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Mesozoic mammaliaform diversity: The effect of sampling corrections on reconstructions of evolutionary dynamics

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ABSTRACT

Recent years have witnessed an explosion of new fossil discoveries and analyses documenting the unappreciated ecological and morphological diversity of Mesozoic Mammaliaformes. In contrast, the taxonomic diversity dynamics through the first 165 million years of mammal evolution have not yet been rigorously analysed, leaving patterns of diversification during this important period open to conjecture. Here, we present a comprehensive statistical analysis of global mammaliaform diversity spanning from the Late Triassic appearance of mammaliaforms (~230 million years ago [hereafter, mya]) to the end Cretaceous mass extinction (66 mya). We analysed 691 occurrences representing 367 genera and 550 species in standard time bins of approximately 10 million years in duration. Significant correlations between diversity and sampling proxies suggest sampling biases in the mammaliaform fossil record. Shareholder quorum subsampling and model-based approaches were used to mediate these biases. After applying these methods, the following patterns were supported: low standing diversity during the Late Triassic–Early Jurassic evolution of early Mammaliaformes (e.g., morganucodonts) was followed by high standing diversity during the Late Jurassic due primarily to the diversification of Eutriconodonta, Multituberculata and Cladotheria. This peak was followed by a fall in diversity during the middle of the Hauterivian–Barremian interval, suggesting that extinctions typically associated with the Jurassic–Cretaceous boundary may instead have occurred later, during the Early Cretaceous. Standing diversity recovered through several fluctuations during the 'mid' Cretaceous (approximately Barremian to Albian), leading to a second peak in the Campanian that reflects the diversification of key clades, including therians. Analyses of geographically restricted datasets illustrate a significant spatial heterogeneity in sampling, with several intervals dominated by North American occurrences. Uneven sampling effort and geographic heterogeneities in the fossil record are significant factors affecting reconstructions of Mesozoic mammaliaform diversity, and correcting these biases can markedly alter observed patterns and their interpretation.

1. Introduction

For decades, the focus of synapsid palaeontology has been on the therapsid response and recovery to the end Permian mass extinction, and the mammalian radiation following the K/Pg mass extinction, which heralded the "Age of Mammals". However, the fossil record of Mesozoic mammaliaforms spans ~2.5 times the duration of the comparatively well-studied record of Cenozoic mammals. Within Mammaliaformes, 11 major clades or functional grades (following Kielan-Jaworowska et al., 2004, and detailed below) formed an ecologically diverse Mesozoic assemblage from the Carnian (Late Triassic, ca 235–229 mya) onwards (Luo, 2007a). Recent fossil discoveries highlight a complex evolutionary history for Mesozoic Mammaliaformes (e.g. Luo et al., 2011), with the traditional scenario of a linear acquisition of mammalian characters being challenged by multiple evolutionary origins of key morphological features such as the tribosphenic molar (Luo et al., 2001) and middle ear ossicles (Luo et al., 2011). Moreover, in contrast to common depictions of early mammaliaforms as small terrestrial and scansorial insectivores, new fossils demonstrate that Mesozoic mammaliaforms invaded a variety of ecological niches, from semi-aquatic to gliding forms, and even dog-sized forms that preyed on juvenile dinosaurs (Hu et al., 2005; Luo and Wible, 2005; Ji et al., 2006; Meng et al.,

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Table 1
Mesozoic stages represented by ~10 myr intervals.

Interval	Stages represented	Duration (myr)
Triassic 3	Carnian	237.0–228.4
Triassic 4	Norian–Rhaetian	228.4–201.3
Jurassic 1	Hettangian–Sinemurian	201.3–190.8
Jurassic 2	Pliensbachian	190.8–182.7
Jurassic 3	Toarcian–Aalenian	182.7–170.3
Jurassic 4	Bajocian–Bathonian	170.3–166.1
Jurassic 5	Callovian–Oxfordian	166.1–157.3
Jurassic 6	Kimmeridgian–Tithonian	157.3–145.0
Cretaceous 1	Berriasian–Valanginian	145.0–133.9
Cretaceous 2	Hauterivian–Barremian	133.9–126.3
Cretaceous 3	Aptian–Albian	126.3–100.5
Cretaceous 4	Cenomanian	100.5–93.9
Cretaceous 5	Turonian–Santonian	93.9–83.6
Cretaceous 6	Campanian	83.6–72.1
Cretaceous 7	Maastrichtian	72.1–66.0

2006; Luo, 2007a). Despite the great attention paid in recent years to this previously unappreciated morphological and ecological diversity of early mammaliaforms, and a series of recent quantitative studies of taxonomic diversity in more basal synapsids (Brocklehurst and Fröbisch, 2014; Brocklehurst et al., 2013; Fröbisch, 2013), there has been little rigorous analysis of mammaliaform diversity dynamics prior to the K/Pg mass extinction (Rose, 2006). Previous approaches have been either broad and qualitative assessments of subclades (Luo, 2007b) or geographically restricted to the North American record (Alroy, 2009) and more specific localities (Wilson, 2005, 2013).

Reconstructing diversity dynamics over deep time is a core theme of palaeobiology (Jablonski, 1999; Raup, 1972; Valentine, 1985). Although the potential effects of geological and anthropogenic biases on accurate taxon counts have been discussed for decades (Raup et al., 1975), it is only more recently that substantial efforts have been made to correct these biases (Alroy, 2000, 2008, 2010; Alroy et al., 2001, 2008; Behrensmeyer et al., 2005; Peters and Foote, 2001; Smith and McGowan, 2007; Smith et al., 2012). A growing number of studies have focussed in particular on biases introduced by differences in outcropping rock area (Crampton et al., 2003; Smith and McGowan, 2007), preservation potential of fossil organisms (Smith, 2001), or evenness and fairness of sampling during standard intervals (Alroy, 2010; Alroy et al., 2001, 2008). These studies suggest that many features of observed diversity curves could be artefacts of changes in fossil preservation, geological sampling, or anthropogenic sampling rather than true biotic signals (e.g. Smith, 2007; Smith et al., 2012). Complex Earth system interactions such as sea level change may drive both sedimentation and ancient biodiversity in the marine realm, suggesting that covariation of fossil taxon counts and potentially biasing factors is not always causal (Peters, 2005; Benson and Butler, 2011; Hannisdal and Peters, 2011; but see Smith and Benson, 2013). However, terrestrial processes may be simpler, with factors such as rock area and collection effort directly biasing taxon counts (e.g. Benson and Upchurch, 2013; Benson et al., 2013; Butler et al., 2011a,b; Upchurch et al., 2011). Here, we present the first quantitative investigation of the global taxonomic palaeodiversity of Mesozoic Mammaliaformes, applying robust sampling-correction approaches to account for geological and anthropogenic biases and reassessing diversity dynamics in early mammal evolution.

2. Methods and materials

2.1. Datasets

2.1.1. Mammaliaform taxa

We have attempted to maximise coverage of Mesozoic mammaliaform occurrence data in the Palaeobiology Database (Alroy et al., 1998), with an extensive literature review and comparison with data in Kielan-Jaworowska et al. (2004). Mammaliaformes was considered as a monophyletic clade, consisting of all descendants of the most recent common ancestor of Morganucodonta and crown Mammalia (Luo et al., 2002; Rowe, 1988; Zhou et al., 2013). Morganucodonts, docodonts and kuehneotherids are successively more closely related outgroups of crown Mammalia, consistent with current phylogenetic studies and nomenclature. The 'crown' Mammalia is defined as the common ancestor of extant monotremes and extant therians and all fossil groups cladistically nested within this clade. Mammalia comprises eutriconodonts, australosphenidans, multituberculates, spalacotheroids, stem cladotherians, stem boreosphenidans, eutherians and metatherians (Kielan-Jaworowska et al., 2004). Stem allotherians, formerly considered to be related to multituberculates, were recently removed from the crown Mammalia (Zhou et al., 2013).

The updated dataset was downloaded from the Paleobiology Database (paleobiodb.org) on 20/02/2013. We then removed ichnofossils and collections with poorly constrained stratigraphic ages (spanning more than two time bins). This filtered version of the dataset comprises 691 occurrences of 367 genera and 550 species, ranging from the Carnian (237–227 mya; Late Triassic) to the Maastrichtian (72.1–66.0 mya; Late Cretaceous). In order to determine the effects of a geographically heterogeneous fossil record on global diversity patterns, two regional datasets were also created via further filtering of the global dataset. These are: (1) a North American dataset consisting of occurrences from the USA, Canada, Mexico and Greenland (288 occurrences of 208 genera and 302 species); and (2) an Asian dataset comprising occurrences from the Russian Federation, China, Japan, Kazakhstan, Kyrgyzstan, Mongolia, Tajikistan and Uzbekistan (255 occurrences of 137 genera and 191 species). These datasets are all provided in the electronic online supplement, along with other data and scripts used to perform our analyses.

2.1.2. Time bins

Occurrences were assigned to standardised time bins, approximately 10 myr (million years) in duration (Table 1) (Alroy, 2000; Alroy et al., 2008). Whereas previous authors have included only Tithonian occurrences in the 'Jurassic 6' time bin, we include both Kimmeridgian and Tithonian occurrences, as 60% of unique occurrences within these stages spanned both intervals (i.e. were defined as 'Kimmeridgian–Tithonian'). The same approach was applied to the 'Cretaceous 3' interval, which has been previously assigned Aptian occurrences only: here it includes both Aptian and Albian occurrences because 24% of occurrences within these stages spanned both intervals.

2.2. Analytical approach

Recent developments in the quantification of vertebrate palaeodiversity curves have increased confidence in reconstructions of ancient diversity patterns by attempting to correct observed taxon counts for sampling biases (e.g. Alroy, 2000; Barrett et al., 2009; Fröbisch, 2008; Irmis and Whiteside, 2011; Lloyd, 2012; Lloyd et al., 2008; Mannion et al., 2011). These methods fall broadly into two classes: (1) model-based approaches that first attempt to quantify the available record using sampling proxies, then construct models of expected diversity to use as a correction factor for observed diversity (Lloyd, 2012; Peters and Foote, 2001; Smith and McGowan, 2007); and (2) sampling standardisation (or subsampling) approaches that simulate an equal, or fair sample of ancient diversity among time intervals based directly on occurrence data, making fewer assumptions about drivers of the record (Alroy, 2010; Alroy et al., 2001, 2008; Kowalewski, 2002). We used both methods to assess the temporal pattern of mammaliaform diversity through the Mesozoic at both the species and genus levels. The application of bias correction approaches that treat the data very differently highlights the most robust temporal trends when their results are congruent (Mannion et al., 2011, 2012; Smith et al., 2012).