.

Pough, F. H., Janis, C. M. & Heiser, J. B. 1999. *Vertebrate Life* (5th edn). Eaglewood Cliffs, New Jersey: Prentice-Hall. 733 pp.

de Queiroz, A. 1999. Do image-forming eyes promote evolutionary diversification? *Evolution* **53**, 1654–64.

Rauhut, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**, 1–213.

Reisz, R. R. & Sues, H.-D. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates. *In* Sues, H.-D. (ed.) *The Evolution of Herbivory in Terrestrial Vertebrates: perspectives from the fossil record*, 9–41. Cambridge, UK: Cambridge University Press.

Rogers, R. R., Swisher, C. C. III, Sereno, P. C., Monetta, A. M., Forster, C. A. & Martínez, R. N. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar dating of dinosaur origins. *Science* **260**, 794–97.

Romer, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XIV. *Lewisuchus admixtus*, gen. et sp. nov., a further thecodont from the Chañares beds. *Brevoria* **390**, 1–13.

Russell, D. A., Béland, P. & McIntosh, J. S. 1980. Paleoecology of the dinosaurs of Tendaguru (Tanzania). *Mémoires de la Société Géologique de la France, nouvelle série* **139**, 169–75.

Sander, P. M. 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **93**, 255–99.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press. 288 pp.

Seebacher, F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* **21**, 51–60.

Sereno, P. C. 1997. The origin and evolution of dinosaurs. *Annual Reviews of Earth and Planetary Sciences* **25**, 435–89.

Sereno, P. C. 1999. The evolution of dinosaurs. *Science* **284**, 2137–47.

Sereno, P. C., Forster, C. A., Rogers, R. R. & Monetta, A. M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* **361**, 64–66.

Sereno, P. C., Zhao, X.-J. & Tan, L. 2010. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. *Proceedings of the Royal Society B* **277**, 199–209.

Sereno, P. C. & Arcucci, A. B. 1994a. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*. *Journal of Vertebrate Paleontology* **14**, 53–73.

Sereno, P. C. & Arcucci, A. B. 1994b. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* **13**, 385–99.

Sereno, P. C. & Novas, F. E. 1992. The complete skull and skeleton of an early dinosaur. *Science* **258**, 1137–40.

Sereno, P. C. & Novas, F. E. 1994. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* **13**, 451–76.

Simpson, G. G. 1953. *The Major Features of Evolution*. New York: Columbia University Press. 434 pp.

Simmons, D. J. 1965. The non-therapsid reptiles of the Lufeng Basin, Yunnan, China. *Fieldiana, Geology* **15**, 1–93.

Storer, R. W. 1971. Adaptive radiation of birds. *In* Farner, D. S., King, J. R & Parkes, K. C. (eds) *Avian Biology (Volume 1)*, 149–88. New York and London: Academic Press.

Sues, H.-D., Clark, J. M. & Jenkins, F. A. Jr. 1994. A review of the Early Jurassic tetrapods from the Clen Canyon Group of the American Southwest. *In* Fraser, N. C. & Sues, H.-D. (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 284–94. Cambridge, UK: Cambridge University Press.

Sues, H.-D. & Reisz, R. R. 1998. Origins and early evolution of herbivory in tetrapods. *Trends in Ecology and Evolution* **13**, 141–45.

Tanner, L. H., Lucas, S. G. & Chapman, M. G. 2004. Assessing the record and causes of Late Triassic extinctions. *Earth Science Reviews* **65**, 103–39.

Tiffney, B. H. 1992. The role of vertebrate herbivory in the evolution of land plants. *Palaeobotanist* **41**, 87–97.

Tucker, M. E. & Benton, M. J. 1982. Triassic environments, climates and reptile evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* **40**, 361–79.

Vijaya, Prasad, G. V. R. & Singh, K. 2009. Late Triassic palynoflora from the Pranhita–Godavari Valley, India: evidence from vertebrate coprolites. *Alcheringa* **33**, 91–111.

Weishampel, D. B. 1984. Evolution of jaw mechanisms in ornithopod dinosaurs. *Advances in Anatomy, Embryology and Cell Biology* **87**, 1–110.

Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) 2004a. *The Dinosauria* (2nd edn). Berkeley: University of California Press. 861 pp.

Weishampel, D. B., Barrett, P. M., Coria, R. A., Le Loeuff, J., Xu Xing, Zhao Xijin, Sahni, A., Gomani, E. M. P. & Noto, C. R. 2004b. Dinosaur distribution. *In* Weishampel, D. B., Dodson, P. & Osmólska, H. (eds) *The Dinosauria* (2nd edn), 517–606. Berkeley: University of California Press.

Weishampel, D. B. & Norman, D. B. 1989. Vertebrate herbivory in the Mesozoic; jaws, plants and evolutionary metrics. *Special Papers of the Geological Society of America* **238**, 87–100.

Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. London: Salamander Books. 192 pp.

Wing, S. L., Sues, H.-D., Tiffney, B. H., Stucky, R. K., Weishampel, D. B., Spicer, R. A., Jablonski, D., Badgley, C. E., Wilson, M. V. H. & Kovach, W. L. 1992. Mesozoic and Early Cenozoic terrestrial ecosystems. *In* Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D. & Wing, S. L. (eds) *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Plants and Animals*, 327–416. Chicago, Illinois: University of Chicago Press.

Xu, X., Clark, J. M., Mo, J.-Y., Choiniere, J., Forster, C. A., Erickson, G. M., Hone, D. W. E., Sullivan, C., Eberth, D. A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.-K., Han, F.-L. & Guo, Y. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* **459**, 940–44.

Yates, A. M., Hancox, P. J. & Rubidge, B. S. 2004. First record of a sauropod dinosaur from the upper Elliot Formation (Early

Jurassic) of South Africa. *South African Journal of Science* **100**, 504–06.

Yates, A., Bonnan, M. & Neveling, J. 2007. A new diverse dinosaur assemblage from the Early Jurassic of South Africa. *Journal of Vertebrate Paleontology* **27** (3-Suppl.), 169A.

Yates, A. M., Bonnan, M. F., Neveling, J., Chinsamy, A. & Blackbeard, M. G. 2010. A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. *Proceedings of the Royal Society B* **277**, 787–94.

Young, C. C. 1951. The Lufeng saurischian fauna. *Palaeontologica Sinica, Series C* **13**, 1–96+pls, 1–12.

Zanno, L. E., Gillette, D. D., Albright, L. B. & Titus, A. L. 2009. A new North American therizinosaurid and the role of herbivory in 'predatory' dinosaur evolution. *Proceedings of the Royal Society B* **276**, 3505–11.

Zawiskie, J. M. 1986. Terrestrial vertebrate faunal succession during the Triassic. *In* Padian, K. (ed.) *The Beginning of the Age of the Dinosaurs*, 353–62. Cambridge, UK: Cambridge University Press.