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Dinosaurs and the Cretaceous Terrestrial Revolution

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The observed diversity of dinosaurs reached its highest peak during the mid- and Late Cretaceous, the 50 Myr that preceded their extinction, and yet this explosion of dinosaur diversity may be explained largely by sampling bias. It has long been debated whether dinosaurs were part of the Cretaceous Terrestrial Revolution (KTR), from 125–80 Myr ago, when flowering plants, herbivorous and social insects, squamates, birds and mammals all underwent a rapid expansion. Although an apparent explosion of dinosaur diversity occurred in the mid-Cretaceous, coinciding with the emergence of new groups (e.g. neoceratopsians, ankylosaurid ankylosaurs, hadrosaurids and pachycephalosaurs), results from the first quantitative study of diversification applied to a new supertree of dinosaurs show that this apparent burst in dinosaurian diversity in the last 18 Myr of the Cretaceous is a sampling artefact. Indeed, major diversification shifts occurred largely in the first one-third of the group's history. Despite the appearance of new clades of medium to large herbivores and carnivores later in dinosaur history, these new originations do not correspond to significant diversification shifts. Instead, the overall geometry of the Cretaceous part of the dinosaur tree does not depart from the null hypothesis of an equal rates model of lineage branching. Furthermore, we conclude that dinosaurs did not experience a progressive decline at the end of the Cretaceous, nor was their evolution driven directly by the KTR.

Keywords: dinosaur; angiosperm; Cretaceous; biodiversity; supertree

1. INTRODUCTION

Dinosaurs are icons of success and failure. According to a long-standing hypothesis (Sloan *et al.* 1986; Sarjeant & Currie 2001; Sullivan 2006), the group was in decline long before its extinction at the end of the Cretaceous Period, 65 Myr ago. However, new evidence (Fastovsky *et al.* 2004; Taylor 2006; Wang & Dodson 2006) suggests a major increase in diversification during the Campanian and Maastrichtian, spanning approximately the last 18 Myr of the Cretaceous, a finding that emphasizes the dramatic nature of the apparently sudden extinction of dinosaurs at the end of the Cretaceous. This Late Cretaceous diversification has been seen as evidence that dinosaurs were part of the Cretaceous explosion of terrestrial life (Fastovsky *et al.* 2004; Weishampel *et al.* 2004) characterized by, among others, the rise of flowering plants, social insects and butterflies, as well as modern groups of lizards, mammals and possibly birds (Hedges *et al.* 1996; Grimaldi 1999; Dilcher 2000; Fountaine *et al.* 2005; Bininda-Emonds *et al.* 2007). (Although an earlier origin for social insects has been suggested (Bordy *et al.* 2004), the interpretation of these fossils is disputed (Genise *et al.* 2005)).

The Cretaceous Period (145–65 Myr ago) has usually been regarded as a time of major reorganization and modernization of ecosystems. In the marine realm, these ecosystem changes have been named collectively the Mesozoic Marine Revolution (Vermeij 1977), characterized by the appearance of new groups of planktonic organisms (e.g. coccoliths, foraminifera, dinoflagellates, diatoms) and new predators among crustaceans, teleost fish and marine reptiles. It has been postulated (Vermeij 1987) that the emergence of such predators selectively favoured the appearance of thicker exoskeletons as a defensive measure in prey groups such as bivalves, gastropods and echinoids. Land-dwelling organisms experienced a similar Cretaceous Terrestrial Revolution (KTR), as we term it here, marked by the replacement of ferns and gymnosperms by angiosperms (Dilcher 2000). (We use the standard one-letter acronym 'K' for the Cretaceous). The explosive radiation of angiosperms, from 125–80 Myr ago, provided new evolutionary opportunities for pollinating insects, leaf-eating flies, as well

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as butterflies and moths, all of which diversified rapidly (Grimaldi 1999). Among vertebrates, squamates (lizards and snakes), crocodilians (J. E. Tarver 2008, unpublished data available upon request) and basal groups of placental mammals and modern birds all underwent major diversifications (Hedges *et al.* 1996; Fountaine *et al.* 2005; Bininda-Emonds *et al.* 2007) although the timing of appearance of modern bird orders (Hedges *et al.* 1996; Dyke 2001) and modern mammal orders (Wible *et al.* 2007) remains controversial.

Dinosaur evolution was marked by the appearance of truly spectacular new forms. Giant sauropods, the dominant herbivores of the Jurassic, were joined by new kinds of ornithischians at the beginning of the Cretaceous. Subsequent new waves of diversification at the beginning of the Late Cretaceous (some 100 Myr ago) produced a diverse fauna of hadrosaurs, neoceratopsians, ankylosaurid ankylosaurs and pachycephalosaurs, among herbivores, as well as new carnivorous groups, including the giant carcharodontosaurines and the smaller troodontids, dromaeosaurs and ornithomimosaurs. Qualitatively then, dinosaurs appear to have been part of the KTR.

As is commonly the case, studies of dinosaur diversity through time have suffered from the lack of a conceptual framework in which 'diversification' is defined, detected and quantified. Furthermore, a proper evaluation of sampling biases (e.g. Raup 1972; Benton *et al.* 2000; Alroy *et al.* 2001) has not been carried out on the group. Two key sampling issues are that the fossil record of a group may be truncated (i.e. lacking its youngest and/or oldest members) and that the number of observed taxa depends to some extent on sampling intensity (proxies for this are the number of localities investigated and the number of specimens collected). Here, we address both issues and use analytical protocols to minimize or mitigate their impact.

At the heart of our analysis is a new supertree of dinosaurs, which represents a development and expansion of an earlier study (Pisani *et al.* 2002), consisting of 440 species (some 70% of the total number of valid species, based on Weishampel *et al.* 2004) and an additional 15 undescribed or indeterminate forms. The tree was constructed using a variety of techniques to ensure that it represents the best possible summary of current knowledge. It is highly resolved (99.2% compared to a fully bifurcating tree) and its nodes are mostly well supported (see the electronic supplementary material), making the tree amenable to diversity analyses. Use of large trees in diversification analyses is commonly two-pronged. Previous workers have used them to fill implied gaps in the fossil record and estimate species richness accordingly (Weishampel & Jianu 2000; Upchurch & Barrett 2005), though never for the whole of Dinosauria. A completely different approach is to use tree shape to search for and date perturbations in diversification patterns that diverge from a simple birth–death model (e.g. Forest *et al.* 2007; Ruta *et al.* 2007). Here we use both approaches to test whether dinosaurs responded to the KTR, by comparing the magnitude and rates of their diversification in the Cretaceous with their diversification patterns in the Triassic and Jurassic.

As with the previous studies (listed above), the focus of this contribution is the non-avian dinosaurs and throughout 'dinosaurs' should be read as meaning non-avian dinosaurs.

2. MATERIAL AND METHODS

(a) *Supertree construction*

We expanded significantly upon a previous list of source trees of dinosaur interrelationships (Pisani *et al.* 2002) with publications up to the end of 2006. This list was then shortened by removing those trees that have not been built through a formal cladistic analysis (i.e. a matrix and character list must be available either as a part of the publication itself, as an electronic appendix, or obtainable from the senior author). Retention of this information allowed us to determine redundant source trees (Bininda-Emonds *et al.* 2004), reinsert out-group(s) discarded in published figures and rerun analyses where the source publication did not provide a standardized (strict) consensus tree. Not all trees could be considered novel and hence independent (Bininda-Emonds *et al.* 2004). When one analysis clearly superseded an earlier work, we retained the later tree and discarded the original. When multiple later works had equal claim, we included them all, but weighted them in tree searches so that their net contribution was equal to one independent tree. Overall, these filters led to a strong skew in the data towards more recent analyses (figure 1), greatly enhancing the chances of recovering a tree that represents current consensus.

Unlike the previous genus-level effort (Pisani *et al.* 2002), we chose to produce a species-level supertree. This decision was bolstered by an authoritative recent compilation of valid names (Weishampel *et al.* 2004) that served as our primary reference for *nomina dubia*, which were purged, and junior synonyms, which were replaced with their senior counterpart. Birds more derived than *Archaeopteryx* and non-dinosaurian taxa were also purged from the source trees. Supraspecific taxa were replaced with all species that could be unequivocally assigned to that higher taxon based on the labelled nodes of source trees (Page 2004), with the exception of genera, which were replaced by their most completely known species. Each source tree was processed in this way and both a tree (Page 1996) and an XML file were produced (these are available for download from http://www.graemetlloyd.com). The latter contains metadata about the source publication, taxa and characters, ensuring a consistent standard of data collection and audit trail for future updates. Standard (Baum 1992) and Purvis (Purvis 1995) MRP matrices were then produced using a modified version of SuperMRP.pl (Bininda-Emonds *et al.* 2005), RadCon (Thorley & Page 2000) and Clann (Creevey & McInerney 2005).

Tree searches were performed following an established protocol (Pisani *et al.* 2002, 2007). First, 5000 heuristic searches were performed in PAUP v. 4b10 (Swofford 2003) with the MulTree option turned off. Trees obtained from these searches were saved and swapped using the tree bisection reconnection algorithm and the MulTree option on (to retain multiple equally optimal trees). The Parsimony Ratchet (Nixon 1999) could not find a better tree. The split-fit supertree (Wilkinson *et al.* 2005*a*) was built analysing the standard MRP matrix using Mix, which is part of the Phylip package (Felsenstein 2000). To enforce Mix to run a compatibility analysis, the threshold parsimony option was set to 2. One hundred heuristic searches were performed, and characters were weighted (as described above) using a specifically generated weight file (Felsenstein 2000).

In order to obtain a well-resolved tree, we undertook some *post hoc* taxon pruning where poorly constrained species, producing unacceptably high numbers (more than 5000) of equally probable supertrees, were removed. Choosing a tree

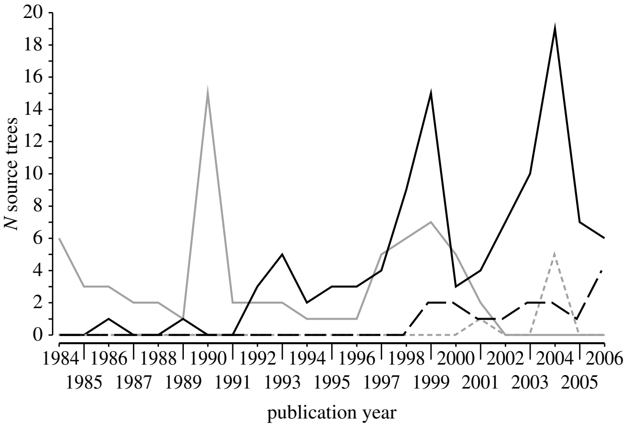

Figure 1. The year of publication of source trees shows a strong skew among included trees towards more recent analyses. Excluded trees include those that were uncorroborated; solid grey line (lacked an accompanying matrix and character list) or redundant; dashed grey line (trees that have been superseded by a later, more comprehensive study). Included trees are either independent; solid black line (are characterized by a unique combination of characters and taxa) or dependent; dashed black line (trees derived from a shared character list, but have differing and non-redundant taxon sets). The latter were down-weighted in the supertree searches so that their summed contribution was equal to that of one independent tree. The three major peaks (1990, 1999 and 2004) correspond to the publication of *The Dinosauria* first edition (Weishampel *et al.* 1990), a *Science* review paper (Sereno 1999) and *The Dinosauria* second edition (Weishampel *et al.* 2004), respectively.

for diversity analyses was based on overall supertree support. Here we used the V1 index (Wilkinson *et al.* 2005*b*), which indicated that support was highest for the standard MRP supertree.

(b) *Diversification metrics*

We calculated the percentage change, per million years, of global species richness among 12 successive time bins of approximately equal duration created by grouping geological stages for three different datasets: (i) a recent database of the known dinosaur record (Weishampel *et al.* 2004), (ii) the same dataset but with some species' first appearances extended back in time as implied by a sister group relationship with an older taxon (Norell 1992) in the supertree, and (iii) a subsampled dataset.

This latter dataset was created using a subsampling method similar to rarefaction. Rarefaction methods have played an important role in ecology (Gotelli & Colwell 2001) and palaeoecology (Raup 1975; Tipper 1979), as they offer the opportunity to examine the effects of taxonomic sampling on measures of species richness. Here we measure sample size as the total number of species occurrences by locality for each of our 12 time bins. Methodologically, our approach is equivalent to setting the global quality of the record as equal to that of the worst part of it. In this case, the worst bin was bin 5 (Pliensbachian—Aalenian), with only 39 occurrences, and this set the number to be subsampled in each case. In order to calculate the mean and 95% error bars, subsampling was performed 1000 times and the number of species observed in 39 randomly drawn occurrences from each bin was recorded. Subsampling was performed using custom-built code (available for download from http://www.graemetlloyd.com) in the freely available statistical programming language 'R' (http://cran.r-project.org/). Note that, in all cases, diversification rates were calculated for each time bin, except the first, as there are no unequivocal dinosaurian fossils, and second, as there is no previous richness value; diversification is infinite.

An alternative approach to quantifying diversification patterns relies on phylogenetic tree shape. Phylogeny is determined by the available taxa and the inferred pattern of relationships, and phylogenetic tree shape reflects large-scale variations in speciation and extinction rates (Mooers & Heard 1997). Topological methods (Bininda-Emonds *et al.* 1999; Katzourakis *et al.* 2001; Chan & Moore 2005; Jones *et al.* 2005) may be used to identify diversification rate shifts in phylogenetic trees, based on comparison between the observed tree and one expected under an equal rates Markov (ERM) model. A diversification shift is simply a change in net speciation rate (i.e. rate of splitting of evolutionary lineages). In the ERM model, such rates are constant, resulting in a constant splitting of lineages. The ERM model is best seen as a standard reference model for measuring significant changes in lineage splitting (Nee 2006). Simply put, given two groups subtended by a node, if one group is significantly more speciose than the other, a diversification rate shift is inferred to have taken place, i.e. a significant departure from an ERM model of clade growth has occurred.

Phylogenetic shifts in diversification were detected using SymmeTREE v. 1.0 (Chan & Moore 2005). Analyses of tree shape are biased when a group is paraphyletic, as a particularly speciose clade (in this case, birds) is represented by a single terminal (*Archaeopteryx*). A modification was thus required in order to account for the absence of birds. Although it was not feasible in the present contribution to include all birds, a hand-drawn phylogeny of the better-known Mesozoic taxa (72 species in total) was inserted at the node subtending *Archaeopteryx* +*Jinfengopteryx*, effectively making the tree a Mesozoic time slice. (This placement of *Jinfengopteryx* is based on the original description (Ji *et al.* 2005), but more recent analyses, e.g. Turner *et al.* (2007), have placed it within Troodontidae.) Polytomies were treated as soft, with the size-sensitive ERM algorithm set to perform 10 000 random resolutions per individual node and 1 000 000 random resolutions for the entire tree. Internal branches within the phylogeny on which diversification shifts are inferred to have occurred were identified using the Δ_2 shift statistic. This process was repeated for time slices of the whole tree as described in Ruta *et al.* (2007) to avoid violating the ERM model.

3. RESULTS

(a) *Ghost ranges account for some irregularities in the diversity curves*

The supertree of dinosaur species is plotted on a geological time scale (Gradstein *et al.* 2004; figure 2*a*; electronic supplementary material) subdivided into 12 approximately equal-length time bins to assess the extent of ghost ranges (Norell 1992). Ghost ranges, minimal basal stratigraphic range extensions implied by the geometry of the phylogenetic tree, indicate missing fossil data, and allow us to correct diversity profiles for the group through the Mesozoic and to compare diversification rates, the proportional change in observed species richness as a function of time, at different points (figure 2*b*, solid line): note how the addition of ghost ranges smoothes the curve. In particular, peaks in observed diversification rate in the Norian and Campanian–Maastrichtian (bins 3 and 12) are greatly reduced when ghost ranges are introduced. This is a minimal correction that does not take account of unknown taxon ranges before the first appearance of the older of a pair of sister groups. In addition, this correction does not address possible upward range extensions. However, peaks in the earliest, Middle and Late Jurassic are still observed after introduction of ghost ranges (figure 2*b*, dashed line).

(b) *Correction for sampling removes some extreme diversity peaks*

To test whether these peaks represent real diversification episodes or are simply the result of unusually intense sampling, we considered the number of dinosaur localities in each stratigraphic stage (Weishampel *et al.* 2004). If sampled localities determine apparent generic diversity, then the diversification measures might be levelled once they are corrected for locality numbers. When the same diversification calculations are applied to these subsamples (with means and 95% CIs plotted as dotted lines in figure 2*b*), much lower values are recovered. These results suggest, but do not prove, that diversity estimates are heavily influenced by sampling, and further that the ghost range corrections, i.e. tree-based estimates of missing diversity, are indeed minimal. It follows that the fluctuations in diversification rate may not necessarily reflect evolutionary signal, and these must be tested rigorously.

(c) *Diversification shifts are concentrated in the lower (earlier) half of the dinosaur tree*

Analysis of diversification rates in our dinosaur supertree using the software SymmeTREE (see §2) shows that statistically significant ($p<0.05$) and substantial ($0.05<p<0.1$) diversification shifts (i.e. multiplications of evolutionary lineages) were heavily concentrated in the first one-third of dinosaurian history (figure 2*a*; electronic supplementary material). The majority occur near the base of the group, in the Late Triassic to Early Jurassic (230–175 Myr ago), and are closely, although not always exactly, associated with the origin of major clades (10 significant shifts: Genasauria, Eurypoda, Cerapoda, Sauropodomorpha, Neotheropoda, Tetanurae, Coelurosauria, Maniraptoriformes, Maniraptora and Oviraptorosauria). Later statistically significant diversification shifts occur in the Aalenian (1; Neosauropoda), Kimmeridgian (2; Ankylosauria, Eumaniraptora), Turonian (1; Euhadrosauria) and Campanian (1; Ceratopsidae). The 15 significant and 11 substantial diversification shifts are distributed as follows: 2 significant and 2 substantial shifts in the Triassic; 11 significant and 7 substantial shifts in the Jurassic; 2 significant and 2 substantial shifts in the Cretaceous. Our results confirm that most of the diversification among dinosaurs occurred early, whereas very little is detected in the remaining two-thirds of their history, i.e. the 120 Myr ago from the Middle Jurassic onwards. When the mean Δ_2 shift statistic, which represents the likelihood that a shift occurred, is plotted against time (figure 2*c*), there is a peak value of 0.58 during the Rhaetian–Sinemurian (Bin 4; 205–190 Myr ago) followed by an overall decrease towards the present. Two-thirds of significant pairwise comparisons between Δ_2 values (Kruskal–Wallis test; $p<0.05$) show bins 4 and 5 (Rhaetian–Aalenian; 205–170 Myr ago) to have higher likelihoods of a diversification shift than all other bins.

The robustness of these results was tested further by 'time slicing' our tree to avoid issues surrounding violation of the ERM model's assumptions (Ruta *et al.* 2007). This involved creating 11 separate trees, one for each of our time bins, which included only the taxa that existed, or are posited to have existed (through range extensions), at that time. Results based upon time-sliced trees strongly support our whole-tree analysis, with 11 out of the 15 significant shifts also occurring in the time-sliced trees. Only one novel significant shift was discovered in the time-sliced trees, coincident with the origin of the sauropod clade Lithostrotia in the Valanginian (140 Myr ago). Again, the highest mean Δ_2 shift statistic (0.69) was found in bin 4, with a general decrease in diversification shift likelihood in later time bins. Similarly, over half of the significant pairwise comparisons between Δ_2 values show time bins 4 and 5 to have had higher likelihoods of a diversification shift. All results are robust even if the controversial taxon *Eshanosaurus* (Xu *et al.* 2001), which is here placed as a therizinosaur and is responsible for pinpointing the date of four of the significant shifts (Tetanurae, Coelurosauria, Maniraptoriformes and Maniraptora), is removed.

4. DISCUSSION

(a) *Diversification shifts are not always concentrated in the lower half of a tree*

Geometric arguments might suggest that it is inevitable to find the majority of diversification shifts low in a phylogenetic tree. To an extent, of course, one can expect statistically significant diversification shifts to occur at the base of the tree, as founding taxa within the clade split and major branches become established. Bats, for example, show a similar early diversification pattern (Jones *et al.* 2005), but ants do not (Forest *et al.* 2007). The reason is that clades do not stop diversifying once they have become established. Studies of the distribution of clade shapes (Gould *et al.* 1977; Valentine 1990; Uhen 1996; Nee 2006) show all possible shapes (after paraphyly has been accounted for), ranging from bottom-heavy to top-heavy, tall and thin, short and broad and even spindle-shaped, e.g. when a clade has been hit hard by an extinction event or other bottlenecking crisis and has then recovered. In the case of dinosaurs, this clade continues to expand up to the end of the Cretaceous and yet, statistically speaking, the Cretaceous expansion cannot be distinguished from an undriven ERM.

(b) *Sampling must be taken into account*

The fossil record of continental vertebrates is clearly patchy, with large temporal gaps between sampling horizons. The seriousness of sampling bias is debated, with opinion ranging from assumptions that the fossil record offers more of a geological than a biological signal (Raup 1972; Alroy *et al.* 2001; Peters & Foote 2002) to acceptance that sampling error does not much modify the apparent macroevolutionary patterns (Sepkoski *et al.* 1981; Benton 1998). Comparisons of cladograms with the fossil record show good congruence in most cases (Norell & Novacek 1992;

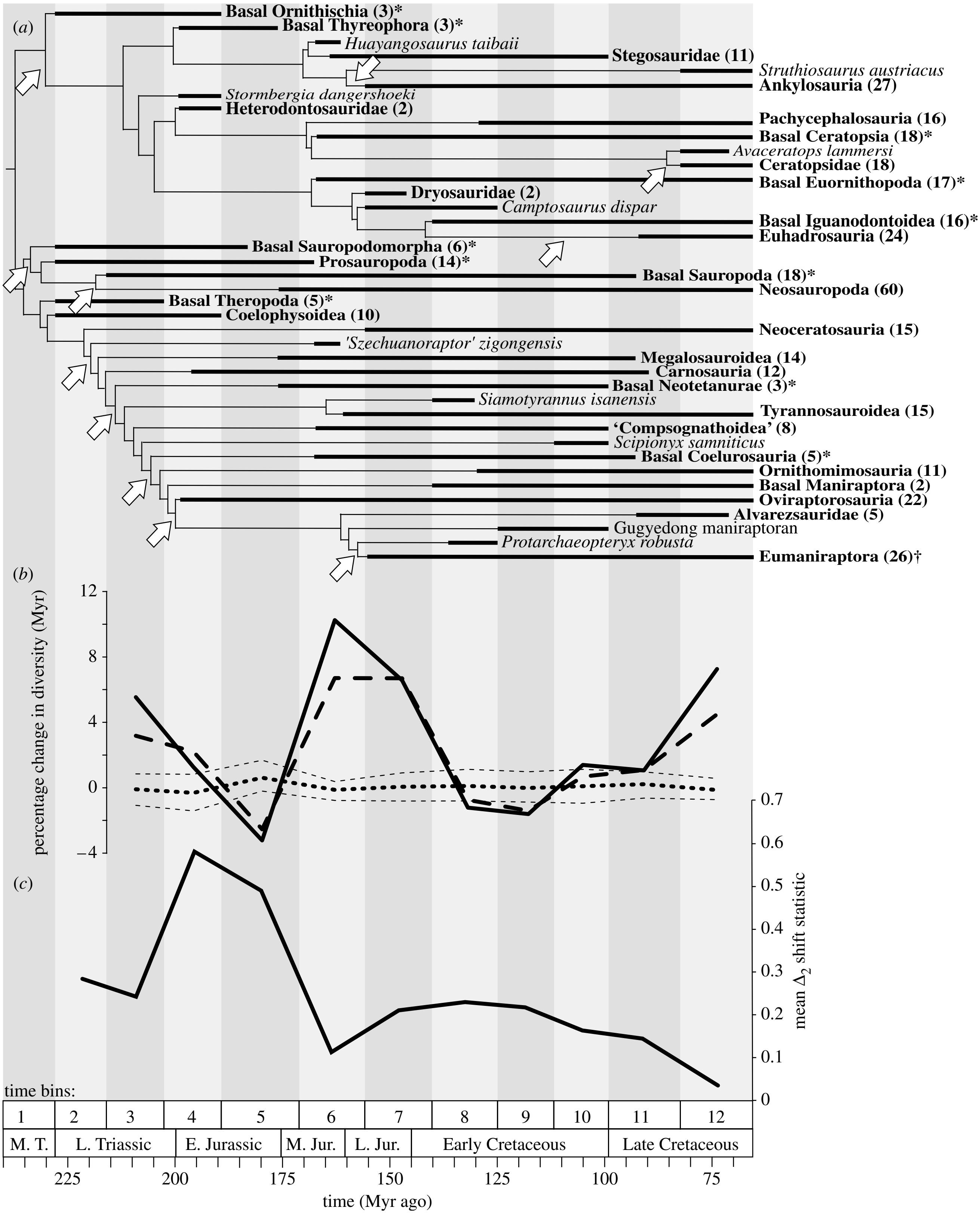

Figure 2. Results of different analyses of dinosaur diversification. (*a*) A summary version of the supertree used here; the 11 statistically significant diversification shifts present in both the entire tree and at least one time slice are marked with white arrows denoting the branch leading to the more speciose clade. Taxa in bold represent the collapsing of a larger clade, the size of which is indicated in parentheses. An '*' indicates the collapsing of a paraphyletic group and a '†' that of an extant clade (i.e. birds). (*b*) Diversification rates based on the raw record (solid line), the raw record plus additional ghost ranges (dashed line) and subsampled data (dotted lines; see text). (*c*) Mean values of Δ_2 shift statistic through time (see text).

Benton *et al.* 2000), thus suggesting that the biological signal is probably adequately represented when assessed at the correct scale. Current efforts (Smith 2007) focus on methods to quantify sampling bias and to determine parts of the fossil record signal that stand out after sampling has been evaluated.

In this paper, we have used the number of dinosaur localities in each time bin as a crude measure of sampling. Other measures could have been area of rock exposure, volume of rock deposited per unit time, total number of geological formations (whether fossiliferous or not) or intensity of worker effort (e.g. measured as the number of palaeontologists working on a specific group). The relative merit of all these measures is the subject of much current debate; we note that the use of any sampling measure to correct diversity figures may be sufficiently heavy-handed that any biological signal may be swamped (Peters & Foote 2002; Smith 2007). For example, there is doubtless a species-area effect (Smith 2001), in which rock area or volume, or number of formations, is linked with the diversity of life. For example, during the times of high sea level, continental margins flood and species on the continental shelf increase in abundance and diversity. Corrections of those diversity figures, obtained by dividing them by shelf area or rock volume, could potentially remove the whole of the biological signal.

Our solution, to offer both the raw data and the sampling-modified data (figure 2*b*), allows comparison of the data without making an assumption that either version is correct, and points to the need for further examination of each of the undoubted biases in our understanding of this fossil record. Before applying a correction factor, we need evidence of how collecting intensity (i.e. number of palaeontologists; number of field days), rock availability and other sampling factors affect the results. The relationship is almost certainly not linear, and that in itself speaks against crude application of sampling corrections. For example, discovery curves for dinosaurs and other fossil taxa, when calibrated against worker effort, show a variety of shapes: that for trilobites is more or less a straight line (Tarver *et al.* 2007), whereas the more intensively studied dinosaurs show a classic logistic shape, where huge efforts at present do not necessarily yield huge numbers of new fossils, after many decades of collection (Benton in press).

(c) *Dinosaurs and the KTR*

There are two issues to be considered in associating dinosaur diversification with the KTR: the timing of that diversification and evidence that dinosaurs did, or did not, benefit from the diversification of angiosperms.

Whereas the raw data show that dinosaurs diversified substantially during the Cretaceous, and especially in the last 18 Myr of the period (Fastovsky *et al.* 2004; Taylor 2006; Wang & Dodson 2006), and we confirm this, we have shown that appearances are deceptive. As we show, and as noted before (Fastovsky *et al.* 2004), much or all of the Campanian and Maastrichtian boost in diversity in the last phases of the Mesozoic is probably an artefact of abundant preservation and intense sampling. Our diversification shift tests indicate that only two significant diversifications happened in the Late Cretaceous, corresponding to the initial diversifications of the euhadrosaurs and the ceratopsids. We therefore do not find evidence for a steadily increasing rate of diversification throughout dinosaurian evolution, nor do we see evidence for the continuing appearance of innovations driving an increasing variety of behavioural strategies, as had been posited (Fastovsky *et al.* 2004).

Previous studies have been equivocal about whether dinosaurs fed on angiosperms. The Late Cretaceous expansion of dinosaurian diversity, found especially on the diversification of herbivorous dinosaurs such as hadrosaurs, ceratopsians, and ankylosaurs, might have suggested that these groups, all of which either arose or diversified substantially only after the origin of angiosperms in the mid-Cretaceous, specialized on an angiosperm diet. Bakker (1978), for example, argued that the ornithopods of the Early Cretaceous fed close to the ground, and so favoured gymnosperms in their diet. Owing to their intense low-level feeding, the only plants that could survive the onslaught were the earliest angiosperms that held their reproductive organs close to the ground. And so, in his words, dinosaurs invented flowers.

This view is disputed (Wedel *et al.* 2000) and there is actually only limited evidence to demonstrate that Cretaceous dinosaurs fed on angiosperms (Barrett & Willis 2001). The patterns of rises and falls in the diversity of Cretaceous dinosaurs and Cretaceous plants, as well as their palaeogeographic distributions, do not suggest any correlation. Coprolites, fossil faeces, are rare and often cannot be attributed to their producer; Cretaceous examples include some with traces of the angiosperm biomarkers oleananes (a group of chemicals with suppressing effects on insect pests), whereas others contain exclusively gymnosperm material. An Early Cretaceous ankylosaur, *Minmi*, has been reported (Molnar & Clifford 2000) with remnants of angiosperm fruits in its gut, and some remarkable coprolites from India show that some dinosaurs ate early grasses (Prasad *et al.* 2005). Fossil occurrences and studies of the teeth and postulated jaw functions of herbivorous dinosaurs suggest that angiosperms were a part of the diet of many dinosaurs, but that gymnosperms were still the major constituent in most cases (Chin & Gill 1996; Barrett & Willis 2001; Ghosh *et al.* 2003). Plant-eating insects and mammals very likely benefited more from the new sources of plant food.

Detailed studies of dinosaurian herbivory and plant evolution (Barrett & Willis 2001) had already suggested there was limited evidence that angiosperm diversification drove the Cretaceous diversification of dinosaurs. Our new evidence confirms that the KTR was a key in the origination of modern continental ecosystems, but that the dinosaurs were not a part of it. Hadrosaurs and ceratopsians showed late diversifications, but not enough to save the dinosaur dynasty from its fate.

Computationally intense analyses were performed using the computer cluster of NUI Maynooth High Performance Computing Centre. Subsampling was performed using modified code taught to G.T.L. by John Alroy as part of the Paleobiology Database Intensive Summer Course in Analytical Paleobiology (http://paleodb.org). We thank Sarda Sahney for help with the figures and discussions concerning subsampling methods and Nicholas Minter for pointing us towards the Genise *et al.* (2005) paper. This manuscript was improved following comments on an earlier draft by Michael P. Taylor and an anonymous reviewer. G.T.L., K.E.D. and J.E.T. acknowledge receipt of NERC studentships NER/S/A/2004/12222, NER/S/A/2003/11241 and NER/S/A/2003/11198A, respectively. M.J.B. and M.R. acknowledge receipt of NERC grant NE/C518973/1. D.W.E.H. is supported by DFG grant RA 1012/-3 as part of Unit 533.

REFERENCES

Alroy, J. M. *et al.* 2001 Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl Acad. Sci. USA* **98**, 6261–6266. (doi:10.1073/pnas.111144698)

Bakker, R. T. 1978 Dinosaur feeding behaviour and the origin of flowering plants. *Nature* **274**, 661–663. (doi:10.1038/274661a0)

Barrett, P. M. & Willis, K. J. 2001 Did dinosaurs invent flowers? Dinosaur-angiosperm coevolution revisited. *Biol. Rev.* **76**, 411–447. (doi:10.1017/S1464793101005735)

Baum, B. R. 1992 Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon* **41**, 3–10. (doi:10.2307/1222480)

Benton, M. J. 1998 The quality of the fossil record of vertebrates. In *The adequacy of the fossil record* (eds S. K. Donovan & C. R. C. Paul), pp. 269–303. New York, NY: Wiley.

Benton, M. J. In press. How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology.*

Benton, M. J., Wills, M. A. & Hitchin, R. 2000 Quality of the fossil record through time. *Nature* **403**, 534–538. (doi:10.1038/35000558)

Bininda-Emonds, O. R. P., Gittleman, J. L. & Purvis, A. 1999 Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* **74**, 143–175. (doi:10.1017/S0006323199005307)

Bininda-Emonds, O. R. P., Jones, K. E., Price, S. A., Cardillo, M., Grenyer, R. & Purvis, A. 2004 Garbage in, garbage out: data issues in supertree construction. In *Phylogenetic supertrees: combining information to reveal the Tree of Life* (ed. O. R. P. Bininda-Emonds), pp. 267–280. Dordrecht, The Netherlands; Berlin, Germany: Kluwer Academic.

Bininda-Emonds, O. R. P., Beck, R. M. D. & Purvis, A. 2005 Getting to the roots of matrix representation. *Syst. Biol.* **54**, 668–672. (doi:10.1080/10635150590947113)

Bininda-Emonds, O. R. P. *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–512. (doi:10.1038/nature05634)

Bordy, E. M., Bumby, A. J., Catuneau, O. & Eriksson, P. G. 2004 Advanced Early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa. *Palaios* **19**, 68–78. (doi:10.1669/0883-1351(2004)019<0068:AEJTII>2.0.CO;2)

Chan, K. M. A. & Moore, B. R. 2005 SymmeTREE: whole-tree analysis of differential diversification rates. *Bioinformatics* **21**, 1709–1710. (doi:10.1093/bioinformatics/bti175)

Chin, K. & Gill, B. D. 1996 Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaios* **11**, 280–285. (doi:10.2307/3515235)

Creevey, C. J. & McInerney, J. O. 2005 Clann: investigating phylogenetic information through supertree analyses. *Bioinformatics* **21**, 390–392. (doi:10.1093/bioinformatics/bti020)

Dilcher, D. 2000 Towards a new synthesis: major evolutionary trends in the angiosperm fossil record. *Proc. Natl Acad. Sci. USA* **97**, 7030–7036. (doi:10.1073/pnas.97.13.7030)

Dyke, G. J. 2001 The evolution of birds in the early Tertiary: systematics and patterns of diversification. *Geol. J.* **36**, 305–315. (doi:10.1002/gj.878)

Fastovsky, D. E., Huang, Y., Hsu, J., Martin-McNaughton, J., Sheehan, P. M. & Weishampel, D. B. 2004 Shape of Mesozoic dinosaur richness. *Geology* **32**, 877–880. (doi:10.1130/G20695.1)

Felsenstein, J. 2000 Phylip v. 3.6. See http://evolution.genetics.washington.edu/phylip.html.

Forest, F., Chase, M. W., Persson, C., Crane, P. R. & Hawkins, J. A. 2007 The role of biotic and abiotic factors in evolution of ant dispersal in the milkwort family (Polygalaceae). *Evolution* **61**, 1675–1694. (doi:10.1111/j.1558-5646.2007.00138.x)

Fountaine, T. M. R., Benton, M. J., Dyke, G. J. & Nudds, R. L. 2005 The quality of the fossil record of Mesozoic birds. *Proc. R. Soc. B* **272**, 289–294. (doi:10.1098/rspb.2004.2923)

Genise, J. F., Bellosi, E. S., Melchor, R. N. & Cosarinsky, M. I. 2005 Comment—advanced Early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa (Bordy *et al.* 2004). *Palaios* **20**, 303–308. (doi:10.2110/palo.2004.p05-C01)

Ghosh, P., Bhattacharya, S. K., Sahni, A., Kar, R. K., Mohabey, D. M. & Ambwani, K. 2003 Dinosaur coprolites form the Late Cretaceous (Maastrichtian) Lameta Formation of India: isotopic and other markers suggesting a C_3 plant diet. *Cret. Res.* **24**, 743–750. (doi:10.1016/j.cretres.2003.08.002)

Gotelli, N. J. & Colwell, R. K. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391. (doi:10.1046/j.1461-0248.2001.00230.x)

Gould, S. J., Raup, D. M., Sepkoski, J. J., Schopf, T. J. M. & Simberloff, D. S. 1977 The shape of evolution; a comparison of real and random clades. *Paleobiology* **3**, 23–40.

Gradstein, F. M. *et al.* 2004 *A geologic time scale 2004.* Cambridge, UK: Cambridge University Press.

Grimaldi, D. 1999 The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann. Miss. Bot. Gard.* **86**, 373–406. (doi:10.2307/2666181)

Hedges, S. B., Parker, P. H., Sibley, C. G. & Kumar, S. 1996 Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226–229. (doi:10.1038/381226a0)

Ji, Q., Ji, S.-A., Lü, J.-C., You, H.-L., Chen, W., Liu, Y.-Q. & Liu, Y.-X. 2005 First avialian bird from China. *Geol. Bull. China* **24**, 197–210.

Jones, K. E., Bininda-Emonds, O. R. P. & Gittleman, J. L. 2005 Bats, clocks, and rocks: diversification patterns in Chiroptera. *Evolution* **59**, 2243–2255. (doi:10.1554/04-635.1)

Katzourakis, A., Purvis, A., Azmeh, S., Rotheray, G. & Gilbert, F. 2001 Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. *J. Evol. Biol.* **14**, 219–227. (doi:10.1046/j.1420-9101.2001.00278.x)

Molnar, R. E. & Clifford, H. T. 2000 Gut contents of a small ankylosaur. *J. Vert. Paleontol.* **20**, 194–196. (doi:10.1671/0272-4634(2000)020[0194:GCOASA]2.0.CO;2)

Mooers, A. O. & Heard, S. B. 1997 Inferring evolutionary process from phylogenetic tree shape. *Q. Rev. Biol.* **72**, 31–54. (doi:10.1086/419657)

Nee, S. 2006 Birth-death models in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **37**, 1–17. (doi:10.1146/annurev.ecolsys.37.091305.110035)

Nixon, K. C. 1999 The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**, 407–414. (doi:10.1111/j.1096-0031.1999.tb00277.x)

Norell, M. A. 1992 Taxic origin and temporal diversity: the effect of phylogeny. In *Extinction and phylogeny* (eds M. J. Novacek & Q. D. Wheeler), pp. 89–118. New York, NY: Columbia University Press.

Norell, M. A. & Novacek, M. J. 1992 The fossil record and evolution: comparing cladistics and paleontological evidence for vertebrate history. *Science* **255**, 1690–1693. (doi:10.1126/science.255.5052.1690)

Page, R. D. M. 1996 TreeView: an application to display phylogenetic trees on personal computers. *Comp. Appl. BioSci.* **12**, 357–358.

Page, R. D. M. 2004 Taxonomy, supertrees, and the Tree of Life. In *Phylogenetic supertrees: combining information to reveal the Tree of Life* (ed. O. R. P. Bininda-Emonds), pp. 247–265. Dordrecht, The Netherlands; Berlin, Germany: Kluwer Academic.

Peters, S. E. & Foote, M. 2002 Determinants of extinction in the fossil record. *Nature* **416**, 420–424. (doi:10.1038/416420a)

Pisani, D., Yates, A. M., Langer, M. C. & Benton, M. J. 2002 A genus-level supertree of the Dinosauria. *Proc. R. Soc. B* **269**, 915–921. (doi:10.1098/rspb.2001.1942)

Pisani, D., Cotton, J. A. & McInerney, J. O. 2007 Supertrees disentangle the chimerical origin of eukaryotic genes. *Mol. Biol. Evol.* **24**, 1752–1760. (doi:10.1093/molbev/msm095)

Prasad, V., Strömberg, C. A. E., Alimohammadian, H. & Sahni, A. 2005 Dinosaur coprolites and the early evolution of grasses and grazers. *Science* **310**, 1177–1180. (doi:10.1126/science.1118806)

Purvis, A. 1995 A modification to Baum and Ragan's method for combining phylogenetic trees. *Syst. Biol.* **44**, 251–255. (doi:10.2307/2413710)

Raup, D. M. 1972 Taxonomic diversity during the Phanerozoic. *Science* **177**, 1065–1071. (doi:10.1126/science.177.4054.1065)

Raup, D. M. 1975 Taxonomic diversity estimation using rarefaction. *Paleobiology* **1**, 333–342.

Ruta, M., Pisani, D., Lloyd, G. T. & Benton, M. J. 2007 A supertree of Temnospondyli: cladogenetic patterns in the most species-rich group of early tetrapods. *Proc. R. Soc. B* **274**, 3087–3095. (doi:10.1098/rspb.2007.1250)

Sarjeant, W. A. S. & Currie, P. J. 2001 The "Great Extinction" that never happened: the demise of the dinosaurs considered. *Can. J. Earth Sci.* **38**, 239–247. (doi:10.1139/cjes-38-2-239)

Sepkoski, J. J., Bambach, R. K., Raup, D. M. & Valentine, J. W. 1981 Phanerozoic marine diversity: a strong signal from the fossil record. *Nature* **293**, 435–437. (doi:10.1038/293435a0)

Sereno, P. C. 1999 The evolution of dinosaurs. *Science* **284**, 2137–2147. (doi:10.1126/science.284.5423.2137)

Sloan, R. E., Rigby, J. K., van Valen, L. & Gabriel, D. 1986 Gradual extinction of dinosaurs and the simultaneous radiation of ungulate mammals in the Hell Creek Formation of McCone County, Montana. *Science* **232**, 629–633. (doi:10.1126/science.232.4750.629)

Smith, A. B. 2001 Large scale heterogeneity of the fossil record: implications for biodiversity studies. *Phil. Trans. R. Soc. B* **356**, 351–367. (doi:10.1098/rstb.2000.0768)

Smith, A. B. 2007 Marine diversity through the Phanerozoic: problems and prospects. *J. Geol. Soc.* **164**, 731–745. (doi:10.1144/0016/76492006-184)

Sullivan, R. M. 2006 The shape of Mesozoic dinosaur richness: a reassessment. *Bull. New Mexico Mus. Nat. Hist. Sci.* **35**, 403–405.

Swofford, D. L. 2003 *PAUP*: phylogenetic analysis using parsimony (*and other methods)*. Sunderland, MA: Sinauer Associates.

Tarver, J. E., Braddy, S. J. & Benton, M. J. 2007 The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Palaeontology* **50**, 177–184. (doi:10.1111/j.1475-4983.2006.00618.x)

Taylor, M. P. 2006 Dinosaur diversity analysed by clade, age, place and year of description. In *Ninth Int. Symp. on Mesozoic terrestrial ecosystems and biota* (ed. P. Barrett), pp. 134–138. Cambridge, UK: Cambridge Publications.

Thorley, J. L. & Page, R. D. M. 2000 RadCon: phylogenetic tree comparison and consensus. *Bioinformatics* **16**, 486–487. (doi:10.1093/bioinformatics/16.5.486)

Tipper, J. C. 1979 Rarefaction and rarefiction: the use and abuse of a method in paleoecology. *Paleobiology* **5**, 423–434.

Turner, A. H., Pol, D., Clarke, J. A., Erickson, G. M. & Norell, M. A. 2007 A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**, 1378–1381. (doi:10.1126/science.1144066)

Uhen, M. D. 1996 An evaluation of clade-shape statistics using simulations and extinct families of mammals. *Paleobiology* **22**, 8–22.

Upchurch, P. & Barrett, P. M. 2005 Phylogenetic and taxic perspectives on sauropod diversity. In *The sauropods: evolution and paleobiology* (eds K. A. Curry Rogers & J. A. Wilson), pp. 104–124. Berkeley, CA: University of California Press.

Valentine, J. W. 1990 The macroevolution of clade shape. In *Causes of evolution: a paleontological perspective* (eds R. M. Ross & W. D. Allmon), pp. 128–150. Chicago, IL: University of Chicago Press.

Vermeij, G. J. 1977 The Mesozoic Marine Revolution: evidence from snails, predators and grazers. *Paleobiology* **3**, 245–258.

Vermeij, G. J. 1987 *Evolution and escalation*. Princeton, NJ: Princeton University Press.

Wang, S. C. & Dodson, P. 2006 Estimating the diversity of dinosaurs. *Proc. Natl Acad. Sci. USA* **103**, 13 601–13 605. (doi:10.1073/pnas.0606028103)

Wedel, M. J., Cifelli, R. L. & Sanders, R. K. 2000 Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Paleontol. Polon.* **45**, 343–388.

Weishampel, D. B. & Jianu, C.-M. 2000 Plant-eaters and ghost lineages: dinosaurian herbivory revisited. In *Evolution of herbivory in terrestrial vertebrates* (ed. H.-D. Sues), pp. 123–143. Cambridge, UK: Cambridge University Press.

Weishampel, D. B., Dodson, P. & Osmólska, H. 1990 *The Dinosauria*. Berkeley, CA: University of California Press.

Weishampel, D. B., Dodson, P. & Osmólska, H. 2004 *The Dinosauria*, 2nd edn. Berkeley, CA: University of California Press.

Wible, J. R., Rougier, G. W., Novacek, M. J. & Asher, R. J. 2007 Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* **447**, 1003–1006. (doi:10.1038/nature05854)

Wilkinson, M. *et al.* 2005*a* The shape of supertrees to come: tree shape related properties of fourteen supertree methods. *Syst. Biol.* **54**, 419–431. (doi:10.1080/10635150590949832)

Wilkinson, M., Pisani, D., Cotton, J. A. & Corfe, I. 2005*b* Measuring support and finding unsupported relationships in supertrees. *Syst. Biol.* **54**, 823–831. (doi:10.1080/10635150590950362)

Xu, X., Zhao, X.-J. & Clark, J. M. 2001 A new therizinosaur from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. *J. Vert. Paleontol.* **21**, 477–483. (doi:10.1671/0272-4634(2001)021[0477:ANTFTL]2.0.CO;2)