

Preface to ‘Late Triassic Terrestrial Biotas and the Rise of Dinosaurs’ Special Issue

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The early Mesozoic records an important transition in the history of the Earth’s terrestrial ecosystems. As they recovered from the largest known mass extinction (the end-Permian event), organisms in these ecosystems transitioned to new forms that eventually evolved into the classic Mesozoic biotas, and laid the foundations for many groups still flourishing today (Fraser 2006; Irmis & Whiteside 2010; Sues & Fraser 2010). All of this was set against a backdrop of dynamic climatic and physical events that shaped these biotas. This early Mesozoic terrestrial transition reached its culmination in many ways during the Late Triassic, when ecosystems had largely recovered from the end-Permian extinction, but had not yet been affected by the end-Triassic mass extinction (Fraser & Sues this volume). Thus, we see a combination of taxa, with some groups that would not survive the end of the Triassic living alongside early representatives of lineages that flourished later in the Mesozoic (e.g., Fraser 2006; Irmis *et al.* 2007; Brusatte *et al.* 2008; Sues & Fraser 2010, this volume) and in some cases are still diverse today. Just one example of this transition, recorded during the Late Triassic, is the origin and diversification of non-avian dinosaurs, the iconic representatives of Mesozoic terrestrial ecosystems (Brusatte *et al.* 2010; Langer *et al.* 2010). Although small and rare components of their respective biotas when they first evolved ~231 Ma, dinosaurs were abundant and had a near-worldwide distribution by the beginning of the Jurassic Period (~201–3 Ma).

Given the importance of the Late Triassic terrestrial transition, it is no surprise that there has been a renaissance in the study of Late Triassic terrestrial biotas, particularly with respect to fossil vertebrates (see recent reviews in Brusatte *et al.* 2010; Sues & Fraser 2010, this volume; Irmis & Whiteside 2010; Langer *et al.* 2010). New fossil discoveries, re-evaluation of existing specimens, and new quantitative meta-analyses of synthetic datasets have significantly changed our view of this transition in the last 15 years. Nonetheless, the last multi-authored volumes to review this transition are over 25 and 15 years old (Padian 1986; Fraser & Sues 1994); no new similar synthetic multi-authored view is available. We hope this volume goes some way towards redressing this situation.

The renewed interest and breadth of research into Late Triassic terrestrial vertebrate palaeontology and need for a new synthesis led the Editors (RJB, RBI and MCL) to convene a special symposium on ‘Late Triassic Terrestrial Biotas and the Rise of Dinosaurs’ for the 2009 Society of Vertebrate Paleontology Annual Meeting in Bristol, United Kingdom. This symposium brought together over 16 presentations

covering numerous aspects of the Late Triassic transition. Many of these new research results are presented for the first time as papers in the present volume. Here, we give a brief description of the ‘state of the art’ in Late Triassic terrestrial vertebrate palaeontology, focusing in part, but not exclusively, on dinosaur origins.

Any evolutionary study in deep time requires a robust geochronologic framework to calibrate the age of fossil taxa and their palaeoenvironmental context. These data are critical for understanding the tempo of change and diversification in particular clades (e.g., early dinosaurs). They are also necessary for comparisons between different fossil assemblages and geological units, because accurate data on stratigraphic ordering of fossil assemblages is essential to determine whether potential differences can be ascribed to variation across space versus time. The study of Late Triassic terrestrial biotas is certainly no exception. Unfortunately, the Late Triassic is particularly devoid of published high-resolution radioisotopic ages (Mundil *et al.* 2010), and these are particularly few for non-marine strata, making correlation between assemblages and to the marine timescale very difficult (Irmis *et al.* 2010; Fraser & Sues this volume). Thus, palynofloral and vertebrate biostratigraphy have been the dominant methods of correlation for non-marine Late Triassic strata (e.g., Litwin *et al.* 1991; Cornet 1993; Lucas 1998, 2010), but this does not afford the precision necessary for detailed comparisons, and its accuracy has certainly been controversial (e.g., Langer 2005; Rayfield *et al.* 2005, 2009; Schultz 2005; Irmis *et al.* 2010).

One bright spot in Late Triassic terrestrial geochronology is the Newark Supergroup of eastern North America, where a ~35 million year record of lacustrine sedimentation from multiple rift basins provides a precise and accurate high-resolution timescale (Kent & Olsen 1999; Muttoni *et al.* 2004; Olsen *et al.* this volume). The Newark Supergroup Astronomically-Calibrated Geomagnetic Polarity Time Scale (Newark APTS) is derived predominantly from the Newark Basin, and consists of high-resolution magnetostratigraphy calibrated by radioisotopic dates and orbitally-paced cyclostratigraphy, allowing for precision of ~20 ka or less (Olsen *et al.* this volume). The high-resolution magnetostratigraphy allows correlation to classic Tethyan marine sections (and thus the marine timescale) (Muttoni *et al.* 2004), and the co-occurrence of extensive palynomorph assemblages allows correlation to existing palynomorph biostratigraphic schemes (Olsen *et al.* this volume). In concert with emerging radioisotopic data from sections containing terrestrial vertebrates

(e.g., Irmis & Mundil 2008, 2010; Ramezani *et al.* 2009), the Newark APTS allows confident correlations between important terrestrial fossil assemblages (Olsen *et al.* this volume).

These absolute age data can also help recast previous vertebrate biostratigraphic schemes as examinations of faunal change rather than strictly a correlation tool. However, for either use, one must have a precise and accurate lithostratigraphic framework, with detailed plots of individual fossil occurrences. Such detailed records have been rare in the past (cf. Rogers *et al.* 1993), but researchers are now beginning to produce such records. For example, a revised lithostratigraphy, along with precise stratigraphic placement of fossil discoveries, has revolutionised our understanding of vertebrate faunal change in the classic Upper Triassic Chinle Formation sections at Petrified Forest National Park, Arizona, USA (Parker & Martz this volume). These data demonstrate a sudden mid-Norian turnover that may correlate with major palaeoenvironmental perturbations (Parker & Martz this volume).

The palaeoenvironmental context of the Late Triassic terrestrial transition has become increasingly important as workers address the processes that affected these ecosystems. Recent studies have identified abrupt palaeoenvironmental changes reflected in the carbon cycle and depositional environment that correlate with major vertebrate faunal changes (e.g., Whiteside *et al.* 2010; Olsen *et al.* this volume; Parker & Martz this volume). Similarly, major differences in coeval assemblages from across the globe may reflect latitudinal or other climatic differences (Fraser 2006; Irmis *et al.* 2007; Nesbitt *et al.* 2009; Ezcurra 2010a; Ezcurra *et al.* this volume; Fraser & Sues this volume; Irmis this volume; Olsen *et al.* this volume). These differences could also explain unusual faunal occurrences, such as the late-surviving giant dicynodonts in north-eastern Europe (Dzik *et al.* 2008; Sulej *et al.* this volume). Further investigation of Late Triassic palaeoenvironments with new analytical methods should prove to be a powerful test of these climatic-biotic hypotheses (e.g., Dunlavey *et al.* 2009; Marynowski & Simoneit 2009).

Among the various tetrapod lineages that originated/radiated during the Late Triassic (e.g., anurans, turtles, lepidosaurs, mammals), archosaurs deserve particular interest for their great diversity, morphological disparity and dominance of terrestrial ecosystems during the remainder of the Mesozoic Era (in the form of dinosaurs, pterosaurs and crocodyliforms) and, during the Cenozoic, in the form of crocodylians and birds (including >10,000 living species). Although the split between the crocodylian and avian lineages occurred very early within the Triassic (Nesbitt *et al.* this volume), a great deal of the cladogenetic events that set the grounds for the latter evolution of archosaurs occurred during the Late Triassic (Brusatte *et al.* this volume; Irmis this volume) including the split of Dinosauria into its main clades (Ornithischia, Sauropodomorpha and Theropoda) and the origin of Crocodyliformes (Pol *et al.* 2009).

Dinosaurs originated from a grade of small gracile archosaurs generally termed 'basal dinosauiromorphs'. Formerly known only from Middle Triassic deposits of Argentina, various recent finds and reanalyses (Dzik 2003; Ezcurra 2006; Ferigolo & Langer 2007; Irmis *et al.* 2007; Nesbitt *et al.* 2007, 2010) have increased both their geographical and chronological record, further enlarged with the recent inclusion of *Saltopus elginensis* in the group (Benton & Walker this volume). Some of these basal dinosauiromorphs may form an unusual clade of long-armed, beaked forms, the silesaurids (Langer *et al.* 2010; Nesbitt *et al.* 2010), with records occurring through most of the Mid–Late Triassic, in Africa, Europe and South and North America.

Following two previous booms of discoveries during the early (Serenó & Novas 1992; Sereno *et al.* 1993) and late (Bonaparte *et al.* 1999; Langer *et al.* 1999) 1990s, the last few years witnessed a burst of exciting discoveries of early dinosaurs. These have included: an herrerasaurid, *Sanjuansaurus gordilloi* (Alcober & Martínez 2010) and two basal sauropodomorphs, *Panphagia protos* (Martínez & Alcober 2009) and *Chromogisaurus novasi* (Ezcurra 2010b), from the Ischigualasto Formation of Argentina; *Tawa hallae*, a new basal theropod, from the Chinle Formation of western USA (Nesbitt *et al.* 2009); the only well known Triassic ornithischian, *Eocursor parvus*, from the lower Elliot Formation of South Africa (Butler *et al.* 2007; Butler 2010); and two new basal sauropodomorphs from the Upper Maleri Formation of India (Novas *et al.* this volume). In addition to a better understanding of the phylogenetic positions of these taxa, reinterpretations of previously known taxa such as *Aliwalia rex* (Yates 2007), *Guaibasaurus candelariensis* (Langer *et al.* this volume), *Heterodontosaurus tucki* (Butler *et al.* 2007, 2008; Porro *et al.* this volume), *Staurikosaurus pricei* (Bittencourt & Kellner 2009) and *Zupaysaurus rougieri* (Ezcurra & Novas 2007), have also helped to unravel basal dinosaur evolution.

Despite these contributions, various aspects of early dinosaur phylogeny remain controversial. Basal ornithischian phylogeny is particularly problematic, with *Eocursor parvus*, *Lesothosaurus diagnosticus* and heterodontosaurids placed in very different positions according to the recent published hypotheses (Serenó 1999; Xu *et al.* 2006; Butler *et al.* 2007, 2008, 2010). Among saurischians, *Guaibasaurus candelariensis* is placed within either the sauropodomorph (Ezcurra 2010b; Novas *et al.* this volume) or theropod (Langer *et al.* this volume) lineages, as is also the case for the very fragmentary *Agnosphitys cromhallensis* (Yates 2007; Ezcurra 2010b). However, the most contentious and longest-lasting issue is the position of herrerasaurids, with recent publications endorsing (Serenó 2007; Nesbitt *et al.* 2009, 2010) or rejecting (Langer & Benton 2006; Irmis *et al.* 2007; Yates 2007; Alcober & Martínez 2010; Ezcurra 2010b; Novas *et al.* this volume) their theropod affinities. The putative herrerasaurid *Chindesaurus bryansmalli* also has an erratic position, and was considered a basal theropod even in phylogenies that excluded core herrerasaurids from the group (Yates 2007; Novas *et al.* this volume). Finally, *Eoraptor lunensis* has also been alternatively nested within (Serenó 2007; Nesbitt *et al.* 2009; Ezcurra 2010b) or outside (Langer & Benton 2006; Yates 2007; Alcober & Martínez 2010) Theropoda.

Serenó (2007) discussed the possible reasons for this discrepancy of opinions. Although there is certainly space for broader taxon and character sampling, and for more precise character state definitions, we believe that this is also a measure of the dynamic nature of the field of research, with numerous studies scrutinising a relatively short segment of evolutionary history. However, among the drawbacks of an ambiguous phylogenetic framework is its limitation as a foundation for ongoing meta-analytical approaches to understanding macroevolution (e.g., Barrett *et al.* this volume). As so often in palaeontology, we hope that further finds and more comprehensive phylogenetic studies may provide a stronger basis for macroevolutionary work.

The palaeobiology and palaeoecology of Late Triassic terrestrial tetrapods and their ecosystems remain relatively little studied, and represent a promising avenue for future research. For example, there has been considerable interest historically in dietary preferences among Triassic tetrapods (e.g., Crompton & Attridge 1986; Galton 1986; Barrett 2000; Reisz & Sues 2000; Small 2002; Barrett *et al.* this volume), particularly focusing on multiple independent origins of herbivory

and the possibility that tetrapod faunal turnover was driven by changes in floral palaeocommunities (e.g., Benton 1983). Recent discoveries of apparently omnivorous and/or herbivorous silesaurids and reevaluations of archosaur phylogeny have led to reexaminations of dietary evolution amongst early dinosaurs and closely related taxa, questioning long held assumptions (Nesbitt *et al.* 2010; Barrett *et al.* this volume). The continued development of such work, combined with careful functional work focusing on exemplar taxa (e.g., Desojo & Vizcaíno 2009; Porro 2009) and better understanding of environmental differences between fossil sites, should begin to yield insights into palaeocommunity structure and evolution.

Historically, work on Triassic biogeography has been qualitative in nature, and has focused on the presence or absence of major barriers to faunal exchange on the Pangaeian supercontinent and the potential influence of climate-driven latitudinal variations in faunas (e.g., Olsen & Galton 1984). Quantitative analyses were pioneered by Shubin & Sues (1991), but have remained relatively scarce, despite the toolkit of possible palaeobiogeographical approaches available. Palaeontologists are now finally beginning to explore these methods in detail: for example, Nesbitt *et al.* (2009) used likelihood-based methods to assess ancestral areas and dispersal events among early dinosaurs, whereas Ezcurra (2010a) used tree-reconciliation analysis and a novel approach in which palaeolatitude is mapped onto area cladograms to examine the biogeography of Triassic tetrapods more broadly. Both studies found quantitative evidence for an important role of palaeolatitude in determining Triassic biogeography. These alternative methodological approaches address subtly different questions, and there is as yet no empirical evidence as to which of the multitude of available biogeographical techniques is most likely to give reliable results. Moreover, these studies represent the tip of the iceberg in terms of possible methodologies and datasets, and it is likely that ongoing work, combined with new data and increasingly detailed phylogenies, will yield further new insights.

Macroevolutionary work on Triassic faunas has generally focused on taxonomic diversity, beginning with the pioneering, although often controversial, global studies of Benton (1983, 1994; see also Brusatte *et al.* this volume), which examined the evidence for Triassic extinction events and their impact on Triassic terrestrial tetrapods. Recent work has stressed that such global analyses should be treated with caution, due to the problems of stratigraphic correlation and the possibilities of differing regional signals (e.g. Irmis this volume). Although no similar global study of all tetrapods has been carried out since Benton (1994), work has focused on individual clades (e.g., Fröbisch 2008; Barrett *et al.* 2009, this volume; Abdala & Ribeiro 2010; Ezcurra 2010b; Brusatte *et al.* this volume; Irmis this volume; Novas *et al.* this volume), and has often attempted to incorporate phylogenetic data on missing lineages. Another new approach looks at diversity shifts (increase in lineage diversification) based on phylogenetic hypotheses (Lloyd *et al.* 2008; Brusatte *et al.* this volume), finding evidence for increases in diversification rate in early dinosaur evolution. Analyses of disparity (morphological diversity) and rates of character evolution have recently been carried out for Triassic archosaur datasets (Brusatte *et al.* 2008, this volume; Cisneros & Ruta 2010), and provide a potentially highly informative counterpart to studies of taxonomic diversity. Methods of ancestral state reconstruction have rarely been applied to Triassic tetrapods, but they have recently been used to investigate topics such as the early evolution of dinosaur body size (Carrano 2006; Irmis this volume).

The elephant in the room for all of these macroevolutionary studies is, however, the effect of uneven spatiotemporal sam-

pling on observed patterns. Recent work has suggested that sampling biases may cause severe problems for studies of taxonomic diversification (e.g., Smith & McGowan 2007; Barrett *et al.* 2009; Butler *et al.* 2011); the effects of uneven fossil record sampling on patterns of disparity and character rates remain largely unstudied, although some theoretical work implies that they should be more robust to such biases (e.g. Ciampaglio *et al.* 2001). Some recent early Mesozoic studies have attempted to correct for geologic biases (e.g., Fröbisch 2008; Lloyd *et al.* 2008; Barrett *et al.* 2009; Irmis this volume), but more comprehensive solutions are necessary. Uneven fossil record sampling is, however, not a reason to abandon such macroevolutionary work: increasingly sophisticated approaches aim to identify and ameliorate sampling biases via sampling standardisation (e.g., Alroy 2010) or multiple regression based modelling approaches (e.g., Marx & Uhen 2010; Benson & Butler in press). Future advances in the understanding of Triassic diversity patterns will require robust new databases, detailed phylogenetic hypotheses, better stratigraphic correlations and careful consideration of sampling biases.

Acknowledgements

We thank the organising and program committees of the Bristol SVP meeting for allowing us to hold the symposium that led to this volume, and the Systematics Association for partially funding attendance for two participants. Our thanks also go to all the vertebrate palaeontologists who participated in and attended the symposium. Many thanks are due to the Royal Society of Edinburgh for their help in producing this volume, with particular thanks to Vicki Hammond, who oversaw and organised the entire publication process, and Andrew Smith for his editorial work. Jeffrey Martz provided the illustration which graces the cover of this volume. Additional thanks are due to all colleagues who reviewed the manuscripts presented herein.

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