COMPLETENESS OF THE DINOSAUR FOSSIL RECORD: DISENTANGLING GEOLOGICAL AND ANTHROPOGENIC BIASES

by

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Abstract

Non-avian dinosaurs were a highly successful clade of terrestrial tetrapods that dominated Mesozoic ecosystems. Their public and scientific popularity makes them one of most intensely researched and understood fossil groups. Key to our understanding of their evolutionary history are interpretations of their changing diversity through geological time. However, spatiotemporal changes in fossil specimen completeness, diagnostic quality, and sampling availability can bias our understanding of a group's fossil record. Methods quantifying the level of skeletal and phylogenetic information available for a fossil group have previously been used to assess potential bias. In this thesis, these methods are used to critically assess the saurischian dinosaur fossil record, including an examination of changes in specimen completeness through research time. Novel metrics are presented that quantify the diagnostic quality of fossil specimens and assemblages. Results suggest that recent changes in our understanding of the dinosaur fossil record mostly derive from taxonomic and stratigraphic revisions. The completeness of the sauropodomorph fossil record is temporally segregated, whereas the theropod record is heavily spatially and environmentally biased, plus shows signs of taphonomic and taxonomic identification bias towards particular subgroups. These results represent a significant contribution to better understanding the nature of the dinosaur fossil record.

An exploration in Time And Relative Dimensions In Space

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Contribution statements

Chapter 2:

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My contribution to this manuscript involved conducting all parts of the research, including data collection, analysis and interpretation of results, as well production of the manuscript. My colleague provided crucial feedback on interpretation of results and drafts of the manuscript.

Chapter 3:

My contribution to this manuscript involved conducting all parts of the research, including data collection, analysis and interpretation of results, as well production of the manuscript. My colleagues designed the basis of the research project, designed the methods behind the analyses used, had major input into the creation of sauropodomorph supertree and provided crucial feedback on interpretation of results and drafts of the manuscript.

Chapter 4:

My contribution to this manuscript involved leading all parts of the research, including data collection, analysis and interpretation of results, as well production of the manuscript. My colleagues provided key data for use in analyses, had methodological input, as an alternate version of the study was previously piloted, and provided feedback on interpretation of results and drafts of the manuscript.

Abbreviations

Data sources

PBDB, Paleobiology Database

Metrics

SCM, Skeletal completeness metric
CCM, Character completeness metric
LoD, Likelihood of diagnosis

Time intervals

T, Triassic
J, Jurassic
K, Cretaceous

Sampling proxies

DBF, Dinsoaur bearing formation
DBC, Dinosaur bearing collection

Methodological implementations

GLS, Generalised least squares
PIC, Phylogenetic independent contrasts
PGLS, Phylogenetic generalised least squares
FDR, False discovery rate
AICc, Akaike's information criterion
p, p-value
R^2, coefficient of determination
W, Wilcoxon statistic
H, Kruskal-Wallis H statistic
λ, lambda
OTU, Operational taxonomic unit

1 | Introduction

Fossils are the windows into the evolutionary history of this planet, providing incredible glimpses into times when life was substantially different to today. Palaeontology has one explicit goal: to understand the history of life on Earth. To achieve this goal palaeontologists are almost entirely reliant on the preserved information available in the fossil record. As a historical science, palaeontology gathers the wealth of information available from the fossil and geological records to create evolutionary hypotheses based on evidence reasoning, and symmetry between the past and present (Benton and Hitchin 1996). The question is, however, can we trust the fossil record to provide a truthful picture of evolutionary history?

The fossil record has long been considered incomplete (Darwin 1859; Teichert 1956; Newell 1959; Foote and Raup 1996; Kidwell and Holland 2002). Therefore, there is a select and finite limit to the information available for our interpretations of ancient life. Its incompleteness is the result of an large number of different spatial and temporal factors relating to organismal biology, environment, and taphonomic and geological processes. It is thought that only a very small percentage of all the organisms that ever lived become fossilised (Teichert 1956; Paul 2009). In most cases, hard tissues, like shells, bones and wood, preferentially survive in comparison to soft tissues. Therefore, soft tissues are often lost unless preserved under exceptional circumstances (Newell 1959). Even between closely related groups, there are strongly different levels of preservation. Ancient environments are also just as prone to uneven representation. Rivers, lakes and marine environments are common in the sedimentary record, whereas mountainous or forest settings are rarely preserved (Newell 1959) due to their distance from depositional sites. There is also an unequal representation of time between different geographical regions and between geological time intervals, as stratigraphic packages have variable accumulation rates (Raup 1972). Fossils in more ancient rocks are also more likely to have been affected by geological processes, greatly enhancing the chances of fossil destruction or misinterpretation due to weathering, erosion or distortion. Therefore, understanding the incompleteness of the fossil record is a pertinent issue, and attempts to recognise and account for its imperfections are of key importance for the field and our interpretations of evolutionary history.

1.1. Approaches to assessing the completeness of the fossil record

On localised scales, it is possible to look at the relative similarity between ancient and modern assemblages of similar faunas to assess the level of missing information (Valentine 1989; Cooper *et al.* 2006). Many taphonomic studies associated with geologically young localities have been able to use this method to assess the levels of faunal completeness (e.g. Behrensmeyer *et al.* 2003; Soligo and Andrews 2005; Bell *et al.* 2010; Carrasco 2013). Attempts have been made to estimate the number of species missing from the fossil record or the true number of taxa that ever lived (Teichert 1956; Valentine 1970; Starrfelt and Liow 2016). However, these estimates seem speculative and have been proven to be problematic (Close *et al.* 2018). It seems that on macroevolutionary scales, the incompleteness of the fossil record cannot be quantified against absolute knowledge of the true pattern of evolutionary history (Benton and Hitchin 1996); therefore, how we approach the analysis of its completeness depends on what we are looking for and what we define to be an acceptably complete record. Different methods have attempted to quantify fossil record completeness in different ways, and in doing so have assessed different aspects of the fossil record.

1.1.1. *Relative completeness*

Raup (1972) found large-scale connections with changes in Phanerozoic diversity and the sedimentary rock record, suggesting major geological controls on the diversity signals we receive. Following this, many early approaches to the issue of quantifying fossil record completeness attempted to calculate the level of fossil-bearing rock preserved, including assessments of sediment accumulation rate (Sadler 1981), resolution of stratigraphic sequences (Schindel 1982), palaeosol formation (Retallack 1984), and the time-averaging of sediment packages (Kowalewski 1996). The desire to assess the completeness of individual taxonomic groups, led to a plethora of fossil occurrence-based metrics. Simple completeness metrics have been devised to quantify the gaps in stratigraphic occurrence ranges of taxa (Benton 1989; Wignall and Benton 1999; Fara and Benton 2000; Mander and Twitchett 2008) and to estimate the number of species with 'true' temporal ranges (Benton and Storrs 1994, 1996; Foote and Raup 1996; Alba *et al.* 2001; Eiting and Gunnell 2009), based on preservation probability assumptions. Stratigraphic congruence methods are also some of the most widely employed to assess the completeness of a fossil record. These seek to quantify the level of consistency between the stratigraphic order of fossil occurrences and branching order of phylogenetic trees by interpreting the percentage of gaps (phylogenetic ghost ranges) as the relative amount of missing information (Dingus 1984; Benton and Storrs 1994, 1996; Springer 1995; Teeling *et al.* 2005; Upchurch and Barrett 2005; Wills 2007, 2008;Dyke *et al.* 2009; O'Connor *et al.* 2011a; Guinot *et al.* 2012). In this regard, a more complete fossil record would provide a strong correlation between phylogenetic hypothesis and stratigraphic occurrences. There have been a variety of different methodological iterations aiming to quantify this general concept (Norell and Novacek 1992), which has led to the development of other novel approaches such as the stratigraphic congruence with character state changes (Angielczyk 2002), and chronophyletic approaches (Dzik 2005). Analyses have found varied completeness signals, with some finding significant congruence (Norell and Novacek 1992; Benton and Storrs 1994) while others have identified crucial gaps (Teeling *et al.* 2005). Some studies have highlighted issues with the methodology of stratigraphic congruence, including assumptions of ancestor-descendant relationships (Norell 1993) and the reliance on phylogenies, which may be misleading (Wagner 2000; Wagner and Sidor 2000). These methods also only focus on large-scale patterns and struggle with methodological consistency, cross-study comparability and interpretational limitations (Angielczyk and Fox 2006).

1.1.2. Specimen completeness

For many years, studies assessing the taphonomic pathways of localised assemblages have used various grading systems based on preserved fossil body sections to assess completeness of specimens (Sander 1992; Kemp and Unwin 1997; Hüngerbühler 1998; Casey *et al.* 2007; McNamara *et al.* 2012a, b; Brown *et al.* 2013; Boessenecker *et al.* 2014). Specifically looking more closely at the vertebrate fossil record, many of these assessments count the number of bones present or provide rough estimates of skeletal completeness and articulation. This type of completeness puts the specimen in the context of natural biotic and ecological interactions, and taphonomic processes like transportation, abrasion, erosion, and chemical weathering. From this, taphonomists can determine detailed preservation histories for an assemblage and therefore can better understand the localised biases acting upon our interpretation of the fossils in question.

In the last two decades these methods have been utilised and adapted for use on the global scale (Benton *et al.* 2004; Fountaine *et al.* 2005; Smith 2007; Dyke *et al.* 2009; Benton 2010). Using these approaches, a high-quality fossil record would be one that contains many highly complete specimens. Early methods for quantifying specimen completeness were relatively subjective, and scored the completeness of fossil specimens by separating preservation quality into four or five simple categories (Benton *et al.* 2004, Fountaine *et al.* 2005, Benton 2008), an approach that was later refined by examining different skeletal regions (Beardmore *et al.* 2012). Subsequently, Mannion and Upchurch (2010a) conceived two completeness metrics that quantify the completeness of individual specimens and species in more detail and with greater accuracy. These metrics are the skeletal completeness metric (SCM) and character completeness metric (CCM). SCM measures the absolute proportion of the skeleton that is preserved for a species, whereas CCM measures the proportion of phylogenetically informative characters preserved. Calculating such metrics enables meaningful comparisons to be drawn between various sampling biases that could influence the record of a group.

Environmental and geological parameters can theoretically influence the quality of fossil specimens (Dingus 1984; Retallack 1984). For example, a high number of localities from depositional settings with higher quality preservation could lead to increased specimen completeness within a time interval. Ecological and biological differences between groups could also influence fossil quality, such as body size and robustness of skeletons (Cooper *et al.* 2006; Brown *et al.* 2013), or environmental preferences (Mannion and Upchurch 2010b). Previous studies have found varying correlations between completeness metrics and changes in diversity and fossil record sampling metrics through time, as well as various geographical and environmental differences between the fossil records of different groups (Mannion and Upchurch 2010a; Brocklehurst *et al.* 2012; Walther and Fröbisch 2013; Brocklehurst and Fröbisch 2014; Cleary *et al.* 2015; Dean *et al.* 2016; Verrière *et al.* 2016; Davies *et al.* 2017; Tutin and Butler 2017; Driscoll *et al.* 2018; Brown *et al.* 2019; Mannion *et al.* 2019a; Lukic-Walther *et al.* 2019), thus highlighting major biases that influence different fossil records to various extents.

1.2. Sampling bias

Adding to taxonomic, environmental, spatial, and temporal incompleteness, is the potential for palaeontologists to unevenly sample and misinterpret the preserved fossil record (Newell 1959; Koch 1978). It has been argued that the natural incompleteness of the fossil record may be less important than human inadequacies (Paul 1992). Studies have noticed biased collection habits of palaeontological field work and research, for example, towards certain time bins, taxonomic groups, formations, and geographic areas (Koch 1978; Hunter and Donovan 2005; Purnell and Donoghue 2005; Smith 2007; Puchalski *et al.* 2008; McGowan and Dyke 2009; Bernard *et al.* 2010; Lloyd *et al.* 2011; Dunhill *et al.* 2013). Variation in historical or geographic sampling by researchers can also potentially influence the level of specimen completeness known for a group, as more effort being allocated to a particular group or a set of localities is likely to yield more complete skeletons (Bernard *et al.* 2010). These sampling habits are known to have changed through research time, and a number of studies have employed the use of historic collection curves to take retrospective views on the understanding of particular fossil records (e.g. Maxwell and Benton 1987; Fara and Benton 2000; Smith 2007). The level of which these cumulative collection curves asymptote has also been employed as a relative fossil record completeness metric (e.g. Kalmar and Currie 2010). Although with each new discovery the knowledge of the fossil record intuitively improves, sampling and collection histories can have strong influences on the understanding of the fossil record. New discoveries have been found to drastically change the shape of diversity curves (Alroy 2000, Alroy *et al*. 2001) and phylogenetic trees (Tarver *et al.* 2007), emphasising a fragile interpretation of certain groups' evolution. Knowing this, recent studies have attempted to consider geographical and temporal sampling biases when interpreting evolutionary signals (e.g. Alroy *et al*. 2001; Lloyd 2011; Benson and Upchurch 2013; Benson *et al.* 2013; Wagner and Marcot 2013;

Brocklehurst 2015; Close *et al.* 2017).

Another potentially important factor acting upon our interpretation of the fossil record is the ability of researchers to confidently and consistently identify different taxonomic groups. The preferential fossilisation and recognition of certain fossil groups enhances our understanding of their evolutionary history (Plotnick and Wagner 2006; Paul 2009). However, poor palaeontological practice (Plotnick and Wagner 2006; Bell *et al.* 2010) and differential diagnostic qualities (Fara 2004; Zeder and Pilaar 2010) of fossil groups can have negative impacts on our interpretations of the fossil record (Sansom *et al.* 2017). Incomplete skeletons may also be difficult to diagnose, resulting in either a reduction in diversity estimates for a group or time bin or, conversely, increasing diversity as a result of taxonomic oversplitting (Brocklehurst and Fröbisch 2014).

1.3. Dinosauria

Non-avian dinosaurs are a highly successful and diverse clade of terrestrial archosaurs, which dominated Mesozoic ecosystems from the Late Triassic until the end of the Cretaceous (66 million years ago [Mya]) when they ultimately became extinct. They exhibit high levels of taxonomic diversity, morphological disparity, body size variation, ecological and niche adaptation, and geographical dispersal. They are likely one of the most intensely studied groups of fossil vertebrates (Benton 2008, 2010), because of scientific and public popularity. Their evolutionary history has received a great deal of attention (Sereno 1997; Sereno 1999; Carrano 2006; Lloyd *et al.* 2008; Brusatte *et al.* 2008a, b; Le Loeuff 2012; Benson and Choiniere 2013; Benson *et al.* 2014; Xu *et al.* 2014; Benson *et al.* 2016; Lloyd *et al.* 2016; Sakamoto *et al.* 2016; Benson *et al.* 2018; Bernardi *et al.* 2018) with many studies attempting to understand the changes in their diversity patterns through time (Barrett and Upchurch 2005; Upchurch and Barrett 2005; Wang and Dodson 2006; Barrett *et al.* 2009; Lloyd 2011; Mannion *et al.* 2011; Upchurch *et al.* 2011; Brusatte *et al.* 2014; Starrfelt and Liow 2016; Tennant *et al.* 2018). However, whether these patterns reflect genuine diversity dynamics, rather than artefacts of an imperfect fossil record remains uncertain. Non-avian dinosaurs are an important tetrapod group and ideal for large-scale assessments of the completeness of the fossil record.

Traditionally, Dinosauria is thought to be composed of two major clades, Saurischia and Ornithischia. Saurischia includes Sauropodomorpha, the long-necked quadrupedal herbivores, and Theropoda, the predominantly carnivorous bipeds. Ornithischia, are a diverse and morphologically disparate group of bipedal and quadrupedal herbivores. Recently, Baron *et al.* (2017) argued for the non-monophyly of Saurischia , and instead proposed an ornithischian-theropod sister relationship that they named Ornithoscelida. Many recent studies have upheld the traditional view of the major dinosaurian relationships (Gauthier 1986; Juul 1994; Novas 1996; Benton 1999, 2004; Langer and Benton 2006; Nesbitt *et al.* 2009a, 2010; Langer 2014; Novas *et al.* 2015; Langer *et al.* 2017; Müller *et al.* 2017), and therefore these are used in this thesis.

Dinosaurs have featured prominently in discussions of the quality of the fossil record (Butler and Upchurch 2007; Benton 2008; Lloyd *et al.* 2008; Barrett *et al.* 2009; Benton 2010; Tarver *et al.* 2011; Mannion and Upchurch 2010a; Brocklehurst *et al.* 2012). Studies have demonstrated that: (1) highly incomplete taxa can still provide important information for our understanding of dinosaur phylogenetic relationships (e.g. Butler and Upchurch 2007); (2) that there are differences in fossil completeness between continents and changing levels of completeness through historical time (Benton 2008); (3) that sampling artefacts influence our interpretation of apparent dinosaur diversification events (Lloyd *et al.* 2008); (4) that the validity of named dinosaurian taxa depends on the researcher (Benton 2010); (5) that there is strong congruence between the ages of phylogenetic tree branching and stratigraphic occurrence ages (Wills *et al.* 2008); (6) that additional finds of new species significantly change dinosaur phylogenetic relationships and our understanding of their evolution (Tarver *et al.* 2011); (7) that the sauropodomorph fossil record varies in completeness through geological and historic time, and may influence understanding of the group's temporal diversity changes (Mannion and Upchurch 2010a); (8) and that Mesozoic avian dinosaurs have a record that may be strongly influenced by diversity changes through time and preservation in Lagerstätten deposits (Brocklehurst *et al.* 2012).

1.4. Objectives

The main goal of this thesis is to quantify the completeness of the dinosaur fossil record and explore new ways of assessing its quality in order to understand potential biases acting on our interpretations of the group's evolutionary history. The thesis addresses some issues in previous completeness studies, by outlining methods to calculate the completeness of all specimens, and efficiently calculate the skeletal body proportions, for different fossil tetrapod groups. The thesis also addresses the findings of previous completeness studies in relation to new discoveries, whilst testing previous results in relation to new statistical methods, and provides a first thorough assessment of the relationship between tetrapod body size and skeletal completeness. The thesis is novel because it addresses the completeness of non-avian theropod fossil record, previously unstudied, and devises new methods to assess the relationship between skeletal completeness and the diagnostic quality of bones.

Chapter 2 quantifies the completeness of the non-avian theropod dinosaur fossil record using the skeletal completeness metric, and takes a detailed look at the spatial, temporal, environmental and taxonomic variation within their record.

Chapter 3 investigates how research history and new discoveries have affected our understanding of the sauropodomorph dinosaur fossil record. Using the skeletal completeness metric I up-date the completeness record of sauropodomorphs ten years after it was initially assessed, and explore possible environmental, phylogenetic and biological explanations for the nature of their record.

Finally, in Chapter 4, I create novel metrics in an attempt to quantify the diagnostic quality, or diagnosability, of non-avian theropod dinosaurs, to test whether there is a taxonomic identification bias acting upon their record. I assess the different diagnostic qualities of different theropods per subgroup, geological formation, time bin and completeness levels, and further assess diagnostic quality on a regional scale by quantifying the differences between system tracts of the Morrison Formation.

2 | Skeletal completeness of the non-avian theropod dinosaur fossil record

2.1. Introduction

Theropods are a major clade of bipedal saurischian dinosaurs. The non-avian species first appeared in the Late Triassic, dispersed and diversified in the Jurassic, became dominant in predatory guilds (Holtz 2012) and gave rise to birds (Padian and Chiappe 1998; Xu *et al.* 2014; Brusatte *et al.* 2015), but ultimately went extinct at the end of the Cretaceous (66 million years ago [Mya]). They were predominantly carnivorous, but some derived lineages evolved omnivorous and herbivorous diets (Barrett 2005; Zanno and Makovicky 2013; Barrett 2014; Novas *et al.* 2015; Lautenschlager 2017). Non-avian theropod fossils have been found on all continents and in all environments, occupying an array of ecological niches (Henderson 1998; Amiot *et al.* 2010; Godefroit *et al.* 2013; Sales *et al.* 2016; Lautenschlager 2017; Frederickson *et al.* 2018), and exhibit high taxonomic diversity, morphological disparity (Brusatte *et al.* 2012a, b; Griffin and Nesbitt 2016; Barta *et al.* 2018) and body size variation (O'Gorman and Hone 2012; Benson *et al.* 2014, 2018).

The quality of the theropod fossil record has never been quantified using specimen completeness metrics. Theropods are an ideal group to assess using these approaches, as their broad geographical and temporal extent may provide insights into large scale biases acting upon the fossil record. Here, we quantitatively assess the fossil record of theropod dinosaurs using the skeletal completeness metric originally developed by Mannion and Upchurch (2010a). SCM was preferred ahead of CCM as it has more obvious connections to natural taphonomic, environmental and weathering processes, for which we were more interested in drawing conclusions on for this study. We also focus on non-avian theropods (here referred to as simply 'theropods'), from the earliest species to the immediate precursors of avians. Avian taxa are excluded because recent studies have already assessed the quality of the Mesozoic bird fossil record (Fountaine *et al.* 2005; Brocklehurst *et al.* 2012; Gardner *et al.* 2016) and additional assessment of Cenozoic birds would be beyond the scope of this study.

Our main aim was to ascertain whether theropod specimen completeness is influenced by spatial and temporal sampling biases. We statistically compare theropod completeness between different geographical regions, depositional environments, and taxonomic subgroups; and the relationship between completeness and changes in rock record, sampling effort, and taxonomic diversity through geological time. By doing so we try to ascertain if there are particular patterns in the theropod fossil record that are indicative of larger scale ecological, geological, geographical or sampling biases, and try to uncover controls acting upon the records of the different theropod subgroups. We hope the results of this study will highlight some of the modern and ancient spatial and temporal inconsistencies of the global fossil record which often go unconsidered when regarding the macroevolutionary understanding of a group. We further hope they can be used to guide future exploration of and research on the theropod fossil record.

2.2. Methodology

2.2.1. Completeness metrics

The skeletal completeness metric (SCM) was proposed by Mannion and Upchurch (2010a) to more objectively estimate the proportion of the total, complete skeleton that is preserved for an individual species. They provided two different definitions for SCM: scored solely on the most complete specimen of a species (SCM1), or as the composite completeness of all known specimens of a species (SCM2). Strong correlations have been found between the two metrics (Mannion and Upchurch 2010a; Cleary *et al.* 2015; Tutin and Butler 2017), but we solely use the latter in this study, as it uses all the information at hand for each species and is more appropriate than arbitrarily nominating a most important specimen (Mannion and Upchurch 2010a; Brocklehurst *et al.* 2012; Brocklehurst and Fröbisch 2014).

Mannion and Upchurch (2010a) used approximations of relative skeletal proportions (e.g., the percentage of the total skeleton made up by any individual bone or skeletal region) to assess specimen completeness for sauropodomorphs. Subsequently, the metric has been refined and altered multiple times. For example, Cleary *et al.* (2015) used different skeletal proportion percentages for ichthyosaur taxa of different geological ages because significant morphological change occurs through time within the group. In contrast to the approximate estimates provided by Mannion and Upchurch (2010a), Brocklehurst and Fröbisch (2014) more precisely estimated the skeletal body proportions of synapsids by modelling each bone as the volume of a cone, cylinder, or a prism, based on skeletal measurements of multiple representatives of morphologically and taxonomically distinct subgroups. The assigned body proportion percentage of each bone was then derived from the average of these representatives. This was further developed by Verierre *et al.* (2016), who modelled bone volumes using more precise natural shapes and mapping two-dimensional outlines, representing each cranial bone, onto the external surface area of the skull (truncated pyramid) to obtain percentage volumes for each.

Although these refinements have made SCM calculations increasingly more precise, they are highly time-consuming to implement, particularly for large and morphologically diverse taxonomic groups like Theropoda. Due to the lack of physical access to specimens or multi-dimensional measurements of every bone (mostly due to varying completeness) we opted not to calculate skeletal

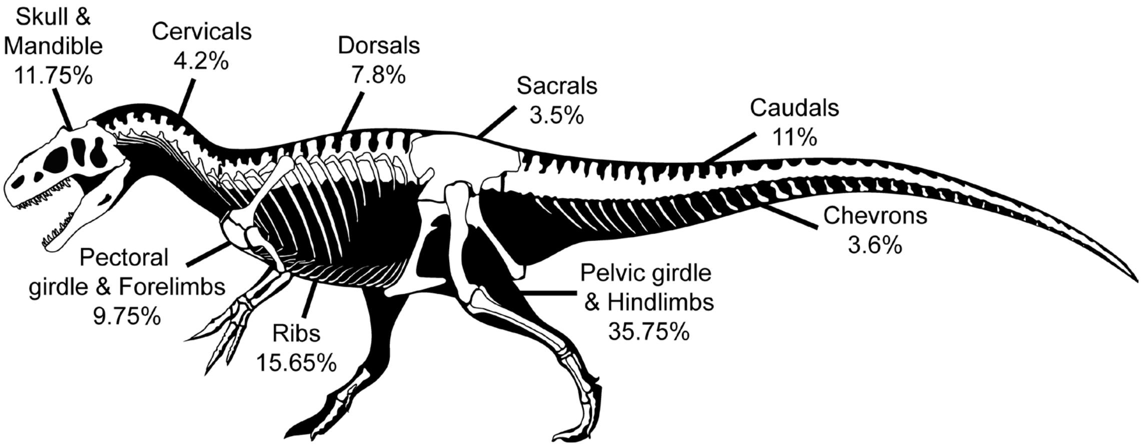


Figure 2.1. Skeletal reconstruction of *Allosaurus fragilis* (modified from http://www.skeletaldrawing.com; original reconstruction by Scott Hartman) illustrating the modelled mean skeletal body proportions of theropods.

proportions using three-dimensional volumes. Instead, we use an alternate but efficient method, whereby we modelled the two-dimensional surface area of each bone for ten morphologically and taxonomically disparate theropod taxa, based on scientifically informed skeletal reconstructions produced by Scott Hartman (www.skeletaldrawing.com): *Herrerasaurus ischigualastensis*, *Coelophysis bauri*, *Majungasaurus crenatissimus*, *Allosaurus fragilis* (Fig. 2.1), *Tyrannosaurus rex*, *Gallimimus bullatus*, *Nothronychus graffami*, composite alvarezsaur (based on *Mononykus olecranus* and *Shuvuuia deserti*), *Khaan mckennai*, and *Velociraptor mongoliensis* (Fig. 2.1, A.1). Choice of the representative skeletal diagrams was based on the availability of distinct species that represent the major groups of Theropoda, as well as how completely known the remains of each species are (see Supporting data). Each skeletal diagram and its constituent bones were traced in Adobe Illustrator (version CC) and the surface areas of individual bones and skeletal regions calculated using a free Illustrator plug-in, Patharea Filter (http://telegraphics.com.au/sw/product/patharea). This enabled us to have precise representative shapes on which to base our relative bone dimensions. All individual skull and mandibular bones were assigned the same proportional percentage of the total skull and mandible, regardless of the varying sizes of the bones.

The lack of the third dimension when estimating proportions is a potential limitation of our approach. To test whether skeletal proportions can be sufficiently well estimated by two-dimensional lateral views, a shape-volume proportioned skeleton of *T. rex* was calculated from the measurements available in the Brochu *et al.* (2003) monograph of 'Sue' (FMNH PR2081), one of the most complete specimens of *T. rex* ever discovered (Table A.1). As in Brocklehurst and Fröbisch (2014), cones, cylinders and prisms were used as the representative shapes for each bone, plus half pyramids, hollow cylinders and cuboids when necessary (see Supporting data). The resulting proportions are highly similar (Pearson's $R^2 = 0.96$, $p = 2.432E\text{-}07$) to those calculated from the two-dimensional skeletal reconstruction. Neither method is perfect, but a strong significant correlation between the results shows that they are coalescing on a relatively consistent set of skeletal proportions. Furthermore, Brown *et al.* (2019) found that there was no statistical difference between the completeness scores of bat taxa calculated using body proportions estimated via three-dimensional (CT scan of extant specimen) or two-dimensional approaches. As a result, we opted for the simpler two-dimensional method, which is easier to apply to a much greater taxonomic sample.

After the proportions were calculated for each skeletal diagram, the percentage values for each individual bone from all ten exemplar taxa (e.g., ten differing values for the femora; see Supporting data) were used to determine a mean value for each bone, which was applied to all theropods when computing completeness scores. Figure 2.1 shows the percentages used for individual regions of the theropod skeleton.

2.2.2. Dataset

We present a comprehensive dataset of 455 valid non-avian theropod species, including specimens that have not yet received formal taxonomic names but have been included as operational taxonomic units (OTUs) within phylogenetic analyses. Many of these OTUs represent isolated specimens of fairly low completeness but their inclusion is justified because they likely represent distinct, unnamed taxa, that can be of great value in regards to understanding phylogenetic relationships, and inclusion provides a better representation of the quality of the fossil record. We excluded all theropod species currently considered to be nomen dubia, *Protoavis texensis* because it is considered to be a chimera, including non-theropod remains (Nesbitt *et al.* 2007), and *Vitakridrinda sulaimani* because the published information on this species is not adequate to score it (Malkani 2006). All published specimens of every taxon were included unless information was lacking for an individual specimen, or if a taxon's composite completeness was already 100%, and any additional specimens made no difference to its completeness score. Completeness data was primarily gathered from figures and descriptive text in the literature, and when necessary from additional online sources, museum catalogues and via personal communication. The dataset includes detailed descriptions of the completeness of each specimen and scores completeness of individual bones from 0–100%, which is then transformed into overall skeletal proportions. See 'Scoring specimen completeness' in Supporting data for a detailed description of how individual bones were scored and how non-typical specimens were treated. Information regarding each taxon's geographical locality (modern- and palaeocoordinates), geological age (stratigraphic stage), sedimentary setting (e.g., siliciclastic or carbonaceous facies) and depositional setting were also gathered from the Paleobiology Database (PBDB: www.paleobiodb.org) and the literature. Body size data were collected as mass estimates (179 taxa) from Benson *et al.* (2018), supplemented by a further 57 calculations of additional taxa from available femoral measurements based on methods described in the same paper (see Cashmore and Butler 2019, Chapter 2). The dataset is up-to-date as of December 2018 (Cashmore and Butler 2019, Chapter 2).

Theropoda has been considered the sister group to Sauropodomorpha within the clade Saurischia in the vast majority of studies on dinosaur relationships (Gauthier 1986; Juul 1994; Novas 1996; Benton 1999, 2004; Langer and Benton 2006; Nesbitt *et al.* 2009a, 2010; Langer 2014; Novas *et al.* 2015; Langer *et al.* 2017; Müller *et al.* 2017). Baron *et al.* (2017) recently argued that Ornithischia and Theropoda are sister groups to the exclusion of Sauropodomorpha, and that herrerasaurids represent basal sauropodomorphs. Other authors have previously considered herrerasaurids as basal dinosaurs outside Saurischia, or basal saurischians outside Theropoda (Ezcurra 2006; Langer and Benton 2006; Irmis *et al.* 2007; Nesbitt *et al.* 2009b; Ezcurra 2010; Nesbitt 2011; Langer 2014; Baron and Barrett 2017; Parry *et al.* 2017). However, we follow the majority of recent studies and include Herrerasauridae within our theropod dataset.

2.2.3. Theropod completeness subdivisions

To examine completeness through time, SCM2 scores of each taxon were used to calculate a mean completeness value for each geological stage-level time bin from the Carnian to Maastrichtian. Stage-level time bins were chosen for ease of comparisons with sampling proxy data and with completeness data from the majority of previous studies. The standard deviation of completeness scores was calculated for each individual stage. Taxa that were present over multiple geological stages, or have an uncertain stratigraphic age, were included in each stage in which they potentially were present. The Triassic and Jurassic (T-J) SCM2 scores were also analysed separately from the Cretaceous (K) in some tests to assess changes in the theropod record through time.

To assess the differing completeness levels within Theropoda we subdivided the SCM2 scores into the following major subgroups: basal Theropoda, basal Neotheropoda, Ceratosauria, basal Tetanurae, Megalosauroidea, Allosauroidea, Megaraptora, basal Coelurosauria, Tyrannosauroidea, Compsognathidae, Ornithomimosauria, Alvarezsauroidea, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae, and non-deinonychosaurian Paraves. See Supporting data or details of which species were assigned to which subgroup, and Figure A.1 for the phylogenetic relationships followed.

To assess the varying quality of the theropod fossil record throughout the world, SCM2 scores were grouped by their hemisphere and between the major continental regions: Africa (30 taxa), Asia (191 taxa), Australasia (8 taxa), Europe (62 taxa), North America (95 taxa), and South America (68 taxa). Antarctica (1 taxon) was excluded from these analyses due to its very limited fossil record.

SCM2 scores were also subdivided according to their inferred sedimentary setting and depositional environment to generally understand global taphonomic influences on the theropod fossil record. Taxa were classified as originating from either siliciclastic or carbonaceous settings, and from aeolian, fluvial channel, alluvial plain, or lacustrine terrestrial environments, or a coastal or open marine setting.

We further separated taxa derived from either conservation Lagerstätten, concentration Lagerstätten, or background (non-Lagerstätten) sedimentary regimes in order to measure the impact that sites of exceptional preservation have had on our understanding of the theropod record. For this study we define conservation Lagerstätten as deposits (and formations) which preserve soft tissues alongside skeletal remains (Eliason *et al.* 2017), and concentration Lagerstätten as unusually dense macro-bone accumulations from a single sedimentary stratum (Behrensmeyer 2007). Assignment of taxa as belonging to either type of Lagerstätte was primarily based on information gathered from the PBDB.

2.2.4. Temporal correlations

The temporal curve of theropod SCM2 completeness was statistically compared to a number of other time series with which it might potentially have a relationship. We first compared the complete theropod SCM2 time series with scores for its component preservational regimes: time series of concentration Lagerstätten, conservation Lagerstätten, non-conservation Lagerstätten, and background SCM2. Additionally, we tested the correlations between temporal changes in total SCM2 and changes in SCM2 curves for specific continental regions, subgroups and depositional environments to understand the different natural and sampling aspects that best explain the complete SCM2 curve. We tested the correlation between SCM2 and changes in non-avian theropod richness through time, derived from the number of taxa in our dataset, and performed separate correlations for various time intervals, with and without conservation and concentration Lagerstätten taxa. Geological stages lacking any data were removed from all correlations where necessary.

We compared theropod SCM2 with stage bin length to assess whether the uneven lengths of stages influenced completeness recovered for individual intervals. Changes in sea level through time were derived from Butler *et al.* (2010), and were compared to theropod SCM2 because sea level has been argued to have a potential influence on the completeness of marine fossil groups (Cleary *et al.* 2015; Tutin and Butler 2017), although whether this relationship holds in the terrestrial realm is subject to debate (Fara 2002). The number of dinosaur-bearing formations (DBFs) and dinosaur-bearing collections (DBCs) for the Carnian to the Maastrichtian were collected from the PBDB. These have been argued to represent proxies for the amount of rock availability and the level of collection effort made on the respective fossil groups (Upchurch *et al.* 2011), which could have a strong influence on the theropod fossil record. However the use of these as sampling proxies has been criticised (Benton *et al.* 2011; Dunhill *et al.* 2014;

Benton 2015; Brocklehurst 2015; Dunhill *et al.* 2018), with formation counts in particular being regarded as information redundant when compared to raw diversity changes (Benton 2015; Dunhill *et al.* 2018). Results from comparisons between completeness and these proxies should therefore be taken with a level of caution. We consequently opted to calculate Good's u as an estimate of sampling coverage for each time bin. This estimates coverage for each geological stage based on the relative proportion of singleton (taxa sampled from one site only) to non-singleton (taxa sampled from two or more sites) taxon occurrences. If a geological stage has a majority of singleton taxa and a minority of non-singleton taxa, it will have low coverage and is therefore poorly sampled; but if there are higher proportions of non-singleton taxa, then the coverage for that stage is higher, suggesting that the fauna is more evenly sampled and better understood. Species-level theropod taxon occurrences per stage were gathered from the PBDB and sampling coverage was calculated using an R function developed by Chao and Jost (2012) (see Appendix A). We also used the number of theropod PBDB occurrences and the number of specimens per taxon (from our dataset) as proxies for relative abundance of theropod fossils and compared the summed number of each per stage with the theropod SCM2 time series. We also tested each major individual time series for trends in the overall patterns through time and whether combinations of observed species richness, fossil record sampling and time bin length provided significant explanations of mean completeness through time.

Theropod completeness through time was also compared with the records of other Mesozoic tetrapod groups for which skeletal completeness studies have been performed: plesiosaurs (Tutin and Butler 2017), ichthyosaurs (Cleary *et al.* 2015) and sauropodomorph (Mannion and Upchurch 2010a) time series. These comparisons aimed to identify shared or diverging completeness signals between the different groups of terrestrial and marine vertebrates.

2.2.5. Non-temporal comparisons

A variety of comparisons of the median and distribution of completeness values were made between subsets of the data, including Triassic, Jurassic and Cretaceous data, the major theropod subgroups, geographical hemispheres and continents, and the preservational regimes, sedimentary settings and depositional environments of each taxon. If a taxon with multiple specimens is known from more than one of these subsets, the taxon's completeness score was replicated in each group when performing statistical comparisons. Some singleton taxa were assigned to multiple depositional settings when one specific setting was not known for certain. SCM2 values are currently also known for bats (Brown *et al*. 2019), plesiosaurs (Tutin and Butler 2017), ichthyosaurs (Cleary *et al.* 2015), parareptiles (Verierre *et al.* 2016), pelycosaurs (Brocklehurst and Fröbisch 2014), and sauropodomorphs (Mannion and Upchurch 2010a) and so they were also compared to the distribution of theropod SCM2.

SCM2 values for individual taxa were also compared with the number of known specimens, modern and palaeolatitudinal coordinates, and with their body mass estimates, if available. For taxa known from multiple localities, the modern and palaeo- latitudes of the type specimen were used for analyses. The relationship between body mass and completeness was further tested by excluding conservation Lagerstätten taxa (which tend to preserve numerous relatively complete specimens of small-sized species), and concentration Lagerstätten taxa, to assess whether these unusually preserved taxa were obscuring any underlying relationship between completeness and body size.

2.2.6. Statistical tests

All statistical analyses were performed in R. Time series plots were produced using the package ggplot2 (Wickham *et al.* 2019) and non-temporal completeness distributions plots were produced using the package vioplot (Adler 2015).

For linear regressions testing the statistical trend in overall patterns of individual time series and correlations between different time series, generalized least-squares regressions (GLS) with a first order autoregressive model (corARMA) were applied to the data using the function gls() in the R package nlme v. 3.1–137 (Pinheiro *et al.* 2018) as the chance of overestimating the statistical significance of regression lines due to temporal autocorrelation is reduced when using GLS. To ensure normality and homoskedasticity of residuals, time series were log-transformed prior to analysis. Likelihood-ratio based pseudo-R^2 values were calculated using the function r.squaredLR() of the R package MuMIn (Bartoń 2018).

The results of fitting GLS autoregressive models to multiple combinations of potential explanatory variables were compared using Akaike's information criterion (AICc), calculated using the function AICc() of the R package qpcR (Spiess 2018). To identify the best combination of variables from those analysed, Akaike weights were calculated using the aic.w() function of the R package phytools (Revell 2019).

Pairwise comparisons of non-temporal range data were performed using non-parametric Mann-Whitney-Wilcoxon tests, which compare the standard deviation and median of datasets. False discovery rate (FDR; Benjamini and Hochberg 1995) adjustments were used to reduce the likelihood of acquiring type I statistical errors over multiple comparisons. Kruskal-Wallis tests, which analyse whether there is a dominance of a specific variable, were used for comparisons of more than two datasets (e.g. subgroups, continents, and depositional settings). GLS models were also used to compare the non-temporal relationship between log-transformed theropod SCM2 and specimen number, body size estimates, latitude and palaeolatitude. The Shapiro-Wilk normality test was used to assess whether theropod latitudinal occurrences have a normal distribution. Hartigans' Dip test was employed using the R package diptest (Maechler 2013) to test the level of bimodality / multimodality of the latitudinal distribution of theropod occurrences.

2.3. Results

2.3.1. Theropod completeness through time

Mean theropod skeletal completeness (Fig. 2.2) ranges between 10% and 48% through the Mesozoic, with notable peaks in the Carnian, Oxfordian-Kimmeridgian and Barremian–Aptian, and lows in the Berriasian and Hauterivian. All stages exhibit relatively wide standard deviations apart from the Bathonian and Berriasian. There is no significant trend in full theropod SCM2 (Table A.2) through time; however, removing either conservation Lagerstätten or all Lagerstätten (Table A.2) taxa does result in a significant negative trend. Mann-Whitney-Wilcoxon tests show there is no significant difference between the distribution of Triassic and Jurassic (W = 1131, p = 0.111), Triassic and Cretaceous (W = 4475, p = 0.5808) and Jurassic and Cretaceous completeness values (W = 18040, p = 0.0506, Fig. A.2). The models that best explain the theropod SCM2 time

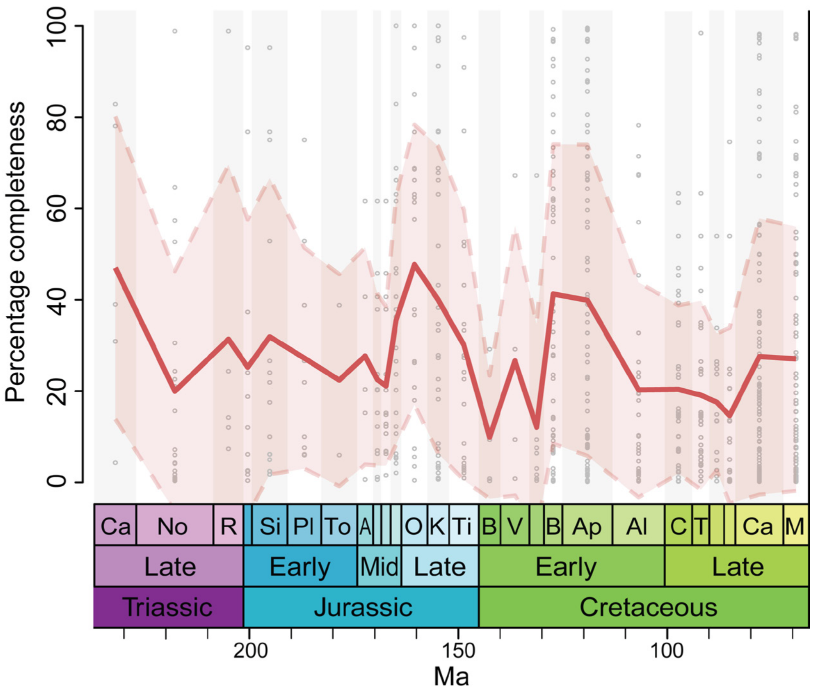


Figure 2.2. Changes in theropod skeletal completeness through time. Mean SCM2 (red line) with one standard deviation from the mean (shaded) and all taxon SCM2 scores per stage (grey circles).

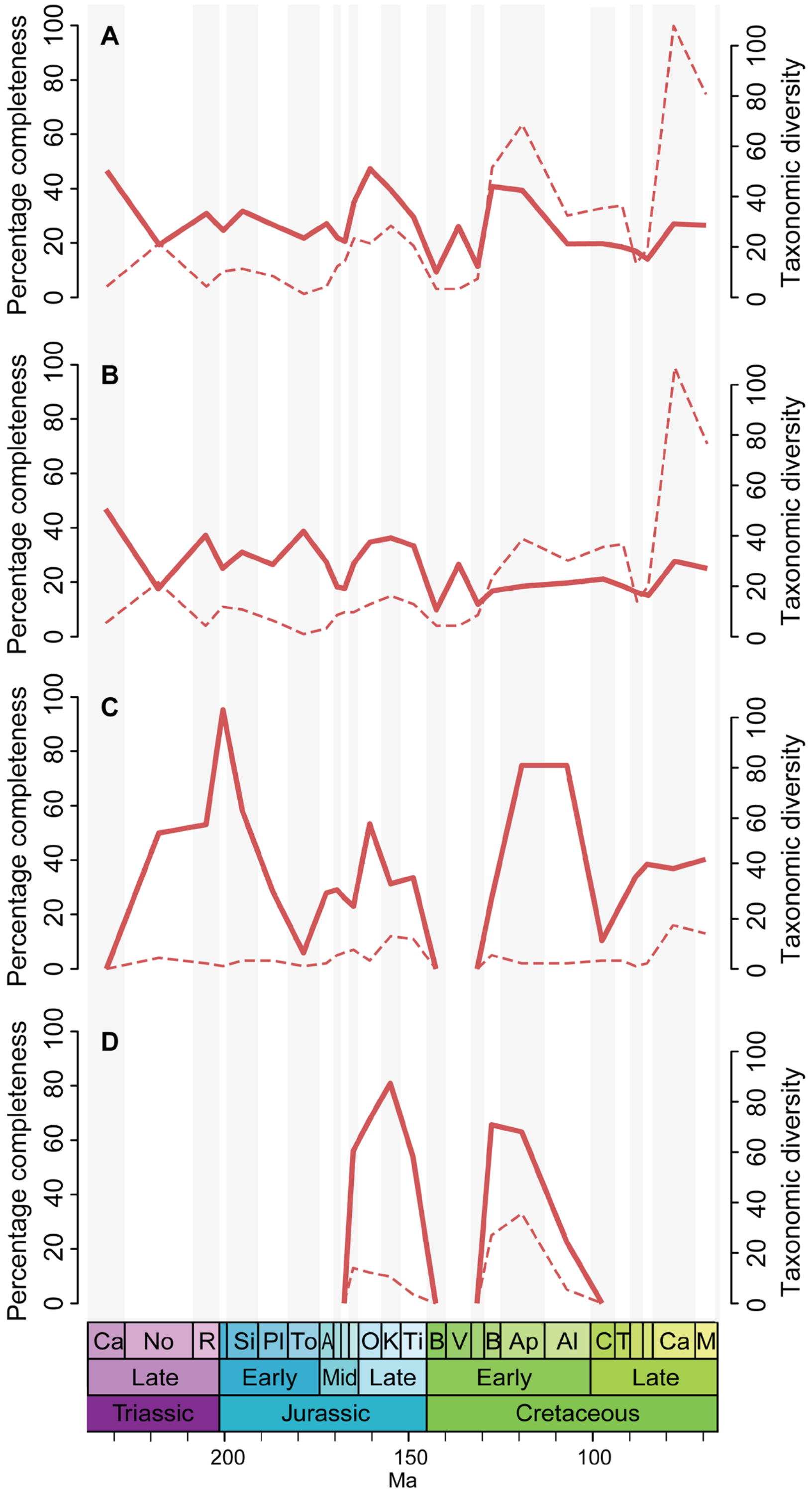


Figure 2.3. Changes in mean theropod SCM2 (red line) and raw taxonomic richness (dashed) through time. A, all data; B, background (non-Lagerstätten); C, concentration Lagerstätten; D, conservation Lagerstätten.

series are those including taxon diversity + sea level, taxon diversity + DBFs, and taxon diversity + DBFs + time bin length as explanatory variables, although all three of these models have weak R^2 values (0.16–0.27) and their coefficients are non-significant (Table A.3).

Table 2.1. Results of pairwise comparisons between theropod SCM2 and taxon richness time series using GLS. Statistically significant results indicated in bold. Abbreviations: T, Triassic; J, Jurassic; K, Cretaceous; Alb., Albian; Car., Carnian; Hett., Hettangian.

Comparison	Slope	t-value	p-value	R2
SCM2 ~ background SCM2	0.8383535	6.452874	**<0.00001**	0.61311125
SCM2 ~ non-conservation Lagerstätten SCM2	1.037552	8.983144	**<0.00001**	0.74077498
SCM2 ~ concentration Lagerstätten SCM2	0.0543674	0.583337	0.5662	0.25960287
SCM2 ~ conservation Lagerstätten SCM2	0.621268	5.365693	**0.003**	0.85500318
SCM2 ~ diversity	0.0919337	1.161717	0.2568	0.0563214
T-J SCM2 ~ T-J diversity	0.154609	1.785366	0.0995	0.06754472
J SCM2 ~ J diversity	0.181148	1.849821	0.0974	0.40019395
J-K SCM2 ~ J-K diversity	0.1962471	2.267968	**0.034**	0.19165969
K SCM2 ~ K diversity	0.2303861	2.953446	**0.0144**	0.46620826
Carn.-Alb SCM2 ~ Carn.-Alb. Diversity	0.1956488	2.523579	**0.0212**	0.21958769
Hett.-Alb. SCM2 ~ Hett.-Alb. Diversity	0.2436681	2.867999	**0.0117**	0.34359297
background SCM2 ~ background diversity	0.086651	1.124616	0.2719	0.05817819

2.3.2. Correlations with theropod taxonomic richness through time

The observed theropod species count gradually rises throughout the Mesozoic, with relative peaks in the Norian, Kimmeridgian and Aptian, and extreme outlying peaks in the Campanian and Maastrichtian (Fig. 2.3A). There is a strong significant trend toward increasing species counts through time (Table A.2). There is no statistically significant correlation between mean theropod SCM2 and observed richness through the entire time series, even when removing Lagerstätten taxa (Table 2.2.1, Fig. 2.3). However, there are weak statistically significant correlations recovered between the Carnian–Albian, Hettangian–Albian, Hettangian–Maastrichtian, and the Berriasian–Maastrichtian. Raw theropod taxonomic richness however does have statistically significant positive correlations with all sampling proxies through time (Table A.4), except time bin length.

2.3.3. Lagerstätten

SCM2 values for concentration Lagerstätten show an extreme peak

Table 2.2. Results of pairwise comparisons between temporal theropod completeness and different fossil record sampling proxies using GLS. Statistically significant results indicated in bold.

Comparison	Slope	t-value	p-value	R2
SCM2 ~ time bin length	0.1649905	1.248291	0.224	0.06382939
SCM2 ~ DBFs	0.041189	0.27681	0.7843	0.00632317
SCM2 ~ DBCs	0.0135006	0.126994	0.9	0.00391274
SCM2 ~ specimen number	0.1037013	2.046558	0.0518	0.14989341
SCM2 ~ PBDB species occurrences	0.0387325	0.542008	0.5928	0.01523463
SCM2 ~ Good's u coverage	0.008923	0.224501	0.8243	0.00530974

completeness in the Hettangian (95%), based on *Syntarsus* (*Coelophysis*) *rhodesiensis*, the sole theropod taxon known from concentration Lagerstätten in this stage. Peaks also occur in the latest Triassic (~50%), Sinemurian (58%), Oxfordian (53%) and Aptian–Albian (75%), while the Mid–Late Jurassic and Late Cretaceous have intermediate completeness levels, and the Toarcian (6%) and Cenomanian (10%) have notably low values (Fig. 2.3C). Theropod conservation Lagerstätten deposits only occur between the Callovian–Tithonian and the Barremian–Albian, all of which, with the exception of the Albian (22%), have relatively high skeletal completeness values, the peak being in the Kimmeridgian (81%) (Fig. 2.3D).

Predictably, values of conservation Lagerstätten SCM2 are significantly higher than those for concentration Lagerstätten (W = 1107, p = 3.53E-05) and background SCM2 (W = 3604, p = 5.61E-15), while taxa from concentration deposits are also significantly different (W = 8879, p = 0.002) than those from background (Fig. A.3). There is a strong significant correlation between conservation Lagerstätten SCM2 with total SCM2 through time (Table 2.2.1) when missing stages are removed.

2.3.4. Correlations with sampling proxies and sea level

There is no significant relationship between mean theropod SCM2 and time bin length (Table 2.2). DBFs and DBCs (Table A.2) show significant trends through time and rise from the Late Triassic onwards, with similar relative peaks

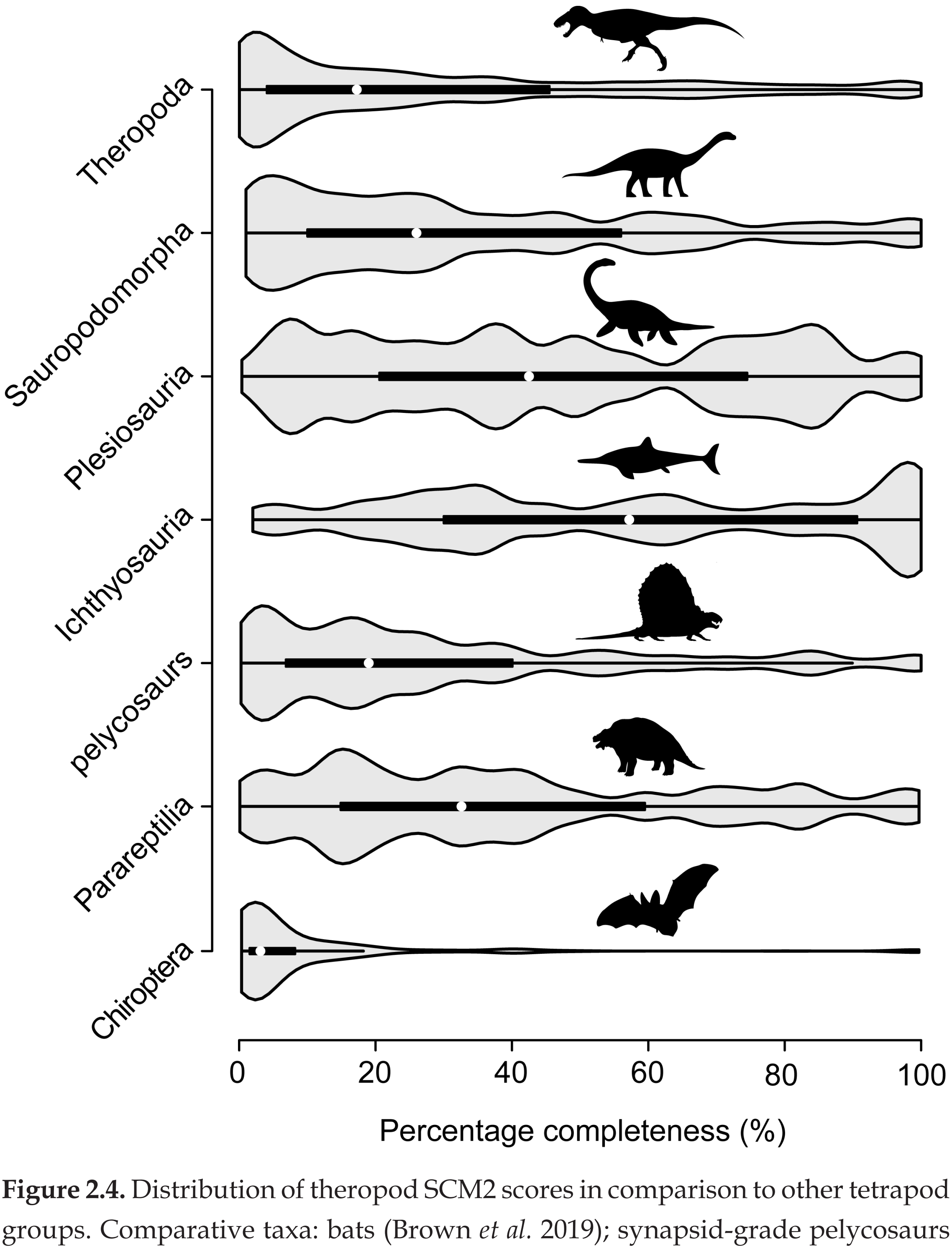


Figure 2.4. Distribution of theropod SCM2 scores in comparison to other tetrapod groups. Comparative taxa: bats (Brown *et al.* 2019); synapsid-grade pelycosaurs (Brocklehurst and Fröbisch 2014); parareptiles (Verrière *et al.* 2016); ichthyosaurs (Cleary *et al.* 2015); plesiosaurs (Tutin and Butler 2017); and sauropodomorphs (Mannion and Upchurch 2010a). Silhouettes used include work by S. Hartman, and D, Bogdanov (see http://phylopic.org/ for full licensing information).

Table 2.3. Results of comparisons of the population median and distribution of theropod completeness values in comparison to other tetrapods, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold. Abbreviations: T, Triassic; J, Jurassic; K, Cretaceous; NC-L, non-conservation Lagerstätten.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Theropod SCM2	Chiroptera SCM2	147953	**9.38E-35**	**1.03E-33**
Theropod SCM2	Parareptile SCM2	12611	**0.000158**	**0.000289**
Theropod SCM2	Pelycosaur SCM2	20065.5	0.210749	0.231824
Theropod SCM2	Ichthyosaur SCM2	10848	**4.05E-17**	**2.23E-16**
Theropod SCM2	Plesiosaur SCM2	15509.5	**3.10E-11**	**1.14E-10**
Theropod SCM2	Sauropodomorph SCM2	32648.5	**0.000668607**	**0.001050668**
Theropod NC-L SCM2	Sauropodomorph SCM2	25315	**3.71E-07**	**1.02E-06**
T-J Theropod SCM2	T-J Sauropodomorph SCM2	4402.5	**0.001515835**	**0.002084273**
T-J Theropod NC-L SCM2	T-J Sauropodomorph SCM2	3494	**4.70E-05**	**0.000103377**
K Theropod SCM2	K Sauropodomorph SCM2	12947	0.372658455	0.372658455
K Theropod NC-L SCM2	K Sauropodomorph SCM2	9982	**0.020704484**	**0.025305481**

in the Late Jurassic, the Aptian–Albian and the latest Cretaceous (Fig. A.4A-B). There is no significant correlation between theropod SCM2 and DBFs and DBCs through time (Table 2.2). Furthermore, theropod SCM2 does not show a significant correlation with either specimen numbers or PBDB occurrences per stage (Table 2.2; Fig. A.4C-D), which both show significant positive trends through time (Table A.2). However, there is a very weak but statistically significant correlation between non-temporal SCM2 score and specimen numbers per taxon ($R^2 = 0.08$, $p = <0.0001$). Good's u sampling coverage, which exhibits no significant trend through time (Table A.2), and has troughs in the Rhaetian, Toarcian and Aalenian, and peaks in the earliest Jurassic, Late Jurassic, and middle and latest Cretaceous (Fig. A.4E), also lacks a significant correlation with theropod SCM2 (Table 2.2). Sea level gradually rises in a stepwise manner throughout the time interval, reaching a high in the Late Cretaceous, and has no significant correlation with SCM2 through time ($R^2 = 0.04$, $p = 0.33$).

2.3.5. Comparison to other tetrapod fossil records

Theropod completeness values range from just above 0 to 100%, with

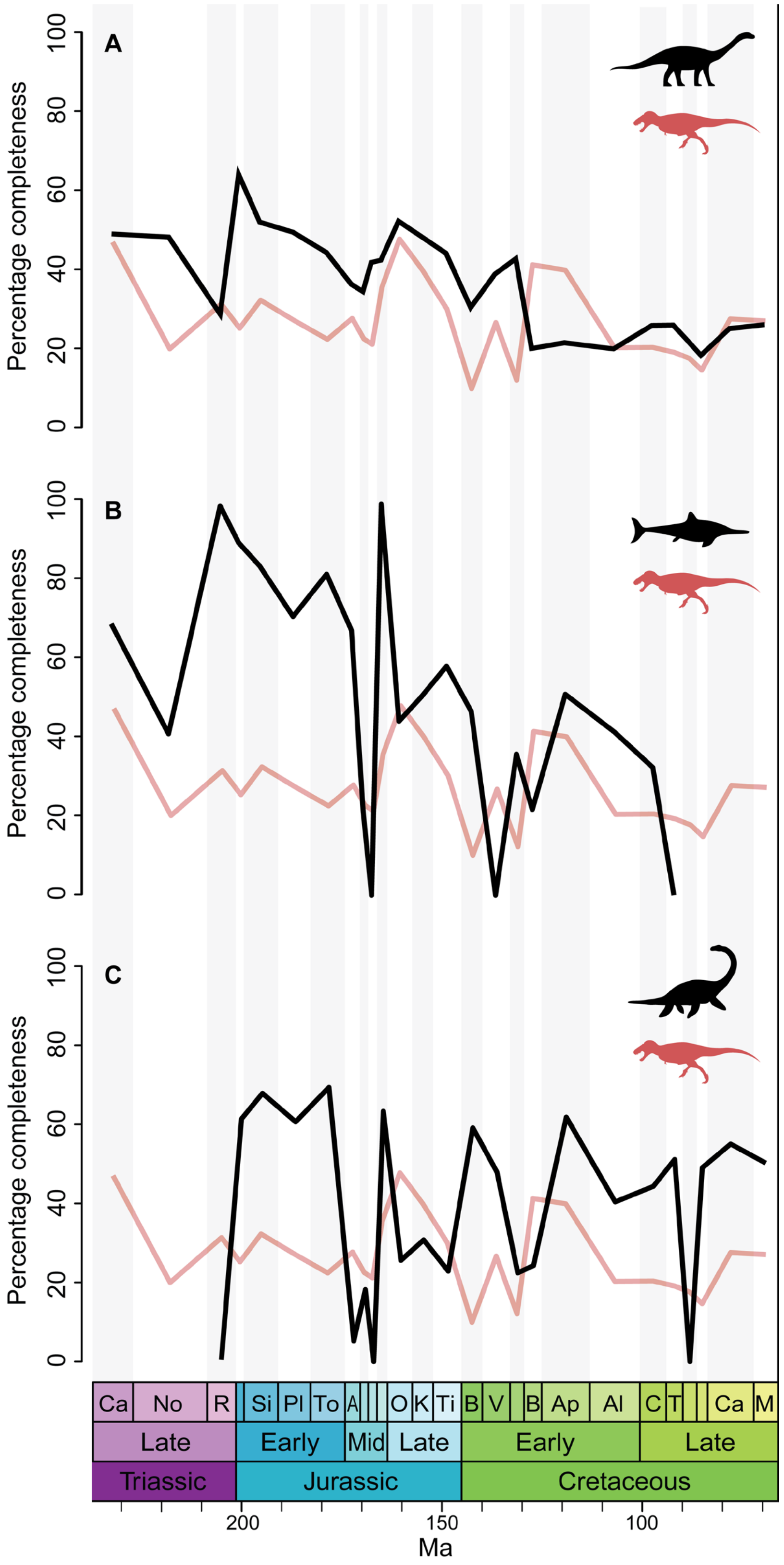


Figure 2.5. Changes in Mesozoic tetrapod mean SCM2 through time. A, sauropodomorphs (Mannion and Upchurch 2010a); B, ichthyosaurs (Cleary *et al.* 2015); C, plesiosaurs (Tutin and Butler 2017). Mean theropod SCM2 (red line) in background for comparison. Silhouettes used include work by S. Hartman and D. Bogdanov (see http://phylopic.org/ for full licensing information).

Table 2.4. Results of pairwise comparisons between the temporal completeness of theropods and other Mesozoic tetrapods using GLS. Statistically significant results indicated in bold. Abbreviations: T, Triassic; J, Jurassic; K, Cretaceous; NC-L, non-conservation Lagerstätten; Sauro., Sauropodomorph; Thero., Theropod.

Comparison	Slope	t-value	p-value	R2
Theropod SCM2 ~ Ichthyosaur SCM2	0.1979274	0.933338	0.3637	0.08656337
Theropod SCM2 ~ Plesiosaur SCM2	-0.06148	-0.41409	0.6834	0.01528748
Theropod SCM2 ~ Sauropodomorph SCM2	0.287613	1.397811	0.175	0.06697955
T-J Theropod SCM2 ~ T-J Sauropodomorph SCM2	0.4715709	1.196002	0.2548	0.04322218
J Theropod SCM2 ~ J Sauropodomorph SCM2	0.2766657	0.5464329	0.5981	0.23139656
J-K Theropod SCM2 ~ J-K Sauropodomorph SCM2	0.2565739	1.119904	0.2754	0.06333257
K Theropod SCM2 ~ K Sauropodomorph SCM2	-0.552647	-1.237971	0.244	0.14381403
NC-L Thero. SCM2 ~ Sauro. SCM2	0.4684724	3.505013	**0.0018**	0.27018894
T-J NC-L Thero. SCM2 ~ T-J Sauro. SCM2	0.6127646	2.916237	**0.0129**	0.3998167
J NC-L Thero. SCM2 ~ J Sauro. SCM2	0.4561594	1.635985	0.1363	0.19013814
J-K NC-L Thero. SCM2 ~ J-K Sauro. SCM2	0.4205787	2.885536	**0.0088**	0.25237022
K NC-L Thero. SCM2 ~ K Sauro. SCM2	-0.167911	-0.636408	0.5388	0.17286784

a median completeness of 17%, which is similar to the median and range of pelycosaur-grade synapsids and sauropodomorphs (Fig. 2.4). Mann-Whitney-Wilcoxon tests reveal theropod SCM2 distribution is statistically no different to pelycosaurs, but is significantly lower in comparison to the sauropodomorph distribution (Table 2.3). Theropods have a significantly less complete skeletal record than Parareptilia, and the marine ichthyosaurs and plesiosaurs (Fig. 2.4, Table 2.3).

Time series comparisons show no significant correlation between theropod and sauropodomorph (Fig. 2.5A), ichthyosaur (Fig. 2.5B), or plesiosaur (Fig. 2.5C) SCM2 through time (Table 2.4). However, when removing taxa known from conservation Lagerstätten, a significant relationship is identified between the theropod and sauropodomorph curves (Table 2.4). A stronger and statistically significant result is found during just the Triassic–Jurassic, even though mean stage-level sauropodomorph completeness is consistently higher (Fig. 2.5A) and sauropodomorph median completeness is significantly higher (Table 2.3) than that of theropods during this interval. In the Cretaceous, mean stage level sauropodomorph completeness drops (also significant drop in sauropodomorph median completeness: W = 5256, p = 0.0001) and the significant differences in

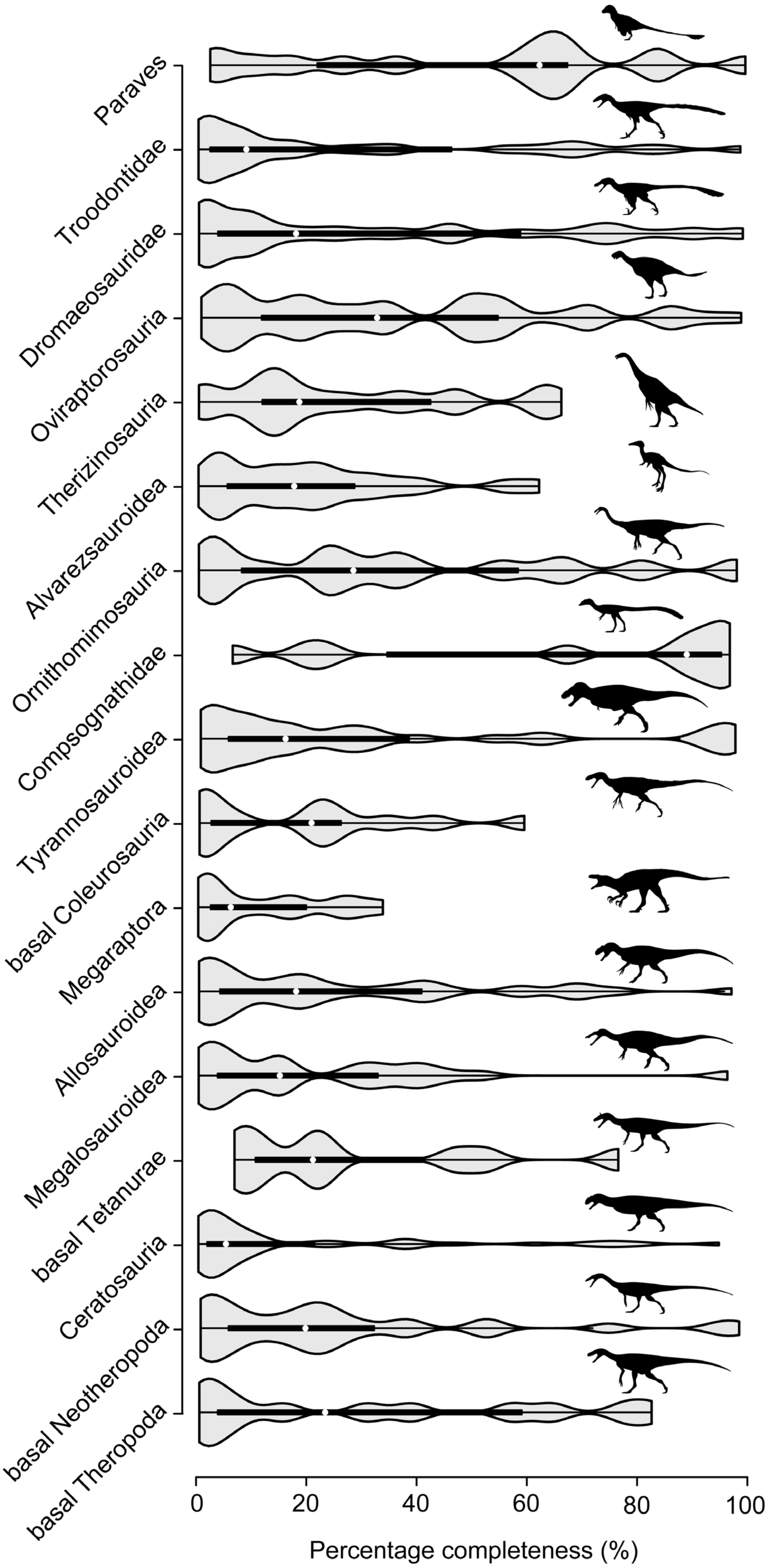

Paraves
Troodontidae
Dromaeosauridae
Oviraptorosauria
Therizinosauria
Alvarezsauroidea
Ornithomimosauria
Compsognathidae
Tyrannosauroidea
basal Coleurosauria
Megaraptora
Allosauroidea
Megalosauroidea
basal Tetanurae
Ceratosauria
basal Neotheropoda
basal Theropoda
0
20
40
60
80
100
Percentage completeness (%)

Figure 2.6. Distribution of theropod SCM2 scores between different theropod subgroups. 'Paraves' indicates non-deinonychosaurian Paraves. Silhouettes used include work by S. Hartman, T Michael Keesey, T. Tischler, J. Conway, Funkmonk, and M. Martyniuk (see http://phylopic.org/ for full licensing information). From top to bottom, silhouettes represent: *Scansoriopteryx heilmanni, 'Troodon' formosus, Velociraptor mongoliensis, Oviraptor philoceratops, Nothronychus mckinleyi, Shuvuuia deserti, Gallimimus bullatus, Compsognathus longipes, Tyrannosaurus rex, Stokesosaurus clevelandi, Australovenator wintonensis, Allosaurus fragilis, Baryonyx walkeri, Cryolophosaurus ellioti, Majungasaurus renatissimus, Coelophysis, Herrerasaurus ischigualastensis.*

median completeness and distribution of scores between them and theropods are lost (Table 2.3).

2.3.6. Theropod subgroups and body size

Compsognathidae have the highest median SCM2 (89%) of any subgroup by a substantial margin (Fig. 2.6), and, like non-deinonychosaurian Paraves, have a markedly different distribution to all other taxonomic groups. Compsognathids have the highest lower quartile and upper quartile completeness compared to any other subgroup. Following these strongly outlying group distributions, Oviraptorosauria (28%) and Ornithomimosauria (33%) have the next highest median SCM2. All remaining subgroups have median SCM2 of < 25%. Basal Tetanurae, Megaraptora, basal Coelurosauria, Alvarezsauroidea and Therizinosauria are all notable for their relatively low completeness ranges and lack of completely known taxa (Fig. 2.6). Ceratosauria and Troodontidae also have particularly low median completeness values. Megaraptora has by far the least complete record of any subgroup, with the second lowest median (5.98%), lowest upper quartile, and a high of only 34%. Kruskall-Wallis tests suggest the variance of completeness distributions is dominated by one or more subgroups ($H = 47.786$, $p = 5.132E-05$). Table A.5 displays the results of pairwise Mann-Whitney-

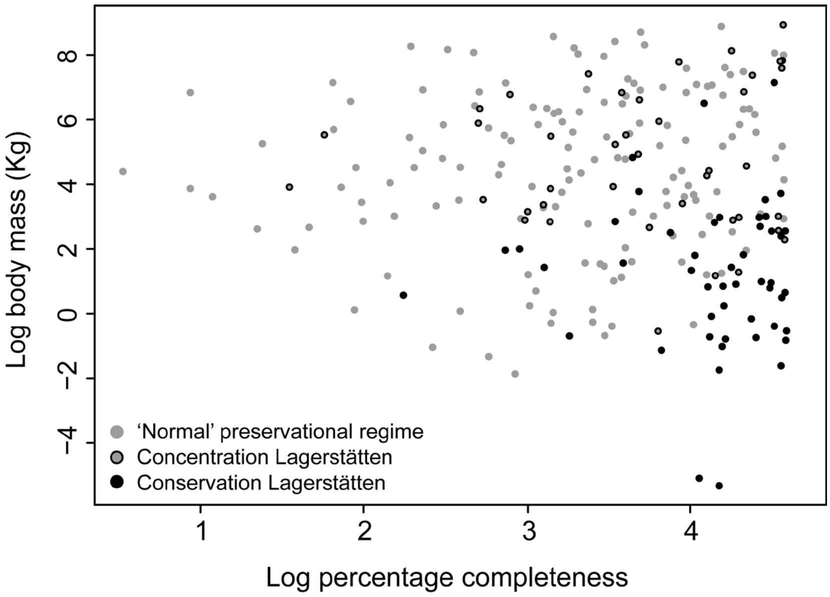


Figure 2.7. Log-transformed scatter distribution of SCM2 values in relation to body mass estimates, primarily sourced from Benson *et al.* (2018). Point colours correspond to different preservational regimes: 'normal' (grey), concentration Lagerstätten (grey with black outline), conservation Lagerstätten (black).

Wilcoxon tests between each subgroup. Compsognathidae is consistently found to have significantly higher SCM2 scores than almost all other subgroups.

GLS time series correlations show the mean temporal SCM2 time series for basal Theropoda, Allosauroidea, Compsognathidae, Alvarezsauroidea, Oviraptorosauria, and non-deinonychosaurian Paraves exhibit statistically significant relationships with total SCM2 (Table A.6, Fig. A.5).

No significant relationship is recovered between theropod SCM2 and body mass estimates ($R^2 = 0.017$, $p = 0.144$) for individual taxa from GLS modelling, even when conservation Lagerstätten taxa ($R^2 = 0.015$, $p = 0.129$) are removed, or when concentration Lagerstätten taxa are additionally removed ($R^2 = 0.02$, $p = 0.09$) (Fig. 2.7).

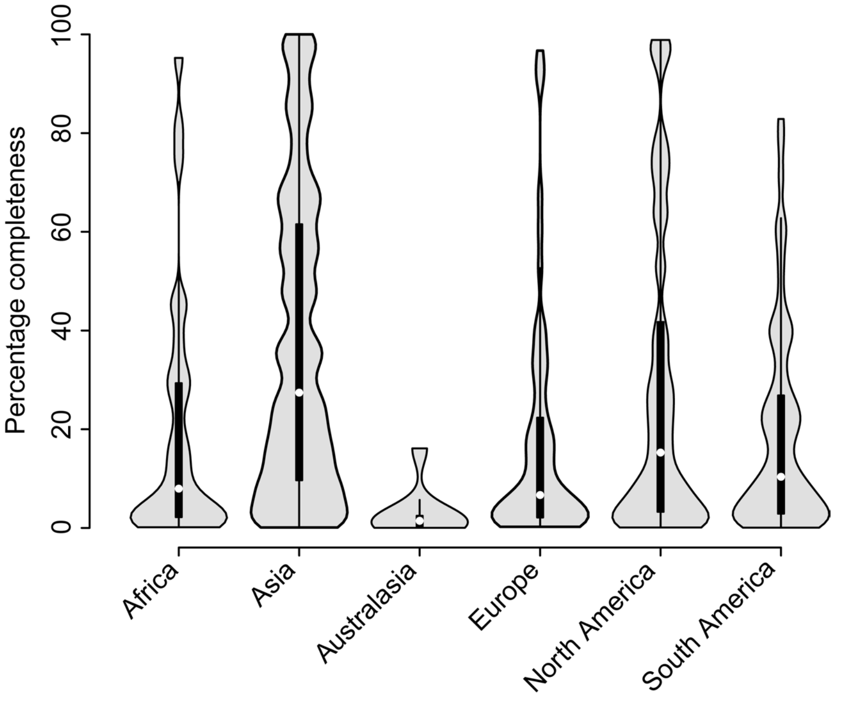


Figure 2.8. Distribution of theropod SCM2 scores between different continents.

2.3.7. Geographical completeness

Taxa from the modern northern hemisphere have a statistically higher distribution of SCM2 values in comparison to those from the southern hemisphere (W = 18724, p = 0.007; Fig. A.6). Kruskall-Wallis tests suggest the variance of completeness distributions between continents is strongly dominated by one or more of them (*H* = 48.929, p = 2.294e09). The range of SCM2 values varies substantially between different continents (Fig. 2.8; Table A.7): Asia has the most complete theropod specimens, with significantly higher SCM2 ranges in comparison to all other continents. North America, South America, Africa and Europe have sequentially lower median values but all share statistically similar distributions of SCM2 scores. Half of European theropods have SCM2 values below 25%. Australasia has the least complete record of any continent, with only eight constituent taxa in this study, none of which are more than 17% complete and a median SCM2 value of 1.45%.

Asia's theropod record extends for the longest geological timespan of any continental record with taxa derived from 21 different geological stages, while

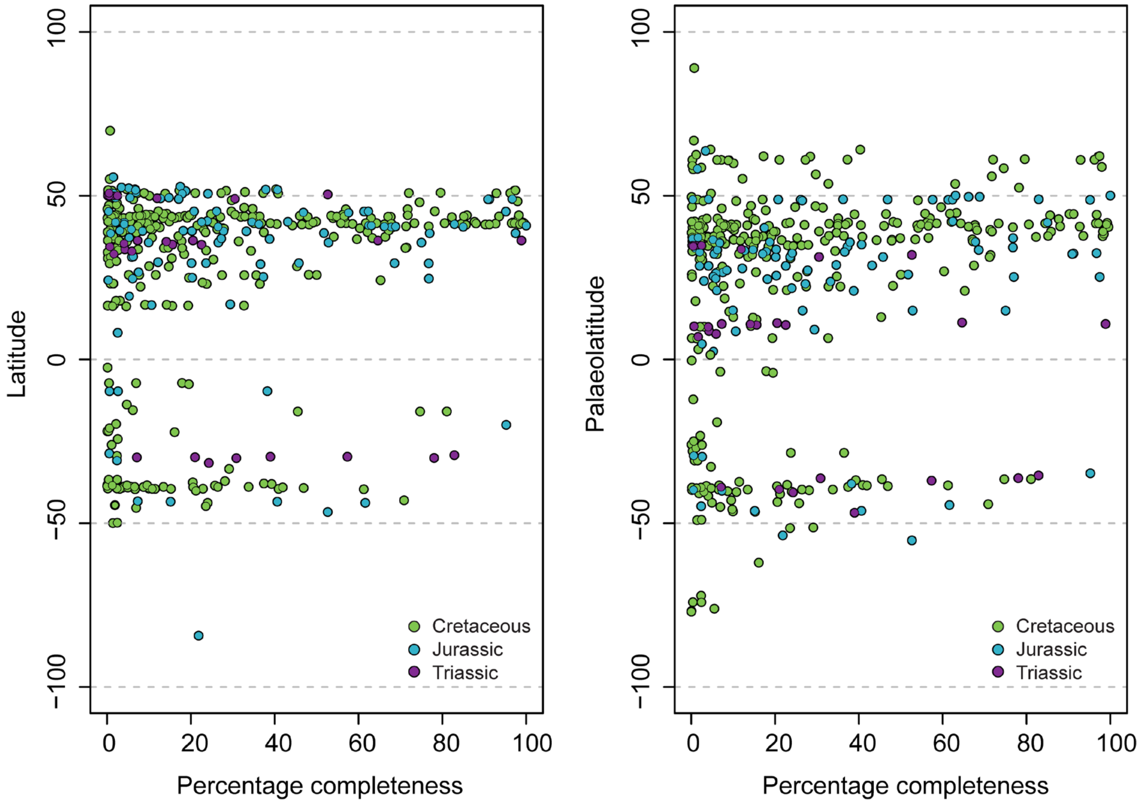


Figure 2.9. Scatter distribution of SCM2 values in relation to geographical coordinates. A, modern latitude. B, palaeolatitude. Point colours correspond to geological age: Triassic (purple), Jurassic (blue), Cretaceous (green).

predictably Australasia has the lowest number of represented geological stages (5) (Fig. A.7). GLS time series correlations reveal that Asian and European SCM2 have strong positive correlations with total theropod SCM2, as well as significant correlations with their component taxonomic richness through time (Table A.8), unlike all other continents.

Figure 2.9 shows modern and palaeolatitudinal distributions of theropod taxon finds in relation to their SCM2 scores. Taxon occurrences are unevenly situated within the northern hemisphere, heavily concentrated from around ~20–55°, but with only one taxon above ~56° N. Here, higher completeness values generally become more frequent at higher latitudes. Towards the equator both occurrences and levels of completeness substantially drop, with only nine occurrences between 10° N and 10° S, and a peak SCM2 score of 38%. Between ~20–

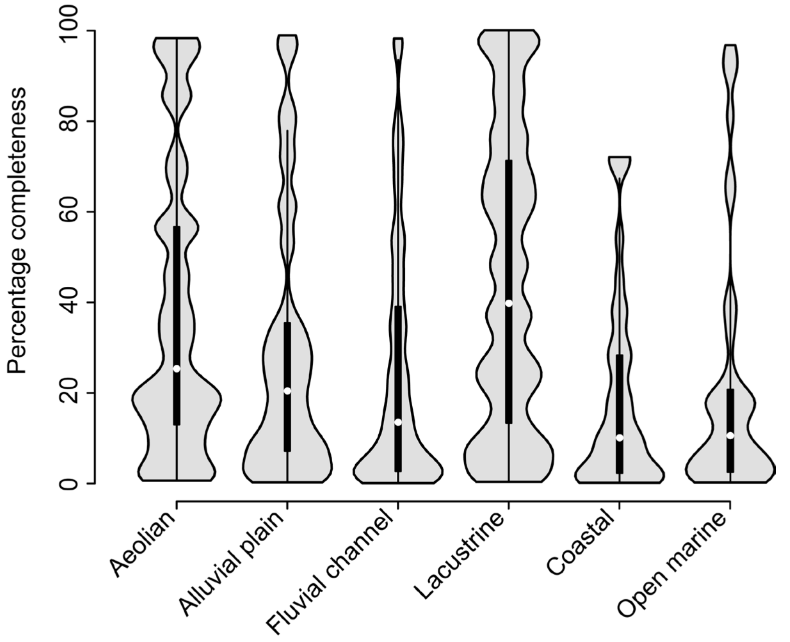


Figure 2.10. Distribution of theropod SCM2 scores between different depositional settings.

50° S there is much less data but a similar peak in occurrences and completeness to the northern hemisphere. Statistically significant Shapiro-Wilk normality and Hartigans' Dip tests suggest the latitudinal density distribution is non-normal ($W = 0.72$, $p < 2.2E\text{-}16$) and non-unimodal ($D = 0.04$, $p = 9.666E\text{-}06$) respectively. Further there is a weak statistically significant positive correlation between latitude and SCM2 value ($R^2 = 0.04$, $p = 0.017$). In contrast, palaeolatitudinal coordinates show there is a more even spread of theropod occurrences within an ancient context (Fig. 2.9B), but the palaeolatitudinal density distribution is still significantly non-normal ($W = 0.82$, $p < 2.2E\text{-}16$) and non-unimodal ($D = 0.04$, $p = 6.631E\text{-}06$). Higher and lower northern palaeolatitudes are better represented, but there is still poor equatorial, polar and general southern representation and completeness.

2.3.8. Sedimentary and depositional setting

There is no significant difference between the range of completeness values of taxa from either siliciclastic or carbonaceous sedimentary settings ($W = 8295.5$, $p = 0.32$; Fig. A.8). On the other hand a statistically significant difference is found between the completeness range of theropods from terrestrial and marine deposits, with taxa from the latter being less complete ($W = 8995.5$, $p = 0.003$; Fig. A.9). Kruskall-Wallis tests suggest one or more settings significantly dominate the distribution of depositional environments ($H = 48.262$, $p = 3.141\text{E-}09$). Lacustrine deposits exhibit statistically higher SCM2 values than all other depositional settings, with the exception of aeolian deposits (Fig. 2.10; Table A.9). The latter has the next highest range of values but a similar median value to taxa from alluvial plains. Fluvial channels, coastal and open-marine settings are sequentially the depositional settings with the least complete specimens, and all exhibit statistically similar completeness ranges (Fig. 2.10).

Figure A.10 shows mean temporal SCM2 based solely on taxa from the six depositional categories. Aeolian and open marine SCM2 curves are the only environmental time series that lack a statistically significant relationship with total SCM2 through time (Table A.10) in GLS correlations.

2.4. Discussion

2.4.1. Comparative completeness

The range of skeletal completeness values observed indicates that the theropod fossil record is one of the poorest of previously assessed tetrapod groups (Fig. 2.4). The bulk of taxa are ~5–10 % complete, numbers of taxa sharply drop above 20% SCM2, with a very gradual but steady decline towards increasing completeness levels. This low level of skeletal completeness for such a well-known group can potentially be explained by the ability of palaeontologists to recognise synapomorphic characters of theropods based on very little fossil material. It could also be explained by a heightened scientific interest in theropods, producing more taxa named from material unlikely to be intensely studied in other tetrapod groups (Benton 2008, 2010). Verrière *et al.* (2016) examined only genus-level taxa of parareptiles, and this may potentially explain the higher completeness of parareptiles in relation to all other terrestrial groups.

When conservation Lagerstätten taxa are excluded from the theropod time series, a significant positive correlation between sauropodomorph and theropod completeness is recovered (Table 2.4). The lack of correlation when conservation Lagerstätten are included emphasises how preservational or ecological exclusion of the large bodied sauropodomorphs from such deposits could be limiting our interpretations of their fossil record. As there are almost no sauropodomorph taxa found in conservation Lagerstätten their fossil record shows differences from other clades that are richly represented in such deposits. Thus, conservation Lagerstätten create a strong signal in the theropod data that obscures an underlying correlation with sauropodomorph completeness. This underlying correlation probably reflects the groups' cohabitation of generally similar palaeoenvironments (Butler and Barrett 2008) and the many overlaps in geographical localities, as well as likely subjection to similar sampling standards through historical time on a global scale (Upchurch *et al.* 2011; Starrfelt and Liow 2016), although on regional scales theropod fossil sampling has been suggested to be potentially heightened in comparison to other dinosaurs (Farlow 1976, 1993; McGowan and Dyke 2009; Horner *et al.* 2011). The non-conservation Lagerstätten theropod and sauropodomorph time series have stronger statistical correlations with each other during the Triassic–Jurassic but diverge in the Cretaceous.

The non-temporal range of sauropodomorph completeness scores is significantly higher than theropods (Table 2.3). Cretaceous data considered alone lacks this significant difference (Table 2.3). However, removing theropod conservation Lagerstätten from this comparison reduces the median and upper quartile range enough to create a statistically significant difference between the Cretaceous records, like all other non-temporal comparisons between the groups. This is intriguing as it suggests that under similar preservation regimes, theropod specimens are significantly less complete than sauropodomorph specimens.

Again, this illustrates how the theropod fossil record is positively influenced by the presence of conservation Lagerstätten.

Following this, the consistently higher levels of sauropodomorph completeness might be caused by ecological or preservational differences between them and theropods. The higher population numbers of the herbivorous and often gregarious (Lockley *et al.* 1986; Upchurch *et al.* 2004; Myers and Fiorollo 2009) sauropodomorphs in Mesozoic ecosystems, as well as their generally more robust skeletons, likely enhances their preservation potential relative to theropods. Large carnivorous theropods would also be expected to be less abundant than their herbivorous contemporaries (Farlow 1993; White *et al.* 1998; Farlow and Planka 2002; Carbone *et al.* 2011) based on typical extant mammalian predator-prey relationships, possibly reducing their preservation potential, although different theropod groups are much more abundant under particular local fossil regimes or within certain localities (Leonardi 1989; Horner *et al.* 2011; Läng *et al.* 2013), and between different environments (Sales *et al.* 2016; Frederickson *et al.* 2018). A drop in sauropod diversity across the Jurassic-Cretaceous boundary (Mannion *et al.* 2011), an environmental preference change from coastal to more depositionally distant inland settings (Mannion and Upchurch 2010b), and a reduction of inland deposits in Europe and North America (Mannion and Upchurch 2011) are possible explanations for the drop in completeness of Cretaceous sauropodomorphs when compared to earlier time intervals. Though our results show inland settings generally preserve more complete theropod specimens, there is no significant difference in the distribution of completeness scores of theropods from coastal settings in comparison to fluvial and alluvial settings (Table A.9). Differences may be exacerbated in the sauropodomorph record. These reasons might explain the lack of correlation between the two time series in the Cretaceous, as well as the drop in sauropodomorph completeness to levels comparable to theropods.

If SCM and CCM generally depict similar completeness signals through time (Mannion and Upchurch 2010a; Tutin and Butler 2017), then comparisons can be drawn between the SCM of theropods and completeness estimates for other Mesozoic terrestrial taxa for which only CCM has been calculated. The non-avian theropod fossil record shows similarities to fluctuations in pterosaur and bird CCM through time. All have time series that begin with relatively high completeness levels, have dramatic reductions in completeness at the Jurassic–Cretaceous boundary, a reduction in completeness and diversity from the Aptian to Albian that reflects the influence of Lagerstätten (see below), and a Maastrichtian fossil record that is taxonomically diverse but has relatively low completeness values (Brocklehurst *et al.* 2012; Dean *et al.* 2016). However, theropod (SCM2) and pterosaur (CCM2) time series reveal no significant correlation for all time bins ($R^2 = 0.13$, $p = 0.08$) or solely the Triassic-Jurassic ($R^2 = 0.17$, $p = 0.99$), and there is also no correlation between theropod (SCM2) and bird (CCM2) time series ($R^2 = 0.05$, $p = 0.8$). However, differences between these time series may have been exacerbated by the use of differing completeness metrics. On the other hand, similarly to the significant similarities in the sauropodomorph and theropod SCM2 records, the sauropodomorph and pterosaur CCM2 time series are significantly correlated during the Triassic-Jurassic (Dean *et al.* 2016), hinting at a potential common causal control of completeness for Triassic-Jurassic terrestrial taxa. Furthermore, like the non-avian theropod record, bird CCM is correlated with observed taxonomic richness through the Jurassic-Cretaceous. Non-avian theropods and birds also show a similar distribution of geographical occurrences and relative continental completeness, with northern landmasses yielding more taxa than the southern, Asia having the most rich and complete (CCM) record, North and South America having relatively abundant but typically less complete records, and there are a few finds in Australia and Antarctica (see Brocklehurst *et al.* 2012). The similarities between the non-avian theropod and bird records are unsurprising given that the latter are direct descendants of the former, considering their similar life histories, ecologies and environmental preferences (Erickson *et al.* 2009; O'Connor *et al.* 2011b), as well as the overlapping geological occurrences. Dean *et al.* (2016) concluded that the similar flight-adapted body plans and fragility of bird and pterosaur skeletons explained their similar patterns of completeness. Likewise, many non-avian theropod groups (e.g. coelurosaurs) had comparable body plans to Mesozoic birds and so at least in part experienced similar preservation biases.

The global similarities highlighted in the theropod, sauropodomorph, avian and pterosaur fossil records could be explained by large scale common cause. Instead of preservational issues dependant on ecological or biological affinities, these temporal similarities could well represent time bins of genuine higher and poorer quality for all terrestrial tetrapods regardless of taxonomic group, most likely controlled by geological and taphonomic histories. Therefore, major components of the terrestrial tetrapod faunas may have generally similar fossil records governed by geological processes and sampling availability. This is somewhat supported, given that the completeness distributions of all terrestrial groups are fundamentally different to the marine Plesiosauria and Ichthyosauria records. As far as can be concluded from our study and previous discussion (Rook *et al.* 2013; Cleary *et al.* 2015; Tutin and Butler 2017), there are fundamental differences between the marine and terrestrial fossil records and tetrapods have consistently higher SCM and CCM values in the marine realm.

2.4.2. Depositional biases

Our results suggest that the best preserved theropod skeletons are those from lacustrine and aeolian deposits, where lack of transport and rapid burial ensured skeletal material was protected from scavenging, weathering, disarticulation and decay. Lacustrine environments are associated with conservation Lagerstätten deposits in the Santana, La Huerguina (Las Hoyas), and Yixian formations, where unique lake conditions (Briggs *et al.* 1997; Gupta *et al.* 2008; Martill et al, 2008; Pan *et al.* 2012) and burial under volcanic ash (Zhou *et al.* 2003; Fürsich *et al.* 2007; Zhou 2014) aided preservation. The high completeness of aeolian deposits likely derives from formations like the Ejinhoro, Bayan Mandahu and Djadokhta of the Gobi Desert, where individuals were rapidly entombed in situ (Jerzykiewicz *et al.* 1993) by sandstorms enabling fully articulated (non-soft tissue) three-dimensional specimens to be preserved in particular horizons. Alluvial, fluvial, coastal and open marine depositional settings generally have incrementally fewer relative occurrences of high completeness, which can likely be attributed to the levels of transportation skeletons underwent before burial. A large quantity of concentration Lagerstätten deposits occur within alluvial plains, which seems to result in the higher numbers of taxa in the 30–40% completeness range for this preservation regime.

44% of taxa in our dataset are derived from fluvial channel deposits and there is a strong statistically significant correlation of fluvial channel SCM2 and total SCM2 (Table A.10). This supports the unsurprising idea that a large component of our understanding of the theropod fossil record is derived from fluvial depositional settings. Although this is likely the case for most terrestrial fossils, as fluvial deposits are commonly preserved, it highlights our reliance on a regime that naturally transports and winnows its sedimentary load, leading to abrasion and disarticulation of skeletal material within it. White *et al.* (1998) found a significant statistical relationship between fluvial channel deposits and lower quality dinosaur fossils in the Hell Creek Formation. Previous studies (Brocklehurst *et al.* 2012; Dean *et al.* 2016) have mentioned the unusually fragmentary nature of the fossil record for other tetrapod groups in the Maastrichtian. For theropods, the Maastrichtian and the preceding Campanian are marked by taxon occurrences that are significantly higher in number than other geological stages but have fundamentally unremarkable levels of skeletal completeness. The Campanian and Maastrichtian alone contain 34% (156/455) of all theropod taxa in our data set, but many species from these intervals are named from relatively incomplete material. One potential driver of this could be the substantial corresponding rise in taxa derived from fluvial channels within the latest Cretaceous (88/156 Campanian and Maastrichtian taxa, 56%) (Fig. A.10C), in comparison to all pre-Campanian stages (105/305 taxa, 34%). Increased preservation within these erosive regimes could at least partially explain the relatively poor levels of completeness. The increased number of occurrences within fluvial settings predominantly corresponds with a few formations in North America, such as the Dinosaur Park (14/15 fluvial channel taxa), Hell Creek (6/6 fluvial channel taxa), and Horseshoe Canyon (5/8 fluvial channel taxa) formations, and also with the Nemegt Formation (17/18 fluvial channel taxa) in Mongolia, and the Iren Dabasu Formation (5/5 fluvial channel taxa) in China. Eliason *et al.* (2017) even noticed a fundamental change to fluvial dominated Late Cretaceous deposits within conservation Lagerstätten.

In addition to the fluvial signal, the significant correlation between lacustrine, alluvial plain and coastal environment SCM2 and total SCM2 (Table A.10) suggests they all significantly impact our understanding of the theropod fossil record. This is however not the case for the aeolian and open marine settings. This again is a foreseeable outcome as these two environments are the most unlikely to consistently preserve theropod fossils.

In theory large scale sea level fluctuations could control the amount of fossil material preserved within different time bins due to variation in continental flooding (Butler *et al.* 2010). The lack of any significant correlation between SCM2 and sea level changes suggests sea level is poorly supported as a large scale control on the theropod fossil record. However, sea level does contribute to the model that best explains changes in SCM2 through time, along with raw diversity (Table A.2). This could indicate some level of sea level influence on specimen completeness but has relatively low explanatory power.

2.4.3. Biological and ecological biases

The wide differences between the non-temporal SCM2 ranges of different theropod subgroups (Fig. 2.6) suggests skeletal completeness may in some ways be influenced by the different abundances, ecologies, body sizes and environmental preferences of different groups of theropods.

Megaraptora has one of the lowest median completeness of any group and no known taxa over 34% complete, which could be explained by generally low number of specimens known for each taxon (75% of taxa known from single specimens), and their common recovery from fluvial channel deposits (67% of taxa) (Table A.11). Its poor record probably also stems from its relatively recent recognition as a group (Benson *et al.* 2010a) and unclear phylogenetic relationships (Porfiri *et al.* 2014; Novas *et al.* 2016; Porfiri *et al.* 2018). Continued finds in relatively unexplored areas of South America and Australasia will likely boost its currently poor skeletal record.

Ceratosaurians and troodontids are known from a wide range of completeness scores but comparatively low median SCM2 (Fig. 2.6) resulting in relatively poor records. 71% of ceratosaurians and 74% of troodontids in our dataset are known from singleton specimens (Table A.11). Though there is some evidence of troodontid rarity within some palaeoecosystems (White *et al.* 1998; Horner *et al.* 2011), some localities like Dinosaur Provincial Park, Alberta, Canada, commonly produce troodontid teeth (Currie and Koppelhus 2015) but limited skeletal material, suggesting locality specific taphonomic biases (Brown *et al.* 2013) may have influenced the relatively poor completeness of their record. The poor ceratosaurian record may derive from a narrow environmental preference. Sales *et al.* (2016) demonstrated that abelisaurid specimens only had a positive association with terrestrial regimes, meaning relatively few abelisaurid fossils were transported to coastal environments, and therefore, they may have more commonly occupied setting relatively far inland. In our dataset, 63% of ceratosaur taxa are found in fluvial channels and 21% are from alluvial plains.

Basal tetanurans, alvarezsauroids, and therizinosaurians all have relatively poor and statistically similar completeness distributions that lack highly complete taxa. Their records may represent a genuine rarity in ancient ecosystems, potentially limited environmental preferences (Butler and Barrett 2008), or a scarcity of finds (Bell *et al.* 2012; Currie and Koppelhus 2015), as 50% of basal tetanurans, 71% of alvarezsauroids, and 63% of therizinosaurians are known from single specimens (Table A.11).

Unlike almost all other theropod groups, the distinctive spinosaurid megalosauroids can be regarded, with some certainty, to have had at least partially piscivorous diets (Charig and Milner 1997; Rayfield *et al.* 2007; Cuff and Rayfield 2013; Sales and Schultz 2017) and relatively specific environmental preferences for fluvial and coastal (Amiot *et al.* 2010; Ibrahim *et al.* 2014; Sales *et al.* 2016) settings. These environments produce numerous but generally poor quality theropod finds. The spinosaurid record reflects this in that there are only ten taxa in our dataset (only 9 classified species) but abundant fossil occurrences are known from specific sites (Läng *et al.* 2013; Medeiros *et al.* 2014; Benyoucef *et al.* 2015), most of which preserve solely teeth. However, isolated from the other megalosauroids their non-temporal distribution of completeness scores is statistically no different to non-spinosaurid megalosauroids ($W = 58$, $p = 0.3669$), and is not significantly lower than any other subgroup except Compsognathidae ($W = 12$, $p = 0.0029$), Oviraptorosauria ($W = 109$, $p = 0.0101$), and non-deinonychosaurian Paraves ($W = 24$, $p = 0.0036$), all of which have relatively unique records in relation to other theropods (see below). The non-significant difference between the distribution of their completeness scores and most theropod subgroups may relate to their heightened association with deposition friendly aquatic settings (Hone *et al.* 2010) and their relative importance within specific palaeoecosystems (Sales *et al.* 2016; Candeiro *et al.* 2018), despite potential rarity on a global scale (Bertin 2010; Hone *et al.* 2010).

Basal theropods, basal neotheropods, megalosauroids, allosauroids, basal coelurosaurians, tyrannosauroids and dromaeosaurids all have relatively unremarkable distributions of completeness values that largely resemble the overall theropod distribution. The generality of their records likely derives from a mixture of specimen numbers per taxon (all groups have singleton specimen taxa close to or above 50%), broad depositional environments (except basal Theropoda and basal Coelurosauria no one depositional setting corresponds to more than 50% of a groups' taxa), and similar preservational regimes (all but Allosauroidea have at least 20% of taxa from concentration deposits) (Table A.11). Unlike the rest of these groups tyrannosauroids have an unusual number of highly complete taxa. This may represent local taphonomic biases towards large bodied animals (Brown *et al.* 2013); however, increased sampling effort in attempts to collect museum display specimens could also have aided their completeness. Species like *Tyrannosaurus rex* are famed for their ability to fascinate and attract the public and are a high commodity for museums and institutions.

Ornithomimosaurians and oviraptorosaurians have very similar distributions that contrast significantly with other subgroups. The fairly consistent number of taxa at all levels of completeness with relatively minor reduction at high levels (Fig. 2.6) suggests that the influences on their preservation differ from most other groups. Intriguingly, both groups have comparable morphological adaptations of the skull (the reduction or total loss of teeth and the development of beaked skulls) and have been suggested to be herbivorous and omnivorous (Barrett 2005, 2014). A further distinction between these subgroups and others is increased gregariousness, as suggested by remains monodominant bonebed assemblages (Kobayashi and Lü 2003; Varricchio *et al.* 2008. Cullen *et al.* 2013; Funston *et al.* 2016), potential communal nesting (Norell *et al.* 1995; Fanti *et al.* 2012; Xu *et al.* 2014) and possibly heightened abundance in comparison to other theropods (White *et al.* 1998). Gregarious behaviour and higher abundance within Mesozoic ecosystems would likely enhance the chances of individuals being preserved, and the chances of preserving complete skeletons due to the heightened density of individuals within local areas.

In contrast to all other groups, the significantly higher completeness distribution of the compsognathid and non-deinonychosaurian paravian records are almost exclusively the result of preservation in exceptional depositional settings, mostly in lacustrine environments (50% and 87% respectively) (Table A.11). Compsognathidae has the highest median completeness of any group and exhibits a bimodal distribution that derives from most taxa preserving in conservation Lagerstätten (70% of taxa) and a few in normal sedimentary regimes (20% of taxa). They are also the most limited theropod subgroup, with only ten taxa in our dataset. By contrast, a striking 93% of non-deinonychosaurian Paraves (14/15 taxa) are solely known from conservation Lagerstätten (Table A.11). Without the presence of exceptional Lagerstätten deposits it is highly unlikely these groups would be as well understood as they currently are. However, differing levels of spatial sampling intensity influences the discovery of such exceptional deposits (Eliason *et al.* 2017), therefore limiting our evolutionary understanding of groups that seem to be dependent on Lagerstätten to consistently preserve in the fossil record (Sales *et al.* 2014).

The statistically significant correlations of mean SCM2 time series for basal Theropoda, Allosauroidea, Compsognathidae, Alvarezsauroidea, Oviraptorosauria, and non-deinonychosaurian Paraves with total SCM2 likely suggests their records are most representative of the overall temporal completeness signals for theropods. The most notable are the basal theropods, which explain the high completeness levels in the Late Triassic, and the compsognathids and non-deinonychosaurian Paraves, which strongly contribute to the mean temporal completeness signal in the Late Jurassic and Early Cretaceous (Table A.6).

Body size has previously been argued to be a strong factor in fossil preservation, with larger, more robust skeletal elements preferentially surviving fossilisation (Cooper *et al.* 2006; Brocklehurst *et al.* 2012; Brown *et al.* 2013), except when elements become too large for easy burial. In this scenario it is expected that very small and very large taxa are less frequently preserved in the fossil record making their skeletons more fragmentary (Cleary *et al.* 2015), which may not reflect original abundance. Brown *et al.* (2013) concluded that there is significant bias towards high abundance and high completeness of large bodied dinosaurs in Dinosaur Provincial Park in Alberta, Canada. Further, Zanno and Makovicky (2013) identified a significant relationship between body mass of closely-related herbivorous Asian theropods and fossil localities, concluding a taphonomic and/or ecological signal was obscuring evolutionary trends in body mass. Studies show that on a global scale the highest completeness scores arise from different size categories dependent on the tetrapod group in question (Cleary *et al.* 2015; Gardner *et al.* 2016; Driscoll *et al.* 2018). On the other hand, Orr *et al.* (2016) argued that because of the role of decay products and adhesion of downward facing bones to the sediment, completeness of a skeleton is not necessarily influenced by size or density of the skeletal elements. Our results of the global theropod record do not recover a relationship between body size and skeletal completeness. We initially thought that this might reflect the many highly complete but small taxa derived from conservation Lagerstätten (Gardner *et al.* 2016). Removal of these taxa, and the further removal of concentration Lagerstätte taxa from the correlation again results in no relationship in either analysis. Because of this we are not convinced that body size of theropods influences the completeness of their fossil record on a global scale. A singular variable cannot adequately explain the differential completeness of all theropod skeletons, but size biases probably strongly influence the record on local scales. Biases that reduce the occurrence and completeness of small taxa under normal depositional regimes also act to limit the occurrence of larger taxa from preservation in conservation Lagerstätten (Zhou and Wang 2010; Gardner *et al.* 2016).

2.4.4. Sampling biases

Our analyses suggest that rock volume or outcrop availability (DBFs), collection effort (DBCs) and sampling coverage (Good's u) are not significant controls on specimen completeness within the theropod fossil record on a global scale. The number of theropod fossil occurrences (PBDB and specimen) through time also has no significant influence on the temporal completeness patterns, but increased specimen numbers do tend to lead to enhanced completeness for individual taxa. GLS model fitting results reveal different combinations of sampling proxy also offer little explanation for the changes in the SCM2 time series (Table A.3). DBFs contribute to two of the best explanatory models but little can be concluded from these due to relatively low R^2 values and AIC weights.

Our results reveal strong spatial biases between different latitudes and continents. The high abundance of theropod remains from northern mid-latitudes and the relative scarcity of specimens at other latitudes strongly suggests a historical focus on Europe, North America, northern Africa and East Asia, and the comparative neglect of South America, southern Africa and Australia (Benton 2008; Tennant *et al.* 2018). This is supported by the significantly higher completeness distributions of theropods from Asia and North America (Fig. 2.8).

The geographical differences in the quality of the theropod fossil record cannot only be due to historical sampling intensity. The latitudinal distribution of theropod occurrences is relatively bimodal in nature, with the dominant occurrences not only coming from the northern but also the southern mid-latitudes within modern and ancient contexts (Fig. 2.9). This suggests that the most productive theropod fossil localities occur in particular latitudinal zones, likely governed by climate and local environment.

Though we have not quantified it here, modern environments and climate likely play an important role in the availability of theropod bearing localities and, therefore, the global understanding of the group. For example, western Europe, the birth place of modern palaeontology, likely has among the highest historical research levels of any continent, but the theropod fossil record is the worst of all studied in terms of quantity and relative quality (SCM2), barring the very limited Australasian and Antarctic records. Benton (2008) similarly found that recent dinosaur species described from European deposits were of the poorest quality in comparison to other continents, and attributed this to historical research efforts and an overfamiliarity with deposits, corroborated by high European theropod Good’s u sampling coverage estimated by Tennant *et al.* (2018). This, however, cannot be solely driven by human sampling effort, but is more likely to reflect the lack of consistent availability of terrestrial Mesozoic horizons yielding fossiliferous material. This may be due to the generally temperate climate, vegetation cover and subsequent erosion in modern day localities. Because of this limited exposure, many of the terrestrial occurrences come from rapidly eroding coastal sections, where even if specimens were originally more complete, elements might be lost. Furthermore, large quantities of the European Jurassic and Cretaceous occurrences are marine, because Europe was an archipelago (possibly making it easier for taxa to end up in marine deposits) (Göhlich and Chiappe 2006; Csiki *et al.* 2010; Csiki-Sava *et al.* 2015), which we have found to be consistently less complete than terrestrial theropod specimens. However, Europe does still preserve many key theropod taxa.

Vast arid areas with little vegetation and high levels of rock exposure such as western North America, Patagonia, northern and southern Africa, and East

Asia provide ideal conditions for the heightened availability of fossiliferous localities and are likely driving the completeness signals seen between different continents and latitudes (Raup 1972, 1976; Wall *et al.* 2009).

On the other hand Australasia's poor record cannot simply be attributed to a significant lack of rock availability. Rich and Vickers-Rich (1997) argued that Australia's poor dinosaur record was the result of deep weathering of land profiles, aided by low topographic relief and by a lack of mountain building causing fossils to either be leached away or eroded through extended exposure. A number of sites with potential to yield vast quantities of dinosaur remains have produced numerous isolated specimens but very few associated skeletons that can be confidently identified at low taxonomic levels (Rich and Vickers-Rich 1997; Hocknull *et al.* 2009; Agnolin *et al.* 2010).

An almost complete absence of occurrences at high latitudes (>60 degrees north and south) and the scarcity and low completeness of theropod occurrences from equatorial regions emphasizes the geographic limitations in our sampling of the theropod fossil record (Fig. 2.9). Reasons for this could be the comparatively limited exploration of fossil bearing localities in these regions, many of which represent challenging environments for fieldwork. The lack of rock exposure due to extensive vegetation overgrowth (e.g. Amazon, Congolese, and Indonesian rainforests) and ice cover (Arctic and Antarctic) vastly reduce the sampling availability, plus extreme weathering processes like frost shattering aid erosion of possible preserved skeletons. There is however potential for further theropod findings in these regions, especially Antarctica which has previously produced a number of new dinosaur species (Olivero *et al.* 1991; Hooker *et al.* 1991; Hammer and Hickerson 1994; Case *et al.* 2000; Salgado and Gasparini 2006; Case *et al.* 2007; Smith and Pol 2007; Cerda *et al.* 2012; Coria *et al.* 2013). In the future, the use of geographic information systems (GIS) and remote sensing to predictively model the distributions of suitable fossil bearing localities may potentially aid our ability to more efficiently sample these challenging environments (see Anemone et al. 2011; Conroy et al. 2012; Emerson et al. 2015; Wills et al. 2018). Being able to accurately predict profitable fossil localities prior to field exploration could potentially enhance the quality of theropod fossil record by vastly increasing the number of newly identified theropod species from original localities, and enabling more efficient discovery of additional specimens of known species.

Furthermore, the spatial spread of sampling is variable through time (Fig. 2.9), and potentially creates another bias on completeness scores. Triassic theropod localities are the most geographically limited, which likely represents the restricted dispersal and diversity of the clade during the period. Jurassic and Cretaceous localities are much more latitudinally spread and far more consistently complete in the northern hemisphere, but both contain sporadic occurrences of low completeness in the southern hemisphere: only three Jurassic and four Cretaceous taxa exceed 50% completeness. Cretaceous occurrences cover the largest latitudinal distance of any period and are the most representative of more equatorial and higher latitudes. The Cretaceous northern hemisphere has produced 58% of the taxa of any age or locality, the majority of which are relatively poorly preserved.

Through time, different continents display different patterns of theropod completeness. The significant correlations between changes in SCM2 for Asian and European taxa and the total SCM2 dataset (Fig. A.7) suggests that these two records best represent the current understanding of the quality of global theropod fossil record greater than other continents. However, both of these records also show significant correlation between changes in SCM2 and taxon richness through time (Table A.8), suggesting changes in observed theropod diversity in these continents may be influenced by the preservation of specimens or vice versa (see below), unlike all other continents.

2.4.5. Lagerstätten influence

In comparison to total SCM2, background SCM2 shows more distinct drops in the Middle Jurassic, and the loss of the Oxfordian and Barremian–Aptian peaks (Fig. 2.3). Background taxon richness is very strongly correlated with total taxon richness throughout the entirety of the Mesozoic (Table A.4).

The relatively high Callovian–Kimmeridgian total SCM2 seems to be mostly driven by the high completeness scores derived from conservation deposits, as the mean background and concentration SCM2 for the stage are relatively low. The high number of taxa derived from conservation Lagerstätten partially explains the richness peak in the Callovian, but a high abundance of concentration deposits seems to contribute the most to enhance the total richness peaks in the Late Jurassic stages (Fig 3C-D). The Barremian and Aptian peaks and subsequent Albian drop in total SCM2 and richness are almost totally derived from conservation Lagerstätten, as 25 and 33 conservation Lagerstätten taxa occur in the former stages, respectively. Results (Table A.2) also indicate that without Lagerstätten included, mean completeness slightly drops through time, showcasing how significant these preservational regimes are for our interpretations of the theropod fossil record.

The influence of concentration and conservation Lagerstätten on theropod faunas is important because a large drop is observed in both total SCM2 and taxon richness across the Jurassic–Cretaceous boundary. This interval has previously been postulated as an extinction event for specific marine and terrestrial groups (Barrett *et al.* 2009; Benson *et al.* 2010b; Starrfelt and Liow 2016; Tennant *et al.* 2016a, b) due to observed drops in diversity. Our findings show the Late Jurassic peak in theropod taxonomic richness is much reduced when Lagerstätten are excluded, resulting in more reasonably similar background richness in both the Tithonian and Berriasian. Though this is simply the theropod record, it may signify that the apparent observed falls in species richness for other groups may be an artefact of preservation, likely controlled by the loss of Lagerstätten taxa and genuinely poor preservation in the earliest Cretaceous.

2.4.6. Impact on evolutionary understanding

The weak but significant correlation between observed taxon richness and specimen completeness throughout varying time intervals (Carnian–Albian, Hettangian–Albian, Jurassic–Cretaceous, Cretaceous) might suggest that changes in observed theropod diversity are influenced by the completeness of specimens, as time intervals with good preservation will yield high taxonomic abundance. This is important because it suggests that our understanding of theropod macroevolution may be influenced by temporal variation in the quality of the fossil record. However, the correlations are not very strong, and are lost depending on the inclusion of a few stages. Exclusion of Triassic stages and inclusion of Cretaceous stages seems to increase the strength of the correlation between richness and completeness (Table 2.2.1). The strongest correlation occurs in just the Cretaceous stages. There is also notable divergence between the taxonomic richness and mean completeness in the Carnian, Rhaetian, Campanian and Maastrichtian.

Alternative explanations for a positive correlation between diversity and completeness are 1) genuine evolutionary events drive diversity change and alter the relative likelihood of preservation of taxa and therefore completeness within a stage (Brocklehurst *et al.* 2012), for example, times of high diversity provide more chance of taxon preservation and vice versa; 2) more fossil specimens or occurrences increase both completeness of taxa and the number of identified taxa of a stage (Brocklehurst *et al.* 2012).

The Carnian has relatively high mean specimen completeness even though raw diversity is low, which suggests that macroevolutionary understanding at the beginning of theropod evolution is not influenced by taxon completeness, specimen counts or abundance. The Carnian theropod signal is anomalous because it has one of the highest standard deviation of scores for any stage (33.2%) and most (60%) taxa are derived from the Ischigualasto Formation of Argentina, which tends to predominantly produce well-preserved skeletons. The subsequent Norian has much reduced completeness but vastly increased specimen count and raw diversity reflecting the proliferation of neotheropods and an increased sampling pool in other formations with poorer preservation regimes. Other stages like the Toarcian, Aalenian, and the Valanginian, which show relatively high mean completeness but low specimen number and taxon abundance are likely the result of relatively poor sampling. Even though there is no negative correlation between skeletal completeness and taxon richness, the Campanian and Maastrichtian are good examples of how increased specimen number and observed diversity does not necessarily equate to higher levels of taxon completeness. These intervals have the highest specimen number (733 combined), highest raw taxon richness (156 combined), and some of the most varied completeness scores of any stage, but with relatively few concentration (24 taxa, 15%) and no conservation Lagerstätten taxa. It could be argued that this peak in richness is the result of numerous taxa being falsely identified from fragmentary, non-overlapping skeletal material (Brocklehurst and Fröbisch 2014) but this seems doubtful considering the derived and likely more diagnostic nature of differing theropod clades during the latest Cretaceous. We would postulate that the numerous fossil rich localities from these stages in North America and East Asia, and the extensive sampling (Upchurch *et al.* 2011; Starrfelt and Liow 2016; Tennant *et al.* 2018) and heightened interest of these stages at the end of the dinosaur record likely explain their extensive outlying peaks in specimen number, raw diversity and the moderate completeness levels at which a majority of taxa are found and named.

Above, and in previous sections, we reveal how there are a number of distinct temporal and spatial inconsistencies in the sampling and completeness of the theropod fossil record. Some geological stages contain more preferable preservational regimes due to geological changes, and therefore they are better sampled. The final stages of the Cretaceous provide an example of this (see Good's u coverage; Fig. A.4). There are also clear spatial biases that suggest sampling of the theropod fossil record has been geographically constrained to the mid-latitudes, possibly biased towards the re-sampling of previously known fossiliferous localities from countries with long histories of palaeontological research. Furthermore, because of the nature of the sedimentary record, theropods which had ecological preferences for fluvial environments will likely be more consistently preserved than others. All of this potential unevenness could be hiding key information, and it is important to take these natural and human sampling biases into consideration when interpreting the evolutionary trends of theropod dinosaurs. For palaeontologists, these should be obvious prerequisites to studying the fossil record and deciphering true evolutionary patterns. However, in future we should be aiming to explore formations and depositional environments from time bins and localities that have not been strongly sampled.

2.5. Conclusions

- Theropod completeness fluctuates through geological time, with notable peaks in the Carnian, Oxfordian-Kimmeridgian and Barremian–Aptian, and prominent lows in the Berriasian and Hettangian.
- Peaks in theropod completeness and raw taxonomic diversity in the Callovian–Kimmeridgian and the Aptian–Albian are driven by the presence of concentration and conservation Lagerstätten. Lagerstätten taxa positively influence the appearance of the theropod fossil record in a significant manner.
- Raw diversity changes through time may be influenced by completeness

of theropod specimens for particular time intervals, but correlations are statistically weak.

- There are no correlations between different sampling proxies and theropod completeness through geological time.
- Theropods have one of the statistically poorest non-temporal distributions of completeness scores of any previously assessed tetrapod group, with many taxa known from low skeletal completeness.
- Theropods have statistically poorer distribution of completeness scores than sauropodomorphs. When Lagerstätten taxa are removed, there is a significant positive correlation between theropod and sauropodomorph completeness time series suggesting a commonality to the preservational biases and sampling standards influencing our understanding of these groups. The poorer theropod fossil record could be due to generally less robust skeletons and predatory population dynamics in comparison to herbivorous and gregarious sauropodomorphs
- Megaraptora has the worst fossil record of any theropod subgroup. The gregarious behaviour of the omnivorous ornithomimosaurians and oviraptorosaurians potentially aids their significantly higher distribution of completeness scores in comparison to many other subgroups. Compsognathids and non-deinonychosaurian Paraves have the most complete records of any theropod subgroup because they are almost exclusively derived from conservation Lagerstätten.
- We recover no significant relationship between the body size of theropod taxa and their skeletal completeness, even when Lagerstätten taxa are removed. This means body size, at least on the global scale, is not a significant bias on the completeness of theropod taxa.
- The consistently best preserved theropod skeletons come from lacustrine and

aeolian deposits. However, the majority of theropod finds come from fluvial channel deposits, a regime that naturally downgrades the quality of fossils through transportation and abrasion. Heightened number of theropods derived from fluvial regimes in the Campanian and Maastrichtian could explain the generally poor quality of material from these time intervals.

- There are strong spatial biases in the theropod fossil record. Historic research interest and sampling effort likely explain the high abundance and significantly higher completeness of theropod remains from northern hemisphere, specifically the northern mid-latitudes. Asia has the statistically best theropod fossil record of any continent, while Australasia has the most limited, however, Europe has a very poor record considering its historic scientific interest. Geographical differences in the quality of the fossil record may be more connected to modern climate, vegetation cover and rock outcrop availability, than to just human sampling.

3 | Ten more years of discovery: revisiting the quality of the sauropodomorph dinosaur fossil record

3.1. Introduction

In their original exploration of the completeness metrics used in this thesis, Mannion and Upchurch (2010a) quantified the completeness of the sauropodomorph fossil record. They identified a number of biases acting upon their record, including a negative relationship between completeness and sea level through time, a positive correlation between completeness and taxonomic diversity changes in the Cretaceous, and a negative trend in specimen completeness through historical time. Subsequent studies have compared completeness of other tetrapod groups to this sauropodomorph record (e.g. Dean *et al.* 2016). However, since its publication a decade ago, 17% of the taxa assessed in Mannion and Upchurch (2010a) have undergone taxonomic revision, and the number of valid sauropodomorph species has increased by 34%.

New discoveries and research can have a strong impact on both the quality and our understanding of the fossil record (Weishampel 1996; Tarver *et al.* 2011; Jouve *et al.* 2017; Tennant *et al.* 2018). In this contribution, we aim to understand how ten years of new and revised data have impacted our knowledge of the fossil record of a major tetrapod group, taking a different approach to that used in some conceptually similar studies (Maxwell and Benton 1987; Sepkoski 1993; Benton and Storrs 1994; Weishampel 1996; Alroy 2000; Tarver *et al.* 2011; Brocklehurst *et* *al.* 2012; Ksepka and Boyd 2012; Nicholsen *et al.* 2015; Close *et al.* 2018; Tennant *et al.* 2018; Marsola *et al.* 2019). We provide a major update on the quality of the sauropodomorph fossil record and expand upon some of the previous analyses that have focused upon it, using more sophisticated statistical approaches to re-evaluate potential correlations between completeness and changes in sea level and taxonomic diversity through geological time. We also provide the first evaluation of how the quality of the sauropodomorph fossil record varies spatially. Finally, we attempt to address some potential key paleobiological and paleoecological influences on the sauropodomorph fossil record by statistically comparing completeness between depositional environments, taxonomic subgroups, and body size classes. The latter is of particular importance for sauropodomorphs, as derived lineages evolved to become the largest terrestrial animals to ever exist (Sander *et al.* 2011; Carballido *et al.* 2017; Benson *et al.* 2018), and body size potentially influences the completeness of a group's fossils (Nicholson 1996; Cooper *et al.* 2006; Noto 2011; Brown *et al.* 2013; Cleary *et al.* 2015), and ultimately our understanding of their record. This is the second re-assessment of its kind for fossil completeness data (Brocklehurst *et al.* 2012), but is the first to consistently use the same metric, and so it enables us to test the longevity of previous conclusions made about the sauropodomorph fossil record. Furthermore, as the results of this study highlight the taxonomic, spatial and temporal gaps in the sauropodomorph fossil record, they may be useful in guiding future exploration and research effort.

3.2. Materials and Methods

3.2.1. Completeness Metrics

Mannion and Upchurch (2010a) proposed two different definitions for their skeletal completeness metric (SCM): SCM1, which is scored solely on the most complete specimen of a species, and SCM2, which is the composite completeness of all known specimens of a species. We solely use the latter metric in this study because it uses all of the available information for each species and it is more appropriate than arbitrarily nominating a 'most important' specimen (Mannion and Upchurch 2010a; Brocklehurst *et al.* 2012; Brocklehurst and Fröbisch 2014). Mannion and Upchurch (2010a) also devised the character completeness metric (CCM) to calculate the number of phylogenetic characters for which a taxon can be scored. This metric is not considered in this study as this approach will in future form part of an independent and comprehensive study of dinosaur CCM following on from Bell *et al.* (2013). Furthermore, SCM and CCM were shown to be strongly correlated with one another by Mannion and Upchurch (2010a).

Mannion and Upchurch (2010a) used approximations of relative skeletal proportions (e.g., the percentage of the total skeleton made up by any individual bone or skeletal region) to assess completeness for sauropodomorphs. Methods of calculating these skeletal proportions have since been revised and refined (Brocklehurst and Fröbisch 2014; Cleary *et al.* 2015; Verierre *et al.* 2016; Cashmore and Butler 2019, Chapter 2) to more precisely estimate the skeletal proportions of different tetrapod groups. However, here we use the proportions defined by Mannion and Upchurch (2010a) to calculate sauropodomorph completeness in order to ensure comparability with this earlier work.

3.2.2. Data

We present a new dataset of 307 sauropodomorph species. This comprises all species currently considered valid. Although this excludes nomina dubia, it includes a small number of specimens that have not yet received formal taxonomic names but which nevertheless are likely to represent distinct species. Skeletal completeness scores of 133 of the taxa were extracted from Mannion and Upchurch (2010a) and personal observations. We calculated skeletal completeness for the remaining 174 newly described or recently revised taxa, published since

Mannion and Upchurch's (2010a) dataset was compiled. These include 141 'new' species (26 were previously included within generic-level completeness scores), and 33 taxa that have been assigned additional specimens or been subject to recent taxonomic revision.

Completeness data were primarily gathered from Figures and descriptive text in the literature, supplemented by additional online sources, museum catalogues, first-hand observation of specimens, and via personal communications. All published specimens of every taxon were included unless information was lacking for an individual specimen, or if a taxon's composite completeness was already 100%, and any additional specimens therefore made no difference to its completeness score. Each specimen's constituent bones were scored from 0–100% completeness and then transformed into completeness scores relative to overall skeletal proportions. Given their rarity, we excluded clavicles, sternal ribs and gastralia from body-proportioned completeness scores. The dataset is up-to-date as of April 2019 (Supporting data).

We subdivided the completeness data into various categories in order to ascertain finer scale signals in the sauropodomorph fossil record. To assess the differing completeness levels within Sauropodomorpha, we subdivided the SCM2 scores into the following major subgroups: non-Sauropoda, non-neosauropodan Sauropoda, Diplodocoidea, non-titanosaurian macronarians and Titanosauria. We also gathered geographical information for each taxon from the Paleobiology Database (PBDB: www.paleobiodb.org), including the hemisphere, continent and modern- and palaeo-latitudinal coordinates for each taxon's holotype locality, to assess the varying spatial completeness of the sauropodomorph fossil record. SCM2 scores were compared to the modern- and palaeo- latitudinal distribution of occurrences and grouped by hemisphere, and between the major continental regions, which are: Africa (44 species), Asia (84 species), Australasia (5 species), Europe (42 species), North America (41 species), and South America (90 species).

Antarctica was excluded from these analyses due to its very limited fossil record (1 species). Although India and Madagascar formed a small isolated continent in the Cretaceous, their species were assigned to their modern continents, Asia and Africa respectively, as analyses were concerned with bias associated with modern spatial distribution. Furthermore, we gathered information regarding each taxon's inferred depositional setting from the literature and the PBDB, and subdivided SCM2 scores between them, to understand global taphonomic influences on the sauropodomorph fossil record. Taxa were classified as originating from (1) fluvial (channel, alluvial plain), (2) lacustrine, (3) 'other' (aeolian, traps/fills) terrestrial environments, and (4) coastal and open marine settings.

To test whether a significant phylogenetic signal is present in sauropodomorph completeness, an informal supertree, comprising 206 species, was constructed in Mesquite (v. 3.6; Madison and Madison 2018), based on an existing supertree (Benson *et al.* 2018) updated via a number of recently published phylogenetic hypotheses (Carballido *et al.* 2017; Tschopp and Mateus 2017; Apaldetti *et al.* 2018; Canudo *et al.* 2018; Díez Díaz *et al.* 2018; González Riga *et al.* 2018; McPhee *et al.* 2018; Müller *et al.* 2018a, b; Pretto *et al.* 2018; Sallam *et al.* 2018; Simón *et al.* 2018; Xu *et al.* 2018; Zhang *et al.* 2018; Filippi *et al.* 2019; Gallina *et al.* 2019; Mannion *et al.* 2019; Zhang *et al.* 2019). The positions of some taxa (e.g. *Atlasaurus*) were highly unstable between analyses, and so were excluded. Several topologies (e.g. Gorscak and O'Connor 2019) were also largely incompatible with the relationships based on other source trees, and thus were also not incorporated. To perform comparative phylogenetic analyses, the supertree was time-scaled using the timePaleoPhy() function in the package paleotree (Bapst and Wagner 2019), with taxon first and last appearance dates used as precise ages, and the "equal" time scaling method employed.

We also collected body mass estimates of 140 species from Benson *et al.* (2018), using the methods presented in that study to calculate 13 additional species body mass estimates, whilst adding three estimates from other literature sources (see Supplementary information). These data were used to test the potential relationship between sauropodomorph body size and skeletal completeness. To assess the relationship between these two aspects of the sauropodomorph fossil record in a phylogenetic context, we employed a reduced version of the composite tree, described above, comprising 129 of the 156 species. These 129 taxa represent species for which body size estimates are available and phylogenetic relationships have been studied in recent literature (see Supporting data).

3.2.2.1. Geological Time Series. Mean SCM2 scores per geological stage-level time bin were used to examine temporal fluctuations in completeness from the Carnian to Maastrichtian (237–66 Ma). Stage-level time bins were chosen as this is the stratigraphic level used in the majority of previous studies and for most sampling proxy data. Stage ages were determined from Walker *et al.* (2018). Taxa that were present over multiple geological stages, or have an uncertain stratigraphic age, were included in each stage in which they potentially were present. The most up-to-date geological ages of each species were gathered from the literature. The ages of the Chinese Middle–Late Jurassic sauropodomorph-bearing units are in a major state of flux (Huang 2019), but we use the most recent dates from the literature for these taxa. Both the mean average and standard deviation of completeness scores were calculated for each individual stage. We also created individual geological time series from solely the species and stages represented in each continent, 10° palaeolatitudinal bin, depositional environment, and sauropodomorph subgroup, in order to reveal specific regional, palaeoclimatic, environmental and taxonomic signals that might be influencing the sauropodomorph record. A geological time series of maximum, minimum and mean body mass estimates per geological stage was also assembled to test the potential temporal relationships with changes in mean skeletal completeness.

3.2.2.2. Historical Species Accumulation and Time Series. To test changes in our understanding of the sauropodomorph fossil record through historical time, we first calculated the species cumulative count and mean SCM2 for each decade from the 1830s until now, based on the species discovered in that decade. We gathered each taxon's discovery date from the literature as the first published description of relevant material. We compared these two variables for all data and separately partitioned by modern continent, taxonomic subgroup and Mesozoic period. Secondly, we produced iterations of our new SCM2 time series using data solely available for each decade from 1949 to pre-2010. These iterations represent the information available for interpreting the sauropodomorph fossil record at the end of each decade, but with the current taxonomic and stratigraphic consensus for each species overprinted. Time series were not produced for any earlier decades as the scarcity of valid taxa named prior to 1940 means that they are unlikely to produce meaningful results. Each historical time series was statistically compared to the newly updated full data set curve.

3.2.3. Statistical Tests

All statistical analyses were performed in R. Time series plots were produced using the package ggplot2 (Wickham *et al.* 2018), non-temporal completeness distributions plots were produced with the package vioplot (Adler 2015), and phylogenetic trees with visually mapped continuous characters were produced through the function contMap() in the package phytools (Revell 2019).

Generalized least-squares regressions (GLS) were employed for linear time series comparisons with the function gls() in the R package nlme (Pinheiro *et al.* 2018), in which a first order autoregressive model (corARMA) is applied to the data, to reduce the chances of overestimating statistical significance due to temporal autocorrelation. Time series were log-transformed prior to analysis to ensure homoscedasticity (constant variance) and normality of residuals. The function r.squaredLR() of the R package MuMIn (Bartoń 2018) was further used to calculate likelihood-ratio based pseudo-R^2 values.

Non-parametric Mann-Whitney-Wilcoxon tests were performed for pairwise comparisons of non-temporal range data. False discovery rate (FDR; Benjamini and Hochberg 1995) adjustments were used to reduce the likelihood of acquiring type I statistical errors over multiple comparisons. GLS models were also applied to test the non-temporal linear relationship between log-transformed body mass estimates and sauropodomorph SCM2. The package chngpt (Fong *et al.* 2017) was used to test for a continuous non-linear relationship between body mass and completeness. Specific non-linear models are fitted to the data by linear regressions to test for sharp changes (breakpoints) or 'thresholds' in the directionality of a relationship between two variables, which happens when there are two different linear relationships in the data. We opted to use three threshold effects (segmented, hinge and upper hinge), following recommendations from Fong *et al.* (2017).

The function phylosig() of the package phytools (Revell 2019) was used to test if species skeletal completeness has a phylogenetic signal. We opted to only consider results from Pagel's lambda to test the phylogenetic signal as it has been determined to perform better than other methods (Münkemüller *et al.* 2012). Phylogenetic independent contrasts (PIC) and phylogenetic generalised least squares (PGLS) linear regression with maximum likelihood methods were further implemented to test the covariance between completeness and body mass whilst considering sauropodomorph phylogenetic relationships. For the former, the function pic() in the R package ape (Paradis *et al.* 2019) was used and polytomies in the input phylogeny were randomly resolved, and for the latter we applied the pgls() function in the R package caper (Orme *et al.* 2018).

3.2.4. Analyses

3.2.4.1. Temporal Correlations. The new time series of sauropodomorph SCM2 through geological time was statistically compared to a number of other time series with which it might potentially have a relationship. We first compared it to the SCM2 time series from Mannion and Upchurch (2010a), and to historical SCM2 time series based on 'degrading' our current dataset. We tested the correlation between SCM2 and changes in 'raw' sauropodomorph diversity through geological time, derived from the number of species in our dataset, and performed separate correlations for various time intervals. We also tested the potential temporal relationship of completeness with the mean, maximum, and minimum body masses of each stage.

Sauropodomorph SCM2 was compared with stage bin length to determine whether our choice of time bins affects our results, as well as with fluctuations in sea level (data derived from Butler *et al.* 2010). To identify shared or diverging completeness signals, the new sauropodomorph completeness time series was also compared with the records of other Mesozoic tetrapod groups for which skeletal completeness studies have been performed, i.e. plesiosaurs (Tutin and Butler 2017), ichthyosaurs (Cleary *et al.* 2015), and theropod dinosaurs (Cashmore and Butler 2019, Chapter 2), and groups for which character completeness studies have been performed, i.e. avialans (Brocklehurst *et al.* 2012), pterosaurs (Dean *et al.* 2016), and crocodylomorphs (Mannion *et al.* 2019). One problem with these clade-level comparisons is that we do not know the extent of the differences that may exist between the up-to-date stratigraphic ages of formations in our sauropodomorph skeletal dataset and the older dates used for other tetrapod groups based on PBDB data. This is unfortunately difficult to overcome without extensive revision of the Mesozoic PBDB data, but we believe the analyses we have performed are still valid and informative.

3.2.4.2. Non-temporal Comparisons. A variety of comparisons of median and distribution of completeness values were made between subsets of the data, including different geological periods, the major sauropodomorph subgroups, geographical hemispheres and continents, and the depositional environments of each species. If a species with multiple specimens occurs in more than one of these subsets, its completeness score was replicated in each group when performing statistical comparisons. The spread of sauropodomorph SCM2 values was also compared to those currently known for pelycosaurs (Brocklehurst and Fröbisch 2014), ichthyosaurs (Cleary *et al.* 2015), parareptiles (Verierre *et al.* 2016), plesiosaurs (Tutin and Butler 2017), bats (Brown *et al.* 2019), and theropod dinosaurs (Cashmore and Butler 2019, Chapter 2).

SCM2 values for individual species were also compared with the modern and palaeolatitudinal coordinates of their type specimens, and with their body mass estimates, when available. Body mass estimates were first compared to SCM2 using a simple linear pairwise correlation. However, it is possible there is an optimal body size that could aid specimen completeness, and this optimum might not lie at either the very small or the large ends of the body size spectrum. It might be expected that most preserved fossil species are of intermediate sizes, and very small and very large taxa are less frequently preserved, likely making their skeletons more fragmentary (e.g. Brown *et al.* 2013). In this scenario, the relationship between body size and completeness would be non-linear; therefore, we also tested for a non-linear relationship between the two variables. Furthermore, species' body mass estimates were compared to completeness whilst taking into account their phylogenetic relationships, in order to assess whether a relationship between completeness and body size is independent of phylogeny.

3.3. Results

3.3.1. Historical sampling changes

3.3.1.1. Species accumulation and changes in historical completeness. As Mannion and Upchurch (2010a) previously showed, the number of identified sauropodomorph species rose steadily through historical time up to the last years of the 20th century, when discoveries began to rise exponentially (Fig. 3.1) (Tennant *et al.* 2018). This trend continued into the early 21st century and has not abated in the last decade, with the rate of discovery increasing further (9.3 species a year) since 2009. The number of named species in the last three decades greatly outnumbers the entirety of discoveries made prior to 1990. All continents exhibit this exponential rise in new discoveries (Fig. 3.1), with Asia and South America being the most extreme, and North America exhibiting a rejuvenation of new discoveries after a long plateau. All subgroups also exhibit the continued rise in new species (Fig. 3.1), with macronarians showing the steepest increase and diplodocoids the gentlest. The number of discoveries of Late Triassic and Jurassic sauropodomorphs has strongly increased, but Cretaceous discoveries have increased the most dramatically (Fig. B.1), with the latter largely driven by discoveries of Titanosauria and South American taxa.

Mean completeness of newly described species per decade fluctuated substantially throughout the 19th century and the first half of the 20th century. In contrast, there has been a steady decline in mean species completeness over the last three decades, with the last decade the lowest on record (excluding the 1860s, in which no new species were discovered) (Fig. 3.1). This seems to be predominantly driven by the African, European and South American records, whereas the Asian, Australasian and North American curves do not display a downward trend in the completeness of newly erected species in the last decade (Fig. 3.1).

3.3.1.2. Changes to geological completeness and diversity curves through historical time. Time series based on our new dataset of mean sauropodomorph completeness values change drastically throughout research time (Fig. 3.2). Prior to the 21st century, each time series shows large fluctuations in the quality of the record per stage, with swings from low to high mean completeness, indicative

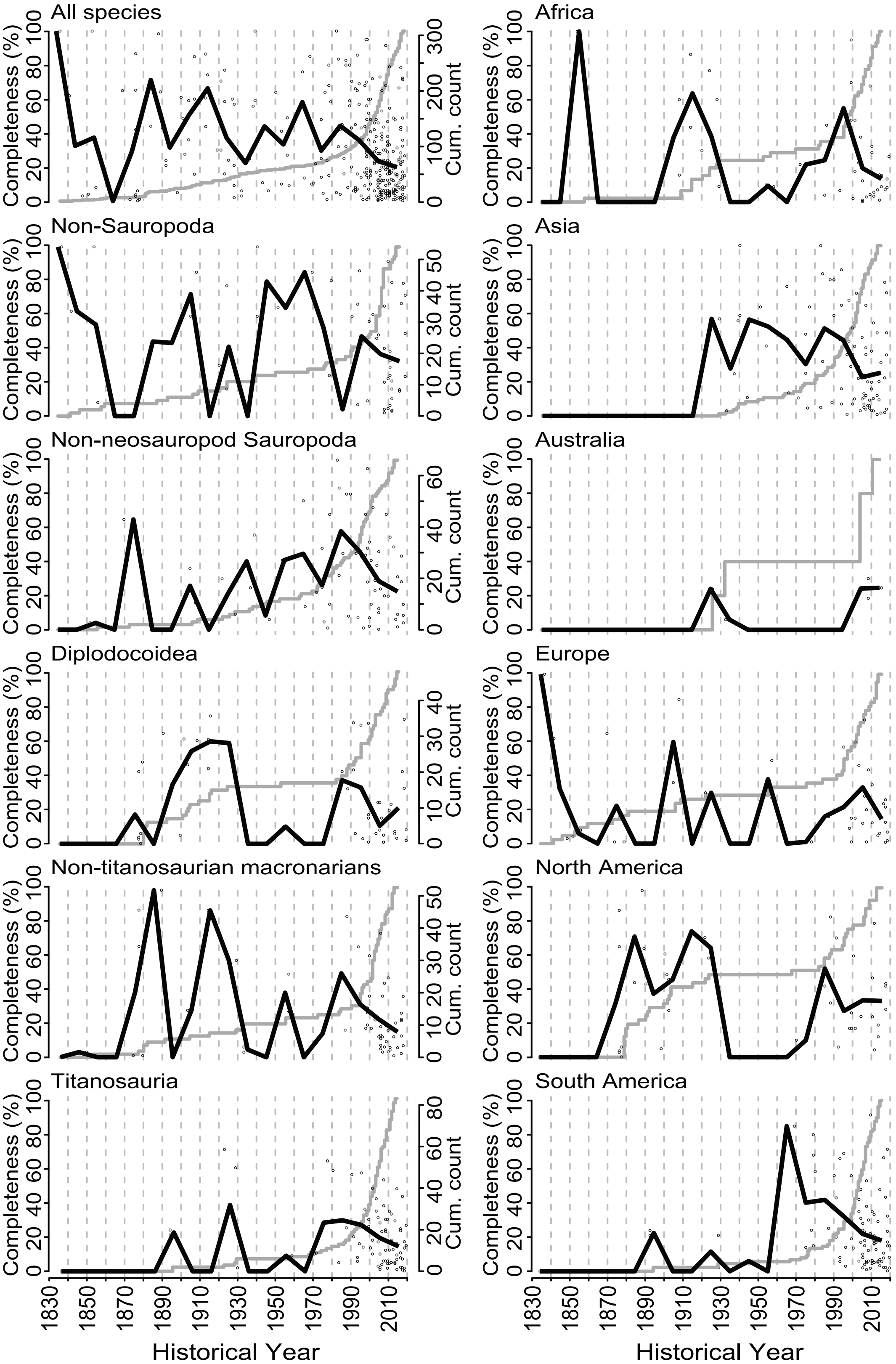


Figure 3.1. Historical accumulation and completeness curves for all sauropodomorph species, each major subgroup, and each continent. Black line, mean SCM2 score per 10 year bin; grey line, cumulative species count; circles, individual

(Fig. 3.1. Continued) species' SCM2 score in relation to first publication date. Abbreviations: cum. count, cumulative species count.

of changes in sampling in stages known from a few species. All of the pre-1990 curves lack a statistically significant correlation with the current completeness curve (Table 1). The curve for data available in 1999 is significantly correlated with the current time series (Table 1), but still contains many alternating peaks and troughs (Fig. 3.2). However, when including data up to 2009, the fluctuations are reduced, resulting in a flatter curve of changes in completeness per stage. This trend continues into the current time series, resulting in a relatively flat curve for most of the Cretaceous (averaging ~20% complete), and higher but generally consistent values for the Triassic–Jurassic (averaging ~40% complete). The current and pre-2010 curves have a strong positively significant correlation (Table 1).

In contrast, a significant difference was recovered between the current completeness curve and the curve presented in Mannion and Upchurch (2010a). Mean completeness is lower in the majority of geological stages in the current curve, with less substantial fluctuations between stages, and a consistent trough in completeness in the earliest Cretaceous that was absent in the Mannion and Upchurch curve (Fig. 3.2). The Mannion and Upchurch (2010a) curve is also significantly different to the pre-2010 curve derived from our data ($R^2 = 0.448$; $p = 0.3814$) (Fig. 3.2).

In contrast to the changes in completeness, raw diversity changes (i.e. fluctuations in the number of species sampled per stage) have become increasingly variable through historical time. Diversity is very low for almost all stages except the Late Jurassic up until the 2000s (Fig. 3.2). With a spate of research and discoveries in predominantly Early Jurassic and Cretaceous strata, diversity now strongly fluctuates between stages. Despite this, changes in raw species diversity for every previous date assessed are significantly correlated with the current time series (Table 1). When Late Jurassic stages are removed the significant correlation is

Table 3.1. Results of pairwise comparisons of time series representing current sauropodomorph SCM2 and raw diversity in relation to past iterations using GLS. Statistically significant results indicated in bold. Abbreviations: M&U (2010), Mannion and Upchurch (2010a); no LJ, removed Late Jurassic stages. Unless specifically stated, 'SCM2' and 'diversity' refers to the current sauropodomorph data.

Comparison	Slope	t-value	p-value	R2
SCM2 ~ SCM2 M&U (2010)	0.050982	0.165225	0.8702	0.458531321
SCM2 ~ SCM2 2009	0.4815371	10.291005	**<0.00001**	0.899401709
SCM2 ~ SCM2 1999	0.4076397	7.896279	**<0.00001**	0.848666106
SCM2 ~ SCM2 1989	0.031612	0.359602	0.7227	0.530537736
SCM2 ~ SCM2 1979	0.033621	0.385478	0.704	0.509055505
SCM2 ~ SCM2 1969	0.037661	0.517804	0.6106	0.49577072
SCM2 ~ SCM2 1959	0.038353	0.527538	0.6039	0.496021615
SCM2 ~ SCM2 1949	0.031879	0.432283	0.6707	0.47332164
diversity ~ diversity 2009	0.7507332	18.046419	**<0.00001**	0.9332359
no LJ diversity ~ diversity 2009	0.7121271	13.702879	**<0.00001**	0.9175663
diversity ~ diversity 1999	0.6262306	8.18947	**<0.00001**	0.7352664
no LJ diversity ~ diversity 1999	0.5718116	5.865903	**<0.00001**	0.6851981
diversity ~ diversity 1989	0.3913624	3.437055	**0.0025**	0.4173742
no LJ diversity ~ diversity 1989	0.1476995	1.059982	0.3032	0.4045711
diversity ~ diversity 1979	0.4253499	4.087849	**0.0006**	0.4506245
no LJ diversity ~ diversity 1979	0.2120439	1.566665	0.1346	0.443022
diversity ~ diversity 1969	0.4198746	3.848375	**0.0011**	0.4238151
no LJ diversity ~ diversity 1969	0.1834932	1.242526	0.2309	0.4367617
diversity ~ diversity 1959	0.4176603	3.709545	**0.0015**	0.41405
no LJ diversity ~ diversity 1959	0.1734618	1.142459	0.2691	0.4295914
diversity ~ diversity 1949	0.4032211	3.336659	**0.0037**	0.390814
no LJ diversity ~ diversity 1949	0.1522655	0.989465	0.3372	0.4051907

still retained between current and 2009 data, and between current and 1999 data, but is lost when compared with changes derived from pre-1990 data (Table 1).

3.3.2. Current understanding of the sauropodomorph fossil record

3.3.2.1. Sauropodomorph completeness through geological time. Mean sauropodomorph skeletal completeness (Fig. 3.2) ranges between 4% and 48% through the stages of the Mesozoic, with minor peaks in the Hettangian Bajocian and Maastrichtian, and notable lows in the Rhaetian, Valanginian and Hauterivian (Fig. 3.2). The most striking observation is that mean completeness noticeably drops across the Jurassic/Cretaceous boundary, and never recovers

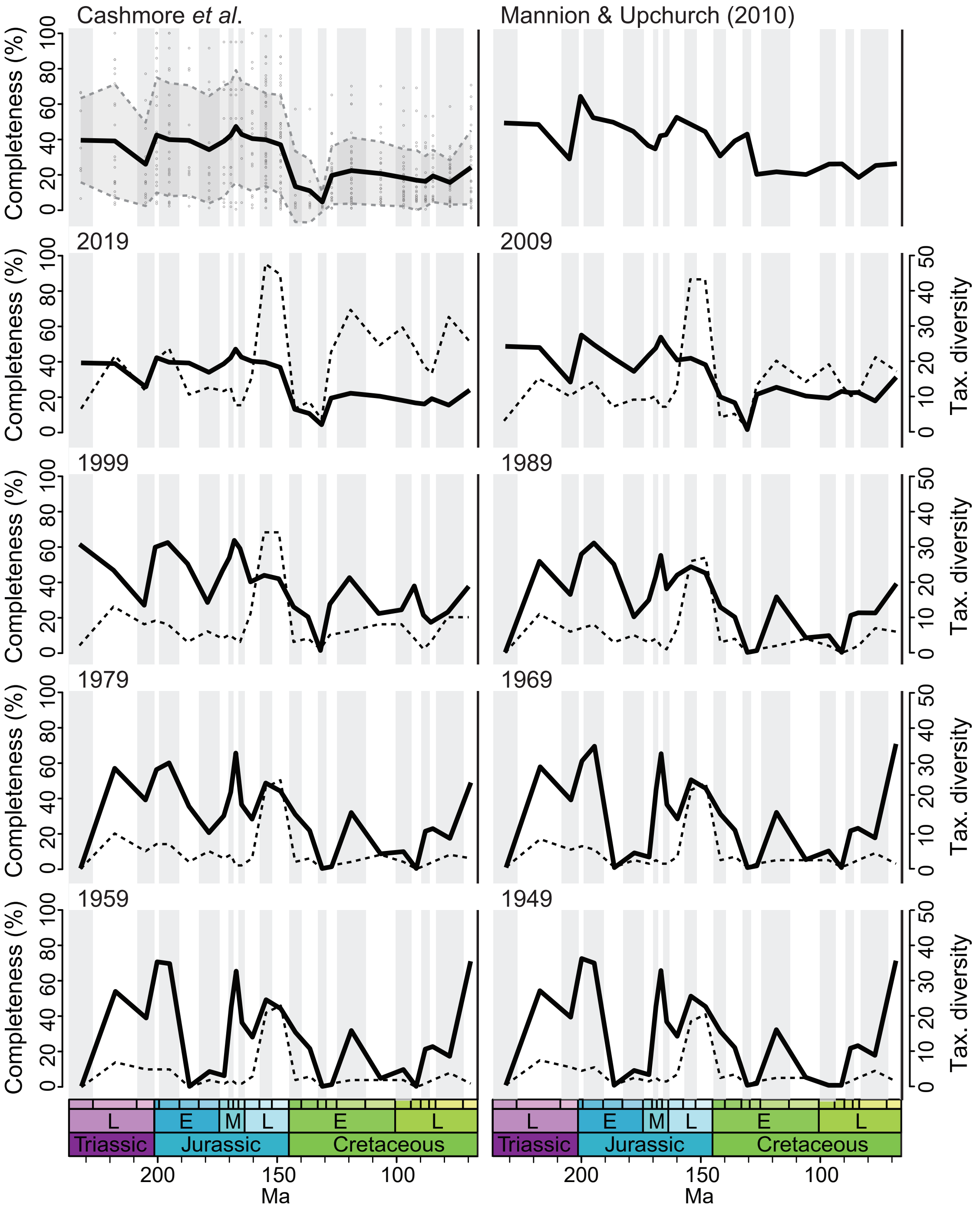


Figure 3.2. Changes in mean sauropodomorph completeness through geological time from our current data set, from Mannion and Upchurch (2010a), and partitioned by available data per research decade based on our current data set, with raw diversity changes for comparison. Black lines, mean SCM2; grey polygon with dashed lines, one standard deviation either side of mean SCM2; dashed lines, raw species diversity; circles, individual species' SCM2 scores. Abbreviations, Tax. diversity, raw taxonomic diversity.

to pre-Cretaceous levels. There is no significant trend in sauropodomorph completeness through time ($R^2 = 0.505$; $p = 0.089$). The Triassic and Jurassic exhibit relatively wide standard deviations, whereas this is narrower in the Cretaceous (Fig. 3.2). Mann-Whitney-Wilcoxon tests show that there is no significant difference between the distributions of Triassic and Jurassic ($W = 2104$, $p = 0.917$) completeness values, but there are strongly significant differences between distributions for the Triassic and Cretaceous ($W = 3474.5$, $p = 0.0002$), Jurassic and Cretaceous ($W = 13122$, $p = 1.32E\text{-}08$), and Triassic–Jurassic and Cretaceous ($W = 16518.5$, $p = 1.02E\text{-}09$) (Fig. B.2A).

3.3.2.2. Correlations with taxonomic diversity through time. Observed sauropodomorph species diversity fluctuates throughout the Mesozoic, with an outlying peak in the Kimmeridgian and Tithonian, and notable lows in the Pliensbachian to Callovian, and Berriasian, Valanginian and Hauterivian (Fig. 3.2). There is no statistically significant trend in raw diversity changes through time ($R^2 = 0.18$; $p = 0.1159$), but there is a strong, significant positive correlation between temporal fluctuations in sauropodomorph completeness and raw species diversity (Table 2). This correlation is non-significant when assessed for the Triassic–Jurassic and Jurassic periods alone (even when Late Jurassic stages are removed), but is still retained in the Cretaceous (Table 2).

3.3.2.3. Comparisons with other tetrapod fossil records. Sauropodomorph species completeness values range from just above 0% to 100%, with a median completeness of 21.5%, which is similar to pelycosaur-grade synapsids, but significantly different to all other previously assessed groups (Table B.1, Fig. B.2B). The non-temporal distribution of sauropodomorph completeness values has remained statistically unchanged since Mannion and Upchurch (2010a) (Table B.1, Fig. B.2B). We also recovered the statistically significant higher completeness distribution of sauropodomorphs in comparison to theropods found by Cashmore and Butler (2019, Chapter 2), but note that the significant difference is lost not only

Table 3.2. Results of pairwise comparisons of current sauropodomorph SCM2 and raw diversity, body mass, other Mesozoic tetrapods, and sea level time series using GLS. Statistically significant results indicated in bold. Abbreviations: Abbreviations: occs., occurrences; non-cons., non-conservation Lagerstätten; LT, Late Triassic; J, Jurassic; EK, Early Cretaceous; K, Cretaceous; Barr., Barremian; Maas., Maastrichtian. Unless specifically stated, 'SCM2' refers to the current sauropodomorph data.

Comparison	Slope	t-value	p-value	R2
SCM2 ~ diversity	0.4115605	4.231914	**0.0003**	0.672395358
LT-EK SCM2 ~ LT-EK diversity	0.4551134	4.4701	**0.0003**	0.708264632
LT-J SCM2 ~ LT-J diversity	-0.021317	-0.321045	0.7537	0.003880958
J SCM2 ~ J diversity	-0.054868	-1.189266	0.2648	0.258319312
J-EK SCM2 ~ J-EK diversity	0.5050091	4.623453	**0.0003**	0.753239437
J-K SCM2 ~ J-K diversity	0.4485924	4.227545	**0.0004**	0.700598115
K SCM2 ~ K diversity	0.581422	7.723001	**<0.00001**	0.790919202
SCM2 ~ mean body mass	0.058566	1.072138	0.2948	0.4678553
SCM2 ~ max body mass	0.0477604	0.930038	0.362	0.4639178
SCM2 ~ min body mass	0.0821301	2.145753	**0.0427**	0.507147
SCM2 ~ Theropod SCM2	0.4664736	2.970759	**0.0067**	0.6037791
LT-J SCM2 ~ LT-J Theropod SCM2	-0.052913	-0.372815	0.7158	0.015112174
J SCM2 ~ J Sauro SCM2	-0.038116	-0.337635	0.7434	0.155188796
J-K SCM2 ~ Theropod SCM2	0.5777531	3.703968	**0.0013**	0.67416404
K SCM2 ~ Theropod SCM2	0.5355767	2.154694	0.0566	0.340339481
non-cons. SCM2 ~ Theropod non-cons. SCM2	0.4404663	2.188271	**0.0386**	0.5647327
LT-J non-cons. SCM2 ~ LT-J Theropod non-c	-0.127089	-0.77155	0.4553	0.04479128
K non-cons. SCM2 ~ K Theropod non-cons. S	0.533012	1.425175	0.1846	0.2188998
SCM2 ~ Ichthyosaur SCM2	0.036865	0.161165	0.8739	0.309655567
SCM2 ~ Plesiosaur SCM2	-0.01771	-0.123095	0.9033	0.434424413
SCM2 ~ sea level	-0.021302	-0.218543	0.8289	0.458622271
LT-J SCM2 ~ LT-J sea level	0.039748	1.786614	0.0993	0.190401
J SCM2 ~ J sea level	-0.02078	-0.861759	0.4112	0.2078029
K SCM2 ~ K sea level	0.4513228	3.532196	**0.0054**	0.5074996
Barr.-Maas. SCM2 ~ Barr.-Maas. sea level	-0.303502	-4.729699	**0.0021**	0.6464949

when using Cretaceous data alone, but also with just Jurassic data (Table B.1).

There is no significant correlation between sauropodomorph completeness and that of either marine reptile group examined (ichthyosaurs and plesiosaurs) through time (Table 2). Unlike Cashmore and Butler (2019, Chapter 2), the sauropodomorph and theropod completeness time series are now significantly correlated when either including or excluding conservation Lagerstätten (Table 2; Fig. B.3A and B). However, the sauropodomorph and theropod Triassic–Jurassic data are no longer significantly correlated. Jurassic and Cretaceous sauropodomorph and

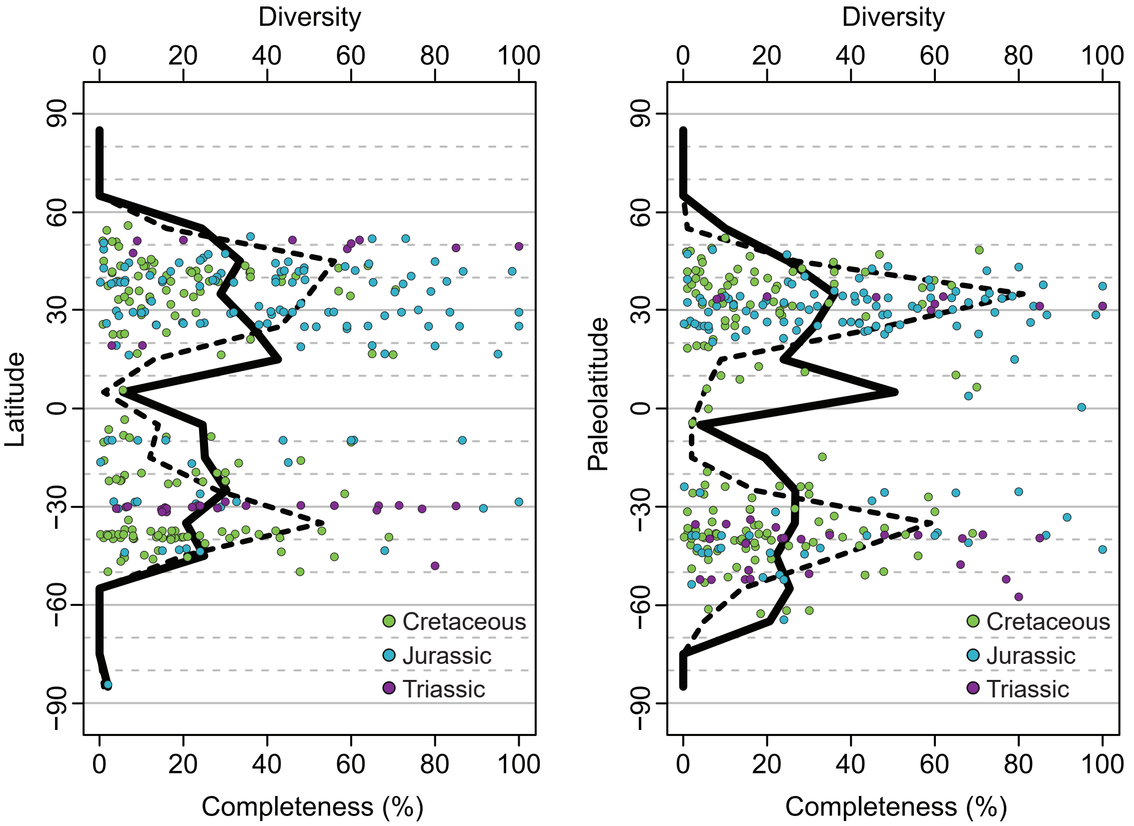


Figure 3.3. Scatter distribution of SCM2 values in relation to geographical coordinates per modern latitude and paleolatitude. Point colours correspond to geological age: Triassic (purple), Jurassic (blue), Cretaceous (green). Black line, mean specimen completeness, and, dashed line, raw taxonomic diversity per 10° latitudinal bin.

theropod data are not significantly correlated when considered separately, but there is a correlation when the Jurassic and Cretaceous data series are combined (Table 2).

3.3.2.4. Geographical completeness. The northern hemisphere has significantly more species at higher completeness levels in comparison to its southern counterpart (W = 13248; p = 0.018). However, this significant difference is lost after accounting for false discovery (adj. p = 0.062) (Fig. B.2C). The latitudinal and palaeolatitudinal spread of occurrences in relation to SCM2 is somewhat bimodal, creating a relatively similar distribution in both hemispheres, with most finds of higher completeness coming from 20–50° N and S in both modern and palaeolatitudinal contexts, but significant drops in numbers of occurrences in palaeoequatorial and high palaeolatitudal regions (Fig. 3.3A). The palaeolatitudinal bin with the highest species diversity in both hemispheres is 30–40°. Mean completeness per palaeolatitudinal bin is mostly in the range of ~19–36%, except for 50–60° N (10%) and 0–10° N and S; the latter pair of bins exhibit the highest (50%) and lowest (4%) mean completeness, respectively (Fig. 3.3B).

The completeness distributions of each continent are all statistically similar to one another (Table B.2; Fig. 3.4A), apart from North America, which is the only continent not to display a 'bottom-heavy' distribution and has significantly more species of higher completeness than Africa, Europe, or South America (Table B.2; Fig. 3.4A). However, only the South American comparison remains significant after adjusting for false discovery. Even though Australasia has the most limited fossil record, with only five species currently recognised, its distribution is still not significantly different to the other continents.

No palaeolatitudinal or continental time series has a continuous temporal stage representation. Whereas Africa, Asia, Europe and South America have species from each epoch, North America only has species from 13 geological stages, and Australasia only from three stages (Table B.3; Fig. B.4). The most comprehensive temporal representation of any palaeolatitudinal bin is for 30–40° N, with 24 stages; this is followed by 20–30° N and 40–50° N (19 stages each), then 30–40° S and 40–50° S (18 stages each). The most equatorial (10° N to 10° S) palaeolatitudinal bins are represented in 11 different geological stages, whilst 10–20° S has only 2 stages, and the high palaeolatitudes of 60–70° S are represented in only three stages, and 50–60° N in only one stage (Table B.4; Fig. B.5). No species are found at higher palaeolatitudes.

The Late Triassic and earliest Cretaceous (Berriasian, Valanginian, Hauterivian) have the poorest geographic extent of sampling, with only 23% and 33% of all palaeolatitudinal bins represented, respectively (Table B.4; Fig. B.5), and species present only in Asia, South America and Europe (Table B.3; Fig. B.4).

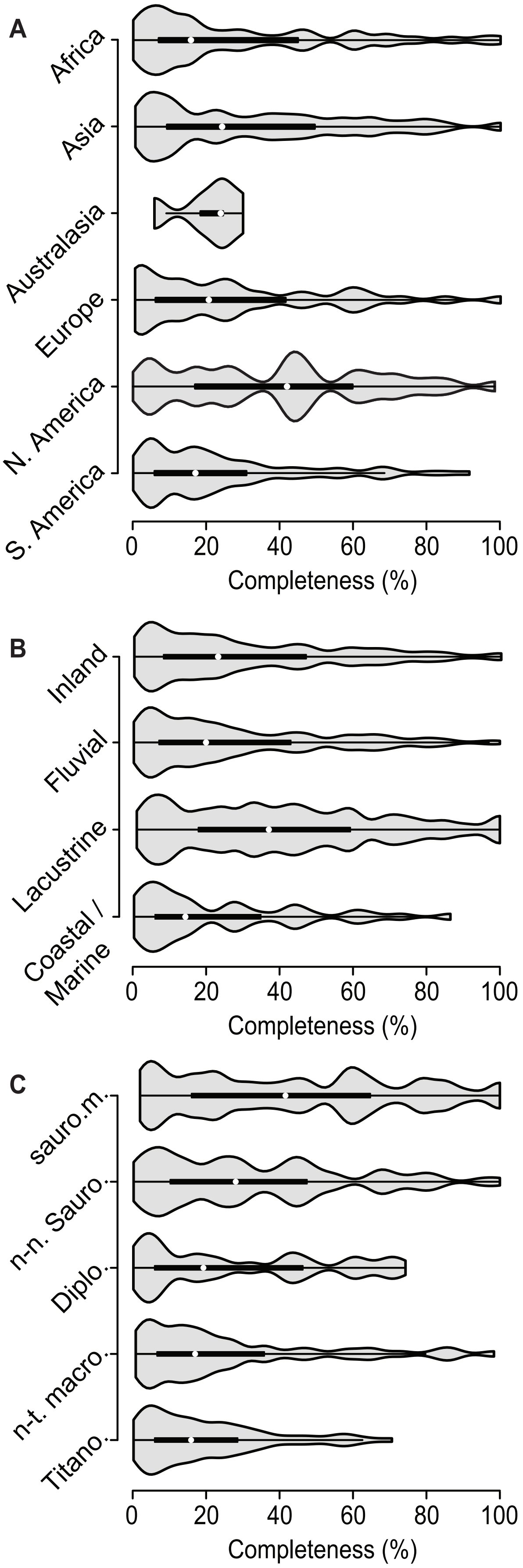


Figure 3.4. Distribution of sauropodomorph SCM2 scores between different A, continents; B, depositional settings, and C, sauropodomorph subgroups. Shaded polygon width represents the relative density of species. Abbreviations: sauro.m, non-Sauropoda; n-n. Sauro., non-neosauropod Sauropoda; Diplo., Diplodocoidea; n-t. macro., non-titanosaurian macronarians; Titano., Titanosauria. Note inland depositional settings includes both the fluvial and lacustrine terrestrial settings, as well as ‘others’ (aeolian, trap/fills).

The Late Jurassic has the joint second-worst palaeolatitudinal representation (33%), as species predominantly occur in the northern hemisphere and there are no occurrences outside of 20–50° N in the Oxfordian. Except for the Bajocian, which has average levels of geographical extent, the Middle Jurassic is also relatively poorly known. The remaining epochs have greater than 66% continental representation, but much more varied palaeolatitudinal representation. The Cretaceous is the only period represented in all occupied palaeolatitudinal bins, and has relatively high levels of palaeolatitudinal representation in its last three quarters (Table B.4; Fig. B.5). The only stage known from every continent is the Albian, which is also known from all palaeolatitudinal bins except 50–60° N, 10––20° S, and 20–30° S.

As stated above, the prominent drop in completeness across the Jurassic/Cretaceous (J/K) boundary is potentially the most interesting pattern in the updated sauropodomorph time series. A Late Jurassic peak in sauropodomorph diversity is consistently seen in North American, European and Asian time series (Fig. B.4), which corresponds to peaks seen in 20–30° N and 30–40° N palaeolatitudinal bins (Fig. B.5). Europe and Asia exhibit diversity drops from this peak into the earliest Cretaceous. However, South America does not exhibit the Late Jurassic peak, and instead shows a gradual diversity rise across the J/K boundary into the earliest Cretaceous, although this is accompanied with a drop in mean completeness (Fig. B.4). Furthermore, there is also little change in raw diversity and completeness in the 40–50° N palaeolatitudinal bin across the J/K boundary, and the Late Jurassic diversity peak is only partially present in one other latitudinal bin, 30–40° S (Fig. B.5).

3.3.2.5. Environmental completeness. In contrast to Mannion and Upchurch (2010a) we find no correlation between sauropodomorph completeness and changes in sea level through the entire Mesozoic, but we find a positive correlation for the Cretaceous when considered alone (Table 2; Fig. B.3C). However, excluding the Berriasian, Valanginian and Hauterivian (i.e. the first three stages of the Cretaceous) results in a significant negative correlation between sea level and completeness for the later Cretaceous (Table 2; Fig. B.3C).

Sauropodomorph species known from concentration Lagerstätten ('bonebeds' such as found in e.g. the Late Jurassic Morrison and Tendaguru formations of North America and Tanzania, respectively) are on average also significantly more complete than species known from non-Lagerstätten deposits ($W = 2701.5$, $p = 0.002$) (Fig. B.2D).

There is no significant difference in the distribution of completeness values between inland and coastal/marine deposits (Fig. 3.4B), even when separated between Triassic–Jurassic and Cretaceous species (Table B.5; Fig. B.2E). Species known from lacustrine deposits are significantly more complete than those from fluvial or coastal/marine settings (Table B.5; Fig. 3.4B). In all inland, coastal, fluvial and lacustrine deposits, the non-temporal distribution of completeness values is statistically much higher in the Triassic–Jurassic than the Cretaceous (Table B.5; Fig. B.2E). Temporal fluctuations in completeness for species found in fluvial, lacustrine or coastal environments each show a drop in mean completeness across the J/K boundary that never recovers to pre-Cretaceous levels (Fig. B.6).

3.3.2.6. Taxonomic subgroup, phylogenetic and body size completeness. Different sauropodomorph groups have contrasting levels of completeness. Non-sauropod sauropodomorphs have the highest distribution of completeness scores, which is significantly different to all other subgroups, except non-neosauropod Sauropoda (Table B.6; Fig. 3.4C). The latter has a distribution of completeness scores that is also not significantly different from any of the other subgroups, except Titanosauria, compared to which it has significantly higher levels of completeness. The remaining subgroups, Diplodocoidea, non-titanosaurian macronarians, and Titanosauria, all have distributions that are not significantly different from one another (Table B.6; Fig. 3.4C). Geological time series show consistently high completeness for non-sauropods, but fluctuations for non-neosauropod sauropod, diplodocoid and non-titanosaurian macronarian completeness, which all exhibit peaks in the Late Jurassic and lows in the earliest Cretaceous. Furthermore, titanosaur completeness gradually rises to moderate completeness levels, along with diversity, through the ‘middle’–Late Cretaceous (Fig. B.7).

Our sauropodomorph supertree, with skeletal completeness mapped on as a continuous character, can be seen in Figure B.8. Basal sauropodomorphs have a heightened abundance of higher completeness clusters, whilst branches with low completeness become more abundant in more derived lineages. Clusters of similar completeness can be seen, for example, among Diplodocidae, which tend to have moderate values, or Rebbachisauridae, which tend to have low levels of completeness. We detect a very strongly significant phylogenetic signal for skeletal completeness ($\lambda = 0.96$; $p = 1.77E-18$) for all sauropodomorphs, and a weaker, but significant signal, in just Sauropoda ($\lambda = 0.31$; $p = 1.70E-05$).

Figure 3.5 displays the relationship between species’ body mass estimates and completeness, as well as the same relationship for data from each of the three Mesozoic periods. The total plot shows data distributed along a broad arc, with species with high completeness known from a wide range of body sizes, species with large body sizes also known from a wide range of completeness scores, and only one species (*Chromogisaurus novasi*) known from small body size and relatively low completeness. We find a very weakly significant negative linear relationship between completeness and body size for all species ($R^2 = 0.03$; $p = 0.037$), but no relationship for solely the Triassic ($R^2 = 0.13$; $p = 0.3$), Jurassic ($R^2 = 0.03$; $p = 0.16$), or Cretaceous ($R^2 = 0.01$; $p = 0.6$) data. We also tested the linear relationship when solely considering Sauropoda, but still found no significant relationship ($R^2 = 0.001$; $p = 0.84$). Non-linear regressions also reveal no significant relationship whilst using either segmented ($p = 0.74$), hinge ($p = 0.65$), or upper hinge ($p = 0.06$) regression models.

Figure 3.6 shows the reduced composite phylogenetic tree with completeness and body size mapped as continuous characters. Phylogenetic independent contrasts reveal no significant relationship between completeness and body mass estimates for all Sauropodomorpha ($R^2 = 0.001$; $p = 0.69$) or solely Sauropoda ($R^2 = 0.02$; $p = 0.16$). Similar results were also found in PGLS tests for all sauropodomorph species ($R^2 = 0.003$; $p = 0.52$), as well as solely Sauropoda ($R^2 = 0.02$; $p = 0.14$).

The mean body mass time series gradually rises from the Carnian to peaks in the Bathonian and Kimmeridgian–Tithonian. There is then a drop in the earliest Cretaceous, a sharp rise to a peak in the Albian, followed by a gradual decline until the end-Cretaceous (Fig. B.3D). Time series correlations between mean, maximum and minimum body mass estimates and mean completeness per time bin reveal no significant correlations for mean and maximum estimates, but a significant positive correlation with minimum estimates (Table 2).

3.4. Discussion

3.4.1. Changes in our understanding of the sauropodomorph fossil record

As Mannion and Upchurch (2010a) showed, the number of identified sauropodomorph species has risen significantly in recent years and this trend is unlikely to halt in the near future. Exploratory fieldwork, detailed revision of historical collections, and applications of new methodological approaches, have all contributed to this increase in newly recognised species over the last few decades. This might indicate that our understanding of the sauropodomorph fossil record and changes in their diversity through time could substantially change in the next 10–20 years if discovery rates continue to rise (e.g. Tarver *et al.* 2011; Jouve *et al.* 2017; Tennant *et al.* 2018).

In general, over the last two decades workers have identified a much greater number of sauropodomorph species from less complete fossil remains than previously (Fig. 3.1). This is probably because of the growing understanding of the group's anatomy and phylogeny, enabling the identification of characteristic traits of various sauropodomorph subgroups with increasing confidence. A heightened scientific and popular interest in dinosaurs over the last few decades might also contribute to this increase in named sauropodomorph species, as highly incomplete material of other tetrapod groups is unlikely to be as intensely studied (Benton 2008, 2010). It is also logistically more likely that researchers will discover fragmentary skeletons with distinctive character-rich elements in the field and in understudied museum collections, than continuously find new, entirely complete skeletons.

Geological time series based on species known from before the year 2000 demonstrate substantial peaks and troughs in completeness, suggesting major fluctuations in preservation between time bins (Fig. 3.2). The downward trend in mean completeness through historical time suggests that completeness curves through geological time might also be destined to become lower and less variable as more species are discovered. As geological stages become more thoroughly sampled, more species are potentially identified from a wider range of completeness scores, and therefore the more likely a stage is to reflect average completeness across all species of the group in question. As our dataset produces roughly the same signals for data available in the last three decades, and there is relatively little change in the overall structure of the completeness time series (Table 1; Fig. 3.2), it is probable that we are beginning to see an accurate representation of the changes of the quality of sauropodomorph record through time (cf. Sepkoski 1993; Alroy 2000). We predict that additional future discoveries will have comparatively minor impacts on these completeness patterns.

In contrast, the lack of correlation between the current or pre-2010 completeness curve and the curve presented in Mannion and Upchurch (2010a) requires explanation (Table 1; Fig. 3.2). Because of similarities between the curves of the three most recent decades (2019, 2009, 1999; Table 1) derived from the data of the current study, the differences between our study and that of Mannion and Upchurch (2010a) must be primarily driven by taxonomic and stratigraphic revisions, rather than the discovery of new taxa. This is understandable as there have been many revisions of existing taxa (e.g. Tschopp *et al.* 2015), and more precise understanding of the stratigraphic ages for numerous formations and species (e.g. McPhee *et al.* 2017). These revisions are therefore critical to understanding the macroevolutionary history of sauropodomorphs and we agree with Jouve *et al.* (2017) that up-to-date taxonomic reviews are vital to understand accurate temporal changes in species diversity for different tetrapod groups.

Temporal changes in the raw diversity time series exhibit considerably larger fluctuations in comparison to time series from previous decades (Fig. 3.2). Tennant *et al.* (2018) found relatively strong increases in 'middle' and Late Cretaceous raw sauropodomorph diversity from 1991 to 2015, and noted the largest rise in subsampled diversity related to an increase of finds in the 'middle' Cretaceous. We also find strong increases in discoveries in the 'middle' and Late Cretaceous, even since 2009, and an additional rise in Early Jurassic occurrences (Fig. 3.2; Fig. B.1). Despite this, a significant correlation between the current curve and all historical time series suggests a roughly consistent understanding of sauropodomorph raw taxic diversity changes through geological time (Tennant *et al.* 2018). However, these correlations result from the prominent and consistently identified diversity peak in the Late Jurassic in all assessed decades, mostly driven by extensive discoveries in the Morrison Formation of North America and, to a lesser extent, the Tendaguru Formation of Tanzania. Therefore, our understanding of sauropodomorph diversity fluctuations outside of the Late Jurassic may yet change with additional findings (Tarver *et al.* 2011; Jouve *et al.* 2017; Tennant *et al.* 2018).

3.4.2. Impact of changes on understanding sauropodomorph evolution

The lowering and flattening of completeness curves through historical time (i.e. more consistent mean stage scores) should indicate that preservation per stage is less likely to influence the diversity changes we observe for a particular taxonomic group. However, the strong positive correlation between completeness and species richness indicates that our understanding of the sauropodomorph record is not free of the influence of preservation (Table 2; Fig. 3.2). This correlation persists after ten years of discovery and numerous taxonomic and stratigraphic revisions. This indicates that specimen completeness might bias our understanding of sauropodomorph diversity changes, although it is difficult to distinguish whether a poor/high quality record is the cause or the symptom of low/high observed diversity. It may be that genuine evolutionary events have driven diversity changes, altering the relative likelihood of preservation of specimens. However, as there is no correlation in the Triassic–Jurassic and Jurassic periods alone (Table 2), this suggests that the Cretaceous record has a strong influence on the total correlation between completeness and diversity, with the increased number of Cretaceous species in recent years likely being the driver. The Cretaceous is notable in having higher numbers of species in comparison to low mean completeness, which suggests that we either have a very good grasp of identifying species at this time (see below), or we are over-splitting isolated specimens into new species and inflating the record. It is likely that the steep increase in Cretaceous discoveries in the last 20 years, especially of often incomplete South American titanosaurs (Fig. 3.1), is driving the current understanding of Cretaceous sauropodomorph diversity changes.

A drop in diversity across the J/K boundary in several taxonomic groups has previously been interpreted as a potential extinction event (e.g. Barrett *et al.* 2009; Benson *et al.* 2010b; Starrfelt and Liow 2016; Tennant *et al.* 2016a, b). This was partially contended by Mannion and Upchurch (2010) because they noted a coincident drop in sauropodomorph completeness. This J/K decline has also been previously recognised in the theropod fossil record (Cashmore and Butler 2019, Chapter 2), and notable drops in completeness can be seen in the crocodylomorph (Mannion *et al.* 2019), avialan (Brocklehurst *et al.* 2012), and pterosaur (Dean *et al.* 2016) fossil records. With the current data, the decrease in sauropodomorph completeness at this boundary is much more severe than in previous studies. Moreover, the significant correlation between completeness and diversity calls the previously postulated extinction 'event' further into question, as there is no certainty that the significant diversity change across the boundary is not an artefact of preservation.

After the severe drop in sauropodomorph completeness at the J/K boundary, which continues through the earliest Cretaceous, completeness never recovers to pre-Cretaceous levels (Fig. 3.2). This shows a clear temporal segregation in the levels of mean completeness, which is corroborated by the statistically significant difference in the range of completeness values between the periods (Fig. B.2A). Because of increased finds through historical time and more even sampling (flattened completeness curves), we can identify periods of deficient preservation and potentially large-scale bias that impinge on our understanding of the sauropodomorph record.

3.4.3. Explaining the current completeness of the sauropodomorph record

3.4.3.1. Comparative completeness. The significant correlation between sauropodomorph and theropod mean completeness through geological time (Table 2) could mean that their records converge on a common dinosaur preservation signal, although the quality of the ornithischian fossil record has not yet been studied. It is possible that this signal is also more broadly representative of the Mesozoic terrestrial record, heralding from a common cause. This type of large-scale megabias in the fossil record would most likely be controlled by a combination of geology, taphonomy and sampling availability. A key similarity in both the sauropodomorph and the non-conservation Lagerstätte theropod fossil records is the fundamental difference in completeness between Cretaceous and pre-Cretaceous species (Fig. B.3B).

Cashmore and Butler (2019, Chapter 2) outlined some of the similarities between the completeness of the non-avian theropod fossil record and those of Mesozoic birds and pterosaurs (both estimated using the CCM). The recently studied CCM of terrestrial crocodylomorphs (Mannion *et al.* 2019) also shares a drop across the J/K boundary (though a very gradual decline in comparison to those other groups) and moderate completeness values in the latest Cretaceous. However, these are very broad similarities and we find no correlation between the current sauropodomorph SCM2 and any of these avialan ($R^2 = 0.02$; $p = 0.79$), pterosaur ($R^2 = 0.46$; $p = 0.30$) or crocodylomorph ($R^2 = 0.43$; $p = 0.82$) CCMs through time. There is also no significant correlation between the Cretaceous sauropodomorph and theropod temporal records (Table 2), and neither is there one in either the Triassic or Jurassic alone. Therefore, the drop in completeness across the J/K boundary seems to be key to the significant correlation recovered between the sauropodomorph and theropod records (Table 2).

Contrasting with the temporal signal, non-temporal sauropodomorph completeness values are significantly higher than those of theropods (Table B.1; Fig. B.2B), which could reflect significant preservational differences between the two groups, derived from palaeobiological or palaeoecological distinctions. Sauropodomorphs were mostly gregarious herbivores and so likely had higher population numbers than non-avian theropods (Upchurch *et al.* 2004; Myers and Fiorollo 2009), possibly enhancing their preservation potential (see Cashmore and Butler [2019, Chapter 2] for further discussion).

3.4.3.2. Geographical sampling bias. Sampling in each geographic hemisphere can be regarded as relatively even for sauropodomorphs (Fig. 3.3). The well-established historical focus of palaeontological research in the northern mid-latitudes is not that apparent in the distribution of the sauropodomorph fossil record, likely because of the huge growth in South American finds in recent decades (Fig. 3.1). Tennant *et al.* (2018) found that the most productive continents for dinosaur discovery have changed through historical time, as new regions became more favourable after exploration. However, the northern hemisphere still has a significantly more complete distribution of non-temporal SCM2 values than its southern counterpart (Fig. B.2C). The non-temporal distributions of completeness values between most continents are statistically similar (Table B.2), suggesting a generality of preservation influences and sampling effort.

The wave of recent palaeontological research has had little impact on the nature of the Australasian record: it is extremely temporally limited in comparison to every other continent (Fig. B.4), but its distribution of scores is not significantly different (Table B.2). This indicates that the quality of finds in Australasia is not a major problem. A similarly very limited Australasian record was also noted for theropod dinosaurs (Cashmore and Butler 2019, Chapter 2). Extreme landscape weathering and leaching of fossils have been suggested as causes of the poor Australasian dinosaur record (Rich and Vickers-Rich 1997). North America is unique for its high mean completeness scores and temporally patchy record (Fig. B.4) (Tennant *et al.* 2018), probably resulting from a combination of fortunate preservation regimes (e.g. Morrison Formation) and discontinuous continental deposition due to palaeoepicontinental seas (Chiarenza *et al.* 2019).

The South American record has seen the most drastic changes. Incredible numbers of South American (especially Cretaceous) sauropodomorph finds in the last thirty years (Fig. 3.1) (e.g. Jesus Faria *et al.* 2015; Pretto *et al.* 2018) suggest discoveries are far from finished (Tennant *et al.* 2018), and therefore current diversity and completeness curves may not be representative of this continent's wealth of potential information. However, it is notable in having the lowest average sauropodomorph completeness of any continent (Fig. 3.4). The low completeness of so many new Cretaceous finds in South America is probably the main driver of the lowering of global completeness through historical time (Fig. 3.2). Tennant *et al.* (2018) noted that the middle–Late Cretaceous sauropodomorph record in Africa, Asia, and South America has seen volatile changes in subsampled diversity and sampling coverage estimation from 1991 to 2015 due to taxonomic revision and new discoveries. Continents such as South America, Africa, Asia, and hopefully Australasia, should provide many more discoveries in future and could drastically change the outlook of the sauropodomorph fossil record and our understanding of diversity patterns.

No continental or latitudinal time series has a continuous fossil record for the entirety of sauropodomorph history (Fig. B.4), suggesting that our understanding of changing sauropodomorph diversity through time is driven by a strong intermix of provincial patterns (Tennant *et al.* 2018; Mannion *et al.* 2019). The Late Jurassic peak in raw diversity is primarily the result of finds from North America. In spite of relative peaks in Europe and Asia (Fig. B.4). the extensive diversity peak in the Kimmeridgian–Tithonian global record is only definitively seen in the North American time series, indicating that our understanding of the diversity changes of this period is heavily influenced by one continent. The South American signal departs radically from the global one (Fig. B.4) and hints at the possibility of an alternate regional evolutionary history in the southern hemisphere.

Although species from the earliest Cretaceous are represented in fewer modern continents than Late Jurassic species (Table B.3), they have been sampled from more varied palaeolatitudinal bins (seven), including 0–10° S (Table B.4).=To an extent, this means that there is a more even palaeolatitudinal sampling of the earliest Cretaceous in comparison to the Late Jurassic, which potentially indicates that the drop in raw diversity at the J/K boundary is a real change. The Cretaceous in general has a relatively even geographical distribution (Fig. 3.3), potentially because stratigraphically younger outcrops are more likely to survive geological processes. The Albian is represented in the most continents and palaeolatitudinal bins, closely followed by the Cenomanian (Table B.3, B.4). It is likely that these two stages have the most even and, in some ways, accurate representation of sauropodomorph diversity. Tennant *et al.* (2018) also found the Albian to have the highest subsampled sauropodomorph diversity, but one of the lowest sampling coverage estimates, indicating a stage with high global occurrence of species known from singleton specimens. However, it should be noted that Tennant *et al.* (2018) excluded species that were not constrained stratigraphically to one geological stage from their analyses, therefore possibly enhancing the diversity of the Albian relative to other less well constrained time bins. We must be cautious about delving too deeply into interpretations from global signals of completeness and diversity changes because they are conglomerations of regional patterns (Benson *et al.* 2016; Close *et al.* 2017; Mannion *et al.* 2019) and, as we demonstrate, regional records have exhibited strong changes through historical time (Fig. 3.1).

An almost complete absence of sauropodomorph finds at high modern latitudes (> 60° in both hemispheres), and a significant drop in occurrences at equatorial latitudes (Mannion *et al.* 2012; Poropat *et al.* 2016), creates a bimodal distribution of species richness and mean completeness per latitudinal bin (Fig. 3.3). This could represent geographically limited sampling opportunities and therefore indicate a significant spatial bias towards finding more sauropodomorphs in mid-latitudinal regions. This might partially be controlled by historical research interest, but probably has more to do with climate dynamics, vegetation cover, and subsequent erosion in modern day localities. Arid areas such as western North America and Patagonia, which have high levels of rock exposure, offer heightened availability of fossiliferous terrestrial Mesozoic horizons and possibly drive the observed latitudinal diversity and completeness signals (Raup 1972, 1976; Wall *et al.* 2009). Limited occurrences in higher and more equatorial latitudes might reflect a lack of consistently exposed fossiliferous localities because of extensive ice cover and vegetation overgrowth respectively, which greatly reduces the chances of successful discoveries. Although there might be a wealth of unsampled data at these latitudes, as species have been found (e.g. *Glacialisaurus hammeri* from Antarctica: Smith and Pol 2007), they need a great deal of effort to access and are much less 'profitable' than mid-latitudinal localities.

3.4.3.3. Climatic biases. The relative paucity of sauropodomorph occurrences from high and low latitudes and palaeolatitudes (Fig. 3.3) is not necessarily evidence of a significant spatial sampling bias, given that species might have been genuinely rare at such latitudes in the Mesozoic. None of the Late Triassic sauropodomorph species are known from equatorial palaeolatitudes (i.e. 30° N or S of the equator) or high latitudes (i.e >50° N or S of the equator), whilst Cretaceous sauropodomorphs have the greatest latitudinal spread, but still exhibit few occurrences of low completeness in equatorial palaeolatitudes (Table B.4; Fig. 3.3). It is possible that, at least at certain time intervals, the low taxonomic abundance and completeness in the low and high latitudes is in part due to climatic barriers, continental dynamics, physiological tolerances, and impact of resource availability on sauropodomorph populations (Nesbitt *et al.* 2009; Whiteside *et al.* 2011; Mannion *et al.* 2012; Poropat *et al.* 2016). However, as explained above, the modern equatorial and high latitudinal belts are regarded as grossly under-sampled due to difficult working conditions. Therefore, a lack of sauropodomorph abundance in similar palaeolatitudes is unsurprising and probably the result of a significant modern spatial sampling bias.

To test this, we downloaded all non-marine body fossil occurrences of Carnian–Maastrichtian tetrapods from the PBDB. We found no significant correlation ($R^2 = 0.28$; $p = 0.18$) between the number of sauropodomorph species and the number of tetrapod occurrences per 10° palaeolatitudinal bin when data from 50–60° N was included. This is because the latter palaeolatitudinal bin contains one sauropodomorph taxon (‘Cloverly titanosauriform’) included in our data set, in strong contrast to the large number of Mesozoic tetrapod occurrences in the same palaeolatitudinal belt (Fig. B.9), resulting in a lack of significant correlation. However, a very strong positive correlation is found when the 50–60° N bin is excluded ($R^2 = 0.82$; $p = 0.0002$). This means that sauropodomorph species distribution is not significantly different to the overall occurrences of all Mesozoic tetrapods, and therefore does not seem to indicate a climatic and ecologically driven absence of sauropodomorph remains at the lowest latitudes. However, the near-absence of sauropodomorphs from palaeolatitudes higher than 50° demonstrates some degree of palaeolatitudinal control on their distribution and therefore the quality of their fossil record. A similar latitudinal pattern is recognised in crocodylomorphs (Mannion *et al.* 2019).

3.4.3.4. Sea level and environmental bias. Variation in continental flooding due to sea level fluctuations has been regarded as a potential control on the amount of continental fossil material preserved within different time bins (Weishampel and Horner 1987; Haubold 1990; Hunt *et al.* 1994; Hedges *et al.* 1996; Sereno 1997; Smith 2001; Chiarenza *et al.* 2019), though no significant relationship has yet to be found (Fara 2002; Butler *et al.* 2010). Sea level highstands have been argued to both hinder and aid terrestrial tetrapod fossil preservation. Theoretically, at times of high sea level there is contracted terrestrial space and so less opportunity for terrestrial organisms to be fossilised, whilst at lower sea levels terrestrial space expands, increasing opportunities for preservation. On the other hand, it has been argued that higher sea levels might increase the quality of terrestrial vertebrate preservation as marine expansion inland reduces transportation distances and increases the chances of remains finding their way into coastal and marine depositional settings (assumed to have a higher preservation potential) (Haubold 1990; Hunt *et al.* 1994; Hedges *et al.* 1996; Sereno 1997; Smith 2001; Chiarenza *et al.* 2019). In contrast, it is thought at times of regression, heightened coastal erosion and longer transportation distance makes fossil preservation less likely even though the expanded terrestrial area probably promotes higher terrestrial diversity (Weishampel and Horner 1987; Chiarenza *et al.* 2019). These opposing mechanisms are not mutually exclusive. Lower sea levels likely create more terrestrial space, but at the same time reduce coastal preservation due to erosional properties, whereas higher sea levels probably reduce terrestrial space, but provide more opportunity for coastal preservation.

In contrast to Mannion and Upchurch (2010a), we now find no correlation between sauropodomorph completeness and changes in sea level throughout the entire time series (Fig. B.3C), and we find a positive correlation solely in the Cretaceous (Table 2). This suggests that sea level is poorly supported as a large-scale control on the sauropodomorph fossil record (Butler *et al.* 2010), but a positive Cretaceous correlation might favour the scenario where reduced terrestrial space aids preservation of terrestrial tetrapods through increased coastal erosion and depositional proximity, as described above. However, this result is likely due to outliers in the earliest Cretaceous, where a substantial sea level regression is concurrent with a drop in mean completeness. Removing the Berriasian, Valanginian and Hauterivian data results in a statistically significant negative correlation for sea level and completeness for the remainder of the Cretaceous. This demonstrates how the earliest Cretaceous differs substantially from the remainder of the sauropodomorph time series, and also how the quality of the remainder of the Cretaceous sauropodomorph record is possibly negatively affected by sea level rise and terrestrial environment contraction. To test whether the differing results found here and in Mannion and Upchurch (2010a) stem from differences in the statistical methodology employed, we compared the mean SCM2 time series from their dataset with fluctuations in sea level using the GLS regression applied in this study. The results maintained a significant negative relationship ($R^2 = 0.52$; $p = 0.008$) between SCM2 and sea level for the entirety of the time series, as reported in Mannion and Upchurch (2010a). This indicates that the differing results found here and in Mannion and Upchurch (2010a) do not stem from statistical tests used, but are probably related to substantial changes in the sauropodomorph SCM2 data in the last 10 years.

The large drop in sea level in the earliest Cretaceous (Fig. B.3C) is accompanied by both low sauropodomorph diversity and completeness, which could be caused by a reduction in fossil preservation in coastal settings due to rapid regression and subsequent erosion of those key environments. The first titanosaurs appeared and diversified as sea level rapidly rose during the remainder of the Early Cretaceous (Gorscak and O'Connor 2016). Their environmental preference changed away from coastal environments (with possibly higher preservation potential) to more inland settings, in combination with contracted localised environmental space (Mannion and Upchurch 2011), and this has been suggested as a partial explanation for the poor quality preservation of Cretaceous sauropodomorphs (Mannion and Upchurch 2010b). However, this makes the assumption that the coastal and marine fossil record preserves significantly more and better-quality terrestrial tetrapod fossils than more inland settings. This is not supported by our data. If fewer sauropodomorph skeletons deposited in coastal settings were to negatively impact the quality of their record, it would be expected that a reduction in diversity and completeness in the coastal realm would be matched with a relative increase (or at least no change) in completeness in the terrestrial realm. However, on average species found from Cretaceous coastal, inland, fluvial and lacustrine deposits are all significantly less complete than their Triassic–Jurassic equivalents. This is true both with and without the inclusion of earliest Cretaceous (Berriasian, Valanginian and Hauterivian) species, to account for the potential cofounding signal of non-titanosaurs living more predominantly in coastal environments in the time interval. There is also no significant difference between the average completeness of species from coastal and inland deposits in any interval (Table B.5; Fig. B.2E), indicating that Cretaceous completeness was not reduced by the expansion or contraction of one or more depositional environments. Therefore, we do not support the conclusion that a shift in Cretaceous sauropodomorphs to environments with lower preservation potential negatively impacted the quality of their record. This suggests the low Cretaceous completeness might be more intrinsically tied to other ecological or biological aspects of sauropodomorphs instead. However, to caveat this assumption, Mannion and Upchurch (2011) found that the total number of inland deposits decreased in North America and Europe during the mid-Cretaceous. Therefore, even if there is no detectable difference between the preservation of inland and coastal sauropodomorph fossils, our ability to sample potential sauropodomorph-bearing inland deposits is limited by the loss of sedimentary record, indicating the influence of larger scale geological processes.

3.4.3.5. Taxonomic and biological bias. Larger, more robust skeletal elements are generally thought to have a higher potential of surviving fossilisation in comparison to smaller, more delicate bones (Von Endt and Ortner 1984; Behrensmeyer *et al.* 2003; Soligo and Andrews 2005; Carrano 2006; Muñoz-Durán and Van Valkenburgh 2006; Farlow *et al.* 2010; Brown *et al.* 2013; Gardner *et al.* 2016). However, taxa with very large body sizes might be prone to greater skeletal fragmentation (Dodson 1990; González Riga and Astini 2007; Yeshurun *et al.* 2007; Bandeira *et al.* 2018), and possible exclusion from geographically constrained sites of exceptional preservation (Tennant *et al.* 2018). Therefore, in theory, both small and very large taxa might potentially be less likely to fossilise in comparison to intermediate size classes, reducing the completeness of such species, and possibly influencing our understanding of their abundance. This means that body size might be a major factor in fossil preservation, and could have a significant influence on the fossil records of different tetrapod groups (Cooper *et al.* 2006; Brocklehurst *et al.* 2012; Brown *et al.* 2013). A number of studies have documented taphonomic body size bias on local scales (Behrensmeyer *et al.* 2003; Soligo and Andrews 2005; Muñoz-Durán and Van Valkenburgh 2006; González Riga and Astini 2007; Brown *et al.* 2013; Zanno and Makovicky 2013), and others have noticed connections between completeness and body size (Cleary *et al.* 2015; Gardner *et al.* 2016; Driscoll *et al.* 2018). Carrano (2006) argued that there is also a sampling and preparation bias against large dinosaurs, as their skeletons are so challenging to collect and prepare thoroughly, but that this had a negligible influence on the overall understanding of evolutionary patterns. In contrast, O'Gorman and Hone (2012) stated that taphonomic processes have accentuated the preservation of large dinosaurs, but concluded that the skew towards them does not fully result from preservation bias, a view also held by Codron *et al.* (2013).

The overall body size-completeness scatterplot (Fig. 3.5) for sauropodomorphs shows a general concave arc that suggests that completeness is relatively high for small body sizes but declines as body size reaches a certain threshold (~1000–3000 kg). The very weak significant negative linear correlation between body size and completeness tentatively supports a trend towards lower completeness at larger body size. However, we find no significant non-linear relationship based on segmented, hinge, or upper hinge breakpoint estimated linear regressions, meaning the connection between the two variables does not seem to be two-sided. There is also no statistically significant correlation between the two variables when we account for phylogenetic relationships (Fig. 3.6). The very weakly significant positive temporal relationship between mean completeness and minimum body size (Fig. B.3D) might suggest the smallest body sizes of a population have an influence the level of completeness in particular time interval (i.e. as minimum body size increases so does specimen completeness). However, this is in opposition to the negative non-temporal correlation

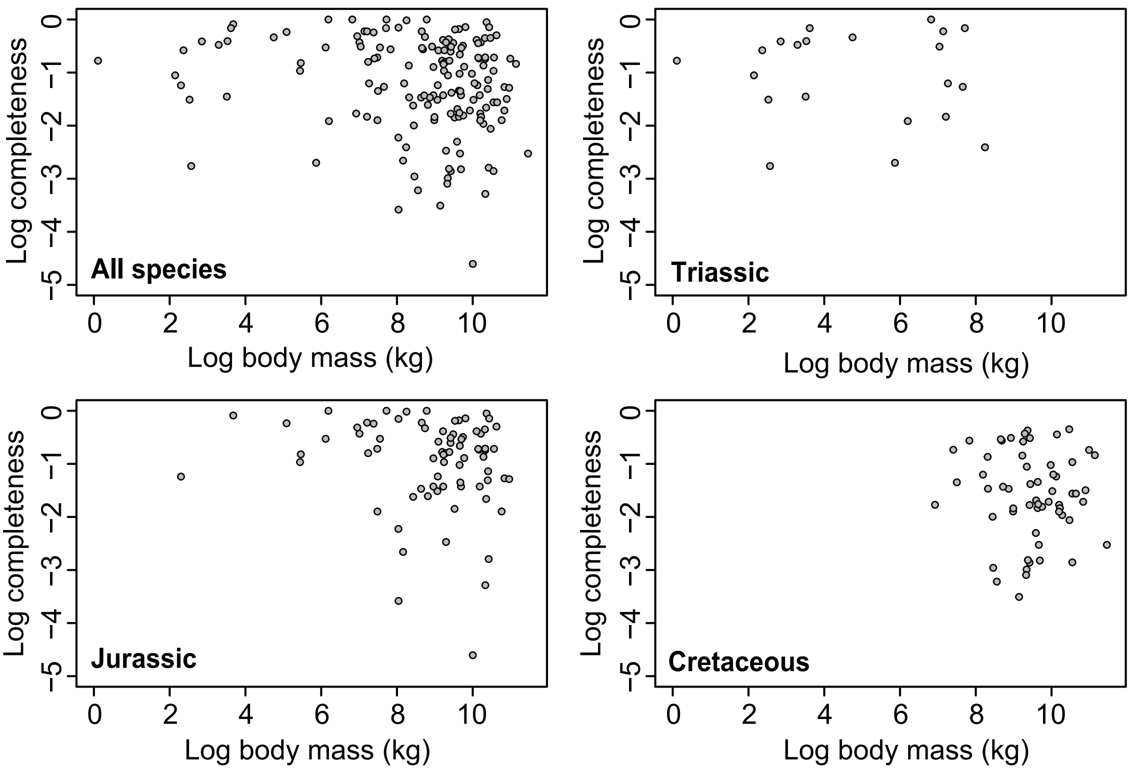


Figure 3.5. Scatter distribution of sauropodomorph SCM2 values in relation to logged body mass estimates, and separated for each Mesozoic geological Period.

described above, and the low explanatory power of the correlation and the lack of relationship between mean completeness and the mean and maximum body mass estimates suggest any control is tentative at best. Collectively, this strongly suggests that there is little relationship between sauropodomorph body size and specimen completeness on the global scale and, therefore, our understanding of the group's evolution might not be hampered by taphonomic size bias. This is somewhat unexpected, but a similar conclusion was reached for the theropod record (Cashmore and Butler 2019, Chapter 2). This also means that on a global scale, body mass cannot explain the much poorer Cretaceous record, despite the massive sizes attained by some titanosaurs. Various localised taphonomic studies show that bone preservation is more closely related to a combination of size, shape (Peterson and Bigalke 2013), density (Moore and Norman 2009), burial temperature (Elder and Smith 1988), substrate adhesion (Orr *et al.*

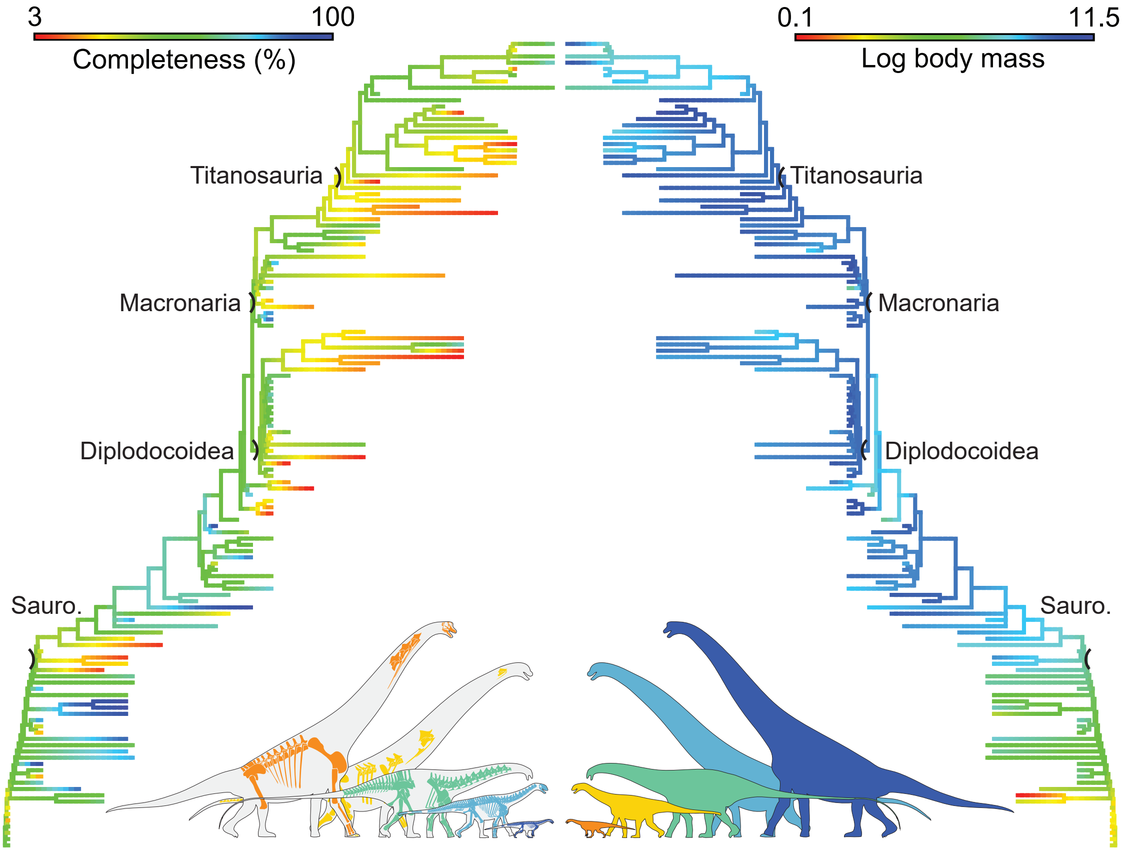


Figure 3.6. Composite trees depicting sauropodomorph relationships with SCM2 scores, and logged body mass estimates, mapped on as continuous characters, and displayed on a red-blue colour spectrum. Red represents low completeness and body size, while blue is high completeness and body size. Silhouettes used include work by S. Hartman (see http://phylopic.org/ for full licensing information). From the foreground to background, silhouettes represent *Riojasaurus incertus*, *Shunosaurus lii*, *Brontosaurus excelsusi*, *Brachiosaurus altithorax*, and *Dreadnoughtus schrani*. Abbreviations: Sauro., Sauropoda.

2016), physical processes (Britt *et al.* 2009; Boessenecker *et al.* 2014; Heijne *et al.* 2019), local taphonomic conditions (Maurer *et al.* 2014; Müller *et al.* 2019), and other less obvious biological factors (McNamara *et al.* 2011; Noto 2011; McNamara *et al.* 2012; Heijne *et al.* 2019) that might show no consistent global trend.

The non-temporal distributions of completeness scores of sauropodomorph subgroups have changed little in comparison to one another over the last 10 years. Mannion and Upchurch (2010a) reported only the mean completeness values of various groups of sauropodomorphs, but the same broad patterns are evident in our re-analysis. Non-sauropod sauropodomorphs have the most complete record, diplodocoids have a moderately complete record (but no complete species), and Titanosauria has the least complete record (Table B.6; Fig. 3.4). The Cretaceous produces considerably less complete sauropodomorph skeletons on average than preceding time intervals (Fig. B.2A), and a large component of that pattern is the consistently low completeness scores for titanosaurs (Fig. 3.4), which dominated many Cretaceous terrestrial faunas, and were the only sauropodomorphs to survive into the latest Cretaceous (Upchurch *et al.* 2004). In comparison, the higher completeness of non-titanosaurs, especially non-sauropod sauropodomorphs, might be the result of the fortunate preservational regimes in particular regions. For example, there are extensive bonebeds in the Late Triassic of western Europe (Sander 1992) and Late Jurassic of the western USA (Carpenter 2013), and productive formations in the Middle–Late Jurassic of China (Li *et al.* 2011), whereas there are no equivalent Cretaceous deposits preserving sauropodomorphs. González Riga and Astini (2007) argued that a particular taphonomic mode (“over-bank bone assemblage”), which disarticulates, re-orientates, and winnows skeletal remains, often preserves titanosaurs and is characteristic of Late Cretaceous Patagonian deposits. The strongly significant phylogenetic signal for completeness demonstrates that there are substantial taphonomic constraints acting on certain sauropodomorph subgroups that do not apply to others. However, this signal only demonstrates that there is a recognisable pattern to the sauropodomorph fossil record, and does not necessarily imply any underlying process (Blomberg and Garland 2002).

We can generally explain the relatively poor titanosaur record and, as a result, that of Cretaceous sauropodomorphs in general, on unfortunate preservational regimes, but there might be subtle biological and ecological influences too. Considering the two most contrasting subgroups, the bauplans of non-sauropodan sauropodomorphs and titanosaurs differ significantly, as do aspects of their physiology (Christiansen 1999), life strategy (Christiansen 1999; Sander and Klein 2006; Griebeler *et al.* 2013; Hofmann and Sander 2014), and ecological and environmental interactions (Barrett and Upchurch 2005), all of which might ultimately influence their respective fossil records. There are large differences in distance between the extremities and the main body of non-sauropod sauropodomorphs and titanosaurs. The long neck, tail, and even limb lengths of many titanosaurs might have led to the loss of many skeletal elements in comparison to non-sauropod sauropodomorphs, as taphonomic studies demonstrate that distal elements are lost first due to heightened disarticulation (e.g. McNamara *et al.* 2012a). Furthermore, large, derived sauropod species have been suggested to have had relatively low population densities in comparison to Cenozoic megaherbivore mammals, permitted by fast population recoveries due to oviparous reproductive strategy and rapid growth rates (Sander and Clauss 2008; Farlow *et al.* 2010; Sander *et al.* 2011; Codron *et al.* 2012, 2013; Sander 2013). This could have influenced the relative likelihood of fossil preservation of large titanosaur species in comparison to early-branching sauropodomorphs. Counterintuitively, juvenile sauropodomorph discoveries are rare, even though they likely constituted the largest proportion of sauropodomorph biomass (Farlow *et al.* 2010; Sander *et al.* 2011). The lack of consistent juvenile preservation has been argued to be the result of their more delicate (less mineralogically developed) skeletons or increased predation risk (Wilson *et al.* 2010; Griebeler and Werner 2011; Noto 2011; Sander *et al.* 2011; Bois and Mullen 2017). Higher ecological specificity (Bonaparte and Coria 2001; Sander *et al.* 2008; Sander *et al.* 2011; Griebeler and Werner 2011; Klein *et al.* 2012) could also have precluded some titanosaur species from consistent preservation in active depositional settings. In contrast, non-sauropod sauropodomorphs are regarded as having high ecological diversity, varying diets (McPhee *et al.* 2017; Müller and Garcia

2019), and different life strategies throughout ontogeny (Otero *et al.* 2019), which might have aided their ecological breadth, possibly enhancing their chances of preservation. Though only speculative, these potential natural influences, in combination with previously mentioned geological biases, may have generated variations in the quality of the sauropodomorph fossil record.

It is also possible that researchers may also be identifying numerous Cretaceous sauropodomorph species from fragmentary remains because of their derived and characteristic morphology. Different bones have varying diagnostic value throughout a skeleton, and which of those bones are most diagnostic depends on the taxonomic group in question (Rofthus 2002, 2005; Polly and Head 2004; Soligo and Andrews 2005; Bell *et al.* 2010; Mannion and Upchurch 2010a; Zeder and Pilaar 2010; Hendy 2011; Carrasco 2012; Richardson 2017). As Mannion and Upchurch (2010a) warned, completeness as defined by SCM and CCM does not necessarily equate to quality, or diagnosability, of specific material. Species known from entire skeletons can possess fewer unique and identifiable characters than species known from a few elements (Mannion and Upchurch 2010a). Though the relative diagnosability of individual sauropodomorph bones and subgroups has not yet been quantified, we can make some generalisations as to the usefulness of different skeletal regions.

In sauropods (especially eusauropods) for example, the presacral vertebrae are extremely character-rich, primarily relating to complex laminae. However, this is not the case for non-sauropod sauropodomorphs, whose presacral vertebrae are relatively undiagnostic. This means there are a greater number of unique characters associated with sauropod presacral vertebrae, and therefore isolated elements are likely to be more distinct and useful for confident taxonomic identification. Researchers also potentially have increased opportunity to recognise diagnostic sauropod characters if we further consider that their vertebral series constitute higher numbers of more robust individual vertebrae, which may give them a greater chance of preservation. The likelihood of preservation of diagnostic bones plays a pivotal role in positive taxonomic identification. Many titanosaur caudal vertebrae can be distinctly procoelous (Otero *et al.* 2011) and often the most common elements found in sauropod-bearing assemblages are caudal vertebrae and limbs (Winkler *et al.* 2000; González Riga and Astini 2007; Britt *et al.* 2009; Molnar 2010; Bandeira *et al.* 2018). It is possible that Cretaceous sauropodomorphs, especially titanosaurs, are more easily identifiable from limited material, enabling recognition of numerous species, but consequently reducing the average skeletal completeness in the period. By contrast, the successful identification of basal forms, especially non-sauropod sauropodomorphs, in some instances could require more complete skeletons if the available material is not significantly diagnostic for them, i.e presacral vertebrae.

On the other hand, there is the possibility that researchers have artificially oversplit Cretaceous species because of the isolated nature of remains (Mannion and Upchurch 2010a), subsequently inflating diversity whilst reducing average skeletal completeness. Benton (2008, 2010) postulated that a dramatic increase in new dinosaur species might have been driven by over detailed study of limited material because of media and career benefits that naming new species provided researchers. However, a satisfying answer to this oversplitting supposition would require a systematic overview of all Cretaceous sauropodomorphs, and therefore we can only speculate here. Although the relative diagnosability of subgroups is probably not the sole explanation for the low titanosaur and Cretaceous completeness scores, it is an additional factor that might influence the quality of the sauropodomorph fossil record.

3.4.3.6. *Specimen collection bias*. Fieldwork collection preferences and museum practice could also potentially influence the signals we perceive in our, and other, completeness studies. For example, there are known historical collection biases towards the sole acquisition of adult ceraptosian dinosaur skulls in some

North American localities (Goodwin and Horner 2010), and favoured dinosaur fossil collection from particular lithologies in the Hell Creek Formation (Lyson and Longrich 2010). An intentional dismissal of any specimen or any particular skeletal section for whatever reason could obviously lead to lower completeness of specimens for a species, and potentially influence correct identification of a species. Lower specimen and lithological, or environmental, sample size likely lower our understanding of diversity, disparity and ecology of a locality, and could affect our evolutionary understanding of a group. On the global scale, there does not seem to be such a clear collection bias towards any skeletal element or lithology associated with sauropodomorph fossils.

After material is collected, there is no guarantee that it quickly makes its way into scientific literature, as many specimens lie unprepared or undescribed for many years. The study presented here, and many previous studies, disregard such a potential wealth of unpublished museum material and so signals we perceive could potentially alter with its inclusion. Museums in close proximity to highly fossiliferous localities, or formations, with a long history of palaeontological collection will likely have a back catalogue of unprepared and undescribed specimens, which could reveal a wealth of new information. When non-published museum material is included in other studies significant changes to have been noted (e.g. Marshall et al. 2018). However, as the collection of this data is beyond the confines of this study, we can only speculate to what sauropodomorph material is available and how this influences our results. If we consider many dinosaur species are described from monospecific specimens, and tend to attract high levels of scientific attention we can suggest it is unlikely there are significant numbers of new species and complete specimens of previously described sauropodomorph species sitting in museum stores.

3.5. Conclusions

This is the first attempt to reassess the quality of the fossil record for a tetrapod group in such a retrospective manner. Through the use of a simple metric to quantify the completeness of fossil specimens, it is possible to keep a detailed track record of the changes in our understanding of a fossil group through historical time. This work acts as a test for the longevity of some of the conclusions made about the fossil record of a particular group. Our key conclusions, which themselves might need revising in ten years time, are as follows:

- Research findings change through historical time and are currently changing rapidly. Ten years of discoveries and revisions to existing taxa since Mannion and Upchurch (2010a)'s initial assessment of the completeness of the sauropodomorph fossil record has led to a number of specific changes, with the consistent fall in mean completeness of finds and the current completeness time series displaying a significantly different pattern. The current curve generally has fewer fluctuations and a much more pronounced drop in completeness in the earliest Cretaceous, with scores staying consistently low in the remainder of the period.
- The major differences between this study and the former are primarily driven by taxonomic and stratigraphic revisions. However, a well-developed understanding of sauropodomorph anatomy and relationships, heightened research interest in dinosaurs, and more thorough sampling in multiple geological stages and new localities has led to the discovery of numerous new species of low completeness, resulting in a reduced mean completeness in the current time series. Our understanding of the sauropodomorph fossil record could further substantially change in the next 10–20 years.
- However, despite major stratigraphic and compositional changes, some over-arching macroevolutionary signals from the sauropodomorph dinosaur fossil

record have remained the same over the last 10 years, including a significant correlation between completeness and diversity, and a significant drop in completeness at the Jurassic-Cretaceous boundary.

- These consistencies suggest that our current understanding of the sauropodomorph diversity changes may be influenced by the completeness of the sauropodomorph fossil specimens, and temporal and spatial sampling, especially in the Cretaceous. Sauropodomorphs have changes in their temporal fossil record that are significantly similar to those of theropod dinosaurs, and further similarities with other Mesozoic terrestrial tetrapods can be identified. Geological processes acting upon all Mesozoic terrestrial deposits may partially control changes in the sauropodomorph fossil record. The sauropodomorph record has relatively even spatial sampling which is likely to have some level of modern climatic control on its heterogeneity. Sauropodomorph completeness also has a strong phylogenetic signal, as early-diverging taxa are generally known from significantly more complete skeletons than more derived forms. However, species body size does not seem to have influenced the completeness of discoveries at the global scale, and therefore has not negatively influenced our understanding of sauropodomorph macroevolution.
- We find it difficult to explain the consistently lower completeness in the Cretaceous, as we cannot confirm that titanosaur environmental preferences significantly altered the quality of their record, and it seems unlikely that extreme body sizes obtained by Cretaceous species have substantial impact the quality of their record. The much lower Cretaceous completeness could, however, be related to sea level fluctuations and its changing influences on the terrestrial record, as well as much unfortunate preservation and increased sampling in those specific formations yielding ‘low-quality’ disarticulated remains. It could also be because of biological and ecological specificities of more

derived sauropodomorphs (e.g. titanosaurs) influencing their preservation likelihood, and/or recognisable remains of more morphologically distinct derived forms, enabling consistent species identification from less complete material.

- Studies of the completeness of the fossil record will never completely quantify the total knowledge collected for a particular fossil group, and so interpretations from these studies are transient. Reassessments, such as this study, will be increasingly necessary in future in order for palaeontologists to keep up with the vast number of discoveries, as well as taxonomic and stratigraphic revisions, that will occur. Research trends should not be ignored when inferring evolutionary processes from the fossil record.

4 | Taxonomic identification bias of theropod dinosaurs: preservation potential and diagnosability

4.1. Introduction

In Chapter 2, (Cashmore and Butler 2019) we assessed how the skeletal completeness of the theropod fossil record influences our understanding of the group using a metric devised by Mannion and Upchurch (2010). Along with other methodologically similar studies (Mannion and Upchurch 2010; Brocklehurst *et al.* 2012), we noted discrepancies between specimen completeness and raw taxonomic diversity at different times and/or localities (high completeness and low raw diversity, or low completeness and high raw diversity) which cannot be explained as a preservation control.

The completeness of a fossil record for a group or an individual specimen does not necessarily equate to 'quality' or the ease of taxonomic recognition (Mannion and Upchurch 2010). Species recognised from little material have been known to possess more unique and identifiable characters than species known from entire skeletons (Mannion and Upchurch 2010), and quantity of skeletal material does not even guarantee identification to low taxonomic levels. If some commonly preserved bones contain more unique characters in certain taxonomic groups than in others, palaeontologists would be able to more readily identify fossils of the former. However, if the diagnostic characters of a taxonomic group are found on skeletal elements unlikely to become fossilized, it therefore becomes less likely that discovered bones belonging to that group will be assigned correctly. The likelihood of preservation of individual diagnostic bones could therefore play a pivotal role in positive taxonomic identification and therefore our understanding of the diversity and evolutionary history of a group. Therefore, it is necessary to try to quantify the diagnostic quality of a fossil record in order to assess if there is a taxonomic identification bias.

Only a few studies have attempted to assess our ability to identify species in relation to preservation (Rofthus 2002; Polly and Head 2004; Rofthus 2005; Soligo and Andrews 2005; Plotnick and Wagner 2006; Bell *et al.* 2010; Zeder and Pilaar 2010; Hendy 2011; Carrasco 2013; Richardson 2017; Müller *et al.* 2018). In this study we quantify the preservation potential of all skeletal elements of theropods and calculate the diagnosability of their constituent bones, in an attempt to understand the influence of differential diagnosability on the taxonomic identification of different theropod species, and ultimately, our understanding of their temporal diversity patterns. We do this by utilising taxonomic diagnoses, which are concise paragraphs that describe key distinguishing traits of an ancient species, demonstrating its taxonomic validity, based on morphological information from fossils. We assess how bone occurrences, character assignments, and species diagnosability varies between different subgroups, geological formations and skeletal completeness levels. We also explore how diagnosability changes on local scales, by assessing specific quarries and environmental regimes of the famous dinosaur-bearing Morrison Formation, western USA. This novel assessment enables us to offer detailed explanations for the nature of the theropod fossil record and evaluate potential controls on our ability to identify species.

4.2. Methodology

4.2.1. Metrics

4.2.1.1. Diagnostic likelihood metric. In order to assess how fossil material influences our ability to confidently diagnose known theropod species we define a new metric that calculates the likelihood of recognising autapomorphies in relation to the preservation potential of individual elements, originally based on the metric used by Richardson (2017). For every known theropod species, we determined which skeletal elements were present or absent in the known fossil material. We then summed the occurrences of each individual element for the entire group (all species) and calculated the relative percentage of each in relation to all other elements, producing a relative preservation potential score for each element of the theropod skeleton (Fig. 4.1). For example, 2.24% of all known preserved theropod elements are maxillae. Furthermore, for each species we also gathered the number of autapomorphies (unique diagnostic characters) that have been identified for each skeletal element within taxonomic diagnoses (see Supporting data for links to the literature references). For example, the maxilla of *Duriavenator hesperis* has two autapomorphic features (Benson 2008). Knowing the number of autapomorphies used to diagnose a species per skeletal element, and how commonly each skeletal element is typically preserved in the theropod fossil record, we can calculate the diagnostic quality of each known theropod species. For each species we multiplied the specific autapomorphy number of each element by the overall preservation proportion of that element within the entire group (Fig. 4.1). For example, the two maxillary autapomorphies of *Duriavenator hesperis* are multiplied by the maxilla's occurrence percentage (2.24%) to produce an element specific diagnosability score of 4.48. This element specific diagnosability score (4.48) is then summed with all the other element specific diagnosability scores, derived from each element present for a taxon, producing an overall raw species diagnosability score. No other elements of Duriavenator hesperis have autapomophic features, so all of the remaining elements have an element specific diagnosability score of 0 (e.g. each element specific group occurrence percentage multiplied by zero autapomorphies), which results in an

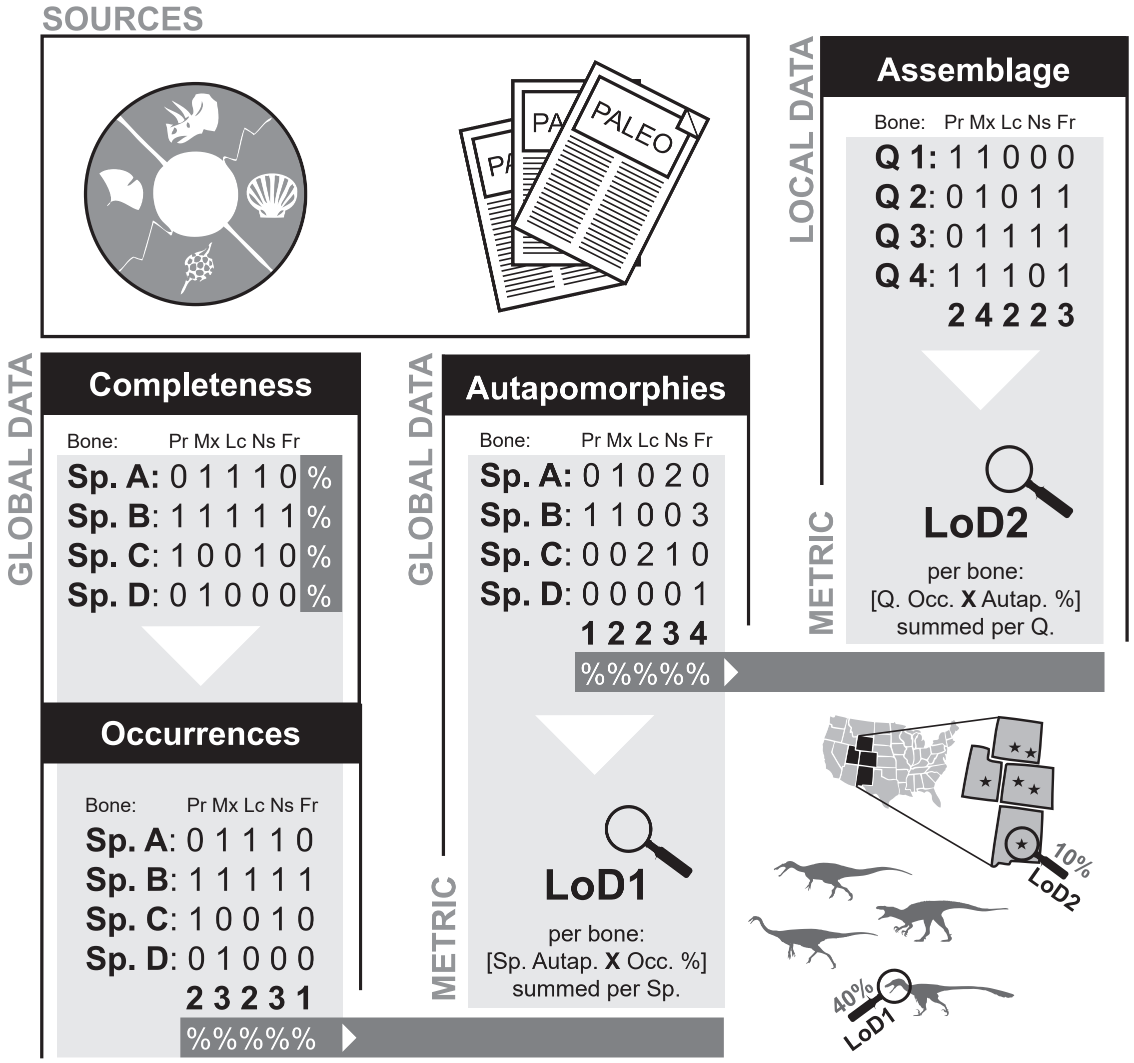


Figure 4.1. Diagrammatical representation of the process and methodology behind Likelihood of Diagnosis metrics. Skeletal completeness, autapomorphy and local assemblage data is gathered from the PBDB and literature sources. Completeness data is utilised to create proportional bone occurrence percentages. These are multiplied by the known autapomorphies of each bone per species, and the resulting scores summed to produce a LoD1 score for a species. Local assemblage data of bone occurrences, for example per palaeontological quarry, is multiplied by the proportion of autapomorphies assigned to each bone of a taxonomic group and summed per assemblage, to produce LoD2 scores.

overall diagnosability score of 4.48 (4.48 + 0) for the species. This score is then scaled between 0-1 in relation to all other species combined diagnosability scores. This here is defined as the Likelihood of Diagnosis 1 (LoD1). With this, we can identify which species were likely to be more easily recognised. To calculate the likelihood of diagnosing all of the known species in a more inclusive grouping of data (i.e. taxonomic subgroups, locality, formations, geological stages), we summed the LoD1 scores for the constituent species.

Alternatively, to assess how likely a specific assemblage or locality is to yield any recognisable theropod species, we use a different iteration of the LoD. Contrasting with the method described above, we initially sum all of the element occurrences of all identified theropod material within an assemblage or locality, resulting in an occurrence list of each element, representative of the number of different taxa a specific element is known for in the assemblage. For example, as far as the literature represents, the only theropod material from Quarry 14 of Como Bluff (Yale Peabody Museum) are skull and mandibular elements of one specimen of Allosaurus fragilis (Supplementary information), resulting in 1 element occurrence of the premaxilla, maxilla, and lacrimal (and so on) for the quarry. However, if another taxon were recognised from these same elements in the quarry then the overall element occurrence for the assemblage would be increased to two, for each of these elements. Once a definitive occurrence list of each element is collated for an assemblage, each element occurrence number (e.g. 1 occurrence of the premaxilla, maxilla and lacrimal in Quarry 14, Como Bluff) is multiplied with the proportion of autapomorphies assigned to that element for the entire group. The latter is derived from summarizing the number of autapomorphies assigned to each bone for all theropods in our dataset, and calculating the relative proportion of each. For example, 2.8%, 5.4%, and 1.8% of all theropod autapomorphies are associated with the premaxilla, maxilla and lacrimal, respectively. Once each element specific diagnosability score is calculated (e.g. 1x2.8, 1x5.4, 1x1.8), they are summed with all of the other element specific scores of the assemblage (e.g. 2.8+5.4+1.8) to create an assemblage specific diagnosability score (e.g. 10). These scores are then also scaled between

0-1 in relation to all other assemblages, and the resulting score defined as LoD2. This enables the assessment of the diagnostic potential of a bone assemblage regardless of the validity of the material but does take into account the number of representative taxa.

4.2.1.2. Completeness metrics. Mannion and Upchurch (2010) devised two completeness metrics to quantify the proportion of information preserved for an individual fossil specimen or species. The first estimates the proportion of a complete skeleton that is preserved, the skeletal completeness metric, and the other determines the number of characters that can be scored, the character completeness metric. We used estimates of completeness to test if there are significant relationships between the diagnostic information available for a species and the quality of preservation of that species. We opted to solely use the skeletal completeness metric (SCM2) as it has more natural connections to taphonomy, sedimentology, depositional environment and weathering, and little philosophical overlap with species diagnoses in comparison to the character completeness metric.

4.2.2. Datasets

We identified the individual skeletal elements referenced in autapomorphy-based taxonomic diagnoses and the number of times they were referenced for all valid theropod species except those solely known from isolated teeth (see Supporting data) (Fig. 4.1). This information was only gathered from taxonomic diagnoses in systematic palaeontology sections and not any additional descriptive text in reference to each species. Species with multiple diagnostic revisions were represented by the most recent revised diagnoses. We opted to use only diagnoses post-1980 as modern cladistic techniques were not strictly conformed to prior to this time, and we only incorporate diagnoses from peer-reviewed publications. Not all diagnoses purely contain autapomorphies, and so we include 'autapomorphic-equivalent' diagnoses, ones using apomorphies and unique combination of characters. All plesiomorphic, synapomorphic and differential diagnostic references to individual elements were removed from scoring as identification of unique characters is key for new species identification. Unique characters referring to entire body partitions (e.g. skull length), integument (e.g. feathers), or fenestrae with multiple element contacts, could not be assigned to specific elements and were therefore removed, but characters associated with multiple specific skeletal elements (e.g. measurement ratios between two bones) were assigned and scored to all of the elements specified. From these scores we then calculated the proportion of diagnoses used per element in comparison to all elements (e.g. 10% of all autapomorphies used to identify theropod species refer to the maxilla).

We utilised the theropod completeness dataset of Cashmore and Butler (2019; see Chapter 2) to obtain skeletal completeness scores, and updated it to include all new theropod species published since that publication. It includes all valid species, as well as non-valid species and phylogenetically informative specimens previously included in cladistic analyses. We believe the inclusion of the latter specimens provides a more representative outlook of the global content of the theropod fossil record than valid species alone.

We then used the completeness data to generate a dataset depicting the presence or absence of each skeletal element for each taxon (Fig. 4.1). In this case, elements with multiple component bones (e.g. teeth, vertebrae, ribs, digits) were treated as one individual element, either present or not. A second iteration also attempted to reflect the true relative abundance of each bone, as we estimated the number of individual teeth, vertebrae, ribs, gastralia and manual and pedal phalanges per species. Due to the nature of the Cashmore and Butler (2019) dataset these estimations had to be projected from raw completeness scores based on the expected number of elements per continuous series for each species. From both of these iterations, we calculated the relative percentage of occurrences of each individual skeletal element, and applied them to different analyses. The relative abundance was used to calculate element preservation potential for comparisons with autapomorphy numbers (Fig. 4.2). By contrast, presence-absence data (or number of species with a specific element) was used in order to estimate diagnostic likelihood and taphonomic preservation. This is because the diagnostic attributes of continuous elements are strongly favoured when we utilise the relative abundance of each individual element as they consist of many more individual bones than the other regions of the skeleton, and so automatically gain high levels of preservation potential and diagnostic likelihood.

We also gathered theropod bone occurrences for 96 theropod-bearing quarries of the Morrison Formation, USA, using a quarry list from a revision of the formation's chronostratigraphy (Maidment and Muxworthy *in press*). We scored bone presence-absence of each taxon found in each quarry based on taxonomic occurrences listed in the PBDB (Fig. 4.1), cross-referenced with Foster (2003), a substantial palaeoecological analysis documenting the vertebrate fauna of the Morrison Formation. Much of the bone data was gathered from other literature and online catalogues where available. All occurrences of any identifiable theropod material was included in the dataset, including specimens indeterminate at low taxonomic levels. We could not obtain adequate information for 39 additional theropod-bearing quarries from the available literature or online catalogues.

Furthermore, most of the quarries have also been associated with a specific stratigraphic sequence and systems tract (Maidment and Muxworthy *in press*), defining their depositional and palaeogeographical contexts. Summarised definitions derived from Maidment and Muxworthy (*in press*) are as follows: STA2 comprises isolated channel fill facies of anastomosing channels and ephemeral lakes, with a moderate accommodation space/sediment input (A/S) ratio, in relatively close association to the Sundance Sea. STB3 is an amalgamated channel belt facies deposited under low A/S conditions and maximum progradation, with isolated channel fill and well-drained floodplain settings near the top of the sequence in some localised areas. STB4 records a key shift to very high A/S conditions with extensive wetland and lacustrine facies across the most of the depositional basin, with the large lake 'Lake T'oo'dichi' occupying a significant portion of areal extent. STC5 exhibits a sharp change from lacustrine dominated deposition to conditions with low accommodation space and sedimentary input, resulting in widespread palaeosol formation within a generally isolated channel fill facies, associated with a well-drained floodplain. STC6 was interpreted as a poorly-drained floodplain and wetland/lacustrine facies association deposited under high A/S conditions with low sedimentary input and comparative geographic restriction due to tectonic migration of mountainous regions over a majority of the former basin sea (Maidment and Muxworthy *in press*).

4.2.3. Global subdivisions and analyses

4.2.3.1. Non-temporal. Species were subdivided into their respective geological formations and the summarised LoD1 of each calculated in order to identify formations of particularly high or low diagnosability that could be influencing our ability to identify theropod species in different temporal and spatial settings. The formations were then ranked and the LoD1 scores compared to the number of valid species found in each respective formation and the mean completeness of each formation.

We also split the data by the major theropod subgroups: basal Theropoda, basal Neotheropoda, Ceratosauria, basal Tetanurae, Megalosauroidea, Allosauroidea, Megaraptora, basal Coelurosauria, Tyrannosauroidea, Compsognathidae, Ornithomimosauria, Alvarezsauroidea, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae, and non-deinonychosaurian

Paraves. We follow the phylogenetic relationships used in Chapter 2, for which species assignment reasoning is outlined in Appendix A. We then calculated the relative proportion of autapomorphies, relative proportion of bone occurrences, and the summarised LoD1 scores for each subgroup. This enabled us to identify the different elements that are most often preserved and are diagnostic for each theropod subgroup. Using this data we could also estimate the likelihood of diagnosing members of each theropod subgroup from each element. We statistically correlated the relative percentage of autapomorphies assigned to each bone with the relative percentage of occurrences of each bone, for all species, and separately for each subgroup. We also compared the subgroup specific LoD1 scores with species diversity and mean completeness per subgroup.

In order to assess how taphonomy influences the occurrence of different skeletal elements and our ability to identify species, we split all theropod species by their completeness scores into 20 categories, each representing a 5% spread of completeness values (i.e. 100–95%, 95–90%, etc). We then summed the number of times each skeletal element was present from all the constituent taxa of each completeness category (taphonomic time). Based on these summed taxon-bone occurrences, we were able to calculate the relative proportion of occurrences of each element within each completeness category (proportioned within each completeness category), and the relative proportion of occurrences of each element throughout all the completeness categories (proportioned through all completeness categories by each element). We therefore were able to create a global sequence of taphonomic loss for theropods, allowing us to determine the relative survivorship of different skeletal elements through taphonomic processes. Following this principle, we also calculated the proportion of autapomorphies assigned to each skeletal element per completeness category and relative to the same specific elements in all completeness categories, in order to assess the taphonomic influence on the identification of unique characters.

4.2.3.2. Temporal. To examine how temporal changes in theropod species richness have potentially been influenced by our ability to diagnose species we calculated the total number of element occurrences and autapomorphies assigned per geological stage-level time bin from the Carnian to Maastrichtian, plus calculated the mean species LoD1 per stage and an overall LoD1 score for each stage. Minimum and maximum stage dates were determined from Walker *et al.* (2018). Stage-level time bins were used for ease of comparisons with sampling proxy data and with completeness data from the majority of previous studies. Species that were present over multiple geological stages, or have an uncertain stratigraphic age, were included in each stage in which they were potentially present. We further split the number of temporal occurrences and autapomorphies by different skeletal regions to assess specific changes in their abundance. The skeletal regions are the skull, mandible, dentition, vertebrae, ribs, pectoral girdle, forelimbs, pelvic girdle, and hind limbs. We tested the temporal relationship between changes in mean species LoD1, stage-level LoD1, raw species diversity, mean completeness, the number of assigned autapomorphies and the number of individual bone occurrences. We also statistically compared the temporal relationship between the number of autapomorphies and bone occurrences per skeletal region.

4.2.4. Localised case study: Morrison Formation

We look at the Morrison Formation, USA, one of the most well-known and richest dinosaur-bearing formations in the world, to assess how the diagnostic quality of individual theropod bones and species change in a spatially and temporally localised assemblage with relatively minor environmental fluctuations.

Firstly, to assess our ability to identify the presently known species in the

Morrison Formation, we calculated the LoD1 for each quarry and systems tract based on tallied species-level LoD1 scores. Unfortunately, the most abundant component of Morrison Formation theropod fauna, *Allosaurus fragilis* (Foster *et al.* 2018), lacks an autapomorphy-based diagnosis. Therefore, it could not naturally be included into the summarised LoD1 scores for each quarry and systems tract. To work around this, we included autapomorphy-based diagnoses of Morrison genera. We scored the autapomorphies in the same manner as species-level diagnoses and thus assigned LoD1 scores for all Morrison material identified to genus-level. This allowed us to include *Allosaurus fragilis*, along with every other occurrence identified as *Allosaurus* sp. Other species of *Allosaurus*, for which species-level diagnoses are available, were scored in the same manner as the global record, as were the remainder of the Morrison species. Collectively, we assigned LoD1 scores to 97 of the sampled Morrison quarries, as these include valid genera and species occurrences for which the individual LoD1 scores could be tallied. 75 of these quarries were previously assigned to systems tracts and so contributed to the summarised scores of the latter.

Separately, we also applied the LoD2 metric to assess the potential of identifying any theropod species within each quarry and systems tract. This utilised the quarry-bone occurrence dataset and enabled us to assess the diagnostic potential of quarries without known valid taxa. We were able to score bone occurrences for 90 Morrison quarries, 71 of which included valid genera and species. Some quarries were excluded as theropod fossil assignments were based on either fragments or trace fossils, or the bone information was not presently available. 69 of these successfully scored quarries have assigned systems tracts, and so contributed to LoD2 scores per systems tract.

Each quarry and systems tract were ranked based on each metric. We then statistically compared the LoD1 and LoD2 scores with one another, to generic richness and number of different taxa per quarry and systems tract. Furthermore, we statistically tested for a correlation between Morrison species LoD1 and the minimum number of individuals of each obtained from our quarry dataset.

4.2.5. Statistical tests and plotting

R was used to perform all statistical tests and initially create all plots. Time series plots were produced using the package ggplot2 (Wickham *et al.* 2018), radial plots and the pyramid plots were created with the package plotrix (Lemon *et al.* 2019), and the taphonomic maps were produced through the base R heatmap() function.

All temporal and non-temporal correlation tests employed generalized least-squares regressions (GLS) for linear comparisons with the function gls() in the R package nlme (Pinheiro *et al.* 2018). First order autoregressive model (corARMA) is applied to the data, to reduce the chances of overestimating statistical significance due to temporal autocorrelation. Prior to analysis time series were log-transformed to ensure normality of residuals and homoscedasticity (constant variance). We further calculated a likelihood-ratio based pseudo-R^2 values by using the function r.squaredLR() of the R package MuMIn (Bartoń 2018).

4.3. Results

4.3.1. Preservation likelihood and taxonomic diagnoses

Figure 4.2A shows the relative proportion of occurrences and autapomorphies assigned to the major regions of the theropod skeleton. Table C.1 outlines the percentage of occurrences and assigned autapomorphies of each skeletal element, and Table C.2 summarises the resultant diagnostic use of the elements for all theropods and each subgroup.

When considering relative abundance of elements we identify that most occurrences come from the vertebrae. This is closely followed by the ribs, hind

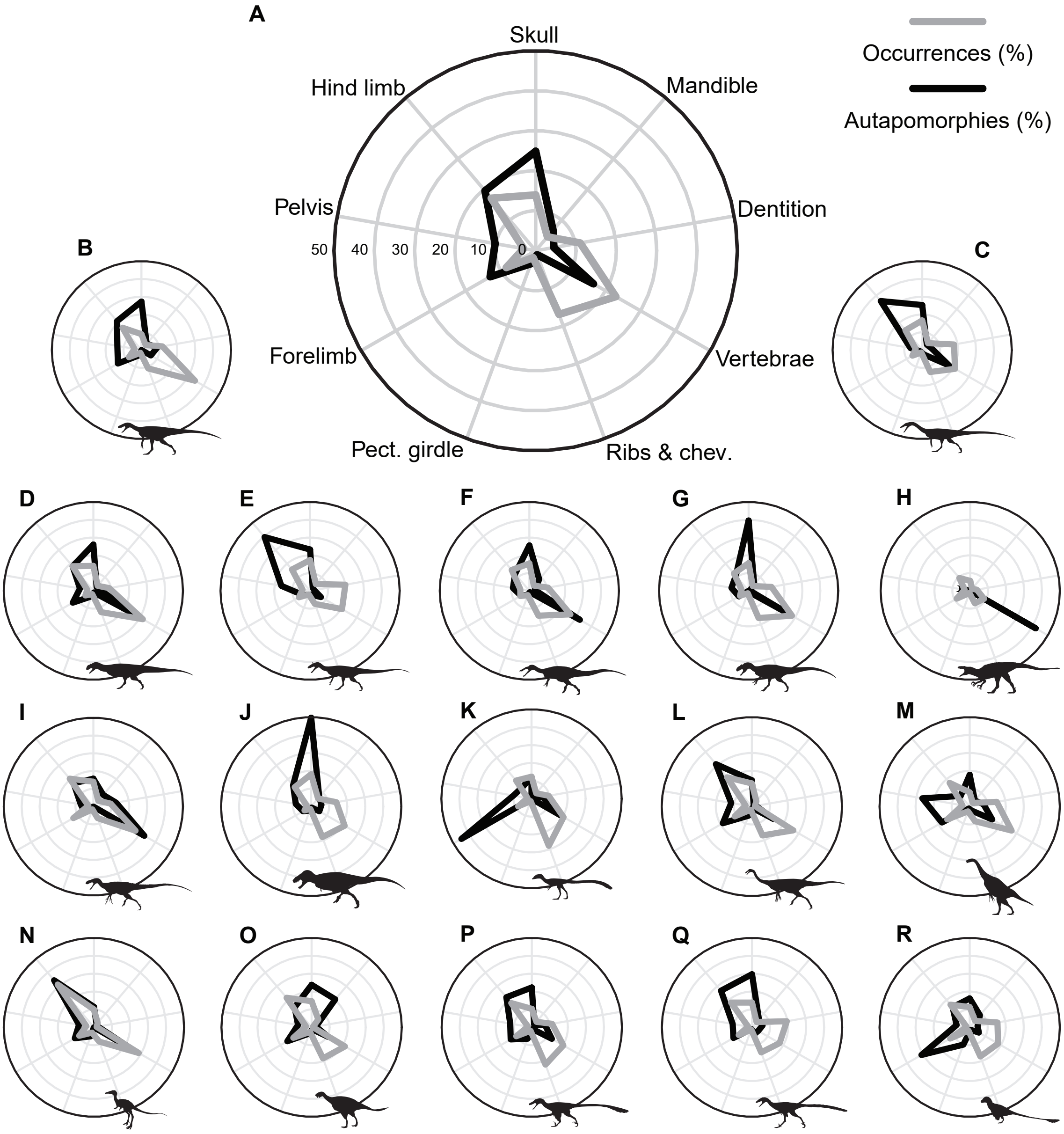


Figure 4.2. Radial plots showing the relative percentage of occurrences of, and autapomorphies assigned to, the major regions of the skeleton, for: A, all theropod species; B, basal Theropoda; C, basal Neotheropoda; D, Ceratosauria; E, basal Tetanurae; F, Megalosauroidea; G, Allosauroidea; H, Megaraptora; I, basal Coelurosauria; J, Tyrannosauroidea; K, Compsognathidae; L, Ornithomimosauria; M, Therizinosauria; N, Alvarezsauroidea; O, Oviraptorosauria; P, Dromaeosauridae; Q, Troodontidae; R, non-avialan Paraves. All subgroup outer circles represent 50%, apart from H, which represents 100%. Abbreviations: chev., chevrons; Pect., Pectoral. Silhouettes used include work by S. Hartman, T Michael Keesey, T. Tischler, J. Conway, Funkmonk, and M. Martyniuk (see http://phylopic.org/ for full licensing information). From A to R, silhouettes represent:

(Fig. 4.2. Continued) *Herrerasaurus ischigualastensis*, *Coelophysis*, *Majungasaurus crenatissimus*, *Cryolophosaurus ellioti*, *Baryonyx walkeri*, *Allosaurus fragilis*, *Australovenator wintonensis*, *Stokesosaurus clevelandi*, *Tyrannosaurus rex*, *Compsognathus longipes*, *Gallimimus bullatus*, *Shuvuuia deserti*, *Nothronychus mckinleyi*, *Oviraptor philoceratops*, *Velociraptor mongoliensis*, *'Troodon' formosus*, *Scansoriopteryx heilmanni*.

limb elements and skull elements (mostly the maxilla and dentary) respectively, whereas the pectoral and pelvic girdles have the most limited preservation potential (Fig. 4.2A). Individual elements with the highest preservation potential are the dorsal and caudal vertebrae, femur and tibia, and the metatarsals and pedal digits respectively (Table C.1). The least are the sternal elements, furcula, carpals, tarsals, and gastralia. We find that most theropod autapomorphies come from the skull (Fig. 4.2A), predominantly from the maxilla and dentary, and the hind limb has the next highest number, with metatarsals, femora and tibiae contributing the most (Table C.1). This is closely followed by the vertebrae with high proportions of autapomorphies attributed to each of the cervicals, dorsals, and caudals. The forelimbs (mostly manual digits, metacarpals and humerus) and pelvic girdle (mostly ilium and pubis) have moderate numbers of unique characters, but the dentition, pectoral girdle and ribs have the least (Fig. 4.2A), in consecutive order.

When taking into account the preservation likelihood we find the major elements that will most likely lead to a positive diagnosis of a theropod species are the metatarsals (Table C.2). These are followed sequentially in rank order by the caudal vertebrae, cervical vertebrae, dorsal vertebrae, maxilla, femur, tibia, ilium, pubis, dentary, manus digits, dentition, humerus, metacarpals, ischium, frontal, astragalus, and then a variety of lower diagnostic likelihoods for the remainder of the available skeleton.

There are significant positive correlations between the percentage of

Table 4.1. Results of pairwise comparisons between the percentage of total occurrences and assigned autapomorphies for each skeletal element per subgroup, using GLS. Statistically significant results indicated in bold. Abbreviations: autap., autapomorphies; occ., occurrences Paraves., non-avialan Paraves.

Comparison	Slope	t-value	p-value	R^2
occ. ~ autap.	1.79	9.24	**0**	0.67
basal Theropoda occ. ~ autap.	1.02	4.14	**0.0001**	0.21
basal Neotheropoda occ. ~ autap.	1.98	4.42	**0**	0.27
Ceratosauria occ. ~ autap.	1.27	5.04	**0**	0.32
basal Tetanurae occ. ~ autap.	1.80	4.88	**0**	0.23
Megalosauroidea occ. ~ autap.	1.38	8.53	**0**	0.63
Allosauroidea occ. ~ autap.	1.51	5.10	**0**	0.31
Megaraptora occ. ~ autap.	0.13	0.22	0.8265	0.18
basal Coelurosauria occ. ~ autap.	1.78	6.00	**0**	0.50
Tyrannosauroidea occ. ~ autap.	1.95	4.92	**0**	0.38
Compsognathidae occ. ~ autap.	0.64	0.80	0.426	0.28
Ornithomimosauria occ. ~ autap.	1.68	6.84	**0**	0.57
Therizinosauria occ. ~ autap.	0.92	4.18	**0.0001**	0.43
Alvarezsauroidea occ. ~ autap.	1.43	9.97	**0**	0.62
Oviraptorosauria occ. ~ autap.	1.64	4.39	**0**	0.25
Dromaeosauridae occ. ~ autap.	1.88	6.41	**0**	0.42
Troodontidae occ. ~ autap.	2.16	6.32	**0**	0.41
Paraves occ. ~ autap.	2.51	3.80	**0.0004**	0.24

total occurrences and assigned autapomorphies for each skeletal element for all theropods, and within all subgroups, apart from Megaraptora and Compsognathidae (Table 4.1). There are also a number of key finding of interest regarding individual subgroups. The most diagnostically useful elements to identify basal theropods and neotheropods are derived from the tibia, whereas cervical characters are by far the most diagnostic for ceratosaurs (Table C.2). All megaraptoran autapomorphies come from the dorsals, sacrals and ilium, with the dorsals being the most diagnostic (Fig. 4.2H, Table C.1). Autapomorphies are heavily weighted in the maxilla for tyrannosauroids and in the manual digits for compsognathids (Table C.1), whereas the dentary is substantially the most diagnostic element of oviraptorosaurs (Table C.2).

On average species are assigned five autapomorphies or autapomorphy-equivalents, whilst 37 is the highest assigned to a species (*Deinocheirus mirificus*).

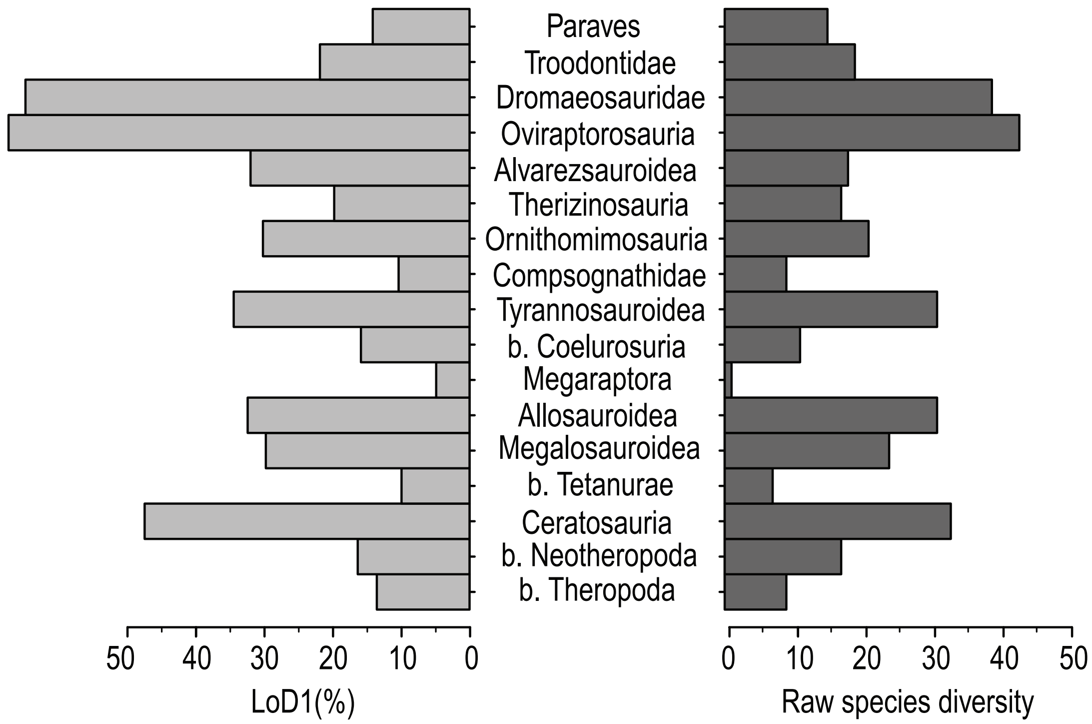


Figure 4.3. Pyramid plot comparing the summarised LoD1 scores to taxonomic diversity of each theropod subgroup. Abbreviations: b., basal; Paraves., non-avialan Paraves.

When taking into account the preservation of different elements, *Deinocheirus mirificus* is the species with the highest likelihood of diagnosis and *Shidaisaurus jinae* is the species with the lowest. The mean relative diagnosability is ~16% of the most diagnostic species, and most species have ~5-20% relative diagnosability. There is a very weak but significant positive relationship between the species LoD1 and completeness score per species ($R^2 = 0.07$; $p = <0.0001$).

When specimen information for each subgroup is collated, we can calculate the diagnostic likelihood of the entire group. We find that Oviraptorosauria and Dromaeosauridae have the highest diagnosability by a substantial margin (Fig. 4.3). The next highest is Ceratosauria, which still has much higher diagnostic likelihood relative to the remaining theropod subgroups. Tyrannosauroidea, Allosauroidea, Alvarezsauroidea, Megalosauroidea and Ornithomimosauria all have moderate diagnostic likelihoods, and the remaining subgroups are all relatively low, with exception of Megaraptora, which has a very low diagnostic likelihood (Fig. 4.3). We find a strong positive relationship between the diagnostic likelihood and the taxonomic diversity of each subgroup ($R^2 = 0.91$; $p = >0.00001$), but no relationship with the mean completeness of each subgroup ($R^2 = 0.02$; $p = 0.63$).

4.3.2. Taphonomic preservation sequence

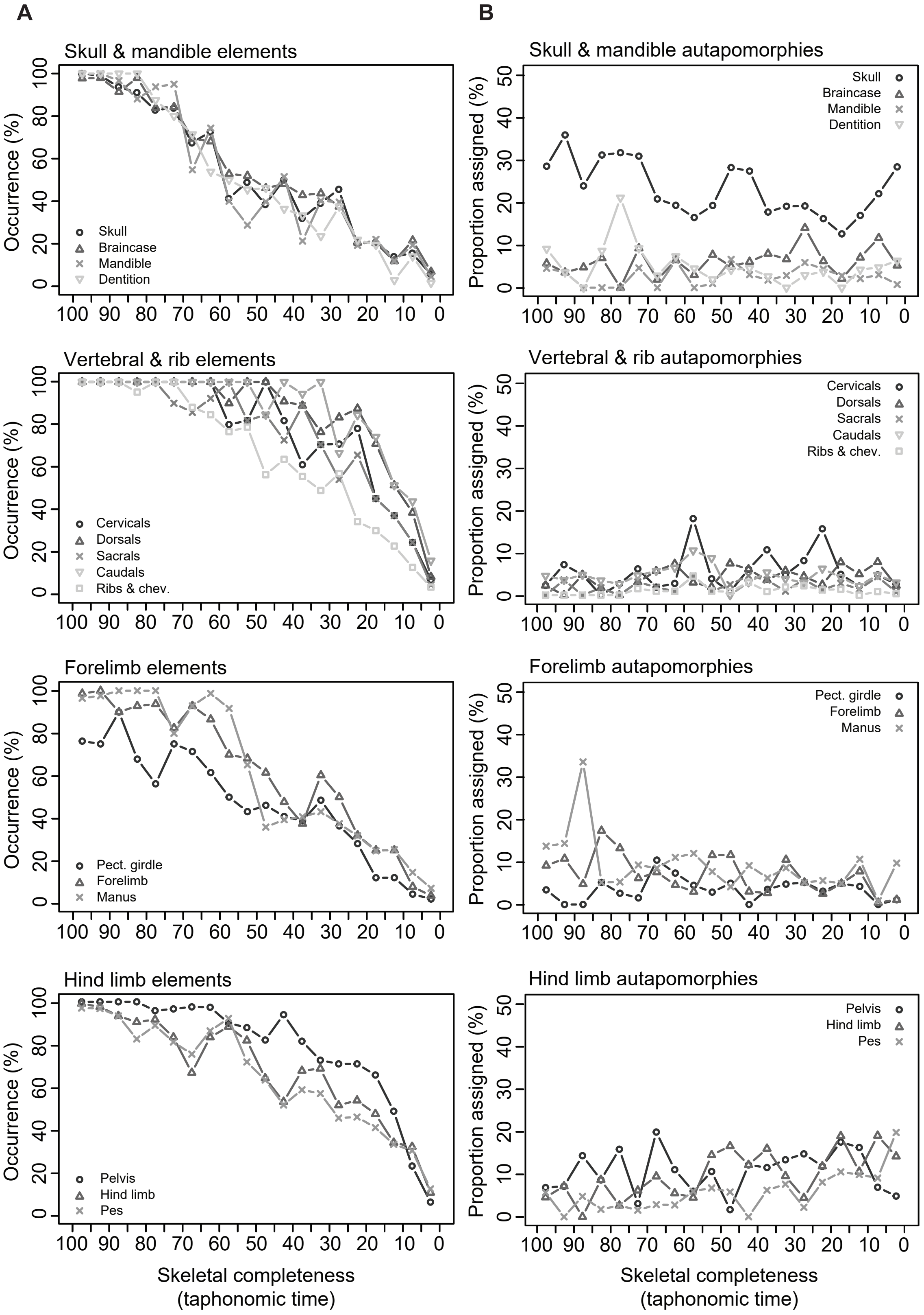
Fig. 4.4 reveals a global taphonomic sequence of bone loss for theropod dinosaurs. It plots the relative proportion of species known to contain each skeletal region (Fig. 4.4A), the relative proportion of autapomorphies assigned to those regions (Fig. 4.4B), and the number of species diagnosed using autapomorphies from those regions (Fig. 4.4C), at different completeness levels. Using this we can track the relative number of occurrences and autapomorphies of each skeletal element per completeness category, therefore, enabling us to make inferences about the survivorship of different skeletal elements and its influence on their diagnostic utility.

Skull and mandibular elements show a consistent negative trend of occurrence loss (Fig. 4.4A). A high proportion of element survival is retained down to 70% completeness. Below this however, the consistency of preservation starts to degrade for most skull and mandibular elements. In contrast to the other skeletal regions, there is relative occurrence stasis in the lowest completeness categories. Similarly, the forelimb elements have a relatively linear taphonomic trend, though the upper forelimb and manus are relatively consistently preserved until ~50% completeness (Fig. 4.4A). The vertebral, rib and hind limb elements have a slower decline in occurrence loss, with a more arched trend. There are high proportions of vertebral and pelvic occurrence until below 20% completeness, when this falls sharply. Notably the occurrences of the vertebrae, pelvis and upper hind limb suddenly drop from 5-10% completeness category too very low relative levels in the 0-5% category.

For most skeletal elements there is no trend in the allocations of autapomorphies through completeness levels, with various fluctuations between bins (Fig. 4.4B). However, even though skull elements are consistently assigned the highest proportion of autapomorphies, there is a notable rise in assignment in the lowest four completeness categories. Furthermore, the hind limb and pes exhibit a gentle increase in autapomorphy numbers as skeletal completeness drops; a pattern which may also be present for the braincase (Fig. 4.4B).

Figure 4.4C reveals little noticeable trend in the number of species diagnosed using most skeletal regions at different completeness levels. Skull, braincase and mandibular autapomorphies result in some of the lowest proportions of diagnosed species, while the dental autapomorphies consistently produce more species. The number of species diagnosed using vertebral autapomorphies fluctuates heavily through completeness levels, while there is a negative trend for manus, slightly positive trend for the pes.

For each skeletal completeness category, we calculated the relative percentage each skeletal region (Fig. 4.5A) and individual element (Fig. C.1A) contributes to the total bone occurrences within it, or, alternatively, what are the most and least common elements species are known from in each completeness category. Skeletal elements are represented on the x-axis, and the twenty skeletal completeness categories are positioned on the y-axis for which taxa were assigned based on their SCM2 scores (Fig. 4.5A, C.1A). As would be expected, within the highest completeness categories the occurrence of almost all elements are even, apart from a relative absence of pectoral elements (Fig. 4.5A, C.1A). Below 75% completeness, the vertebrae, pelvic girdle and hind limb become the dominant constituents of each completeness category, and this is maintained for almost all of the lower completeness levels (Fig. 4.5A, C.1A). Below 20% completeness there is also a relative increase in the proportion of pelvic and upper hind limb element


A
B
Skull & mandible elements
Occurrence (%)
Skull
Braincase
Mandible
Dentition
Skull & mandible autapomorphies
Proportion assigned (%)
Skull
Braincase
Mandible
Dentition
Vertebral & rib elements
Cervicals
Dorsals
Sacrals
Caudals
Ribs & chev.
Vertebral & rib autapomorphies
Cervicals
Dorsals
Sacrals
Caudals
Ribs & chev.
Forelimb elements
Pect. girdle
Forelimb
Manus
Forelimb autapomorphies
Pect. girdle
Forelimb
Manus
Hind limb elements
Pelvis
Hind limb
Pes
Hind limb autapomorphies
Pelvis
Hind limb
Pes
0
20
40
60
80
100
0
10
20
30
40
50
100 90 80 70 60 50 40 30 20 10 0
Skeletal completeness
(taphonomic time)
Skeletal completeness
(taphonomic time)

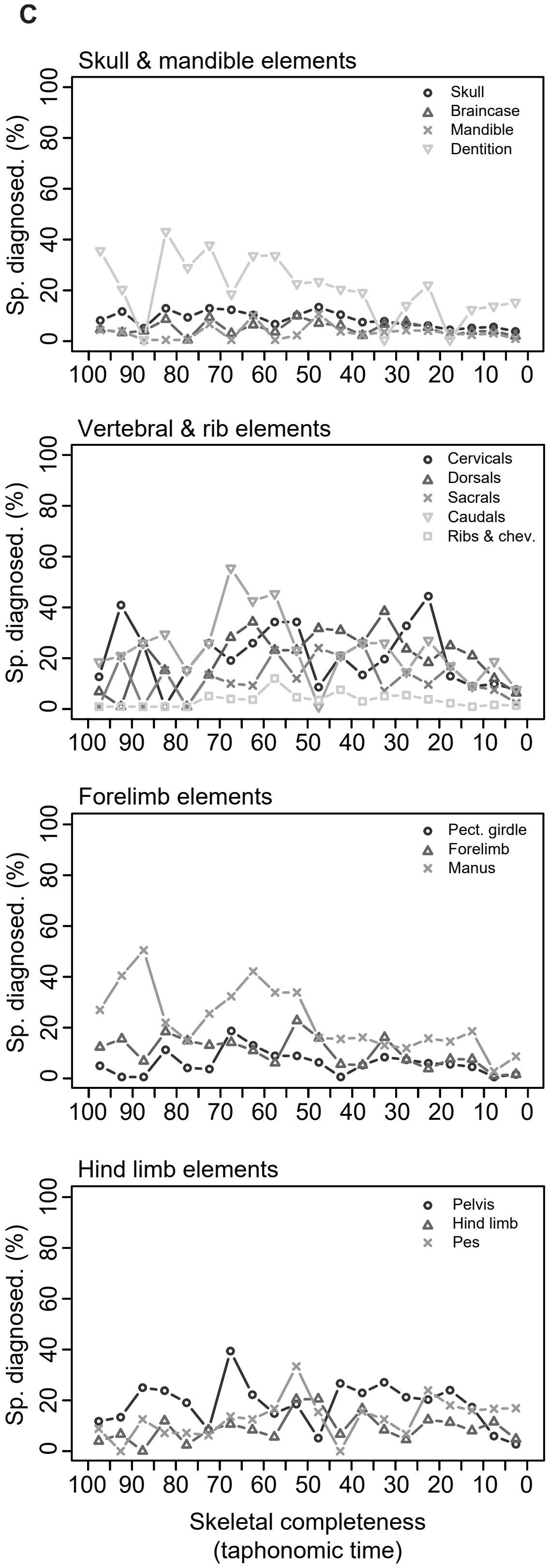


Figure 4.4. Survivorship curves representing: A, global sequence of theropod bone loss through 'taphonomic time' (completeness level) per major skeletal region; B, the resultant autapomorphies assigned to each skeletal region per completeness category, and C, the relative proportion of species diagnosed using different skeletal elements per completeness category.

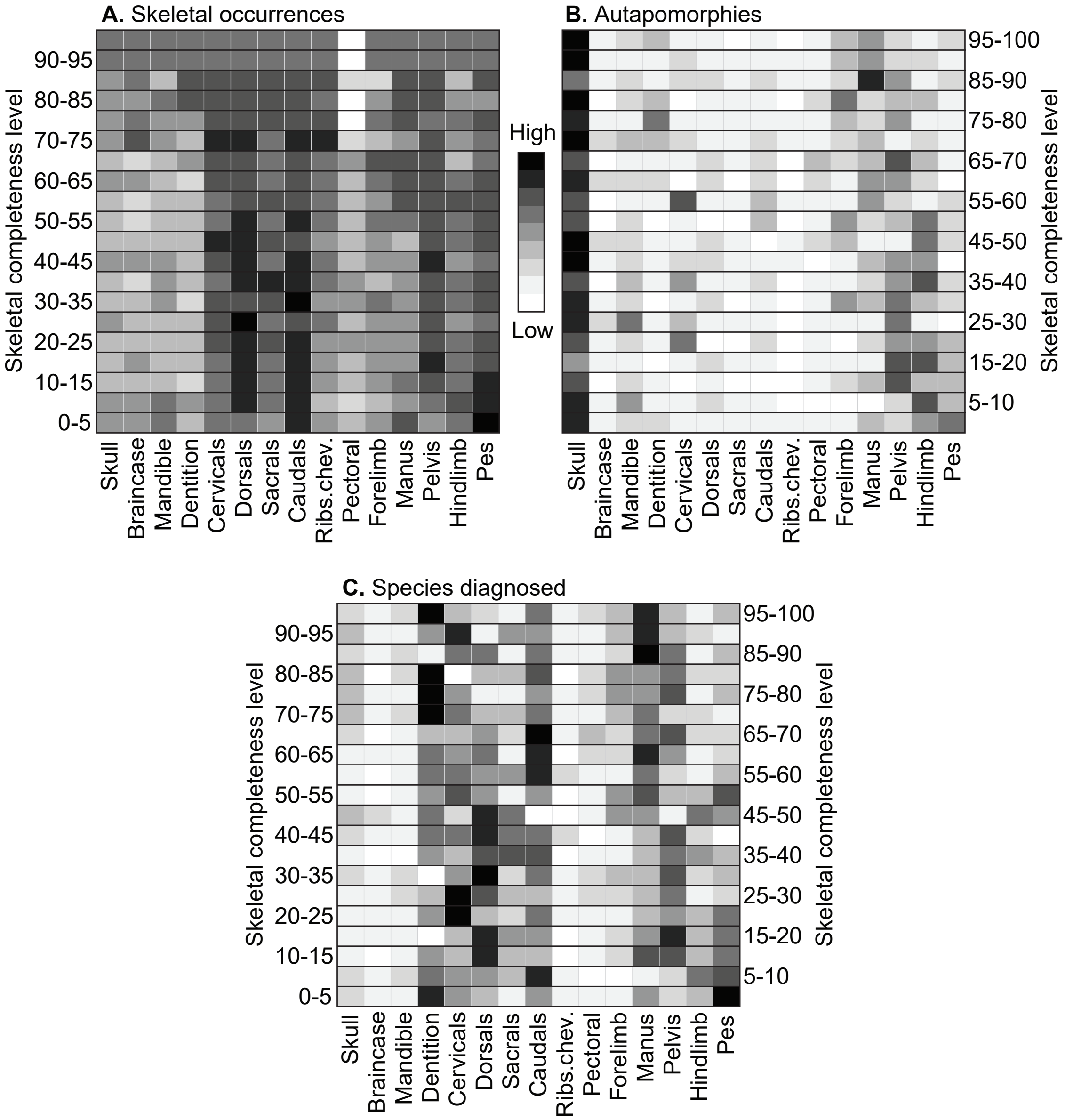


Figure 4.5. Taphonomic heat maps representing the relative proportion of: A, skeletal region occurrences; B, assigned autapomorphies, and C, species diagnosed using different skeletal regions, within in each 5% completeness category.

occurrences. Metatarsals and pedal digits make up relatively high proportions of occurrences within the lower completeness categories. The highest proportion of element occurrences in the 0–5% category are the maxilla, dentary, tibia, pedal digits and metatarsals (Fig. C.1A).

Figure 4.5B and C.1B show the relative number of autapomorphies assigned to different skeletal regions and individual elements, respectively, within each completeness category. Expectedly, this reveals the most autapomorphies assigned to species are from the skull at most completeness levels. However, in the highest completeness categories most autapomorphies come from either the premaxilla, maxilla, lacrimal, nasal, teeth, metacarpals or manual digits. In lower completeness categories, the teeth, vertebrae, pelvic elements, and upper hind limb are consistently assigned the highest proportion of autapomorphies within respective categories (Fig. C.1B). The dentary also shows distinctive intermittent peaks in autapomorphy assignment at various completeness levels, mostly below 60% completeness (Fig. C.1B). At low completeness levels the pelvis, hind limb and pes contribute substantially more to the proportion of assigned autapomorphies (Fig. 4.5B), and this is particularly notable for the metatarsals (Fig. C.1B). In 0-5% category, the maxilla, metatarsals and frontal contribute the highest proportion of all autapomorphies assigned to each element (Fig. C.1B).

Figure 4.5C and C.1C show the relative proportion of species diagnosed using autapomorphies of each skeletal region and individual element, respectively, within each completeness category. This shows the elements that are used to diagnose the highest number of species consistently derives from dentition and vertebrae. At lower completeness levels the higher proportion of species being diagnosed using the manus shifts towards the hind limb. Individual skull elements are moderately responsible for the diagnosing species at higher completeness levels, but become less utilised at lower completeness levels. The maxilla and metatarsals are used to diagnose the highest proportion of species at the lowest completeness levels.

4.3.3. Temporal changes

The number of element occurrences and number of autapomorphies fluctuate through geological time (Fig. 4.6). For both of these time series there are relative peaks in the Late Triassic, Late Jurassic, mid-Early Cretaceous

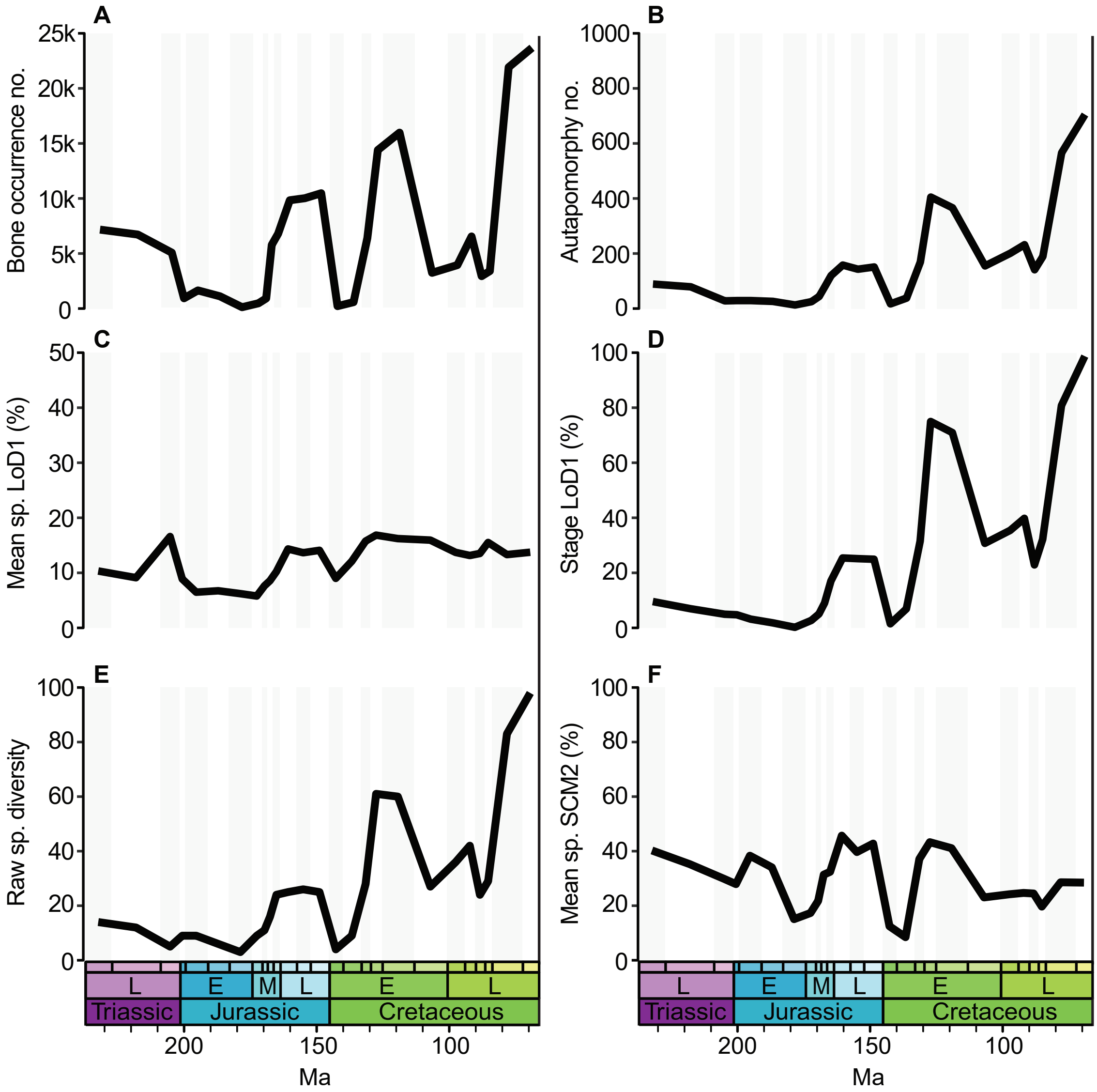


Figure 4.6. Changes through geological time in: A, bone occurrence numbers; B, assigned autapomorphies; C, mean species LoD1; D, stage-level LoD1; E, raw species diversity, and F. mean species SCM2.

and latest Cretaceous, and substantial troughs in the Early-Middle Jurassic, earliest Cretaceous, and a partial drop in the mid-Cretaceous. However, the autapomorphic peaks are relatively moderate in comparison to the lows. Stage-level diagnostic likelihood also very closely follows this same pattern, but is most akin to the autapomorphy time series (Fig. 4.6). The mean species diagnostic likelihood reveals little fluctuation in comparison, with relative peaks in the latest Triassic and Late Jurassic, a consistent low in the Early-Middle Jurassic, a drop at the Jurassic-Cretaceous boundary, and a relatively unfluctuating plateau in the remainder of the Cretaceous. Raw species diversity also very closely resembles the same patterns as the element occurrences, autapomorphies, and stage-level diagnosability (Fig. 4.6). Mean completeness for species assigned autapomorphic characters has peaks in the Carnian, Sinemurian–Pliensbachian, Late Jurassic, and mid-Early Cretaceous, and lows in the Middle Jurassic and earliest Cretaceous. Table 4.2 reveals strong significant positive correlations between all time series except between mean species LoD1, and raw species diversity and mean SCM2.

Figure C.2 shows how the temporal fluctuations in element occurrence and autapomorphies changes between different skeletal regions. For almost all skeletal regions, bone occurrence curves exhibit very similar patterns to the total data (described above), except the mandible, and the pectoral and pelvic girdles, which have relatively constrained fluctuations. The autapomorphy curves have more inconsistencies. The skull and hind limb autapomorphies resemble the total data most closely, but the skull in particular exhibits exceptional rise in autapomorphies in the latest Cretaceous. Mandibular autapomorphies show relatively little fluctuation through time and an outlying rise in the latest Cretaceous. Autapomorphies of the vertebrae uniquely do not share a peak in the latest Cretaceous, but a low rise and a peak in the mid-Early Cretaceous. The pectoral and pelvic girdles generally exhibit a gradual rise to a peak in autapomorphies in the latest Cretaceous. Forelimb autapomorphies occur as extreme outlying peaks in the mid-Early Cretaceous and the latest Cretaceous. Table C.3 reveals that all skeletal elements have significant positive correlations between the number of bone occurrences and the assigned autapomorphies through time.

Table 4.2. Results of pairwise comparisons between time series representing the number of individual bone occurrences, number of assigned autapomorphies, mean species LoD1, stage-level LoD1, raw species diversity, and mean completeness, using GLS. Statistically significant results indicated in bold.

Comparison	Slope	t-value	p-value	R^2
mean sp. LoD1 ~ stage-level LoD1	0.21	5.17	**0**	0.69
mean sp. LoD1 ~ autap.	0.17	3.26	**0.0033**	0.61
mean sp. LoD1 ~ bone occ.	0.12	2.93	**0.0073**	0.63
mean sp. LoD1 ~ diversity	0.13	1.86	0.0756	0.55
mean sp. LoD1 ~ SCM2	0.16	1.51	0.143	0.56
stage-level LoD1 ~ autap.	1.01	21.47	**0**	0.97
stage-level LoD1 ~ bone occ.	0.61	8.79	**0**	0.90
stage-level LoD1 ~ diversity	1.13	16.62	**0**	0.96
stage-level LoD1 ~ SCM2	1.17	5.17	**0**	0.81
autap. ~ bone occ.	0.62	9.41	**0**	0.91
autap. ~ diversity	1.15	23.70	**0**	0.97
autap. ~ SCM2	1.23	5.99	**0**	0.82
bone occ. ~ diversity	1.18	6.94	**0**	0.76
bone occ. ~ SCM2	1.95	6.99	**0**	0.76
diversity ~ SCM2	1.01	4.61	**0.0001**	0.72

4.3.4. Geological formations

The formation with by far the highest likelihood of species diagnosis is the Yixian Formation, China, which is comprised of 31 species, almost double the diversity of next highest formation (Table C.4). There is a significant positive correlation between the LoD1 score and the number of identified species per formation ($R^2 = 0.56$; $p = <0.0001$). However, there are couple of outlying formations with low species number and relatively high LoD1 scores (e.g. Baharije, Aïn el Guettar, Toqui), and some with reasonable species numbers but notably low LoD1 scores (e.g. Lufeng, Shaximiao, Sao Khua) (Table C.3). There is also a relative weak but significant correlation between the LoD1 scores and the mean SCM2 scores of each formation ($R^2 = 0.2$; $p = <0.0001$) and only a very weak significant correlation between formation SCM2 and species diversity ($R^2 = 0.09$; $p = 0.0005$).

Table 4.3. Results of pairwise comparisons between LoD1, LoD2, generic diversity, and all taxon richness per quarry and systems tract of the Morrison Formation as defined by Maidment and Muxworthy (*in press*), using GLS. Statistically significant results indicated in bold. Abbreviations: Syst., Systems.

Comparison	Slope	t-value	p-value	R^2
Quarry LoD1 ~ LoD2	0.24	5.60	**0**	0.29
Quarry LoD1 ~ all taxa diversity	0.68	9.66	**0**	0.57
Quarry LoD1 ~ generic diversity	0.92	13.38	**0**	0.72
Quarry LoD2 ~ all taxa diversity	1.18	5.21	**0**	0.26
Quarry LoD2 ~ generic diversity	1.49	5.89	**0**	0.31
Syst. Tract LoD1 ~ LoD2	0.75	18.80	**0**	0.99
Syst. Tract LoD1 ~ generic diversity	1.07	19.44	**0**	0.98
Syst. Tract LoD2 ~ all taxa diversity	1.33	12.03	**0.0003**	0.95
Syst. Tract LoD2 ~ generic diversity	1.41	16.97	**0.0001**	0.98

4.3.5. Local study: Morrison Formation

The Morrison Formation is ranked as the eighth-best formation in the world for ease of diagnosing theropod species (Table C.3). Within it, we can identify the quarries and the stratigraphic sequence systems tracts with the highest and lowest diagnostic use and potential.

Quarry 9 from Como Bluff of systems tract STC6 has the highest ranked LoD1 score, followed closely by the Cleveland-Lloyd Dinosaur Quarry (STB4) (Table C.5). The latter has the highest LoD2 score, whereas the former has a much lower score for this metric. Immediately successive to the Cleveland-Lloyd Dinosaur Quarry, the Bone Cabin Quarry (STC6), Felch Quarry 1 (STB3) and Dry Mesa Quarry (STB4) all have LoD2 scores substantially higher than the remaining Morrison quarries (Table C.5). There are strong significant correlations between quarry LoD1 scores, and generic and all taxon diversity, and there are relatively weak, but still significant correlations between quarry LoD2 scores and diversity (Table 4.3). In contrast, there is no correlation between Morrison taxon LoD1 scores and the estimated minimum number of individuals derived from quarry data ($R^2 = 0.01$; $p = 0.8$). There is a greater level of variation of quarry LoD2 scores than LoD1 (Table C.5) because of its different methodological approach, but there is

Table 4.4. Chronostratigraphic changes in LoD1 and LoD2 per systems tract of the Morrison Formation, as defined by Maidment and Muxworthy (*in press*), with the number of times specimens of different taxonomic levels were identified. Abbreviations: Strat., Stratigraphic.

Systems Tract	LoD1	LoD1 (%)	LoD2	LoD2 (%)	Species	Genera	Indet.
STC6	314.68	100.00	880.29	97.74	23	19	13
STC5	158.25	50.29	664.27	73.75	8	19	5
STB4	253.71	80.63	900.69	100.00	14	25	25
STB3	82.81	26.32	219.71	24.39	3	7	2
STA2	12.98	4.12	16.94	1.88	0	3	1
Unknown strat. location	146.77	46.64	430.85	47.84	7	16	18

still and weak significant correlation between the respective quarry scores (Table 4.3). However, there are a number of quarries with discrepant diagnoses scores. For example, the Louise Quarry (STC6) has a moderate LoD1 score but the lowest LoD2 score, and the previously mentioned Bone Cabin Quarry (STB4) has a very high LoD2 score but much reduced LoD1 score.

Table 4.4 summarises the diagnostic scores of each Morrison systems tract. Systems tract STA2 and STB3 have the lowest diagnosability scores for either metric. By contrast, systems tracts STC6 and STB4 have the highest LoD1 and LoD2 scores, respectively, and both have the second highest scores for the opposing metrics. This suggests diagnosability levels generally increase through time in the Morrison Formation, which is supported by a very strong significant correlation between LoD1 and LoD2. This, in turn, tracks an increase in identified taxa through the formation (Table 4.4), supported by strong significant correlations (Table 4.3) between diagnosability and raw diversity.

4.4. Discussion

4.4.1. Preservation likelihood, identifiable characters and natural bias

Our results reveal different theropod species and subgroups have varying levels of diagnostic quality. The strong relationship between subgroup LoD1 and species richness is a potential bias on our ability to identify species of different groups, as some groups may be known to have relatively low/high diversity because of the lower/higher diagnostic tendencies, controlled by preferential preservation of specific elements and the morphological characters identifiable from them.

The three most diagnostic subgroups are Ovraptorosauria, Dromaeosauridae, and Ceratosauria. The element with the highest diagnostic likelihood for oviraptorosaurs is the dentary (Table C.2). Overall, skull elements show relative lower survival rate than other parts of the skeleton, but the dentary in particular occupies a high proportion of occurrences known at lower completeness (Fig. C.1). Highly diagnostic oviraptorosaur mandibles are fused along the midline, likely making them more robust to taphonomic survival, and in turn leading to heightened diagnostic utility. Heightened occurrences of oviraptorosaur mandibles also partially explain the extreme rise in mandibular occurrences during the Late Cretaceous (Fig. C.2). Following the dentary, oviraptorosaurs do not have any other standout diagnostic elements. However, they do have an incredibly even spread of diagnostic traits across different portions of the skeleton. 87% of oviraptorosaur bones have been assigned at least one autapomorphic character, with reasonable diagnostic utility seen in the premaxilla, caudals, metacarpals, manual digits, femur and metatarsals (Table C.1). The most diagnostic elements for ceratosaurs and dromaeosaurids are cervical vertebrae and the metatarsals, respectively, which both have high levels of preservation occurrence and diagnostic likelihood (Fig. 4.4). The two groups also have a greater range of elements with relatively high proportion of diagnostic use (Table C.2), for example, 63% and 75% of ceratosaur and dromaeosaurid bones have assigned autapomorphies, respectively, with relatively high diagnostic utility in the tibia and metatarsals in the former (Table C2). This reveals that for a theropod species to be relatively easily diagnosable, it needs a combination of unique characters in elements that preferentially survive, and a range of unique characters evenly spread throughout the skeleton, thus combating differential preservation regimes.

Basal tetanuran, megaraptoran, and compsognathid species have the least likelihood of diagnosis (Fig. 4.3). These subgroups exhibit a limited range of unique characters specific to a few elements, with only 35, 5%, and 33% autapomorphic bone coverage, respectively (Table C.2). This limits the scope of bones in which these taxa are readily identified in comparison to other groups. Megaraptora is an exceptional example, whereby unique characters are only associated with three elements, the dorsals, sacrals and ilium. If these elements are not preserved in an assemblage, it is likely quite difficult to identify new species of this group. This may be why megaraptorans were only recently described (Benson *et al.* 2010a), why they have a very poor fossil record (Chapter 2, Cashmore and Butler 2019), and why our understanding of their evolution and phylogenetic relationships is relatively limited (Porfiri *et al.* 2014, 2018; Novas *et al.* 2016). The low diversity of the compsognathid record is related to necessity of exceptional preservation quality (Chapter 2, Cashmore and Butler 2019), as almost all species are derived from conservation Lagerstätten. Dependence on identification of unique characters associated with the manus (Table C.1), elements that have relatively low taphonomic survival, likely hinders positive identification in poorer preservation regimes. Although non-avialan Paraves have slightly higher autapomorphy bone coverage and higher diversity, the latter also likely applies to them, as they too have almost exclusively been discovered in similar Lagerstätten. Low average autapomorphy bone coverage can also explain the noticeably average to poor diagnosability of the remaining non-monophyletic theropod subgroups: basal Theropoda, basal Neotheropoda, and basal Coelurosauria (Fig. 4.3, Table C.1). Species at the base of clades may be hindered by their morphological generality, because they possess morphological features that are similar to many clades.

Our data suggests that basal and non-monophyletic theropod groups have a relatively limited range of skeletal elements that provide recognisable autapomorphies (Table C1), and generally, LoD increases in more derived theropod subgroups (Fig. 4.3). Therefore, it is possible that there is a positive relationship between phylogenetic position and LoD score, suggesting theropod taxa that lie at the base or just outside monophyletic groups could be less easily identifiable than more derived forms, which are more morphologically distinct. This may also explain why basal theropods are often identified from few specimens of relatively high completeness, as they require better quality of preservation to be confidently identified in their basal positions, whereas more derived species can be more easily identified from fewer preserved elements. Though we do not have similar relevant autapomorphy data, in Chapter 3, we also conclude that it is possible that more derived and morphologically distinct sauropodomorphs are more easily identified from less complete material than basal forms. This potential phylogenetic bias towards the identification of more derived, or more morphologically disparate, forms could have strong consequences for our ability to correctly recreate phylogenetic relationships and understand the evolutionary history of particular tetrapod groups.

For most subgroups there is a positive relationship between LoD1 and diversity. However, Alvarezsauroidea records relatively high diagnosability but has fewer species than other groups with similar LoD1 scores, such as Megalosauroidea, Allosauroidea Tyrannosauroidea, and Ornithomimosauria (Fig. 4.3). In fact, they have comparable diversity to Therizinosauria and Troodontidae, both of which have substantially lower LoD1 scores. The tibia and metatarsals constitute the most diagnostic alvarezsaur elements, two skeletal elements that preferentially survive fossilisation relative to most, and they exhibit an average autapomorphy bone coverage of 52%. The lack of diversity does not seem to be related to inadequate preservation of the group's most diagnostic elements, as for the most part, they have some of the highest proportion of alvarezsauroid element occurrences. This, however, could possibly be associated with the clade's genuine rarity in palaeoecosystems, meaning species diversity will always remain comparatively low even though they have relatively highly diagnostic skeletons.

4.4.2. Preservation likelihood, identifiable characters and human bias

Generally, there are no obvious trends in the number of autapomorphies assigned to, and species diagnosed from, most skeletal elements at different completeness levels (Fig. 4.4). Most exhibit relatively minor fluctuations in the proportion of assigned autapomorphies or species diagnosed, resulting in relatively flat lying curves. This suggests that at most completeness levels species are identified with no recognisable bias towards particular skeletal elements. However, the increased proportion of autapomorphies of the skull in the lowest four completeness categories (0-20% SCM2) and the increasing proportion of hind limb autapomorphies through taphonomic time (Fig. 4.4) suggests identification of species at lower completeness levels is dominated by the use of certain skull and hind limb elements. By observing the element-specific taphonomic maps (Fig. C.1B) we can associate these relative rises mostly to the assignment of autapomorphies to the maxilla, frontal, metatarsals and pedal digits. This may imply that these elements are assigned more autapomorphies at low completeness levels than would potentially be expected. Potentially, this highlights a research trend to extensively scrutinise material of low completeness, which in turn could be associated with a potential taxonomic identification bias (Benson 2008, 2010; Brocklehurst *et al.* 2012), and, as a result, have possibly led researchers to oversplit isolated remains of certain species. A 'novelty bias' may explain this pattern: identifications of new fossil species are easier to publish and receive much greater attention and citations than indeterminate specimens. This is especially true for dinosaurs, which media and the public have a greater investment in when compared to other ancient groups. However, this autapomorphy increase is not greatly reflected in the number of species diagnosed from these elements, as Figure 4.4.C demonstrates relatively flat curves with no trend through lower completeness levels. This means that although material of low completeness are being assigned potentially more autapomorphies than would be expected there is no relative increase in species identified based on these increased autapomorphies. This therefore suggests there is no obvious taxonomic identification bias, but assignment of many autapomorphic characters at lower levels for specific elements could potentially result in overly split taxa.

Following this, it is noteworthy that Allosauroidea and Tyrannosauroidea have relatively high species diversity, close to that of Ceratosauria, but comparatively low LoD1 scores (Fig. 4.3), on par with Ornithimosauria and Alvarezsauroidea. Figure 4.2 shows that both Allosauroidea and Tyrannosauroidea have a much higher proportion of skull autapomorphies than other theropod subgroups, and Table C.1 shows this is mostly due to maxillary assignments. 13.9% of all tyrannosauroid autapomorphies are assigned to the maxilla, the highest proportion of any subgroup. High species diversity but average diagnostic potential could potentially have resulted from higher diversity in palaeoecosystems, but it could also be evidence of intense scrutiny of their skull elements, which may lead to taxonomic oversplitting.

4.4.3. Localised differential diagnosability

We find strong differences in the diagnostic quality of theropod dinosaurs in different geological formations, and formations with higher levels of diagnosability in general produce more identified species. This localised spatial and temporal variation in the quality of the fossil record likely has a major influence on the 'global' record. The Yixian Formation is by far the most diagnostic formation (Table C.4). This conservation Lagerstätten was deposited under unique depositional conditions (Pan *et al.* 2012) enabling exquisite level of fossil completeness, and subsequent palaeontological use. Due to its preservation quality, the Yixian would be expected to have the highest level of diagnostic utility. However, other formations with similar depositional conditions and/or standard of preservation, like the La Huerguina (Las Hoyas), Solnhofen and Santana formations, rank much lower, producing only handfuls of diagnosed species. The difference between these formations might lie in the extent of the depositional accommodation space available of the Yixian, its greater rock exposure, and/or its lacustrine depositional setting, which may have attracted comparatively higher theropod populations than the coastal settings of the other formations. Following the Yixian, the highest ranking formations were mostly deposited under varying fluvial-lacustrine conditions (e.g. Nemegt, Barun Goyot, Dinosaur Park, Morrison), deriving from broadly similar modern environments, consisting of vast arid areas with high rock exposure and little vegetation. The high diagnosability of these formations is likely due in part to these ideal conditions for consistent fossil preservation. A large number of these high ranking formations are also latest Cretaceous in age, which likely leads to the high levels of autapomorphy assignments, stage LoD1 and species diversity within the time frame.

Our results demonstrate that the global differences in the quality of the fossil record can be attributed to changes on more local temporal and spatial scales. Five systems tracts of the Morrison Formation bearing theropod remains reveal very different diagnostic qualities (Table 4.4). Maidment and Muxworthy (*in press*) associated each of these systems tracts with discrete sedimentological, environmental and tectonic conditions. From the environmental definitions outlined in the section 4.2.2, we can identify a very clear association between poorly drained, lacustrine dominated facies and increased diagnostic likelihood of theropod species, as system tracts STB4 and STC6 have the highest LoD1 and

LoD2 scores and produce the highest number of valid species identifications (Table 4.4). In Chapter 2 (Cashmore and Butler 2019), we found theropod completeness to be significantly higher in lacustrine depositional settings than any other deposit type, as these stationary bodies of water do not transport sediment loads, and are less likely to winnow skeletons, ensuring higher quantities of skeletal preservation, therefore likely enhancing the chances of diagnosing species. The sampling pool of these system tracts may also have been increased because of seasonal congregation patterns of theropod species (Peterson *et al.* 2017). Lacustrine environments were also possibly more preferable living habitats, and/or they force higher populations of animals to congregate in confined depositional areas near evaporating bodies of water during times of seasonal aridity (Peterson *et al.* 2017). Furthermore, the heightened connectivity of wetland palaeoenvironments (Whitlock *et al.* 2018) possibly enables higher populations of species to accumulate in comparison to fluvial dominated periods, where large rivers act as environmental barriers (Whitlock *et al.* 2018), particularly to smaller species. The nature of the depositional environment in systems tract STB4 and STB6 also permitted the development of extensive bonebeds. For example, the Cleveland-Lloyd Dinosaur Quarry and Mygatt-Moore Quarry are exceptional accumulative pond deposits (Gates 2005; Foster *et al.* 2016, 2018; Peterson *et al.* 2017), unique in relation to the majority of Morrison deposits (Foster 2003, 2016), yielding a high abundance of finds, mostly of *Allosaurus*, which increases the overall diagnostic utility of these systems tracts.

Between these two most diagnostic systems tracts there are however noticeable differences. STB4 has the highest LoD2 score and STC6 has the highest LoD1 score, which indicate different qualities to their records. LoD2 corresponds more to preservation within different assemblages as it predominantly relies on bone occurrence data. This means a higher LoD2 score likely reflects higher quantity of material. LoD1 on the other hand is concerned with recognition of species. This is reflected in the relative number of identified species within the two system tracts, whereby STC6 has preserved significantly more species-level identifications than STB4, which has higher numbers of individuals of indeterminate identification (Table 4.4). This demonstrates a localised comparison between quantity and quality. Within STB4 there are a number of famous dinosaur-bearing bone beds including Cleveland-Lloyd Dinosaur Quarry, Dinosaur National Monument Quarry and Dry Mesa Quarry (Table C.5). These deposits accumulate great masses of skeletal material, but it may be hard to associate elements together into single individuals of a species. This seems possibly less of a problem in system tract STC6, whereby species identification is relatively consistent over more quarries (Table C.5), and may be because it contains a number of microvertebrate sites, like in Como Bluff (Carrano and Velez-Juarbe 2006; Foster *et al.* 2016).

STA2 and STB3 have the lowest diagnosability scores of any systems tract and both were deposited in predominantly well-drained floodplain settings with isolated channels. It is likely that this environment constrained the preservation of theropod bones in these system tracts as fluvial channels produce relatively incomplete theropod skeletons (Chapter 2, Cashmore and Butler 2019), as remains recovered are more than likely transported from other environments (Bandeira *et al.* 2018). However, STC5 exhibits relatively high LoD1 and LoD2 scores within a well-drained floodplain. Its low accommodation space and palaeosol formation likely have has some positive influence on theropod fossil preservation within this environment (Retallack 1998), and ultimately our ability to identify higher proportion of species.

These results clearly demonstrate a relative taxonomic identification bias controlled by localised environmental and tectonic changes (Maidment and Muxworthy *in press*). Without distinct shifts to wetland-dominated environments it is possible that the Morrison Formation would not have produced such a rich dinosaur fauna. In comparative geological settings, the Karoo Basin of South Africa, Walther and Fröbisch (2013) also find some evidence for a significant geological bias acting upon the anomodont fossil record, whilst Irmis *et al.* (2013) concluded non-biotic control on diversity estimates. Therefore, variation of facies control within a basin can be of high importance to the quality of that specific record, but in turn can strongly impact the global signals we receive, and our understanding of evolutionary change of particular groups.

4.4.4. Impact on evolutionary understanding

The highly significant correlations between almost all time series (Table 4.2, Fig. 4.6) strongly reaffirms intuitive relationships between fossil preservation and our ability to identify species, as we clearly identify more unique characters and more species when there is more information available. This is to be expected. The low relative fluctuation in the species LoD1 time series and its lack of correlation with raw species diversity indicates that there is possibly little taxonomic identification bias on geological time scales, as theropod species from varying time bins have generally the same likelihood of identification. However, the Carnian–Norian, Early Jurassic and earliest Cretaceous stand out with noticeable lows within the species LoD1 curve (Fig. 4.6). Though the difference between these lows and the highs are minor, it does demonstrate that there are time bins that potentially possess generally more or less diagnostic species. In contrast, stage level LoD1 fluctuates dramatically through time and mirrors the changes in raw species diversity, autapomorphy number and bone occurrences (Fig. 4.6), suggesting that there are time bins with strong diagnostic differences. We interpret this discrepancy between the generally flat species LoD1 curve, and the fluctuating stage-level LoD1 curve, as meaning the likelihood of identifying individual theropod species changes little, but within time bins the level of available material must strongly influence the chances of successfully diagnosing species.

If there were to be a noticeable worker bias, we would expect time bins to have divergent likelihoods in comparison to species diversity, for example. This means, on macroevolutionary scales, researchers are not identifying more or less species in particular time bins than they should. As bone occurrences, autapomorphies, likelihood of diagnosis, and species diversity curves all demonstrate the same patterns, there is clear redundancy in the information revealed, and they are all intuitively linked. This therefore suggests the occurrences of bone material is the strongest influence on changes in theropod diversity, which is likely controlled by local scale differential geological processes (Barrett *et al.* 2009; Alroy 2010; Mannion *et al.* 2011; Dunhill *et al.* 2013, 2014).

4.4.5. Diagnosability and fossil completeness

The relationship between diagnosability and skeletal completeness seems to fluctuate slightly depending on the scale used. Our results demonstrate a very weak significant relationship between species-specific LoD1 and formation LoD1 and SCM2, but no relationship between mean subgroup LoD1 and mean SCM2, and no apparent relationship on geological time scales. Furthermore, our global taphonomic curves and maps (Fig. 4.4, 4.5, C.1) demonstrate that there is no distinct change in the autapomorphies assigned to theropod species throughout different completeness levels, apart from the increase at low levels for the skull and hindlimb. It may be the case there are some preservational regimes and taxa that require more complete skeletons for diagnosis, such as compsognathids. However, the lack of any strong relationship confirms what has been previously suggested, that diagnosability, or the quality of the fossil record, has relatively little connection with the completeness of fossil material (Mannion and Upchurch 2010a; Brocklehurst *et al.* 2012). Therefore, records with low specimen completeness, defined by SCM and CCM, may give false impressions of a lack of understanding of the evolutionary changes in that record. The opposite is also potentially true of a highly 'complete' record.

4.4.6. Limitations and application of diagnosability metrics

The novel metrics we apply in this study attempt to quantify the diagnostic quality of fossil material and critically assess taxonomic identification from an anthropomorphic perspective. However, here we acknowledge a couple of methodological limitations that should be recognised when considering our results.

The diagnostic elements of 55 species were removed from our relative autapomorphy proportioning because they were known from differential, plesiomorphic and synapomorphic diagnoses, or they were simply unavailable. Therefore, our diagnostic character sampling pool is partially limited. An overabundance of material and exceptional level of research on some taxa, such as *Allosaurus fragilis* and *Tyrannosaurus rex*, has resulted in complex systematic history but, surprisingly, a lack of up-to-date formal diagnoses. Though our results suggest a key relationship between element occurrence and autapomorphy assignments, those two species in particular, are examples of a discrepancy between fossil occurrence and the formalised identification of taxonomically distinct traits. A lack of formalised autapomorphic diagnosis does not necessarily mean that these species are hard to recognise in the field or in collections; in fact, the opposite seems to be true, with their bones being common and readily identified, although the basis for those taxonomic identifications may not necessarily be clear. Therefore, in reality these species may have a high diagnosability that is not captured by our analysis. This highlights a particular problem with the LoD1 metric, whereby autapomorphy number is effectively considered to control the recognition of species. Table C.2 best illustrates this limitation, as a large number of elements are considered to have zero diagnosability for each theropod subgroup, as there are no autapomorphic characters associated with those elements. Lack of autapomorphies does not mean that a particular element is unrecognisable to a clade or even species; therefore, LoD1 scores may be slightly misleading as estimates of our ability to identify taxa. This issue, however, is not easy to overcome.

The LoD2 metric also has some methodological problems. It equates the autapomorphies of the entire fossil group with an assemblage localised in time and space. That assemblage likely contains taxa for whose unique characters are isolated to particular bones; therefore, by incorporating a global autapomorphy proportion we are artificially associating diagnostic traits of other subgroups to those present in the assemblage. Scores from this metric, in contrast to LoD1, are more representative of element occurrence data and therefore has more in common with completeness metrics, like SCM, than anthropomorphic identification of a taxon.

Furthermore, our occurrence data for the global theropod fossil record is constrained to the completeness data collection presented in Chapter 2 (Cashmore and Butler 2019), and does not incorporate the vast majority of indeterminate theropod material from around the world, or all specimens recognised in museum catalogues for all taxa. To gather such a detailed record is unrealistic but it should be noted that the bone preservation likelihood of occurrence is based on a representative theropod fossil record of the most diagnosable material. Therefore, there might be minor circularity in the comparison between proportioned autapomorphies and occurrences. The Morrison quarry bone data also has similar issues. Large amounts of detailed quarry data were collected from the literature and online catalogues, but the available information is not a comprehensive list of all preserved theropod material. A number of theropod-bearing quarries could not be scored and the details of preserved material from scored quarries is reliant on the information available, and so is likely not totally representative of all the material collected.

4.4.7. *Implications for theropod research*

Our results are highly relevant for theropod systematists, as they summarise the output of human interpretation for theropod species diagnosis, and illustrate worker focus and perception. This enables us to highlight areas of natural morphological and phylogenetic bias, and any possible human perception bias towards or against the diagnosis of particular skeletal elements or theropod groups, which could be impinging the ability of researchers to diagnose species.

We demonstrate that the relative number of identified elements and derived autapomorphic features varies substantially depending on the theropod group in question. Taxa that are phylogenetically close to the base of clades, and non-monophyletic grades, generally have fewer elements with autapomorphic features than more derived groups, meaning their species will likely have less chance of confident identification from incomplete specimens. Basal members of clades will likely have more plesiomorphic features in common with outgroups, or other more directly descendant monophyletic groups. These close similarities mean, for example, that some early theropods have been difficult to consistently distinguish from other early saurischian dinosaurs, and may underpin some of the recent lack of consensus on their phylogenetic relationships (Langer et al. 2017; Müller et al. 2017; Baron et al. 2017; Baron and Barrett 2017; Parry et al. 2017). Similar issues have also been identified for basal coelurosaurs (Rauhut and Xu 2005; Butler and Upchurch 2007; Choiniere et al. 2010; Novas et al. 2012; Choiniere et al. 2014; Hendrickx et al. 2015; Azuma et al. 2016). The limited and relatively poorly diagnostic megaraptoran fossil record means the phylogenetic position of this clade is also still highly contentious (Benson et al. 2010a; Porfiri et al. 2014, 2018; Novas et al. 2016). In the immediate future, work should focus on a thorough reassessment and investigation of basal theropod, basal coelurosaurian, and megaraptoran morphology and relationships. Without a thorough grasp of these, our ability to understand the process, and rate, of adaptive radiations of more derived groups may be inadequate. Moreover, a clichéd but necessary suggestion is for future explorative fieldwork to aim for new localities from time bins likely to yield new species of basal theropod forms. Recently many new basal dinosaurs have been unearthed in key localities in South America (e.g. Müller et al. 2014, 2015, 2016, 2018; Pretto et al. 2015, 2018), which should significantly enlighten our understanding of basal dinosaur relationships in the coming years.

Another major issue for theropod researchers is the reliance on sites of exceptional preservation to preserve and identify compsognathids and paravians (Supplementary data). Our apparent inability to identify species of these potentially diverse clades in non-exceptional deposits means we have a very geographically and temporally isolated understanding of their evolution. Successfully identifying new compsognathid and paravian species from less complete material is key to improving understanding of their evolution.

In future, it would be preferable for theropod workers to solely use autapomorphic features to define new species. Most recent descriptions do use autapomorphic features or a unique combination of characters, but there are still a relatively large number of valid theropod species that do not have such diagnoses (60 species), the majority of which have not been reassessed since before the advent of modern cladistic and taxonomic practice. Of upmost importance is the need to provide diagnoses for key species such as *Allosaurus fragilis* and *Tyrannosaurus rex*. The lack of clear definitions of such taxa could be hampering identification of separate species and the interpretations of intraspecific morphological and ontogenetic diversity within key formations. Generally, however, we suggest workers should expand their search for autapomorphies across the skeleton, rather than focusing on a few select skeletal elements, such as, for example, the maxilla in Tyrannosauroidea. However, this is understandably difficult, as some skeletal elements are more diagnostic for different groups, leading those elements to naturally attract the most attention from researchers. However, an awareness of this issue is required in future to reduce the level of character skew towards, and diagnostic reliance on, a few select elements in certain groups (Fig. 4.2).

4.5. Conclusions

We create two novel metrics in an attempt to quantify the likelihood of diagnosing fossil species, clades, temporal or spatial assemblages, and assess the gap between fossil occurrence and anthropogenic understanding of the fossil record. These diagnosability metrics, named LoD1 and LoD2, utilise formalised autapomorphic taxonomic diagnoses from the published literature in conjunction with bone occurrence data sets. We applied these metrics to the theropod fossil record in order to identify a potential taxonomic identification bias acting upon their record. Our results as follows:

- The most often preserved elements of the theropod skeleton are the vertebrae and ribs, followed by the hind limb, skull (mostly maxilla and dentary), and forelimb. On average, theropod species are diagnosed by five autapomorphies or autapomorphy-equivalent characters, mostly related to the skull, particularly the maxilla and dentary, and the hind limb, with the metatarsals, femur and tibia withholding the highest number of unique characters.
- There is a strong significant relationship between bone occurrence and autapomorphy assignment for all theropods, for almost all individual theropod subgroups, and through geological time. Our ability to identify unique characters from theropod remains seems largely controlled by presence of useful elements.
- We find that the elements most likely lead to a positive diagnosis of a theropod species are the metatarsals. The theropod subgroups with the highest diagnosability are Oviraptorosauria, Dromaeosauridae and Ceratosauria,

whilst the subgroups with the lowest scores are basal Theropoda, basal Tetanurae, Compsognathidae and Megaraptora. These within-group differences are largely due to the distribution level of unique characters in a theropod skeleton, with high autapomorphy distribution enabling increased likelihood of diagnosing species. However, at low completeness levels there are noticeable increases in autapomorphies associated with the skull (e.g. maxilla) and the hindlimb (e.g. metatarsals). This we interpret as a potential human induced character identification bias due to intense investigation of isolated remains, which may have led to oversplitting of some species.

- There is a strong significant relationship between subgroup diagnosability score and species diversity, which might indicate that the diagnosability of different groups may strongly influence our understanding of their fossil record and subsequent macroevolution. Species diagnosability exhibits relatively little fluctuation through geological time, but stage level diagnosability, fluctuates in accordance with bone occurrence, autapomorphy assignment and species richness changes, which all have strong significant positive correlations. We interpret this as being the result of little to no researcher identification bias in any particular geological time bin, but our recognition of species and our understanding of diversity changes may well be strongly controlled by geological processes changing the availability of theropod fossils.
- We find different geological formations have contrasting diagnostic quality, and generally more species are identified from formations with higher levels of diagnosability. Detailed examination of the changing diagnostic quality of the Morrison Formation reveals strong environmental association of poorly drained, lacustrine/wetland dominated facies and increased diagnostic likelihood of theropod species, which is ultimately controlled by local climatic and tectonic fluctuations.

5 | Summary and Perspectives

5.1. Conclusions

In this thesis, quantitative methods have been employed to assess the level of skeletal and diagnostic information available for saurischian dinosaurs, in an attempt to understand the potential natural and anthropogenic biases influencing our understanding of their evolutionary history. The results presented here represent an important contribution to the ever-growing studies on fossil record bias.

In Chapter 2, results show that peaks in raw taxonomic diversity and the completeness of the theropod fossil record during the Late Jurassic and 'middle' Cretaceous were driven by the presence of Lagerstätten, though only marginal statistical evidence was recognised for a control of specimen completeness on observed diversity changes through time. However, the diagnostic utility of theropod specimens in different geological stages strongly corresponds with observed diversity changes, along with the number of bone occurrences and autapomorphies assigned to species per stage (Chapter 4). This strong connection seems to indicate observed diversity changes are fundamentally reliant on the underlying occurrences of bones, which is an intuitively obvious conclusion, but provides further evidence of a strong geological and taphonomic control on theropod diversity trends.

The theropod record constitutes many taxa of low completeness, but there are notable differences between phylogenetic subgroups. Megaraptorans have by far the least complete record of any group, which is likely exacerbated by their low diagnosability, whereas compsognathids and non-deinonychosaurian

Paraves have a very highly complete record, which is exclusively due to preservation in conservation Lagerstätten, as these groups too have relatively low diagnostic utility. Oviraptorosaurs, dromaeosaurids and ceratosaurs, on the other hand, have high diagnostic utility because of even distribution of skeletal autapomorphies and select elements of high diagnosability that preferentially survive taphonomic processes. However, the high completeness of oviraptorosaur skeletons in comparison to dromaeosaurids and ceratosaurs could be related to their ecological distinctiveness, as well as the environmental preferences of the latter groups. Although there is further evidence of potential environmental and ecological controls on completeness, taxon body size appears not to act as such a control on a global scale.

Furthermore, strong spatial biases are identified in the theropod record, with high completeness in Asia, a very limited record in Australiasia, and a poor European record, plus strong diagnostic differences between formations. Modern climate and landscape evolution are a potential cause of such differences, whereby consistent access to fossil-bearing localities and good preservation necessitate vast arid areas with little vegetation. However, even within one formation there are strong environmental controls on fossil occurrences and the relative diagnosability of assemblages, as the Morrison Formation displays strong inclination towards higher diagnostic utility within wetland and lacustrine facies. Spatiotemporal differences in basin deposition on relatively small scales likely strongly influence the spatial biases we see on continental scales, and in turn, the evolutionary signals we detect.

Chapter 3 reveals there have been significant changes to our understanding of the sauropodomorph fossil record in the last ten years, due mostly to taxonomic and stratigraphic revisions. This suggests interpretations from studies such as those presented in this thesis may change over time, highlighting the need for quantitative studies to keep up-to-date with new discoveries. However, even with such shifts, the over-arching trends in the sauropodomorph record have remained broadly the same, including a significant relationship between completeness and observed taxonomic diversity and a drop in completeness at the Jurassic–Cretaceous boundary, which to a lesser extent is also observed in the theropod record. There is potentially a significant similarity between the sauropodomorph and theropod records, indicating a level of geological control on dinosaurian and possibly even all Mesozoic tetrapod records. In contrast to theropods, the sauropodomorph record is affected less by spatial bias and more by temporal bias, as Cretaceous sauropodomorphs have significantly and consistently less complete skeletons than pre-Cretaceous species. Even though phylogenetic signals of completeness are detected for sauropodomorphs, it is difficult to attribute an explanation of the low Cretaceous completeness to either shifts in sauropodomorph environmental preferences or body size evolution. Possible explanations may relate to sea level changes and their subsequent influence on the terrestrial record, and/or biological or ecological specificities influencing the preferential preservation and identification of less complete material.

5.2. Comparisons to other completeness studies

As in this thesis, numerous recent studies have adopted the metrics originally outlined in Mannion and Upchurch (2010a) to assess the fossil record completeness of various tetrapod groups. We now have a detailed understanding of the fossil records of sauropodomorph (Mannion and Upchurch 2010a; Chapter 3) and non-avian theropod (Chapter 2, Cashmore and Butler 2019) dinosaurs, Mesozoic (Brocklehurst *et al.* 2012) and Cenozoic (Gardner *et al.* 2016) birds (an alternate metric is used in the latter), pterosaurs (Dean *et al.* 2016), crocodylomorphs (Mannion *et al.* 2019), plesiosaurs (Tutin and Butler 2017), ichthyosaurs (Cleary *et al.* 2015), mosasaurs (alternate metrics; Driscoll *et al.* 2018), pelycosaur-grade synapsids (Brocklehurst and Fröbisch 2014), parareptilians (Verrière *et al.* 2016), anomodonts (Walther and Fröbisch 2013), non-mammalian cynodonts (Lukic-Walther *et al.* 2019), Mesozoic and early Cenozoic eutherians (Davies *et al.* 2017), and bats (Brown *et al.* 2019). I am also aware of a number of currently in progress assessments of other tetrapod groups, including early tetrapods, sauropterygians, pinnipedomorphs, and cynodonts (using alternative metrics to Lukic-Walther *et al.* 2019). Projects have also begun using similar metrics to assess acanthodian and shark fossil records. This relative standardisation in assessing tetrapod fossil record completeness is positive for the field, as the data is comparable, and results become more meaningful with every new study.

As a result, researchers are beginning to have a more detailed understanding of the fossil record of different tetrapod groups and the major biases that could potentially be acting upon them. As is to be expected there are mixed signals depending on the group in question. Studies have reported positive relationships (Mannion and Upchurch 2010; Brocklehurst *et al.* 2012; Walther and Fröbisch 2013; Dean *et al.* 2016; Cashmore and Butler 2019), a negative relationship (Brocklehurst and Fröbisch 2014), and no relationship (Cleary *et al.* 2015; Davies *et al.* 2017; Tutin and Butler 2017; Driscoll *et al.* 2018; Brown *et al.* 2019; Mannion *et al.* 2019) between changes in mean completeness and diversity through time. Positive relationships suggest some level of control of specimen completeness on our understanding on tetrapod evolutionary history, whilst the negative correlation was argued to be due to taxonomic over-splitting. The groups with no relationship are the only marine and mammalian tetrapod groups studied, which suggests their records are controlled by significantly different preservation regimes to other mostly reptilian study groups, and that there are key differences between the fossil records of major tetrapod clades and between the terrestrial and marine realm. It is becoming increasingly clear that marine tetrapods and even semi-aquatic terrestrial tetrapods, such as crocodylomorphs, have substantially better fossil records than fully terrestrial tetrapods. This is almost certainly due to consistent proximity to depositional settings. Subtler differences in environmental association have also been shown to have a strong impact on the completeness of different tetrapod fossil records. This is strongly demonstrated by the reliance of the flying tetrapod preservation on non-typical regimes, such as conservation Lagerstätten (pterosaurs and birds) and cave deposits (bats). Furthermore, almost all studies find major spatiotemporal sampling biases acting upon different tetrapod records. These mostly consist of preferentially higher completeness in the northern hemisphere, contributed to mostly by Asia and North America, and modern and palaeo- mid-latitudes. Therefore, within the context of other studies, we can suggest that the nature of the dinosaur record is subject to certain limitations that are common to the fossil records of terrestrial reptiles and typical sampling availability.

5.3. Future directions

Many of the above mentioned studies, including this thesis, have focussed on the Mesozoic reptilian fossil record. Eight studies have included Palaeozoic (Walther and Fröbisch 2013; Brocklehurst and Fröbisch 2014; Verrière *et al.* 2016; Lukic-Walther *et al.* 2019) or Cenozoic (Gardner *et al.* 2016; Davies *et al.* 2016; Brown *et al.* 2019; Mannion *et al.* 2019) aged groups. Of these, the clades with Palaeozoic records have records that extend into the Mesozoic, and of the Cenozoic studies one used an alternate, simplified metric (Gardner *et al.* 2016), and another used different temporal constraints to other studies (Davies *et al.* 2016). Therefore, we have a comparatively limited global understanding of patterns of specimen completeness in the fossil record of Palaeozoic and Cenozoic clades. Immediate future research should aim to move away from assessments of Mesozoic tetrapod groups and focus more on the Palaeozoic and Cenozoic. Notable mammalian groups that would provide useful comparisons and significant enhancement of our understanding of the global tetrapod record would be cetaceans and carnivores.

Chapters 2 and 3 assessed the completeness of the saurischian dinosaur fossil records in detail. In the near future, it would be desirable for the ornithischian dinosaur fossil record to be studied in a similar manner, so we can have complete understanding of the potential biases acting upon the dinosaur fossil record. It would be of keen interest to determine whether the ornithischian temporal record is substantially different from the saurischian, or if the two converge on the same general pattern. This could have strong implications for our understanding of the dinosaur fossil record.

Completeness studies, using the metrics proposed by Mannion and Upchurch (2010a), do however have limitations. As SCM and CCM are simple quantifications of how much morphological information is available in comparison to a minimum that should be available (e.g. every identified species known from complete skeletons), they are incapable of assessing the missing fossil record, such as spatial, environmental or temporal gaps. For example, as there is a complete lack of identified bat specimens in the Paleocene, Brown et al. (2019) were unable to significantly address the preservation issues influencing a crucial period in bat evolution. In this regard, quantifications of the completeness of specimens can provide misleading interpretations of the quality of a record. A few complete specimens can artificially inflate a temporally and spatially isolated record. To combat such limitations, future studies could attempt to combine skeletal and character completeness metrics with relative completeness approaches, like stratigraphic congruence analyses, to gain a more thorough understanding of the particular issues underlying the fossil records of different groups.

Another methodological issue of studies like that presented in this thesis, is the relative inability to distinguish between cause and effect. For example, simple correlation tests between mean completeness and diversity time series only show that there is a potential relationship, but do not elucidate what relationship. We can only speculate as to whether a positive correlation means lower completeness of specimens in a given time bin influences our ability to identify more species, or the fewer species controls the amount of material available to us. In future, studies could potentially take advantage of the novel methodology used in Chapter 4 of this thesis, and attempt to quantify the diagnostic quality of skeletal material to help elucidate the relationship between specimen completeness and our understanding of the evolution of different groups. Using such methods, it would also be interesting to compare the contrasting levels of diagnostic quality between different tetrapod clades within the same formations or the same depositional environments. It would be advantageous to expand studies into other geological time periods as well, exploring how diagnostic quality may change depending on the geological age. One would expect diagnostic quality to increase through time, as faunas become more reminiscent of modern taxa. The most potentially insightful aspects of the research presented in this thesis is the generation of global occurrence and diagnostic potential datasets. From these we can unpick the fossil records of groups, effectively element by element, providing strong reasons for the nature of their specific records.

I believe that future specimen-based completeness studies should focus more closely on the connections between fossil completeness and environmental, ecological and biological factors, which could be influencing our understanding of the evolution of different groups. Though global macroevolutionary scale signals are informative, their amalgamation of localised signals means they have limited scope to provide reasons for the nature of different tetrapod fossil records. Studies of localised assemblages provide a wealth of information to disentangle the taphonomic pathways of fossils from a particular locality and/or specific animal group. However, most of these studies are difficult to extrapolate to larger scales. Future completeness studies could work to equate these differing scales, possibly with the goal of classifying regions and time bins in generalised taphonomic categories. I hope that the work undertaken in Chapter 4 could aid taphonomic studies including theropod material, as the bone occurrence dataset and taphonomic pathways could be utilised as a global basis for comparisons to local assemblage pathways. Finally, another key area of potential investigation would be to analyse the effects of modern day climate on the fossil record of different tetrapod groups. Statistically comparing specimen completeness data to regional precipitation levels or estimates of vegetation cover could provide credence to some of the claims made in this thesis.

References

ADLER, D. 2015. vioplot: Violin plot. R package version 0.2. https://cran.r-project.org/web/packages/vioplot/index.html

AGNOLIN, F. L., EZCURRA, M. D., DIEGO, F. P. and SALISBURY, S. W. 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology*, **8**, 257-300.

ALBA, D. M., AGUSTI, J. and MOYÀ-SOLÀ, S. 2001. Completeness of the mammalian fossil record in the Iberian Neogene. *Paleobiology*, **27**, 79-83.

ALROY, J. 2000. Successive approximations of diversity curves: ten more years in the library. *Geology*, **28**, 1023-1026.

ALROY, J. 2010. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *The Paleontological Society Papers*, **16**, 55-80.

ALROY, J., MARSHALL, C. R., BAMBACH, R. K., BEZUSKO, K., FOOTE, M., FÜRSICH, F. T., HANSEN, T. A., HOLLAND, S. M., IVANY, L. C., JABLONSKI, D. and JACOBS, D. K., 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences*, **98**, 6261-6266.

AMIOT, R., BUFFETAUT, E., LÉCUVER, C., WANG, X., BOUDAD, L., DING, Z., FOUREL, F., HUTT, S., MARTINEAU. F., ALFREDO MEDEIROS, M., MO, J., SIMON, L., SUTEETHORN, V., SWEETMAN, S., TONG, G., ZHANG, F. and ZHOU, Z. 2010. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology*, **38**, 139-142.

ANEMONE, R., EMERSON, C., CONROY, G. 2011. Finding fossils in new ways: An artificial neural network approach to predicting the location of productive fossil localities. *Evolutionary Anthropology*, **20**, 169-180.

ANGIELCZYK, K. D. 2002. A character-based method for measuring the fit of a cladogram to the fossil record. *Systematic Biology*, **51**, 176-191.

ANGIELCZYK, K. D., and FOX, D. L. 2006. Exploring new uses for measures of fit of phylogenetic hypotheses to the fossil record. *Paleobiology*, **32**, 147-165.

APALDETTI, C., MARTÍNEZ, R. N., CERDA, I. A., POL, D., and ALCOBER, O. 2018. An early trend towards gigantism in Triassic sauropodomorph dinosaurs. *Nature Ecology & Evolution*, **2**, 1227.

AZUMA, Y., XU, X., SHIBATAL, M., KAWABE, S., MIYATA, K. and IMAI, T. 2016. A bizarre theropod from the Early Cretaceous of Japan highlighting mosaic evolution among coelurosaurians. *Scientific Reports*, **6**, 20478.

BANDEIRA, K. L., BRUM, A. S., PÊGAS, R. V., CIDADE, G. M., HOLGADO, B., CIDADE, A., and DE SOUZA, R. G. 2018. The Baurusuchidae vs Theropoda record in the Bauru Group (Upper Cretaceous, Brazil): a taphonomic perspective. *Journal of Iberian Geology*, **44**, 25-54.

BAPST, D. W. and WAGNER, P. J. 2019. paleotree: Paleontological and Phylogenetic Analyses of Evolution. R package version 3.3.0. https://cran.r-project.org/web/packages/paleotree/index.html

BARON, M. G. and BARRETT, P. M. 2017. A dinosaur missing-link? *Chilesaurus* and the early evolution of ornithischian dinosaurs. *Biology Letters*, **13**, 20170220.

BARON, M. G., NORMAN, D. B. and BARRETT, P. M. 2017. A new hypothesis of dinosaur relationships and early dinosaur evolution. *Nature*, **543**, 501-506.

BARRETT, P. M. 2005. The diet of ostrich dinosaurs (Theropoda: Ornithomimosauria). *Palaeontology*, **48**, 347-358.

BARRETT, P. M. 2014. Paleobiology of herbivorous dinosaurs. *Annual Review of Earth and Planetary Sciences*, **42**, 207-230.

BARRETT, P. M. and UPCHURCH, P. 2005. Sauropod diversity through time: possible macroevolutionary and palaeoecological implications, pp. 125–156. *In* K. A. Curry-Rogers, and J. A. Wilson (eds). *The sauropods. Evolution and Paleobiology*. University of California Press, Berkeley, 349 pp.

BARRETT, P. M., MCGOWAN, A. J., and PAGE, V. 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2667-2674.

BARTA, D. E., NESBITT, S. J. and NORELL, M. A. 2018. The evolution of the manus of early theropod dinosaurs is characterized by high inter- and intraspecific variation. *Journal of Anatomy*, **232**, 80-104.

BARTOŃ, K. 2018. MuMIn: Multi-model inference. R package version 1.42.1. https://cran.r-project.org/web/packages/MuMIn/index.html

BARTOŃ, K. 2018. MuMIn: Multi-model inference. R package version 1.42.1.

BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T., FURRER, H. and JOHNSON, C. 2012. Death, decay and disarticulation: modelling the skeletal taphonomy of marine reptiles demonstrated using *Serpianosaurus* (Reptilia; Sauropterygia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **337**, 1-13.

BEHRENSMEYER, A. K. 2007. Bonebeds through Time. 65-102. *In* ROGERS, R. R., EBERTH, D. A. and FIORILLO, A. R. (eds). *Bonebeds, Genesis, Analysis, and Paleobiological Significance*. The University of Chicago Press, Chicago and London, 499 pp.

BEHRENSMEYER, A. K., STAYTON, C. T. and CHAPMAN, R. E. 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology*, **29**, 52-70.

BELL, C. J., GAUTHIER, J. A. and BEVER, G. S. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary Herpetofaunal Stability Hypothesis. *Quaternary International*, **217**, 30-36.

BELL, P. R., CURRIE, P. J. and LEE, Y. N. 2012. Tyrannosaur feeding traces on *Deinocheirus* (Theropoda:? Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia. *Cretaceous Research*, **37**, 186-190.

BELL, M. A., UPCHURCH, P., MANNION, P. D. and LLOYD, G. T. 2013. Using the character completeness metric to examine completeness of Mesozoic dinosaurs: A Maastrichtian high and a paleoequatorial low. *Society of Vertebrate Paleontology Annual Meeting, Program and Abstracts*, p. 84.

BENJAMINI, Y. and HOCHBERG, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289-300.

BENSON, R. B. J. 2018. Dinosaur Macroevolution and Macroecology. *Annual Review of Ecology, Evolution, and Systematics*, **49**, 379-408.

BENSON, R. B. J. and CHOINIERE, J. N. 2013. Rates of dinosaur limb evolution provide evidence for exceptional radiation in Mesozoic birds. *Proceedings of the Royal Society B: Biological Sciences,* **280**, 20131780.

BENSON, R. B., and UPCHURCH, P. 2013. Diversity trends in the establishment of terrestrial vertebrate ecosystems: interactions between spatial and temporal sampling biases. *Geology*, **41**, 43-46.

BENSON, R. B. J., CARRANO, M. T. and BRUSATTE, S. L. 2010a. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften*, **97**, 71-78.

BENSON, R. B., BUTLER, R. J., LINDGREN, J. and SMITH, A. S. 2010b. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 829-834.

BENSON, R. B., MANNION, P. D., BUTLER, R. J., UPCHURCH, P., GOSWAMI, A. and EVANS, S. E. 2013. Cretaceous tetrapod fossil record sampling and faunal turnover: implications for biogeography and the rise of modern clades. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 88-107.

BENSON, R. B., CAMPIONE, N. E., CARRANO, M. T., MANNION, P. D., SULLIVAN, C., UPCHURCH, P. and EVANS, D. C. 2014. Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biology*, **12**, e1001853.

BENSON, R. B. J., BUTLER, R. J., ALROY, J., MANNION, P. D., CARRANO, M. T. and LLOYD, G. T. 2016. Near-stasis in the long-term diversification of Mesozoic tetrapods. *PLoS Biology*, **14**, e1002359.

BENSON, R. B., HUNT, G., CARRANO, M. T. and CAMPIONE, N. 2018. Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology*, **61**, 13-48.

BENTON, M. J. 1989. Mass extinctions among tetrapods and the quality of the fossil record. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, **325**, 369-386.

BENTON, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, **354**, 1423–1446.

BENTON, M. J. 2004. Origin and relationships of Dinosauria. 7-24. *In* WEISHAMPEL, D. B., DODSON, P. and H. OSMÓLSKA, H. (eds). *Dinosauria.* Second Edition. University of California Press, Berkeley, 861 pp.

BENTON, M. J. 2008. Fossil quality and naming dinosaurs. *Biology Letters*, **4**, 729-732.

BENTON, M. J. 2010. Naming dinosaur species: the performance of prolific authors. *Journal of Vertebrate Paleontology*, **30**, 1478-1485.

BENTON, M. J. 2015. Palaeodiversity and formation counts: redundancy or bias? *Palaeontology*, **58**, 1003-1029.

BENTON, M. J. and STORRS, G. W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology*, **22**, 111-114.

BENTON, M. J. and STORRS, G. W. 1996. Diversity in the past: comparing cladistic phylogenies and stratigraphy. 19-40. *In* HOCHBERG, M. E., CLOBERT, J. and BARBAULT, R. (eds). *Aspects of the genesis and maintenance of biological diversity*. Oxford University Press, Oxford, 316 pp.

BENTON, M.J., and HITCHIN, R. 1996. Testing the quality of the fossil record by groups and by major habitats. *Historical Biology*, **12**, 111-157.

BENTON, M. J., WILLS, M. A. and HITCHIN, R. 2000. Quality of the fossil record through time. *Nature*, **403**, 534-537.

BENTON, M. J., TVERDOKHLEBOV, V. P. and SURKOV, M. V. 2004. Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia. *Nature*, **432**, 97-100.

BENTON, M. J., DUNHILL, A. M., LLOYD, G. T. and MARX, F. G. 2011. Assessing the quality of the fossil record: insights from vertebrates. *Geological Society, London, Special Publications*, **358**, 63-94.

BENYOUCEF, M., LÄNG, E., CAVIN, L., MEBARKI, K., ADACI, M. and BENSALAH, M. 2015. Overabundance of piscivorous dinosaurs (Theropoda: Spinosauridae) in the mid-Cretaceous of North Africa: The Algerian dilemma. *Cretaceous Research*, **55**, 44-55.

BERNARD, E. L., RUTA, M., TARVER, J. E. and BENTON, M. J. 2010. The fossil record of early tetrapods: Worker effort and the end-Permian mass extinction. *Acta Palaeontologica Polonica*, **55**, 229–239.

BERNARDI, M., GIANOLLA, P., PETTI, F. M., MIETTO, P. and BENTON, M. J. 2018. Dinosaur diversification linked with the Carnian Pluvial Episode. *Nature Communications*, **9**, 1499.

BERTIN, T. 2010. A catalogue of material and review of the Spinosauridae. *PalArch's Journal of Vertebrate Palaeontology*, **7**, 1-39.

BLOMBERG, S. P. and GARLAND Jr., T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, **15**, 899-910.

BOESSENECKER R. W., PERRY, F. A. and SCHMITT, J. G. 2014. Comparative Taphonomy, Taphofacies, and Bonebeds of the Mio-Pliocene Purisima Formation, Central California: Strong Physical Control on Marine Vertebrate Preservation in Shallow Marine Settings. *PLoS ONE*, **9**, e91419

BRIGGS, D. E., WILBY, P. R., PEREZ-MORENO, B. P., SANZ, J. L. and FREGENAL-MARTÍNEZ, M. 1997. The mineralization of dinosaur soft tissue in the Lower Cretaceous of Las Hoyas, Spain. *Journal of the Geological Society*, **154**, 587-588.

BRITT, B. B., EBERTH, D. A., SCHEETZ, R. D., GREENHALGH, B. W. and STADTMAN, K. L. 2009. Taphonomy of debris-flow hosted dinosaur bonebeds at Dalton Wells, Utah (Lower Cretaceous, Cedar Mountain Formation, USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280**, 1-22.

BROCHU, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, **22**, 1-138.

BROCKLEHURST, N. 2015. A simulation-based examination of residual diversity estimates as a method of correcting for sampling bias. *Palaeontologia Electronica*, **18**, 1-15.

BROCKLEHURST, N. and FRÖBISCH, J. 2014. Current and historical perspectives on the completeness of the fossil record of pelycosaurian-grade synapsids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **399**, 114–126.

BROCKLEHURST, N., UPCHURCH, P., MANNION, P. D. and O'CONNOR, J. 2012. The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. *PLoS ONE*, **7**, e39056.

BROWN, C. M., EVANS, D. C., CAMPIONE, N. E., O'BRIEN, L. J. and EBERTH, D. A. 2013. Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 108-122.

BROWN, E, E., CASHMORE, D. D., SIMMONS, N. B., BUTLER, R. J. 2019. Quantifying the completeness of the bat fossil record. *Palaeontology*, **61**, 757-776.

BRUSATTE, S. L., BENTON, M. J., RUTA, M. and LLOYD, G. T. 2008a. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science*, **321**, 1485-1488.

BRUSATTE, S. L., BENTON, M. J., RUTA, M., and LLOYD, G. T. 2008b. The first 50 Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters*, **4**, 733-736.

BRUSATTE, S. L., BUTLER, R. J., PRIETO-MÁRQUEZ, A. and NORELL, M. A. 2012a. Dinosaur morphological diversity and the end-Cretaceous extinction. *Nature Communications*, **3**, 804.

BRUSATTE, S. L., SAKAMOTO, M., MONTANARI, S. and HARCOURT SMITH, W. E. H. 2012b. The evolution of cranial form and function in theropod dinosaurs: insights from geometric morphometrics. *Journal of Evolutionary Biology*, **25**, 365-377.

BRUSATTE, S. L., BUTLER, R. J., BARRETT, P. M., CARRANO, M. T., EVANS, D. C., LLOYD, G. T., MANNION, P. D., NORELL, M. A., PEPPER, D. J., UPCHURCH, P. and WILLIAMSON. 2014. The extinction of the dinosaurs. *Biological Reviews*, **90**, 628-642.

BRUSATTE, S. L., O'CONNOR, J. K. and JARVIS, E. D. 2015. The origin and diversification of birds. *Current Biology*, **25**, R888-R898.

BUTLER, R. J. and UPCHURCH, P. 2007. Highly incomplete taxa and the phylogenetic relationships of the theropod dinosaur *Juravenator starki. Journal of Vertebrate Paleontology*, **27**, 253-256.

BUTLER, R. J. and BARRETT, P. M. 2008. Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. *Naturwissenschaften*, **95**, 1027–1032.

BUTLER, R. J., BENSON, R. B., CARRANO, M. T., MANNION, P. D. and UPCHURCH, P. 2010. Sea level, dinosaur diversity and sampling biases: investigating the 'common cause' hypothesis in the terrestrial realm. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**, 1165-1170.

CANDEIRO, C. R. A., GIL, L. M. and DE CASTRO, P. E. P. 2018. Large-sized theropod *Spinosaurus*: an important component of the carnivorous dinosaur fauna in southern continents during the Cretaceous. *BSGF - Earth Sciences Bulletin*, **189**, 15.

CANUDO, J. I., CARBALLIDO J. L., GARRIDO, A. and SALGADO, L. 2018. A new rebbachisaurid sauropod from the Aptian–Albian, Lower Cretaceous Rayoso Formation, Neuquén, Argentina. *Acta Palaeontologica Polonica*, **63**, 679-691.

CARBALLIDO, J. L. POL, D., OTERO, A., CERDA, I. A., SALGADO, L., GARRIDO, A. C., RAMEZANI, J., CÚNEO, N. R. and KRAUSE, J. M. 2017. A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20171219.

CARBONE, C., TURVEY, S. T. and BIELBY, J. 2011. Intra-guild competition and its implications for one of the biggest terrestrial predators, *Tyrannosaurus rex. Proceedings of the Royal Society of London B: Biological Sciences*, **278**, 2682–2690.

CARPENTER, K. 2013. History, sedimentology, and taphonomy of the Carnegie Quarry, Dinosaur National Monument, Utah. *Annals of Carnegie Museum*, **81**, 153-233.

CARRANO, M. T. 2006. Body-size evolution in the Dinosauria. 225–268. *In* CARRANO, M. T., GAUDIN, T. J., BLOB, R. W., WIBLE, J. R. (eds). *Amniote Paleobiology*. University of Chicago Press, Chicago and London, 547 pp.

CARRANO, M. T. and VELEZ-JUARBE, J. 2006. Paleoecology of the Quarry 9 vertebrate assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **237**, 147-159.

CARRASCO, M. A. 2013. The impact of taxonomic bias when comparing past and present species diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 130-137.

CASE, J. A., MARTIN, J. E., CHANEY, D. S., REGUERO, M., MARENSSI, S. A., SANTILLANA, S. M. and WOODBURNE, M. O. 2000. The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. *Journal of Vertebrate Paleontology*, **20**, 612-614.

CASE, J. A., MARTIN, J. E. and REGUERO, M. 2007. A dromaeosaur from the Maastrichtian of James Ross Island and the Late Cretaceous Antarctic dinosaur fauna. *In* COOPER, A. K., RAYMOND, C. R., *et al.* (eds). *Antarctica: A Keystone in a Changing World*. Online Proceedings of the 10th ISAES X, USGS Open-File Report 2007-1047, Short Research Paper 083, 4 pp.

CASEY, M. M., FRASER, N. C. and KOWALEWSKI, M. 2007. Quantitative taphonomy of a Triassic reptile *Tanytrachelos ahynis* from the Cow Branch Formation, Dan River Basin, Solite quarry, Virginia. *Palaios*, **22**, 598-611.

CASHMORE, D. D. and BUTLER, R. J. 2019. Skeletal completeness of the non-avian theropod dinosaur fossil record. *Palaeontology*. doi:10.1111/pala.12436

CASHMORE, D. D. and BUTLER, R. J. 2019. Data from: Skeletal completeness of the non-avian theropod dinosaur fossil record. Dryad Digital Repository. https://datadryad.org/review?doi=doi:10.5061/dryad.37c840g

CERDA, I. A., CARABAJAL, A. P., SALGADO, L., CORIA, R. A., REQUERO, M. A., TAMBUSSI, C. P. and MOLY, J. J. 2012. The first record of a sauropod dinosaur from Antarctica. *Naturwissenschaften*, **99**, 83-87.

CHAO, A. and JOST, L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533-2547.

CHARIG, A. J. and MILNER, A. C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin-Natural History Museum Geology Series*, **53**, 11-70.

CHIARENZA, A. A., MANNION, P. D., LUNT, D. J., FARNSWORTH, A., JONES, L. A., KELLAND, S. J. and ALLISON, P. A. 2019. Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature communications*, **10**, 1091.

CHOINIERE, J. N., CLARK, J. M., FORSTER, C. A. and XU, X. 2010. A basal coelurosaur (Dinosauria: Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucaiwan, People's Republic of China. *Journal of Vertebrate Paleontology*, **30**, 1773-1796.

CHOINIERE, J. N., CLARK, J. M., FORSTER, C. A., NORELL, M. A., EBERTH, D. A., ERICKSON, G. M., CHU, H. and XU, X. 2014. A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. *Journal of Systematic Palaeontology*, **12**, 177-215.

CHRISTIANSEN, P. 1999. On the head size of sauropodomorph dinosaurs: implications for ecology and physiology. *Historical Biology*, **13**, 269-297.

CLEARY, T. J., MOON, B. C., DUNHILL, A. M. and BENTON, M. J. 2015. The fossil record of ichthyosaurs, completeness metrics and sampling biases. *Palaeontology*, **58**, 521-536.

CLOSE, R. A., BENSON, R. B., UPCHURCH, P. and BUTLER, R. J. 2017. Controlling for the species-area effect supports constrained long-term Mesozoic terrestrial vertebrate diversification. *Nature Communications*, **8**, 15381.

CLOSE, R. A., EVERS, S. W., ALROY, J. and BUTLER, R. J. 2018. How should we estimate diversity in the fossil record? Testing richness estimators using sampling-standardised discovery curves. *Methods in Ecology and Evolution*, **9**, 1386-1400.

CODRON, D., CARBONE, C., MÜLLER, D. W. and CLAUSS, M. 2012. Ontogenetic niche shifts in dinosaurs influenced size, diversity and extinction in terrestrial vertebrates. *Biology Letters*, **8**, 620-623.

CODRON, D., CARBONE, C. and CLAUSS, M. 2013. Ecological Interactions in Dinosaur Communities: Influences of Small Offspring and Complex Ontogenetic Life Histories. *PLoS ONE*, **8**: e77110

CONROY, G., EMERSON, C., ANEMONE, R., TOWNSEND, K. E. B. 2012. Let your fingers do the walking: A simple spectral signature model for "remote" fossil prospecting. *Journal of Human Evolution*, **63**, 79-84.

COOPER, R. A., MAXWELL, P. A., CRAMPTON, J. S., BEU, A. G., JONES, C. M. and MARSHALL, B. A. 2006. Completeness of the fossil record: estimating losses due to small body size. *Geology*, **34**, 241-244.

CORIA, R. A., MOLY, J. J., REGUERO, M., SANTILLANA, S. and MARENSSI, S. 2013. A new ornithopod (Dinosauria; Ornithischia) from Antarctica. *Cretaceous Research*, **41**, 186-193.

CSIKI, Z., VREMIR, M., BRUSATTE, S. L. and NORELL, M. A. 2010. An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. *Proceedings of the National Academy of Sciences*, **107**, 15357-15361.

CSIKI-SAVA, Z., BUFFETAUT, E., ŐSI, A., PEREDA-SUBERBIOLA, X. and BRUSATTE, S. L. 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *ZooKeys*, **469**, 1-169.

CUFF, A. R. and RAYFIELD, E. J. 2013. Feeding Mechanics in Spinosaurid Theropods and Extant Crocodilians. *PLoS ONE*, **8**, e65295.

CULLEN, T. M., RYAN, M. J., SCHRÖDER-ADAMS, C., CURRIE, P. J. and KOBAYASHI, Y. 2013. An ornithomimid (Dinosauria) bonebed from the Late Cretaceous of Alberta, with implications for the behavior, classification, and stratigraphy of North American ornithomimids. *PLoS ONE*, **8**, e58853.

CURRIE, P. J. and KOPPELHUS, E. B. 2015. The significance of the theropod collections of the Royal Tyrrell Museum of Palaeontology to our understanding of Late Cretaceous theropod diversity. *Canadian Journal of Earth Sciences*, **52**, 620-629.

DARWIN, C. 1859. *On The Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life*. London: John Murray, 458pp.

DAVIES, T. W., BELL, M. A., GOSWAMI, A. and HALLIDAY, T. J. 2017. Completeness of the eutherian mammal fossil record and implications for reconstructing mammal evolution through the Cretaceous/Paleogene mass extinction. *Paleobiology*, **43**, 521-536.

DE SOUZA CARVALHO, I., SALGADO, L., LINDOSO, R. M., DE ARAÚJO-JÚNIOR, H. I., NOGUEIRA, F. C. C. and SOARES, J. A. 2017. A new basal titanosaur (Dinosauria, Sauropoda) from the Lower Cretaceous of Brazil. *Journal of South American Earth Sciences*, **75**, 74-84.

DEAN, C. D., MANNION, P. D. and BUTLER, R. J. 2016. Preservational bias controls the fossil record of pterosaurs. *Palaeontology*, **59**, 225-247.

DÍEZ DÍAZ , V. D., GARCIA, G., PEREDA-SUBERBIOLA, X., JENTGEN-CESCHINO, B., STEIN, K., GODEFROIT, P. and VALENTIN, X. 2018. The titanosaurian dinosaur *Atsinganosaurus velauciensis* (Sauropoda) from the Upper Cretaceous of southern France: New material, phylogenetic affinities, and palaeobiogeographical implications. *Cretaceous Research*, **91**, 429-456.

DINGUS, L. 1984. Effects of stratigraphic completeness on interpretations of extinction rates across the Cretaceous-Tertiary boundary. *Paleobiology*, **10**, 420-438.

DRISCOLL, D. A., DUNHILL, A. M., STUBBS, T. L. and BENTON, M. J. 2018. The mosasaur fossil record through the lens of fossil completeness. *Palaeontology*, **62**, 51-75.

DUNHILL, A. M., BENTON, M. J., NEWELL, A. J., and TWITCHETT, R. J. 2013. Completeness of the fossil record and the validity of sampling proxies: a case study from the Triassic of England and Wales. *Journal of the Geological Society*, **170**, 291-300.

DUNHILL, A.M., HANNISDAL, B. and BENTON, M. J. 2014. Disentangling rock record bias and common-cause from redundancy in the British fossil record. *Nature Communications*, **5**, 4818.

DUNHILL, A. M., BESTWICK, J., NAREY, H. and SCIBERRAS, J. 2016. Dinosaur biogeographical structure and Mesozoic continental fragmentation: a network-based approach. *Journal of Biogeography*, **43**, 1691-1704.

DUNHILL, A.M., HANNISDAL, B., BROCKLEHURST, N. and BENTON, M. J. 2018. On formation-based sampling proxies and why they should not be used to correct the fossil record. *Palaeontology*, **61**, 119-132.

DYKE, G. J., MCGOWAN, A. J., NUDDS, R. L. and SMITH, D. 2009. The shape of pterosaur evolution: evidence from the fossil record. *Journal of Evolutionary Biology*, **22**, 890-898.

DZIK, J. 2005. The chronophyletic approach: stratophenetics facing an incomplete fossil record. *Special Papers in Palaeontology*, **73**, 159-183.

EITING, T. P. and GUNNELL, G. F. 2009. Global completeness of the bat fossil record. *Journal of Mammalian Evolution*, **16**, 151-173.

ELDER, R. L. and SMITH, G. R. 1988. Fish taphonomy and environmental inference in paleolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62**, 577-592.

ELIASON, C. M., HUDSON, L., WATTS, T., GARZA, H. and CLARKE, J. A. 2017. Exceptional preservation and the fossil record of tetrapod integument. *Proceedings of the Royal Society B*, **284**, 20170556.

EMERSON, C., BOMMERSBACH, B., NACHMAN, B., ANEMONE, R. 2015. An Object-Oriented Approach to Extracting Productive Fossil Localities from Remotely Sensed Imagery. *Remote Sensing*, **7**, 15848.

ERICKSON, G. M., RAUHUT, O. W. M., ZHOU, Z., TURNER, A. H., INOUYE, B. D., HU, D. and NORELL, M. A. 2009. Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. *PLoS ONE*, **4**, e7390.

EZCURRA, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan and Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas*, **28**, 649–684.

EZCURRA, M. D. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. Journal of Systematic *Palaeontology*, **8**, 371-425.

FANTI, F., CURRIE, P. J. and BADAMGARAV, D. 2012. New specimens of *Nemegtomaia* from the Baruungoyot and Nemegt formations (Late Cretaceous) of Mongolia. *PLoS ONE*, **7**, e31330.

FARA, E. 2002. Sea-level variations and the quality of the continental fossil record. *Journal of the Geological Society*, **159**, 489-491.

FARA, E. 2004. Estimating minimum global species diversity for groups with a poor fossil record: a case study of Late Jurassic–Eocene lissamphibians. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **207**, 59-82.

FARA, E., and BENTON, M. J. 2000. The fossil record of Cretaceous tetrapods. *Palaios*, **15**, 161-165.

FARLOW, J. O. 1976. A consideration of the trophic dynamics of a Late Cretaceous large-dinosaur community (Oldman Formation). *Ecology*, **57**, 841-857.

FARLOW, J. O. 1993. On the rareness of big, fierce animals: Speculations about the body sizes, population densities, and geographic ranges of predatory mammals and large carnivorous dinosaurs. *American Journal of Science*, **293A**, 167–199.

FARLOW, J. O. and PLANKA, E. R. 2002. Body size overlap, habitat partitioning and living space requirements of terrestrial vertebrate predators: implications for the paleoecology of large theropod dinosaurs. *Historical Biology*, **16**, 21-40.

FILIPPI, L. S., SALGADO, L. and GARRIDO, A. C. 2019. A new giant basal titanosaur sauropod in the Upper Cretaceous (Coniacian) of the Neuquén Basin, Argentina. *Cretaceous Research*, **100**, 61-81.

FONG, Y., HUANG, Y., GILBERT, P. B. and PERMAR, S. R. 2017. chngpt: threshold regression model estimation and inference. *BMC Bioinformatics*, **18**, 454.

FOOTE, M. and RAUP, D. M. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology*, **22**, 121-140.

FOOTE, M. and SEPKOSKI, J. J. Jr. 1999. Absolute measures of the completeness of the fossil record. *Nature*, **398**, 415-417.

FOSTER, J. R. 2003. Paleoecological Analysis of the Vertebrate Fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, USA. *New Mexico Museum of Natural History and Science*, **23**.

FOSTER, J. R., MCHUGH, J. B., PETERSON, J. E. and LESCHIN, M. F. 2016, Major bonebeds in mudrocks of the Morrison Formation (Upper Jurassic), northern Colorado Plateau of Utah and Colorado. *Geology of the Intermountain West,* **3**, 33–66.

FOSTER, J. R., HUNT-FOSTER, R. K., GORMAN, M. A., TRUJILLO, K. C., SUAREZ, C., MCHUGH, J. B., PETERSON, J. E., WARNOCK, J. P. and SCHOENSTEIN, H. E. 2018. Paleontology, taphonomy, and sedimentology of the Mygatt-Moore Quarry, a large dinosaur bonebed in the Morrison Formation, western Colorado—Implications for Upper Jurassic dinosaur preservation modes. *Geology of the Intermountain West*, **5**, 23-93.

FOUNTAINE, T. M., BENTON, M. J., DYKE, G. J. and NUDDS, R. L. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society of London B: Biological Sciences*, **272**, 289-294.

FREDERICKSON, J. A., ENGEL, M. H. and CIFELLI, R. L. 2018. Niche Partitioning in Theropod Dinosaurs: Diet and Habitat Preference in Predators from the Uppermost Cedar Mountain Formation (Utah, USA). *Scientific reports*, **8**, 17872.

FRICKE, H. C., HENCECROTH, J. and HOERNER, M. E. 2011. Lowland–upland migration of sauropod dinosaurs during the Late Jurassic epoch. *Nature*, **480**, 513.

FUNSTON, G. F., CURRIE, P. J., EBERTH, D. A., RYAN, M. J., CHINZORIG, T., BADAMGARAV, D. and LONGRICH, N. R. 2016. The first oviraptorosaur (Dinosauria: Theropoda) bonebed: evidence of gregarious behaviour in a maniraptoran theropod. *Scientific Reports*, **6**, 35782.

FÜRSICH, F. T., SHA, J., JIANG, B. and PAN, Y. 2007. High resolution palaeoecological and taphonomic analysis of Early Cretaceous lake biota, western Liaoning (NE-China). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**, 434-457.

GALLINA, P. A., APESTEGUÍA, S., CANALE, J. I. and HALUZA, A. 2019. A new long-spined dinosaur from Patagonia sheds light on sauropod defense system. *Scientific reports*, **9**, 1392.

GARDNER, E. E., WALKER, S. E. and GARDNER, L. I. 2016. Palaeoclimate, environmental factors, and bird body size: A multivariable analysis of avian fossil preservation. *Earth-Science Reviews*, **162**, 177-197.

GATES, T. A. 2005. The Late Jurassic Cleveland-Lloyd dinosaur quarry as a drought-induced assemblage. *Palaios*, **20**, 363-375.

GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. Memoir of the California Academy of Sciences, 8, 1–55.

GODEFROIT, P., DEMUYNCK, H., DYKE, G., HU, D., ESCUILLIÉ, F. and CLAEYS, P. 2013. Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nature Communications*, **4**, 1394.

GÖHLICH, U. B. and CHIAPPE, L. M. 2006. A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature*, **440**, 329-332.

GONZÁLEZ RIGA, B. J. G. and ASTINI, R. A. 2007. Preservation of large titanosaur sauropods in overbank fluvial facies: a case study in the Cretaceous of Argentina. Journal of South American *Earth Sciences*, **23**, 290-303.

GONZÁLEZ RIGA, B. J. G., MANNION, P. D., POROPAT, S. F., ORTIZ DAVID, L. D. and CORIA, J. P. 2018. Osteology of the Late Cretaceous Argentinean sauropod dinosaur *Mendozasaurus neguyelap*: implications for basal titanosaur relationships. *Zoological Journal of the Linnean Society*, **184**, 136-181.

GOODWIN, M. B. and HORNER, J. R. 2010. Historical collecting bias and the fossil record of Triceratops in Montana. *In* Ryan M. J., Chinnery-Allgeier B. J., and Eberth D. A. (eds). *New perspectives on horned dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 567 pp.

GORSCAK, E. and O'CONNOR, P. M. 2016. Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history. *Biology Letters*, **12**, 20151047.

GORSCAK, E. and O'CONNOR, P. M. 2019. A new African Titanosaurian Sauropod Dinosaur from the middle Cretaceous Galula Formation (Mtuka Member), Rukwa Rift Basin, Southwestern Tanzania. *PloS One*, **14**, e0211412.

GRIEBELER, E. M. and WERNER, J. 2011. The life cycle of sauropod dinosaurs, pp 263-275. *In* KLEIN, N., REMES, K., GEE, C. T. and SANDER, P. M. (eds). *Biology of the sauropod dinosaurs: Understanding the life of giants*. Indiana University Press, Bloomington, 344 pp.

GRIEBELER, E. M., KLEIN, N. and SANDER, P. M. 2013. Aging, maturation and growth of sauropodomorph dinosaurs as deduced from growth curves using long bone histological data: an assessment of methodological constraints and solutions. *PloS ONE*, **8**, e67012.

GRIFFIN, C. T. and NESBITT, S. J. 2016. Anomalously high variation in postnatal development is ancestral for dinosaurs but lost in birds. *Proceedings of the National Academy of Sciences*, **113**, 14757-14762.

GUINOT, G., ADNET, S. and CAPPETTA, H. 2012. An Analytical Approach for Estimating Fossil Record and Diversification Events in Sharks, Skates and Rays. *PLoS ONE,* **7**, e44632.

GUPTA, N. S., CAMBRA-MOO, O., BRIGGS, D. E., LOVE, G. D., FREGENAL-MARTÍNEZ, M. A. and SUMMONS, R. E. 2008. Molecular taphonomy of macrofossils from the Cretaceous Las Hoyas Formation, Spain. *Cretaceous Research*, **29**, 1-8.

HAMMER, W. R. and HICKERSON, W. J. 1994. A crested theropod dinosaur from Antarctica. *Science*, **264**, 828-830.

HAUBOLD, H. 1990. Dinosaurs and fluctuating sea levels during the Mesozoic. *Historical Biology*, **4**, 75-106.

HEDGES, S. B., PARKER, P. H., SIBLEY, C. G. and KUMAR, S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature*, **381**, 226.

HEIJNE, J., KLEIN, N. and SANDER, P. M. 2019. The uniquely diverse taphonomy of the marine reptile skeletons (Sauropterygia) from the Lower Muschelkalk (Anisian) of Winterswijk, The Netherlands. *PalZ*, **93**, 69-92.

HENDERSON, D. M. 1998. Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison Formation theropods. *Gaia*, **15**, 219-226.

HENDY, A. J. 2011. Taphonomic overprints on Phanerozoic trends in biodiversity: lithification and other secular megabiases. 19-77. *In* ALLISON, P.A. and BOTTIER, D. J. (eds). *Taphonomy: Process and Bias Through Time*, Springer, Dordrecht.

HOCKNULL, S. A., WHITE, M. A., TISCHLER, T. R., COOK, A. G., CALLEJA, N. D., SLOAN, T. and ELLIOTT, D. A. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE*, **4**, e6190.

HOFMANN, R. and SANDER, P. M. 2014. The first juvenile specimens of *Plateosaurus engelhardti* from Frick, Switzerland: isolated neural arches and their implications for developmental plasticity in a basal sauropodomorph. *PeerJ*, **2**, e458.

HOLTZ, T. R. 2012. Theropods. 347-378. *In* BRETT-SURMAN, M. K., HOLTZ, T. R. and FARLOW, J. O. (eds). *The Complete Dinosaur*. Indian University Press, Bloomington and Indianapolis, 1112 pp.

HONE, D. W. E., XU, X. and WANG, D. Y. 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. *Vertebrata PalAsiatica*, **48**, 19-26.

HOOKER, J. J., MILNER, A. C. and SEQUEIRA, S. E. K. 1991. An ornithopod dinosaur from the Late Cretaceous of West Antarctica. *Antarctic Science*, **3**, 331-332.

HORNER, J. R., GOODWIN, M. B. and MYHRYOLD, N. 2011. Dinosaur census reveals abundant *Tyrannosaurus* and rare ontogenetic stages in the Upper Cretaceous Hell Creek Formation (Maastrichtian), Montana, USA. *PLoS ONE*, **6**, e16574.

HUANG, D. 2019. Jurassic integrative stratigraphy and timescale of China. *Science China Earth Sciences*, **62**, 223-255.

HÜNGERBÜHLER, A. 1998. Taphonomy of the prosauropod dinosaur Sellosaurus, and its implications for carnivore faunas and feeding habits in the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **143**, 1-29.

HUNT, A. P., LOCKLEY, M. G., LUCAS, S. G. and MEYER, C. A. 1994. The global sauropod fossil record: *Gaia*, **10**, 261-279.

HUNTER, A. W. and DONOVAN, S. K. 2005. Field sampling bias, museum collections and completeness of the fossil record. *Lethaia*, **38**, 305–314.

IBRAHIM, N., SERENO, P. C., DAL SASSO, C., MAGANUCO, S., FABBRI, M., MARTILL, D. M., ZOUHRI, S., MYHRVOLD, N. and IURINO, D. A. 2014. Semiaquatic adaptations in a giant predatory dinosaur. *Science*, **345**, 1613-1616.

IRMIS, R. B., NESBITT, S. J., PADIAN, K., SMITH, N. D., TURNER, A. H., WOODY, D. and DOWNS, A. 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. *Science*, **317**, 358–361.

IRMIS, R. B., WHITESIDE, J. H. and KAMMERER, C. F. 2013. Non-biotic controls of observed diversity in the paleontologic record: an example from the Permo-Triassic Karoo Basin of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 62-77.

JERZYKIEWICZ, T., CURRIE, P. J., EBERTH, D. A., JOHNSTON, P. A., KOSTER, E. H. and ZHENG, J. J. 1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Canadian Journal of Earth Sciences*, **30**, 2180-2195.

JESUS FARIA, C. C., GONZÁLEZ RIGA, B., CANDEIRO, C. R. A., MARINHO, T. S., ORTIZ DAVID, L., SIMBRAS, F. M., CASTANHO, R. B., MUNIZ, F. P. and COSTA PEREIRA, P. V. L. G. 2015. Cretaceous sauropod diversity and taxonomic succession in South America. *Journal of South American Earth Sciences*, **61**, 154–163.

JOUVE, S., MENNECART, B., DOUTEAU, J. and JALIL, N. E. 2017. Biases in the study of relationships between biodiversity dynamics and fluctuation of environmental conditions. *Palaeontologia Electronica*, **20**, 1-21.

JUUL, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana*, **31**, 1–38.

KALMAR, A., and CURRIE, D. J. 2010. The completeness of the continental fossil record and its impact on patterns of diversification. *Paleobiology*, **36**, 51-60.

KEMP, R. A. and UNWIN, D. M. 1997. The skeletal taphonomy of *Archaeopteryx*: a quantitative approach. *Lethaia*, **30**, 229-238.

KIDWELL, S. M. and HOLLAND, S. M. 2002. The quality of the fossil record: implications for evolutionary analyses. *Annual Review of Ecology and Systematics*, **33**, 561-588.

KLEIN, N., SANDER, P. M., STEIN, K., LE LOEUFF, J., CARBALLIDO, J. L. and BUDDETAUT, E. 2012. Modified laminar bone in *Ampelosaurus atacis* and other titanosaurs (Sauropoda): implications for life history and physiology. *PLoS ONE*, **7**, e36907.

KOBAYASHI, Y. and LÜ, J.−C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, **48**, 235–259.

KOCH, C. F. 1978. Bias in the published fossil record. *Paleobiology*, **4**, 367-372.

KOWALEWSKI, M. 1996. Time-averaging, overcompleteness, and the geological record. *The Journal of Geology*, **104**, 317-326.

KSEPKA, D. T. and BOYD, C. A. 2012. Quantifying historical trends in the completeness of the fossil record and the contributing factors: an example using Aves. *Paleobiology*, **38**, 112–125.

LÄNG, E., BOUDAD, L., MAIO, L., SAMANKASSOU, E., TABOUELLE, J., TONG, H., and CAVIN, L. 2013. Unbalanced food web in a Late Cretaceous dinosaur assemblage. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **381**, 26-32.

LANGER, M. C. 2014. The origins of Dinosauria: much ado about nothing. *Palaeontology*, **57**, 469-478.

LANGER, M. C. and BENTON, M. J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology*, **4**, 309–358.

LANGER, M. C., EZCURRA, M. D., RAUHUT, O. W. M., BENTON, M. J., KNOLL, F., MCPHEE, B. W., NOVAS, F. E., POLL, D. and BRUSATTE, S. L. 2017. Untangling the dinosaur family tree. *Nature*, **551**, E1-E3.

LAUTENSCHLAGER, S. 2017. Functional niche partitioning in Therizinosauria provides new insights into the evolution of theropod herbivory. *Palaeontology*, **60**, 375-387.

LE LOEUFF, J. 2012. Paleobiogeography and biodiversity of Late Maastrichtian dinosaurs: how many dinosaur species went extinct at the Cretaceous-Tertiary boundary? *Bulletin de la Sociéte Géologique de France*, **183**, 547-559.

LEHMANN, O. E., EZCURRA, M. D., BUTLER, R. J. and LLOYD, G. T. 2019. Biases with the Generalized Euclidean Distance measure in disparity analyses with high levels of missing data. *Palaeontology*, **62**, 837-849.

LEMON, J., BOLKER, B., OOM, S., KLEIN, E., ROWLINGSON, B., WICKHAM, H., TYAGI, A., ETERRADOSSI, O., GROTHENDIECK, G., TOEWS, M., KANE, J., TURNER, R., WITTHOFT, C., STANDER, J., PETZOLDT, T., DUURSMA, R., BIANCOTTO, E., LEVY, O., DUTANG, C., SOLYMOS, P., ENGELMANN, R., HECKER, M., STEINBECK, F., BORCHERS, H., SINGMANN, H., TOAL, T., OGLE, D., BARAL, D., GROEMPING, U. and VENABLES, B. 2019. plotrix: Various Plotting Functions. R package version 3.7-6. https://cran.r-project.org/web/packages/plotrix/index.html.

LEONARDI, G. 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. 165-178. *In* GILLETTE, D. D. and LOCKLEY, M. G. (eds). *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, 454 pp.

LI, K., YANG, C. and HU, F. 2011. Dinosaur assemblages from the Middle Jurassic Shaximiao Formation and Chuanjie Formation in the Sichuan-Yunnan Basin, China. *Volumina Jurassica*, **9**, 21-42.

LLOYD, G. T. 2011. A refined modelling approach to assess the influence of sampling on palaeobiodiversity curves: new support for declining Cretaceous dinosaur richness. *Biology Letters*, **8**, 123-126.

LLOYD, G. T., BAPST, D. W., FRIEDMAN M. and DAVIS, K. E. 2016. Probabilistic divergence time estimation without branch lengths: dating the origins of dinosaurs, avian flight and crown birds. *Biology Letters*, **12**, 20160609.

LLOYD, G. T., DAVIS, K. E., PISANI, D., TARVER, J. E., RUTA, M., SAKAMOTO, M., HONE, D. W. E., JENNINGS, R. and BENTON, M. J. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2483-2490.

LLOYD, G. T., YOUNG, J. R. and SMITH, A. B. 2011. Taxonomic structure of the fossil record is shaped by sampling bias. *Systematic Biology*, **61**, 80-89.

LOCKLEY, M. G., HOUCK, K. J. and PRINCE, N. K. 1986. North America's largest dinosaur trackway site: Implications for Morrison Formation paleoecology. *Geological Society of America Bulletin*, **97**, 1163-1176.

LUKIC-WALTHER, M., BROCKLEHURST, N., KAMMERER, C. F. and FRÖBISCH, J. 2019. Diversity patterns of nonmammalian cynodonts (Synapsida, Therapsida) and the impact of taxonomic practice and research history on diversity estimates. *Paleobiology*, **45**, 56-69.

LYSON, T. R. and LONGRICH, N. R. 2010. Spatial niche partitioning in dinosaurs from the latest Cretaceous (Maastrichtian) of North America. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1158-1164.

MADDISON, W. P. and MADDISON, D. R. 2018. Mesquite: a modular system for evolutionary analysis. Version 3.6. http://www.mesquiteproject.org

MAECHLER, M. 2013. diptest: Hartigan's Dip Test Statistic for Unimodality - Corrected. R package version 0.75-5.

MAIDMENT, S. S. and MUXWORTHY, A. (In press). A chronostratigraphic framework for the Upper Jurassic Morrison Formation, western USA.

MALKANI, M. S. 2006. Biodiversity of saurischian dinosaurs from the latest Cretaceous Park of Pakistan. *Journal of Applied and Emerging Sciences*, **1**, 108-140.

MANDER, L., and TWITCHETT, R. J. 2008. Quality of the Triassic–Jurassic bivalve fossil record in northwest Europe. *Palaeontology*, **51**, 1213-1223.

MANNION, P. D. and UPCHURCH, P. 2010a. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology*, **36**, 283-302.

MANNION, P. D. and UPCHURCH, P. 2010b. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology*, **36**, 2, 253-282.

MANNION, P. D. and UPCHURCH, P. 2011. A re-evaluation of the 'mid-Cretaceous sauropod hiatus' and the impact of uneven sampling of the fossil record on patterns of regional dinosaur extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **299**, 529-540.

MANNION, P. D., UPCHURCH, P., CARRANO, M. T. and 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**, 157–181.

MANNION, P. D., BENSON, R. B., UPCHURCH, P., BUTLER, R. J., CARRANO, M. T. and BARRETT, P. M. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecology and Biogeography,* **21**, 898-908.

MANNION, P. D., CHIARENZA, A. A., GODOY, P. L. and CHEAH, Y. N. 2019a. Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity. *Palaeontology*, **62**, 615-637.

MANNION, P. D., UPCHURCH, P., SCHWARZ, D. and WINGS, O. 2019b. Taxonomic affinities of the putative titanosaurs from the Late Jurassic Tendaguru Formation of Tanzania: phylogenetic and biogeographic implications for eusauropod dinosaur evolution. *Zoological Journal of the Linnean Society*, **185**, 784-909.

MARSHALL, C. R., FINNEGAN, S., CLITES, E. C., HOLROYD, P. A., BONUSO, N., CORTEZ, C., DAVIS, E., DIETL, G. P., DRUCKENMILLER, P. S., ENG, R. C., GARCIA, C., ESTES-SMARGIASSI, K., HENDY, A., HOLLIS, K. A., LITTLE, H., NESBITT, E. A., ROOPNARINE, P., SKIBINSKI, L., VENDETTI, J. and WHITE, L. D. 2018. Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. *Biology letters*, **14**, 20180431.

MARTILL, D. M., BRITO, P. M. and WASHINGTON-EVANS, J. 2008. Mass mortality of fishes in the Santana Formation (Lower Cretaceous, ?Albian) of northeast Brazil. *Cretaceous Research*, **29**, 649-658.

MAURER, A. F., PERSON, A., TÜTKEN, T., AMBLARD-PISON, S. and SÉGALEN, L. 2014. Bone diagenesis in arid environments: an intra-skeletal approach. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **416**, 17-29.

MAXWELL, W. D. and BENTON, M. J. 1987. Mass extinctions and data bases: changes in the interpretation of tetrapod mass extinction over the past 20 years. 156-160. *In* CURRIE, P. J. and KOSTER, E. H., (eds). *4th Symposium on Mesozoic Terrestrial Ecosystems, Occasional Paper of the Tyrrell Museum of Palaeontology*, Alberta, **3**.

MCGOWAN, A. J. and DYKE, G. J. 2009. A surfeit of theropods in the Moroccan Late Cretaceous? Comparing diversity estimates from field data and fossil shops. *Geology*, **37**, 843-846.

MCNAMARA, M. E., ORR, P. J., ALCALÁ, L., ANADÓN, P. and PEÑALVER, E. 2012a. What controls the taphonomy of exceptionally preserved taxa—environment or biology? A case study using frogs from the Miocene Libros Konservat-Lagerstätte (Teruel, Spain). *Palaios*, **27**, 63-77.

MCNAMARA, M. E., ORR, P. J., MANZOCCHI, T., ALCALA, L., ANADON, P. and PEÑALVER, E. 2012b. Biological controls upon the physical taphonomy of exceptionally preserved salamanders from the Miocene of Rubielos de Mora, northeast Spain. *Lethaia*, **45**, 210-226.

MCPHEE, B. W., BORDY, E. M., SCISCIO, L. and CHOINIERE, J. N. 2017. The sauropodomorph biostratigraphy of the Elliot Formation of southern Africa: Tracking the evolution of Sauropodomorpha across the Triassic–Jurassic boundary. *Acta Palaeontologica Polonica*, **62**, 441–465.

MCPHEE, B.W., BENSON, R.B., BOTHA-BRINK, J., BORDY, E.M. and CHOINIERE, J.N., 2018. A giant dinosaur from the earliest Jurassic of South Africa and the transition to quadrupedality in early sauropodomorphs. *Current Biology*, **28**, 3143-3151.

MEDEIROS, M. A., LINDOSO, R. M., MENDES, I. D. and DE SOUZA CARVALHO, I. 2014. The Cretaceous (Cenomanian) continental record of the laje do coringa flagstone (Alcântara formation), northeastern South America. *Journal of South American Earth Sciences*, **53**, 50-58.

MOLNAR, R. E. 2010. Taphonomic observations on eastern Australian Cretaceous sauropods. *Alcheringa*, **34**, 421–429.

MOORE, J. R. and NORMAN, D. B. 2009. Quantitatively evaluating the sources of taphonomic biasing of skeletal element abundances in fossil assemblages. *Palaios*, **24**, 591-602.

MÜLLER, R. T. and GARCIA, M. S. 2019. Rise of an empire: analysing the high diversity of the earliest sauropodomorph dinosaurs through distinct hypotheses. *Historical Biology*, 1-6.

MÜLLER, R. T., LANGER, M. C. and AIRES, A. S. S. 2014. New dinosauriform (Ornithodira, Dinosauromorpha) record from the Upper Triassic of southern Brazil. *Paleontological Research*, **18**, 118-122.

MÜLLER, R. T., DA ROSA, Á. A. S., DA SILVA, L. R., AIRES, A. S. S., PACHECO, C. P., PAVANATTO, A. E. B. and DIAS-DA-SILVA, S. 2015. Wachholz, a new exquisite dinosaur-bearing fossiliferous site from the Upper Triassic of southern Brazil. *Journal of South American Earth Sciences*, **61**, 120-128.

MÜLLER, R. T., LANGER, M. C. and DIAS-DA-SILVA, S. 2016. Biostratigraphic significance of a new early sauropodomorph specimen from the Upper Triassic of southern Brazil. *Historical Biology*, **29**, 187-202.

MÜLLER, R. T., LANGER, M. C., PACHECO, C. P. and DIAS-DA-SILVA, S. 2017. The role of ontogeny on character polarization in early dinosaurs: a new specimen from the Late Triassic of southern Brazil and its implications. *Historical Biology*, doi: 10.1080/08912963.2017.1395421

MÜLLER, R. T., LANGER, M. C., BRONZATI, M., PACHECO, C. P., CABREIRA, S. F. and DIAS-DA-SILVA, S. 2018a. Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a remarkably well-preserved dinosaur from the Upper Triassic of southern Brazil. *Zoological Journal of the Linnean Society*, **184**, 1187-1248.

MÜLLER, R. T., LANGER, M. C. and DIAS-DA-SILVA, S. 2018b. An exceptionally preserved association of complete dinosaur skeletons reveals the oldest long-necked sauropodomorphs. *Biology letters*, **14**, 20180633.

MÜLLER, R. T., GARCIA, M. S., DA-ROSA, Á. A. S. and DIAS-DA-SILVA, S. 2018c. Under pressure: Effect of sedimentary compression on the iliac morphology of early sauropodomorphs. *Journal of South American Earth Sciences*, **88**, 345-351.

MÜNKEMÜLLER, T., LAVERGNE, S., BZEZNIK, B., DRAY, S., JOMBART, T., SCHIFFERS, K. and THUILLER, W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, **3**, 743-756.

MUÑOZ-DURÁN, J. and VAN VALKENBURGH, B. 2006. The Rancholabrean record of Carnivora: taphonomic effect of body size, habitat breadth, and the preservation potential of caves. *Palaios*, **21**, 424-430.

MYERS, T. S. and FIORILLO, A. R. 2009. Evidence for gregarious behavior and age segregation in sauropod dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **274**, 96–104.

NESBITT, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**, 1–292.

NESBITT, S. J., IRMIS, R. B. and PARKER, W. G. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. *Journal of Systematic Palaeontology*, **5**, 209-243.

NESBITT, S. J., SMITH, N. D., IRMIS, R. B., TURNER, A. H., DOWNS, A. and NORELL, M. A. 2009a. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science*, **326**, 1530-1533.

NESBITT, S. J., IRMIS, R. B., PARKER, W. G., SMITH, N. D., TURNER, A. H. and 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. and TSUJI, L. A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, **464**, 95–98.

NEWELL, N. D. 1959. The nature of the fossil record. *Proceedings of the American Philosophical Society*, **103**, 264-285.

NICHOLSON, R. A. 1996. Bone degradation, burial medium and species representation: debunking the myths, an experiment-based approach. *Journal of Archaeological Science*, **23**, 513-533.

NICHOLSON, D. B., MAYHEW, P. J. and ROSS, A. J. 2015. Changes to the Fossil Record of Insects through Fifteen Years of Discovery. *PLoS ONE,* **10,** e0128554.

NORELL, M. A. 1993. Tree-based approaches to understanding history; comments on ranks, rules and the quality of the fossil record. *American Journal of Science*, **293**, 407.

NORELL, M. A., and NOVACEK, M. J. 1992. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics*, **8**, 319-337.

NORELL, M. A., CLARK, J. M., CHIAPPE, L. M. and DASHZEVEG, D. 1995. A nesting dinosaur. *Nature*, **378**, 774.

NOTO, C. R. 2011. Hierarchical control of terrestrial vertebrate taphonomy over space and time: discussion of mechanisms and implications for vertebrate paleobiology. 287-336. *In* ALLISON, P. A. and BOTTJER, D. J. (eds). *Taphonomy: Process and Bias Through Time*, Springer, Dordrecht.

NOVAS, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology*, **16**, 723–741.

NOVAS, F. E., EZCURRA, M. D., AGNOLIN, F. L., POL, D. and ORTÍZ, R. 2012. New Patagonian Cretaceous theropod sheds light about the early radiation of Coelurosauria. *Revista del Museo Argentino de Ciencias Naturales*, **14**, 57-81.

NOVAS, F. E., SALGADO, L., SUÁREZ, M., AGNOLIN, F. L., EZCURRA, M. D., CHIMENTO, N. R., DE LA CRUZ, R., ISASI, M. P., VARGAS, A. O. and RUBILAR-ROGERS, D. 2015. An enigmatic plant-eating theropod from the Late Jurassic period of Chile. *Nature*, **522**, 331-334.

NOVAS, F. E., ARANCIAGA ROLANDO, A.M. and AGNOLIN, F. L. 2016. Phylogenetic relationships of the Cretaceous Gondwanan theropods *Megaraptor* and *Australovenator*: the evidence afforded by their manual anatomy. *Memoirs of Museum Victoria*, **74**, 49–61.

O'CONNOR, A., MONCRIEFF, C. and WILLS, M. A. 2011a. Variation in stratigraphic congruence (GER) through the Phanerozoic and across higher taxa is partially determined by sources of bias. *Geological Society, London, Special Publications*, **358**, 31-52.

O'CONNOR, J., ZHOU, Z. and XU, X. 2011b. Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds. *Proceedings of the National Academy of Sciences*, **108**, 19662-19665.

O'GORMAN, E. J. and HONE, D. W. E. 2012. Body size distribution of the dinosaurs. *PLoS ONE*, **7**, e51925.

O'CONNOR, A., MONCRIEFF, C. and WILLS, M. A. 2011. Variation in stratigraphic congruence (GER) through the Phanerozoic and across higher taxa is partially determined by sources of bias. *Geological Society, London, Special Publications*, **358**, 31-52.

OLIVERO, E., GASPARINI, Z., RINALDI, C. and SCASSO, R. 1991. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island): paleogeographical implications, 617-622. *In* THOMSON, M. R. A., CRAME, J.

A. and THOMSON, J. W. (eds). *Geological Evolution of Antarctica*. Cambridge University Press, Cambridge, 736 pp.

ORME, D., FRECKLETON, R., THOMAS, G., PETZOLDT, T., FRITZ, S., ISAAC, N. and PEARSE, W. 2018. Caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 1.0.1. https://cran.r-project.org/web/packages/caper/index.html

ORR, P. J., ADLER, L. B., BEARDMORE, S. R., FURRER, H., MCNAMARA, M. E., PEÑALVER-MOLLÁ, E. and REDELSTORFF, R. 2016. "Stick 'n' peel": explaining unusual patterns of disarticulation and loss of completeness in fossil vertebrates. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **457**, 380–388.

OTERO, A., CANALE, J. I., HALUZA, A. and CALVO, J. O. 2011. New titanosaur with unusual haemal arches from the Upper Cretaceous of Neuquén Province, Argentina. *Ameghiniana*, **48**, 655-662.

OTERO, A., CUFF, A. R., ALLEN, V., SUMNER-ROONEY, L., POL, D. and HUTCHINSON, J. R. 2019. Ontogenetic changes in the body plan of the sauropodomorph dinosaur *Mussaurus patagonicus* reveal shifts of locomotor stance during growth. *Scientific Reports*, **9**, 7614.

PADIAN, K. and CHIAPPE, L. M. 1998. The origin and early evolution of birds. *Biological Reviews*, **73**, 1-42.

PAN, Y., SHA, J., FUERSICH, F. T., WANG, Y., ZHANG, X. and YAO, X. 2012. Dynamics of the lacustrine fauna from the Early Cretaceous Yixian Formation, China: implications of volcanic and climatic factors. *Lethaia*, **45**, 299-314.

PARADIS, E., BLOMBERG, S., BOLKER, B., BROWN, J., CLAUDE, J., CUONG, H. S., DESPER, R., DIDIER, G., DURAND, B., DUTHEIL, J., EWING, R. J., GASCUEL, O., GUILLERME, T., HEIBL, C., IVES, A., JONES, B., KRAH, F., LAWSON, D., LEFORT, V., LEGENDRE, P., LEMON, J., MARCON, E.,

MCCLOSKEY, R., NYLANDER, J., OPGEN-RHEIN, R., POPESCU, A-A., ROYER-CARENZIM, K., SCHLIEP, K. STRIMMER K. and DE VIENNE, D. 2019. ape. Analyses of Phylogenetics and Evolution. R package version 5.3. https://cran.r-project.org/web/packages/ape/index.html

PARRY, L. A., BARON, M. G. and VINTHER, J. 2017. Multiple optimality criteria support Ornithoscelida. *Royal Society Open Science*, **4**, 170833.

PAUL, C. R. C. 1992. How complete does the fossil record have to be? *Revista Española de Paleontologia*, **7**, 127-133.

PAUL, C. R. 2009. The fidelity of the fossil record: the improbability of preservation. *Palaeontology*, **52**, 485-489.

PETERSON, J. E. and BIGALKE, C. L. 2013. Hydrodynamic behaviors of pachycephalosaurid domes in controlled fluvial settings: a case study in experimental dinosaur taphonomy. *Palaios*, **28**, 285-292.

PETERSON, J. E., WARNOCK, J. P., EBERHART, S. L., CLAWSON, S. R. and NOTO, C. R. 2017. New data towards the development of a comprehensive taphonomic framework for the Late Jurassic Cleveland-Lloyd Dinosaur Quarry, Central Utah. *PeerJ*, **5**, e3368.

PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D., HEISTERKAMP, S. and WILLIGEN, B. V. 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137. https://cran.r-project.org/web/packages/nlme/index.html

PLOTNICK, R. E., and WAGNER, P. J. 2006. Round up the usual suspects: common genera in the fossil record and the nature of wastebasket taxa. *Paleobiology*, **32**, 126-146.

POLLY, P. D. and HEAD, J. J. 2004. Maximum-likelihood identification of fossils: taxonomic identification of Quaternary marmots (Rodentia, Mammalia) and identification of vertebral position in the pipesnake *Cylindrophis* (Serpentes, Reptilia). 197-221. *In* ELEWA, A. M. T. (ed). *Morphometrics: Applications in Biology and Paleontology*. Springer, Berlin, Heidelberg.

PORFIRI, J. D., NOVAS, F. E., CALVO, J. O., AGNOLIN, F. L., EZCURRA, M. D. and CERDA, I. A. 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research*, **51**, 35-55.

PORFIRI, J. D., VALIERI, R. D. J., SANTOS, D. D. and LAMANNA, M. C. 2018. A new megaraptoran theropod dinosaur from the Upper Cretaceous Bajo de la Carpa Formation of northwestern Patagonia. *Cretaceous Research*, **89**, 302-319.

POROPAT, S. F., MANNION, P. D., UPCHURCH, P., HOCKNULL, S. A., KEAR, B. P., KUNDRÁT, M., TISCHLER, T. R., SLOAN, T., SINAPIUS, G. H. K., ELLIOT, J. A. and ELLIOTT, D. A. 2016. New Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Scientific Reports*, **6**, 34467.

PRETTO, F. A., SCHULTZ, C. L. and LANGER, M. C. 2015. New dinosaur remains from the late triassic of southern Brazil (Candelária sequence, Hyperodapedon assemblage zone). *Alcheringa: An Australasian Journal of Palaeontology*, **39**, 264-273.

PRETTO, F. A., LANGER, M. C. and SCHULTZ, C. L. 2018. A new dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Brazil provides insights on the evolution of sauropodomorph body plan. *Zoological Journal of the Linnean Society*, **185**, 388-416.

PUCHALSKI, S. S., EERNISSE, D. J., and JOHNSON C. C. 2008. The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora). *American Malacological Bulletin*, **25**, 87-96.

PURNELL, M. A., and DONOGHUE, P. C. 2005. Between death and data: biases in interpretation of the fossil record of conodonts. *Special Papers in Palaeontology*, **73**, 7-25.

RAUHUT, O. W. and XU, X. 2005. The small theropod dinosaurs Tugulusaurus and Phaedrolosaurus from the Early Cretaceous of Xinjiang, China. *Journal of Vertebrate Paleontology*, **25**, 107-118.

RAUP, D. M. 1972. Taxonomic diversity during the Phanerozoic. *Science*, **177**, 1065-1071.

RAUP, D. M. 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology*, **2**, 289-297.

RAYFIELD, E. J., MILNER, A. C., XUAN, V. B. and YOUNG, P. G. 2007. Functional morphology of spinosaur 'crocodile-mimic' dinosaurs. *Journal of Vertebrate Paleontology*, **27**, 892-901.

REMES, K., ORTEGA, F., FIERRO, I., JOGER, U., KOSMA, R., FERRER, J. M. M., IDE, O. A., MAGA, A. 2009. A New Basal Sauropod Dinosaur from the Middle Jurassic of Niger and the Early Evolution of Sauropoda. *PLoS ONE*, **4**, e6924.

RETALLACK, G. 1984. Completeness of the rock and fossil record: some estimates using fossil soils. *Paleobiology*, **10**, 59-78.

RETALLACK, G. J. 1997. Dinosaurs and dirt. *DinoFest International*, 345-359.

REVELL, L. J. 2019. phytools: Phylogenetic Tools for Comparative Biology (and Other Things). R package version 0.6-60. https://cran.r-project.org/web/packages/phytools/index.html

RICH, T. H. and VICKERS-RICH, P. 1997. Future directions for dinosaur research in Australia. *Dinofest International Proceedings*, 275-277.

RICHARDSON, W. 2017. Does taxonomic identification bias affect diversity analyses on dinosaurs? *The Palaeontology Association Newsletter*, **96**, Grant Reports, 94-97.

ROFTHUS, T. A. 2002. Relationship between taphonomic damage and taxonomic identifiability: Implications for paleoecologic analysis. *Geological Society of American Abstract Programs*, **34**, 36.

ROFTHUS, T. A. 2005. Taphonomic damage and taxonomic identifiability: Implications for secular bias in the fossil record. *Geological Society of American Abstract Programs*, **37**, 118.

ROOK, D. L., HEIM, N. A. and MARCOT, J. 2013. Contrasting patterns and connections of rock and biotic diversity in the marine and non-marine fossil records of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 123-129.

SADLER, P. M. 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *The Journal of Geology*, **89**, 569-584.

SAKAMOTO, M., BENTON, M. J. and VENDITTI, C. 2016. Dinosaurs in decline tens of millions of years before their final extinction. *Proceedings of the National Academy of Sciences*, **113**, 5036-5040.

SALES, M. A. F., SCHULTZ, C. L. 2017. Spinosaur taxonomy and evolution of craniodental features: Evidence from Brazil. *PLoS ONE*, **12**, e0187070.

SALES, M. A. F., CASCON, P. and SCHULTZ, C. L. 2014. Note on the paleobiogeography of Compsognathidae (Dinosauria: Theropoda) and its paleoecological implications. *Anais da Academia Brasileira de Ciências*, **86**, 127-134.

SALES, M. A. F., LACERDA, M. B., HORN, B. L. D., DE OLIVEIRA, I. A. P. and SCHULTZ, C. L. 2016. The "χ" of the Matter: Testing the Relationship between Paleoenvironments and Three Theropod Clades. *PLoS ONE*, **11**, e0147031.

SALGADO, L. and GASPARINI, Z. 2006. Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas*, **28**, 119-135.

SALLAM, H. M., GORSCAK, E., O'CONNOR, P. M., EL-DAWOUDI, I. A., EL-SAYED, S., SABER, S., KORA, M. A., SERTICH, J. J. W., SEIFFERT, E. R. and LAMANNA, M. C. 2018. New Egyptian sauropod reveals Late Cretaceous dinosaur dispersal between Europe and Africa. *Nature Ecology & Evolution*, **2**, 445.

SANDER, P. M. 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**, 255-299.

SANDER, P. M. 2013. An evolutionary cascade model for sauropod dinosaur gigantism-overview, update and tests. *PLoS ONE*, **8**, e78573.

SANDER, P. M. and CLAUSS, M. 2008. Sauropod gigantism. *Science*, **322**, 200-201.

SANDER, P. M., PEITZ, C., JACKSON, F. D. and CHIAPPE, L. M. 2008. Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology. *Palaeontographica Abteilung A*, 69-107.

SANDER, P. M., CHRISTIAN, A., CLAUSS, M., FECHNER, R., GEE, C. T., GRIEBELER, E. M., GUNGA, H-C., HUMMEL, J., MALLISON, H., PERRY, S. F., PREUSCHOFT, H., RAUHUT, O. W. M., REMES, K., TÜTKEN, T., WINGS, O. and WITZEL, U. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews*, **86**, 117-155.

SANSOM, R. S., WILLS, M. A. and WILLIAMS, T. 2017. Dental data perform relatively poorly in reconstructing mammal phylogenies: morphological partitions evaluated with molecular benchmarks. *Systematic Biology*, **66**, 813-822.

SCHINDEL, D. E. 1982. Resolution analysis: a new approach to the gaps in the fossil record. *Paleobiology*, **8**, 340-353.

SEPKOSKI, J. J. 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology*, **19**, 43-51.

SERENO, P. C. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences*, **25**, 435-489.

SERENO, P. C. 1999. The evolution of dinosaurs. *Science*, **284**, 2137-2147.

SIMÓN, E., SALGADO, L. and CALVO, J. O. 2017. A new titanosaur sauropod from the Upper Cretaceous of Patagonia, Neuquén Province, Argentina. *Ameghiniana*, **55**, 1-30.

SMITH, A. B. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **356**, 351-367.

SMITH, A. B. 2007. Intrinsic versus extrinsic biases in the fossil record: contrasting the fossil record of echinoids in the Triassic and early Jurassic using sampling data, phylogenetic analysis, and molecular clocks. *Paleobiology*, **33**, 310-323.

SMITH, N. D. and POL, D. 2007. Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica*, **52,** 657-674.

SOLIGO, C. and ANDREWS, P. 2005. Taphonomic bias, taxonomic bias and historical non-equivalence of faunal structure in early hominin localities. *Journal of Human Evolution*, **49**, 206-229.

SPIESS, A.-N. 2018. QpcR: Modelling and Analysis of Real-Time PCR Data. R package v. 1.4-1. https://cran.r-project.org/web/packages/qpcR/index.html

SPRINGER, M. S. 1995. Molecular clocks and the incompleteness of the fossil record. *Journal of Molecular Evolution*, **41**, 531-538.

STARRFELT, J. and LIOW, L. H. 2016. How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **371**, 20150219.

TARVER, J. E., BRADDY, S. J. and BENTON, M. J. 2007. The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Palaeontology*, **50**, 177-184.

TARVER, J. E., DONOGHUE, P. C. J. and BENTON, M. J. 2011. Is evolutionary history repeatedly rewritten in light of new fossil discoveries? *Proceedings of the Royal Society B: Biological Sciences*, **278**, 599-604.

TEELING, E. C., SPRINGER, M. S., MADSEN, O., BATES, P., O'BRIEN, S. J. and MURPHY, W. J. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science*, **307**, 580-584.

TEICHERT, C. 1956. How many fossil species? *Journal of Paleontology*, **30**, 967-969.

TENNANT, J. P., CHIARENZA, A. A. and BARON, M. 2018. How has our knowledge of dinosaur diversity through geologic time changed through research history? *PeerJ*, **6**, e4417.

TENNANT, J. P., MANNION, P. D. and UPCHURCH, P. 2016b. Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nature Communications*, **7**, 12737.

TSCHOPP, E. and MATEUS, O. 2017. Osteology of *Galeamopus pabsti* sp. nov. (Sauropoda: Diplodocidae), with implications for neurocentral closure timing, and the cervico-dorsal transition in diplodocids. *PeerJ*, **5**, e3179

TSCHOPP, E., MATEUS, O. and BENSON, R. B. 2015. A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). *PeerJ*, **3**, e857.

TUTIN, S. L. and BUTLER, R. J. 2017. The completeness of the fossil record of plesiosaurs, marine reptiles from the Mesozoic. *Acta Palaeontologica Polonica*, **62**, 563.

TÜTKEN, T., PFRETZSCHNER, H. U., VENNEMANN, T. W., SUN, G. and WANG, Y. D. 2004. Paleobiology and skeletochronology of Jurassic dinosaurs:

implications from the histology and oxygen isotope compositions of bones. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **206**, 217-238.

UPCHURCH, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions: Biological Sciences*, **349**, 365-390.

UPCHURCH, P. and BARRETT, P. M. 2005. A taxic and phylogenetic perspective on sauropod diversity. 104–124. *In* CURRY ROGERS, K. and WILSON, J. A. (eds). *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley, 349 pp.

UPCHURCH, P., BARRETT, P. M. and DODSON, P. 2004. Sauropoda. 259–322. *In* WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). *Dinosauria.* Second Edition. University of California Press, 861 pp.

UPCHURCH, P., MANNION, P. D., BENSON, R. B., BUTLER, R. J., and CARRANO, M. T. 2011. Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. 209-240. *In* McGOWAN, A. J. and SMITH, A. B. S. (eds). *Comparing the geological and fossil records: implications for biodiversity studies.* Geological Society, London, Special Publications, 358.

VALENTINE, J. W. 1970. How many marine invertebrate fossil species? A new approximation. *Journal of Paleontology*, **44**, 410-415.

VALENTINE, J. W. 1989. How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology*, **15**, 83-94.

VARRICCHIO, D. J., SERENO, P. C., ZHAO, X., TAN, L., WILSON, J. A. and LYON, G. H. 2008. Mud-trapped herd captures evidence of distinctive dinosaur sociality. *Acta Palaeontologica Polonica*, **53**, 567–578.

VERRIÈRE, A., BROCKLEHURST, N. and FRÖBISCH, J. 2016. Assessing the completeness of the fossil record: comparison of different methods applied to parareptilian tetrapods (Vertebrata: Sauropsida). *Paleobiology*, **42**, 680-695.

VON ENDT, D. W. and ORTNER, D. J. 1984. Experimental effects of bone size and temperature on bone diagenesis. *Journal of Archaeological Science*, **11**, 247-253.

WAGNER, P. J. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology*, **49**, 65-86.

WAGNER, P. J., and SIDOR, C. A. 2000. Age rank/clade rank metrics-sampling, taxonomy, and the meaning of "stratigraphic consistency". *Systematic Biology*, **49**, 463-479.

WAGNER, P. J. and MARCOT, J. D. 2013. Modelling distributions of fossil sampling rates over time, space and taxa: assessment and implications for macroevolutionary studies. *Methods in Ecology and Evolution*, **4**, 703-713.

WALKER, J. D., GEISSMAN, J. W., BOWRING, S. A. and BABCOCK, L. E. 2018. Geologic Time Scale v. 5.0, *Geological Society of America*, https://doi.org/10.1130/2018.CTS005R3C

WALL, P. D., IVANY, L. C. and WILKINSON, B. H. 2009. Revisiting Raup: exploring the influence of outcrop area on diversity in light of modern sample-standardization techniques. *Paleobiology*, **35**, 146-167.

WALTHER, M. and FRÖBISCH, J. 2013. The quality of the fossil record of anomodonts (Synapsida, Therapsida). *Comptes Rendus Palevol*, **12**, 495-504.

WANG, S. C., and DODSON, P. 2006. Estimating the diversity of dinosaurs. *Proceedings of the National Academy of Sciences*, **103**, 13601-13605.

WEISCHAMPEL, D. B. 1996. Fossils, phylogeny, and discovery: a cladistic study of the history of tree topologies and ghost lineage durations. *Journal of Vertebrate Paleontology*, **16**, 191-197.

WEISCHAMPEL, D. B. and HORNER, J. R. 1987. Dinosaurs, habitat bottlenecks, and the St. Mary River Formation. *Occasional Paper of the Tyrrell Museum of Palaeontology*, **3**, 224-229.

WHITE, P. D., FASTOVSKY, D. E. and SHEEHAN, P. M. 1998. Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. *Palaios*, **13**, 41-51.

WHITESIDE, J. H., GROGAN, D. S., OLSEN, P. E. and KENT, D. V. 2011. Climatically driven biogeographic provinces of Late Triassic tropical Pangea. *Proceedings of the National Academy of Sciences*, **108**, 8972-8977.

WHITLOCK, J. A., TRUJILLO, K. C. and HANIK, G. M. 2018. Assemblage-level structure in Morrison Formation dinosaurs, western interior, USA*. Geology of the Intermountain West*, **5**, 9-22.

WICKHAM, H., CHANG, W., HENRY, L., PEDERSEN, T. L., TAKAHASHI, K., WILKE, C. and WOO, K. 2019. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R Package version 3.1.1. https://cran.r-project.org/web/packages/ggplot2/index.html

WIGNALL, P. B., and BENTON, M. J. 1999. Lazarus taxa and fossil abundance at times of biotic crisis. *Journal of the Geological Society*, **156**, 453-456.

WILLS, M. A. 2007. Fossil ghost ranges are most common in some of the oldest and some of the youngest strata. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2421-2427.

WILLS, M. A., BARRETT, P. M. and HEATHCOTE, J. F. 2008. The modified gap excess ratio (GER*) and the stratigraphic congruence of dinosaur phylogenies. *Systematic Biology*, **57**, 891-904.

WILLS, S., CHOINIERE, J. N. and BARRETT, P. M. 2018. Predictive modelling of fossil-bearing locality distributions in the Elliot Formation (Upper Triassic–Lower Jurassic), South Africa, using a combined multivariate and spatial statistical analyses of present-day environmental data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **489**, 186-197.

WINKLER, D. A., GOMANI, E. M. and JACOBS, L. L. 2000. Comparative taphonomy of an Early Cretaceous sauropod quarry, Malawi, Africa. *Paleontological Society of Korea Special Publication*, **4**, 99-114.

XU, X., ZHOU, Z., DUDLEY, R., MACKEM, S., CHUONG, C. M., ERICKSON, G. M. and VARRICCHIO, D. J. 2014. An integrative approach to understanding bird origins. *Science*, *346*, 1253293.

XU, X., UPCHURCH, P., MANNION, P. D., BARRETT, P. M., REGALADO-FERNADEZ, O. R., MO, J., MA, J. and LIU, H. 2018. A new Middle Jurassic diplodocoid suggests an earlier dispersal and diversification of sauropod dinosaurs. *Nature Communications*, **9**, 2700.

YESHURUN, R., MAROM, N. and BAR-OZ, G. 2007. Differential fragmentation of different ungulate body-size: a comparison of gazelle and fallow deer bone fragmentation in Levantine prehistoric assemblages. *Journal of Taphonomy*, **5**, 137-148.

ZANNO, L. E. and MAKOVICKY, P. J. 2013. No evidence for directional evolution of body mass in herbivorous theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122526.

ZEDER, M. A. and PILAAR, S. E. 2010. Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, *Ovis*, and goats, *Capra*. *Journal of Archaeological Science,* **37**, 225-242.

ZHANG, Q. N., YOU, H. L., WANG, T. and CHATTERJEE, S. 2018. A new sauropodiform dinosaur with a ‘sauropodan’ skull from the Lower Jurassic Lufeng Formation of Yunnan Province, China. *Scientific Reports*, **8**, 13464.

ZHANG, Q. N., WANG, T., YANG, Z. W. and YOU, H. L. 2019. Redescription of the Cranium of *Jingshanosaurus xinwaensis* (Dinosauria: Sauropodomorpha) from the Lower Jurassic Lufeng Formation of Yunnan Province, China. *The Anatomical Record*. doi:10.1002/ar.24113.

ZHOU, Z. 2014. The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and implications. *National Science Review*, **1**, 543-559.

ZHOU, Z. and WANG, Y. 2010. Vertebrate diversity of the Jehol Biota as compared with other Lagerstätten. *Science China Earth Sciences*, **53**, 1894-1907.

ZHOU, Z., BARRETT, P. M. and HILTON, J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, **421**, 807.

Supplementary information

Supporting data

Chapter 2: The supporting datasets for Chapter 2 ("Skeletal completeness of the non-avian theropod dinosaur fossil record") are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.37c840g

This consists of the skeletal completeness dataset, including specimen information, completeness scores, spatial and temporal occurrence data for non-avian theropod dinosaurs.

Chapter 3: The supporting datasets for Chapter 3 ("Ten more years of Discovery: revisiting the quality of the sauropodomorph dinosaur fossil record") are available on the attached USB memory stick.

This consists of the skeletal completeness dataset, including specimen information, completeness scores, and spatial and temporal occurrence data for sauropodomorph dinosaurs.

Chapter 4: The supporting datasets for Chapter 4 ("Taxonomic identification bias of theropod dinosaurs: preservation potential and diagnosability") are available on the attached USB memory stick.

This consists of an updated version of the theropod skeletal completeness dataset from Chapter 2; an occurrence dataset calculating the presence-absence and relative abundance of each theropod bone; a diagnoses dataset, outlining the autapomorphies assigned to each valid theropod species; and, a Morrison quarry dataset, listing the bone occurrences associated with each.

Appendices

Additional figures, tables, R code, taxonomic justification and data collection methodology, for chapters 2, 3 and 4 follow this page

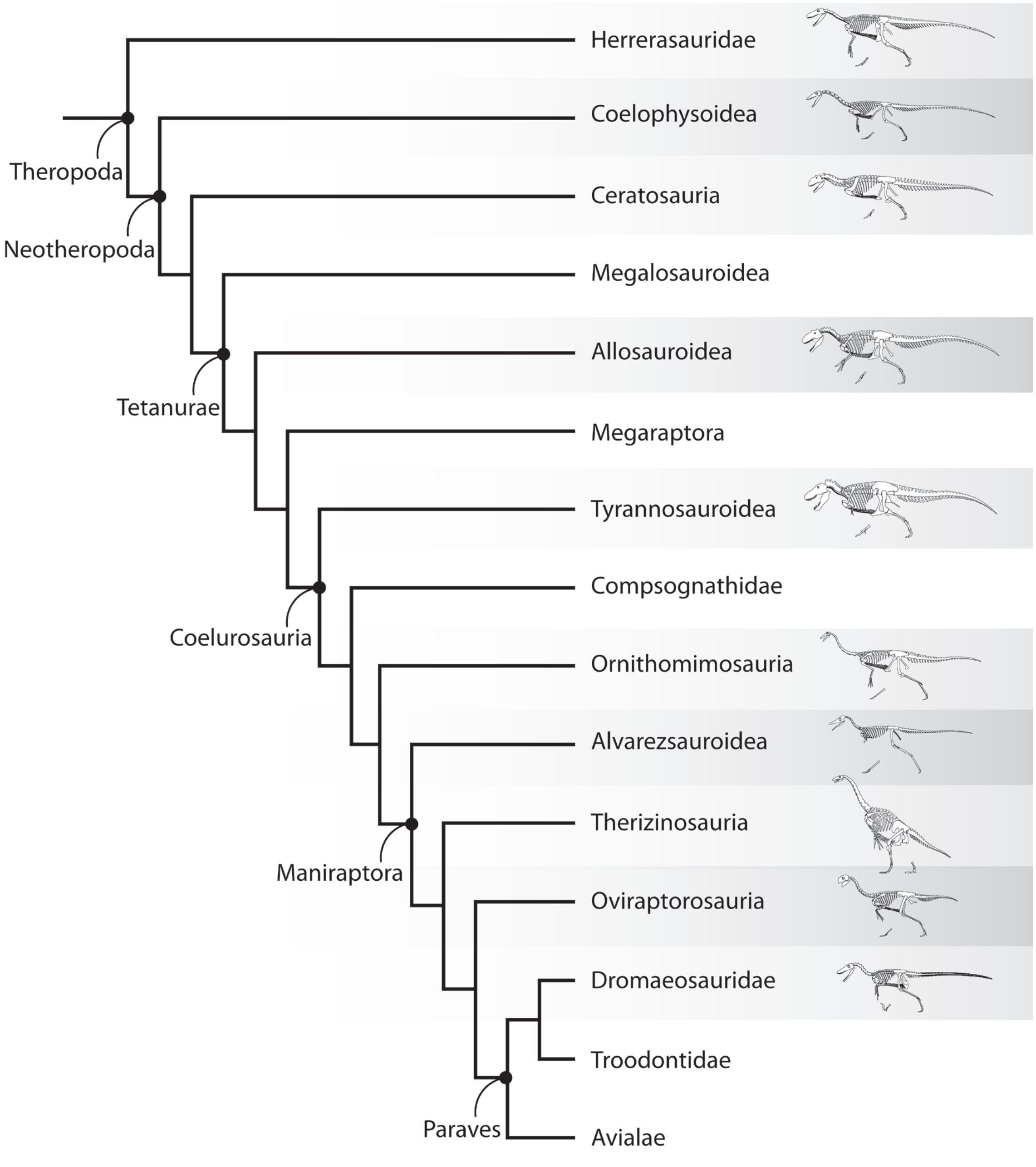


Figure A.1. Theropod phylogenetic relationships followed in this study, with representative skeletal diagrams used in the calculation of mean 2D body proportions. From Top to Bottom: *Herrerasaurus ischigualastensis*, *Coelophysis bauri*, *Majungasaurus crenatissimus*, *Allosaurus fragilis*, *Tyrannosaurus rex*, *Gallimimus bullatus*, *Nothronychus graffami*, composite alvarezsaur (based on *Mononykus olecranus* and *Shuvuuia deserti*), *Khaan mckennai*, and *Velociraptor mongoliensis.*

Table A.1. Comparative skeletal body proportions for *Tyrannosaurus rex* calculated by two-dimensional surface area, and three-dimensional shape-volume methods (see Supplementary data: 'Datasheet'). Abbreviations: SH, Scott Hartmann.

Skeletal region	***T. rex* 2D surface area (%) (SH skeletal diagram)**	***T. rex* 3D volume (%) (Brochu *et al*. 2003)**
Skull and mandible	16.27	16.33
Skull	10.31	10.9
Mandible	5.96	5.43
Vertebrae, chevrons	34.02	34.24
Cervical vertebrae	3.1	2.8
Dorsal vertebrae	8.6	10.1
Sacral vertebrae	4.82	7.42
Caudal vertebrae	12	11.92
Chevrons	5.5	2
Ribs, gastralia	13.43	10.74
Cervical ribs	1.73	0.54
Dorsal ribs and gastralia	11.7	10.2
Pectoral girdle and forelimbs	4.3	2.28
Pectoral Girdle	3.4	2.1
Forelimbs	0.9	0.18
Pelvic girdle and hindlimbs	31.1	36.51
Pelvic girdle	17.6	16.81
Hindlimbs	13.5	19.7

Table A.2. Results of tests for temporal trends in different time series using GLS. Statistically significant results indicated in bold.

Comparison	Slope	t-value	p-value	R^2
SCM2 ~ Stage mid-points	0.075368	1.610064	0.1205	0.11945231
non-conservation Lagerstätten SCM2 ~ Stage mid-points	0.083431	3.135847	**0.0045**	0.25880199
background SCM2 ~ Stage mid-points	0.097078	2.997134	**0.0062**	0.24919675
diversity ~ Stage mid-points	-0.36585	-3.10086	**0.0049**	0.44397363
non-conservation Lagerstätten diversity ~ Stage mid-points	-0.34881	-3.057935	**0.0054**	0.46703975
background diversity ~ Stage mid-points	-0.32453	-3.117001	**0.0047**	0.48343348
DBFs ~ Stage mid-points	-1.00126	-2.762489	**0.0108**	0.73582621
DBCs ~ Stage mid-points	-11.6612	-2.198482	**0.0378**	0.5913766
Good’s u coverage ~ Stage mid-points	-0.11647	-0.7327789	0.4708	0.13419717
specimen number ~ Stage mid-points	-1.7965	-2.589194	**0.0161**	0.29964354
PBDB species occurrences ~ Stage mid-points	-2.3579	-2.304103	**0.0302**	0.58854967
sea level ~ Stage mid-points	-316.05	-4.769932	**1.00E-04**	0.88822335

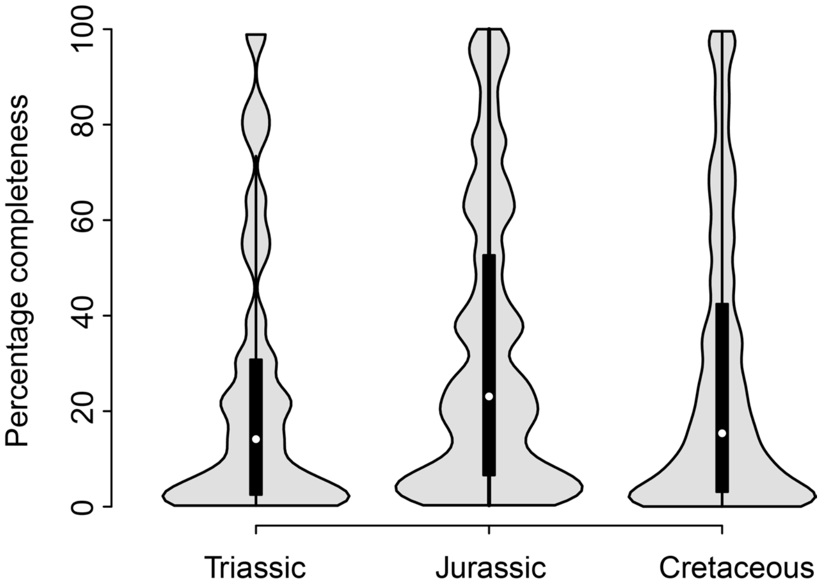


Figure A.2. Distribution of theropod SCM2 scores between the Triassic, Jurassic, and Cretaceous.

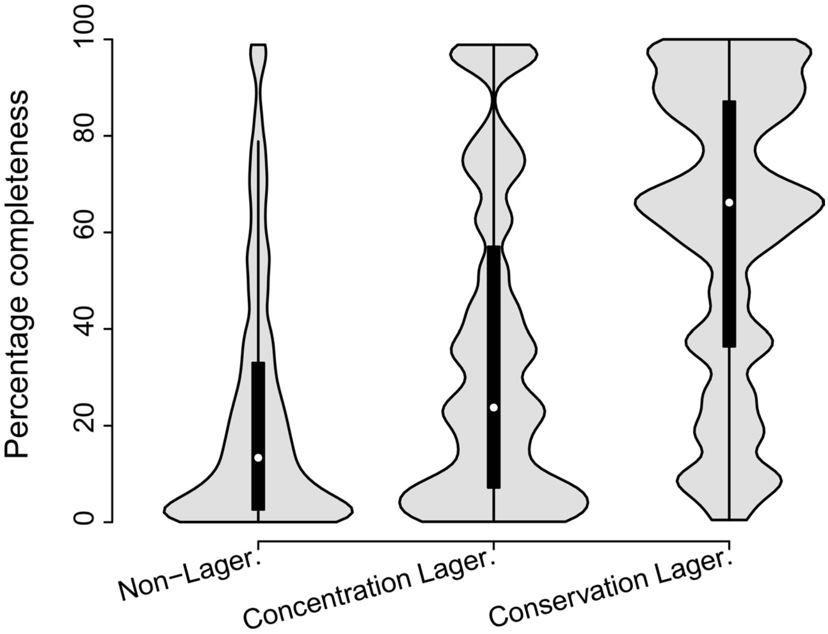


Figure A.3. Distribution of theropod SCM2 scores between non-Lagerstätten deposits, concentration Lagerstätten and conservation Lagerstätten. Abbreviations: Lager., Lagerstätten.

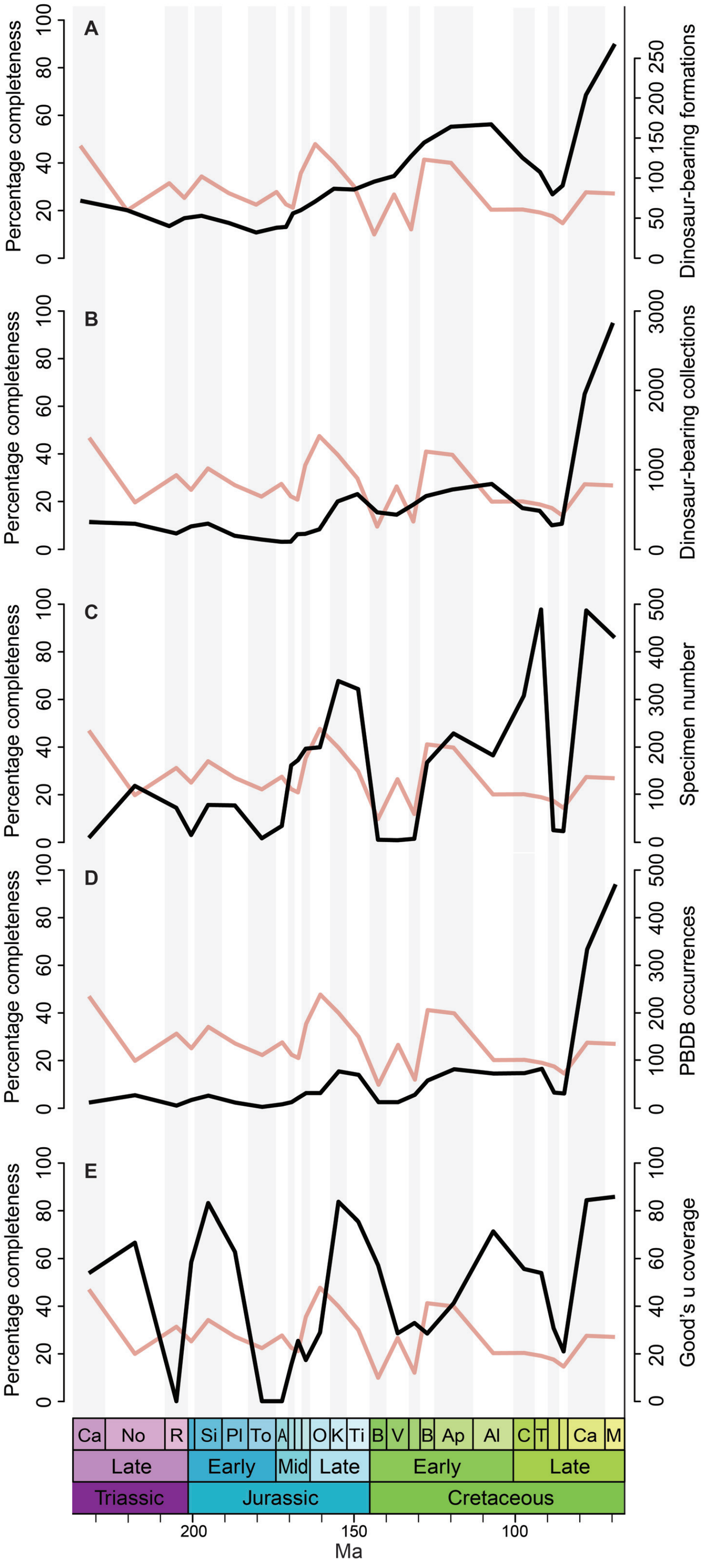


Figure A.4. Changes in theropod sampling proxies through time. A, DBFs; B, DBCs; C, specimen number; D, PBDB occurrences; E, Good's u coverage; Mean theropod SCM2 (red line) in background for comparison.

Table A.3. Results of model-fitting analyses testing the best explanations of theropod SCM2. The three models receiving the highest AIC weights are highlighted in bold, but coefficients in all three are non-significant. Abbreviations: DBCs, dinosaur-bearing collections; DBFs, dinosaur-bearing formations.

Comparison	R^2	AIC weight
SCM2 ~ diversity + DBCs + DBFs + sea level + time bin length	0.3059662	0.00365127
SCM2 ~ diversity + DBCs + DBFs + sea level	0.24415882	0.01007664
SCM2 ~ diversity + DBCs + DBFs + time bin length	0.27360307	0.01689083
SCM2 ~ diversity + DBCs + sea level + time bin length	0.29588794	0.02532619
SCM2 ~ diversity + DBFs + sea level + time bin length	0.30520641	0.03011533
SCM2 ~ DBCs + DBFs + sea level + time bin length	0.10017642	0.0010444
SCM2 ~ diversity + DBCs + DBFs	0.20138146	0.03295448
SCM2 ~ diversity + DBCs + sea level	0.22949148	0.0525073
SCM2 ~ diversity + DBCs + time bin length	0.19743874	0.03091078
SCM2 ~ diversity + DBFs + sea level	0.24169432	0.06461755
SCM2 ~ diversity + DBFs + time bin length	0.26920958	**0.10447672**
SCM2 ~ diversity + sea level + time bin length	0.23903995	0.06174793
SCM2 ~ DBCs + DBFs + sea level	0.06269514	0.00411032
SCM2 ~ DBCs + DBFs + time bin length	0.09231157	0.00623948
SCM2 ~ DBCs + sea level + time bin length	0.09718118	0.00669143
SCM2 ~ DBFs + sea level + time bin length	0.09607689	0.00658593
SCM2 ~ diversity + DBCs	0.09163148	0.03418154
SCM2 ~ diversity + DBFs	0.16609726	**0.10391984**
SCM2 ~ diversity + sea level	0.21151145	**0.21520809**
SCM2 ~ diversity + time bin length	0.10395867	0.04082574
SCM2 ~ DBCs + DBFs	0.0501708	0.01913405
SCM2 ~ DBCs + sea level	0.05667722	0.02092254
SCM2 ~ DBCs + time bin length	0.06855077	0.02466773
SCM2 ~ DBFs + sea level	0.04767159	0.01849145
SCM2 ~ DBFs + time bin length	0.0784205	0.02833167
SCM2 ~ sea level + time bin length	0.09595893	0.03637077

Table A.4. Results of pairwise comparisons between raw theropod diversity and sampling proxy time series using GLS. Statistically significant results indicated in bold.

Comparison	Slope	t-value	p-value	R^2
diversity ~ background diversity	0.9928629	15.648196	**<0.00001**	0.9377634
diversity ~ non-conservation Lagerstätten diversity	1.0521869	24.952043	**<0.0001**	0.9740413
diversity ~ concentration Lagerstätten diversity	0.5898083	3.437195	**0.0026**	0.6252264
diversity ~ conservation Lagerstätten diversity	0.362598	5.98282	**0.0019**	0.8570393
background diversity ~ concentration Lagerstätten diversity	0.5655796	3.007105	**0.007**	0.6039452
background diversity ~ conservation Lagerstätten diversity	0.2031351	2.179183	0.0812	0.6547771
diversity ~ time bin length	0.2500325	0.871255	0.3922	0.3254386
diversity ~ DBCs	0.9153822	3.920037	**0.0006**	0.5636925
diversity ~ DBFs	1.406682	4.093491	**0.0004**	0.5705903
diversity ~ specimen number	0.509456	7.633065	**<0.00001**	0.7967368
diversity ~ PBDB species occurrence	0.8283545	10.749578	**<0.00001**	0.8751722
diversity ~ Good's u coverage	0.2214601	3.256892	**0.0033**	0.5173324

Table A.5. Results of comparisons of the population median and distribution of completeness values between different theropod subgroups, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold. Abbreviations: Paraves, non-deinonychosaurian Paraves.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
basal Theropoda	basal Neotheropoda	181	0.71593922	0.839377016
basal Theropoda	Ceratosauria	399	0.136787222	0.310051036
basal Theropoda	basal Tetanurae	57	0.871759819	0.940947106
basal Theropoda	Megalosauroidea	182	0.428611634	0.656071908
basal Theropoda	Allosauroidea	258	0.601751759	0.787610713
basal Theropoda	Megaraptora	95	0.197808115	0.4076046
basal Theropoda	basal Coelurosauria	94	0.405904275	0.642543358
basal Theropoda	Tyrannosauroidea	229	0.991060988	0.99840218
basal Theropoda	Compsognathidae	22	**0.011152934**	0.058077597
basal Theropoda	Ornithomimosauria	152	0.651718129	0.819165852
basal Theropoda	Therizinosauria	118	0.888881004	0.944436067
basal Theropoda	Alvarezsauroidea	147	0.606315062	0.787610713
basal Theropoda	Oviraptorosauria	230	0.444364065	0.664104537
basal Theropoda	Dromaeosauridae	278	0.948145346	0.997129224
basal Theropoda	Troodontidae	202	0.678771007	0.828053929
basal Theropoda	Paraves	57	0.113825008	0.276432162
basal Neotheropoda	Ceratosauria	945	**0.028971399**	0.115795194
basal Neotheropoda	basal Tetanurae	122	0.567653311	0.764364855
basal Neotheropoda	Megalosauroidea	396	0.588388192	0.78451759
basal Neotheropoda	Allosauroidea	572	0.745803943	0.857907245
basal Neotheropoda	Megaraptora	223	0.108448799	0.269467216
basal Neotheropoda	basal Coelurosauria	206	0.515175681	0.734401302
basal Neotheropoda	Tyrannosauroidea	520	0.882220737	0.944436067
basal Neotheropoda	Compsognathidae	57	**0.004867619**	**0.039798373**
basal Neotheropoda	Ornithomimosauria	304	0.152683955	0.330333726
basal Neotheropoda	Therizinosauria	244	0.644319454	0.818948092
basal Neotheropoda	Alvarezsauroidea	318	0.854038279	0.929193648
basal Neotheropoda	Oviraptorosauria	468	0.066706236	0.197218437
basal Neotheropoda	Dromaeosauridae	620	0.683126702	0.828053929
basal Neotheropoda	Troodontidae	474	0.551508567	0.757627931
basal Neotheropoda	Paraves	117	**0.017152417**	0.077757622
Ceratosauria	basal Tetanurae	130	**0.013192558**	0.064078139
Ceratosauria	Megalosauroidea	531.5	0.126920462	0.2976066
Ceratosauria	Allosauroidea	779	0.060015862	0.181381272
Ceratosauria	Megaraptora	314	0.979416001	0.997129224
Ceratosauria	basal Coelurosauria	301	0.549433952	0.757627931
Ceratosauria	Tyrannosauroidea	674.5	**0.010559058**	0.058077597
Ceratosauria	Compsognathidae	57	**0.000106322**	**0.007229925**
Ceratosauria	Ornithomimosauria	426	**0.002355698**	**0.029124996**
Ceratosauria	Therizinosauria	299	**0.011530111**	0.058077597
Ceratosauria	Alvarezsauroidea	395	**0.036856669**	0.128525822
Ceratosauria	Oviraptorosauria	586	**2.43E-05**	**0.003308291**
Ceratosauria	Dromaeosauridae	860	**0.011306371**	0.058077597
Ceratosauria	Troodontidae	659.5	0.169305038	0.359773205
Ceratosauria	Paraves	147	**0.000264721**	**0.012000681**
basal Tetanurae	Megalosauroidea	164	0.241097337	0.468417683
basal Tetanurae	Allosauroidea	233	0.352187078	0.591326451
basal Tetanurae	Megaraptora	89	0.059135911	0.181381272

Table A.5. Continued

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
basal Tetanurae	basal Coelurosauria	81	0.34340851	0.591326451
basal Tetanurae	Tyrannosauroidea	211	0.6080818	0.787610713
basal Tetanurae	Compsognathidae	21	**0.02880556**	0.115795194
basal Tetanurae	Ornithomimosauria	122	0.567653311	0.764364855
basal Tetanurae	Therizinosauria	95	1	1
basal Tetanurae	Alvarezsauroidea	130	0.434351652	0.656353607
basal Tetanurae	Oviraptorosauria	193	0.497659944	0.72535734
basal Tetanurae	Dromaeosauridae	251	0.748764056	0.857907245
basal Tetanurae	Troodontidae	190	0.300081013	0.545728594
basal Tetanurae	Paraves	45	0.102507373	0.264463338
Megalosauroidea	Allosauroidea	475	0.673154955	0.828053929
Megalosauroidea	Megaraptora	191	0.282970152	0.534499176
Megalosauroidea	basal Coelurosauria	179	0.7800367	0.876735465
Megalosauroidea	Tyrannosauroidea	444	0.501349926	0.72535734
Megalosauroidea	Compsognathidae	42	**0.001217836**	**0.024820771**
Megalosauroidea	Ornithomimosauria	265	0.08823848	0.244906801
Megalosauroidea	Therizinosauria	199	0.278110643	0.532718979
Megalosauroidea	Alvarezsauroidea	270	0.750668839	0.857907245
Megalosauroidea	Oviraptorosauria	370	**0.009801413**	0.058077597
Megalosauroidea	Dromaeosauridae	521	0.304732759	0.545728594
Megalosauroidea	Troodontidae	399	0.955640203	0.997129224
Megalosauroidea	Paraves	88	**0.003131609**	**0.033415574**
Allosauroidea	Megaraptora	295	0.179087068	0.37470525
Allosauroidea	basal Coelurosauria	273	0.688015397	0.828053929
Allosauroidea	Tyrannosauroidea	692	0.621189339	0.796997643
Allosauroidea	Compsognathidae	68	**0.001698734**	**0.025669764**
Allosauroidea	Ornithomimosauria	427	0.131946525	0.304147922
Allosauroidea	Therizinosauria	332	0.52895527	0.741628007
Allosauroidea	Alvarezsauroidea	432	0.970046187	0.997129224
Allosauroidea	Oviraptorosauria	636	**0.030651669**	0.115795194
Allosauroidea	Dromaeosauridae	812.5	0.369258012	0.612427923
Allosauroidea	Troodontidae	625	0.813060616	0.898993852
Allosauroidea	Paraves	159	**0.010207606**	0.058077597
Megaraptora	basal Coelurosauria	62	0.405904275	0.642543358
Megaraptora	Tyrannosauroidea	153	0.090800551	0.2469775
Megaraptora	Compsognathidae	12	**0.000831985**	**0.024820771**
Megaraptora	Ornithomimosauria	81	**0.009283746**	0.058077597
Megaraptora	Therizinosauria	66	0.053089683	0.175451959
Megaraptora	Alvarezsauroidea	84	0.087051614	0.244906801
Megaraptora	Oviraptorosauria	116	**0.001936651**	**0.02633845**
Megaraptora	Dromaeosauridae	187	0.074931024	0.216821686
Megaraptora	Troodontidae	153	0.383903906	0.629047363
Megaraptora	Paraves	26	**0.001155785**	**0.024820771**
basal Coelurosauria	Tyrannosauroidea	203	0.351505843	0.591326451
basal Coelurosauria	Compsognathidae	19	**0.00324282**	**0.033415574**
basal Coelurosauria	Ornithomimosauria	113	0.054183693	0.175451959
basal Coelurosauria	Therizinosauria	96	0.304965979	0.545728594
basal Coelurosauria	Alvarezsauroidea	131	0.698544764	0.833351648

Table A.5. Continued

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
basal Coelurosauria	Oviraptorosauria	178	**0.032359377**	0.118942576
basal Coelurosauria	Dromaeosauridae	237	0.225363977	0.450727953
basal Coelurosauria	Troodontidae	193	0.839034001	0.92023084
basal Coelurosauria	Paraves	38	**0.005180577**	**0.039798373**
Tyrannosauroidea	Compsognathidae	90	**0.009932522**	0.058077597
Tyrannosauroidea	Ornithomimosauria	450	0.292498509	0.544928728
Tyrannosauroidea	Therizinosauria	334	0.656537337	0.819165852
Tyrannosauroidea	Alvarezsauroidea	437	0.778338111	0.876735465
Tyrannosauroidea	Oviraptorosauria	679	0.108975712	0.269467216
Tyrannosauroidea	Dromaeosauridae	890	0.982465559	0.997129224
Tyrannosauroidea	Troodontidae	658	0.411038766	0.642543358
Tyrannosauroidea	Paraves	179	**0.03624376**	0.128525822
Compsognathidae	Ornithomimosauria	207	**0.02576812**	0.113047235
Compsognathidae	Therizinosauria	157	**0.003439839**	**0.033415574**
Compsognathidae	Alvarezsauroidea	186	**0.001301644**	**0.024820771**
Compsognathidae	Oviraptorosauria	340	**0.010861098**	0.058077597
Compsognathidae	Dromaeosauridae	365	**0.005267432**	**0.039798373**
Compsognathidae	Troodontidae	256	**0.001460045**	**0.024820771**
Compsognathidae	Paraves	105	0.102507373	0.264463338
Ornithomimosauria	Therizinosauria	305	0.407655304	0.642543358
Ornithomimosauria	Alvarezsauroidea	392	0.103062918	0.264463338
Ornithomimosauria	Oviraptorosauria	608	0.808539055	0.898993852
Ornithomimosauria	Dromaeosauridae	723	0.48230045	0.712965882
Ornithomimosauria	Troodontidae	537	0.120299466	0.287030304
Ornithomimosauria	Paraves	153	0.151501197	0.330333726
Therizinosauria	Alvarezsauroidea	240	0.429341175	0.656071908
Therizinosauria	Oviraptorosauria	345	0.230419447	0.454160069
Therizinosauria	Dromaeosauridae	450	0.966411559	0.997129224
Therizinosauria	Troodontidae	342	0.350920257	0.591326451
Therizinosauria	Paraves	80	**0.03017729**	0.115795194
Alvarezsauroidea	Oviraptorosauria	333	**0.030303097**	0.115795194
Alvarezsauroidea	Dromaeosauridae	466	0.518400919	0.734401302
Alvarezsauroidea	Troodontidae	362	0.713696463	0.839377016
Alvarezsauroidea	Paraves	76	**0.005137682**	**0.039798373**
Oviraptorosauria	Dromaeosauridae	1219	0.209631751	0.425521165
Oviraptorosauria	Troodontidae	892	**0.039801198**	0.135324075
Oviraptorosauria	Paraves	253	0.153022241	0.330333726
Dromaeosauridae	Troodontidae	823	0.339238491	0.591326451
Dromaeosauridae	Paraves	236	0.055966508	0.177010351
Troodontidae	Paraves	130	**0.015619417**	0.073249681

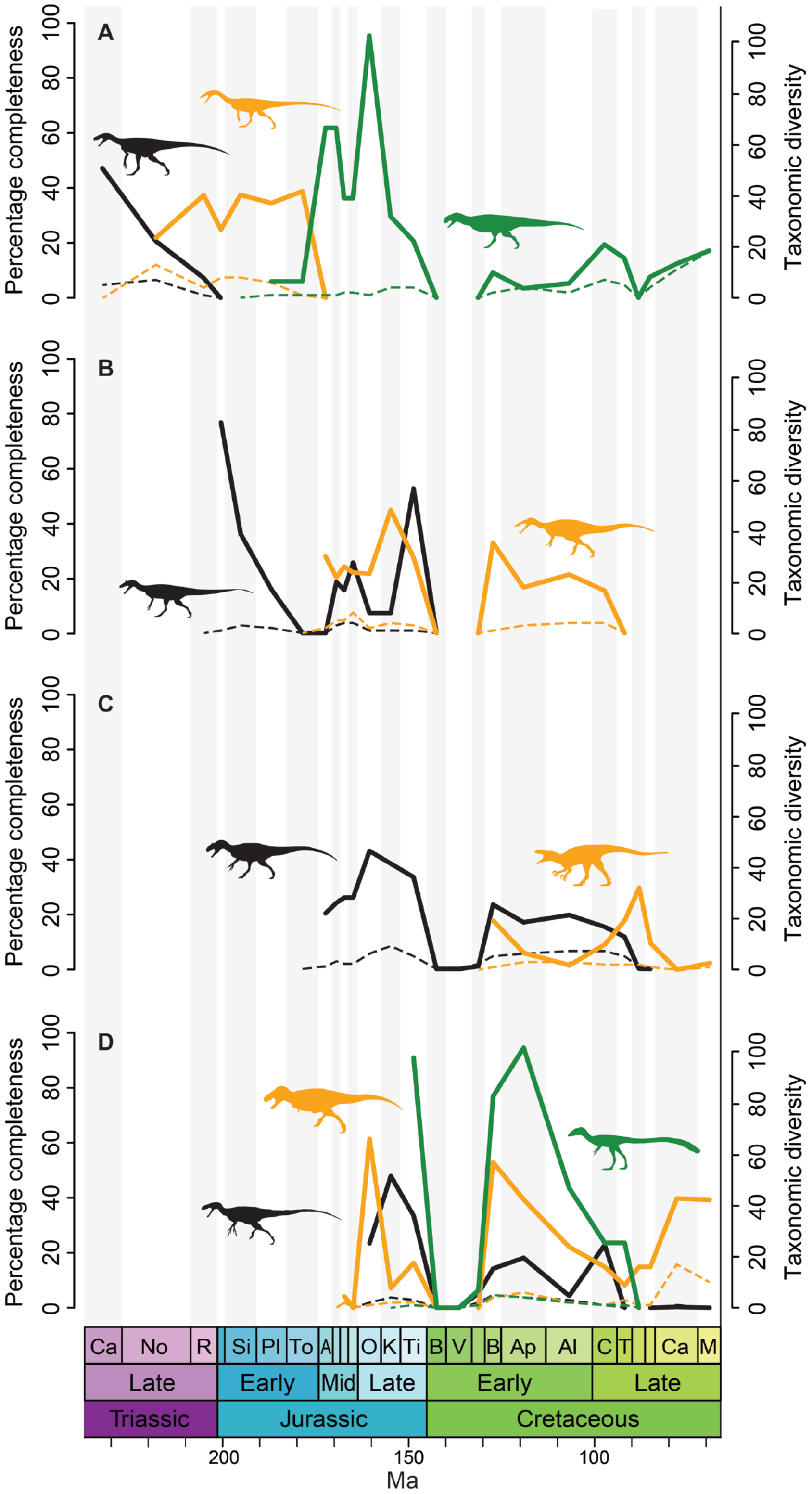


Figure A.5A-D. Changes in mean SCM2 (line) and raw taxonomic richness (dashed) through time for each individual theropod subgroup. A, basal Theropoda (black), basal Neotheropoda (yellow), Ceratosauria (green); B, basal Tetanurae (black), Megalosauroidea (yellow); C, Allosauroidea (black), Megaraptora (yellow); D, basal Coelurosauria (black), Tyrannosauroidea (yellow), Compsognathidae (green). Continued on next page.

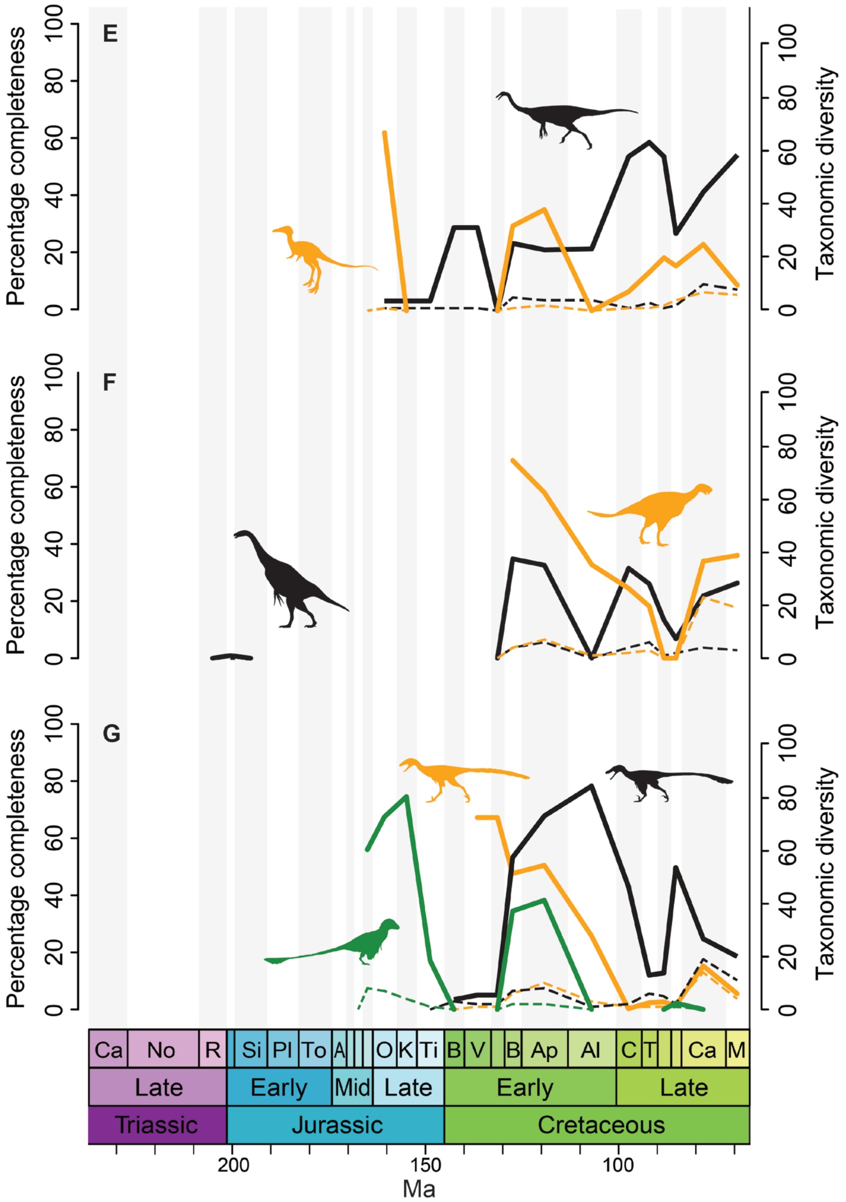


Figure A.5E-G. Changes in mean SCM2 (line) and raw taxonomic richness (dashed) through time for each individual theropod subgroup. E, Ornithomimosauria (black), Alvarezsauroidea (yellow); F, Therizinosauria (black), Oviraptorosauria (yellow); G, Dromaeosauridae (black), Troodontidae (yellow), non-deinonychosaurian Paraves (green).

Table A.6. Results of pairwise comparisons between subgroup and total theropod time series using GLS. Statistically significant results indicated in bold. Abbreviations: basal Thero., basal Theropoda; Neothero., basal Neotheropoda; Cerato., Ceratosauria; basal Tet., basal Tetanurae; Megalo., Megalosauroidea; Allo., Allosauroidea; Megarap., Megaraptora; basal Coeluro., basal Coelurosauria; Tyranno., Tyrannosauroidea; Compsog., Comsognathidae; Ornitho., Ornithomimosauria; Theriz., Therizinosauria; Alvarez., Alvarezsauroidea; Ovirap., Oviraptorosauria; Dromaeo., Dromaeosauridae; Trood., Troodontidae; Paraves, non-deinonychosaurian Paraves.

Comparison	Slope	t-value	p-value	R^2
basal Thero. SCM2 ~ total SCM2	4.591412	4989392	**<0.0001**	0.999999999
basal Thero. SCM2 ~ basal Thero. diversity	1.158491	8454002	**<0.0001**	1
Neothero. SCM2 ~ total SCM2	1.0123988	2.3489364	0.0786	0.419789243
Neothero SCM2 ~ Neothero. diversity	-0.158893	-1.803547	0.1456	0.58508538
Cerato. SCM2 ~ total SCM2	0.6023672	0.8597107	0.4026	0.37783809
Cerato SCM2 ~ Cerato. diversity	-0.0404306	-0.138133	0.8919	0.349982275
basal Tet. SCM2 ~ total SCM2	-1.383278	-1.311084	0.2312	0.208187402
basal Tet. SCM2 ~ basal Tet. diversity	0.0231961	0.045894	0.9647	0.018631972
Megalo. SCM2 ~ total SCM2	0.4143701	1.613727	0.141	0.179308139
Megalo. SCM2 ~ Megalo. diversity	-0.162273	-0.950938	0.3665	0.088848894
Allo. SCM2 ~ total SCM2	2.522232	3.040814	**0.0103**	0.435985056
Allo. SCM2 ~ Allo. diversity	1.7231823	3.805884	**0.0025**	0.46525277
Megarap. SCM2 ~ total SCM2	-0.327976	-0.3229233	0.7562	0.007699365
Megarap. SCM2 ~ Megarap. diversity	-0.7062613	-0.989335	0.3555	0.106372436
basal Coeluro. SCM2 ~ total SCM2	1.457234	1.5924097	0.1553	0.268779258
basal Coeluro. SCM2 ~ basal Coeluro. diversity	1.253774	2.075756	0.0766	0.398481086
Tyranno. SCM2 ~ total SCM2	1.0944997	1.9799496	0.0733	0.270975598
Tyranno. SCM2 ~ Tyranno. diversity	0.5133818	3.298114	**0.0071**	0.434505988
Compsog. SCM2 ~ total SCM2	1.994524	6.769062	**0.0005**	0.888015196
Compsog. SCM2 ~ Compsog. diversity	0.597453	1.218847	0.2686	0.216969518
Ornitho. SCM2 ~ total SCM2	-0.679655	-1.802629	0.0966	0.634232736
Ornitho. SCM2 ~ Ornitho. diversity	-0.0491069	-0.204998	0.841	0.537028954
Theriz. SCM2 ~ total SCM2	2.599432	1.627131	0.1477	0.099425923
Theriz. SCM2 ~ Theriz. diversity	1.565148	3.372108	**0.0119**	0.622224357
Alvarez. SCM2 ~ total SCM2	1.196222	2.930834	**0.022**	0.554600829
Alvarez. SCM2 ~ Alvarez. diversity	-0.0972171	-0.313592	0.763	0.029946671
Ovirap. SCM2 ~ total SCM2	1.3595165	6.218125	**0.0016**	0.883761304
Ovirap. SCM2 ~ Ovirap. diversity	0.200187	1.700463	0.1498	0.516802306
Dromaeo. SCM2 ~ total SCM2	0.8572948	1.6833439	0.1232	0.448906317
Dromaeo. SCM2 ~ Dromaeo. diversity	-0.0934046	-0.31558	0.7588	0.305693527
Trood. SCM2 ~ total SCM2	0.8953126	0.709145	0.4962	0.252450529
Trood. SCM2 ~ Trood. diversity	0.7777052	1.500938	0.1676	0.364257051
Paraves SCM2 ~ total SCM2	3.017637	7.563749	**0.0006**	0.918360788
Paraves SCM2 ~ Paraves diversity	1.092799	2.677638	**0.0439**	0.588938131

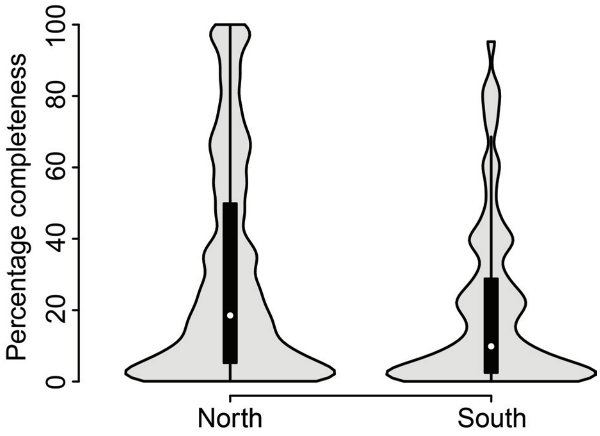


Figure A.6. Distribution of theropod SCM2 scores between different hemispheres.

Table A.7. Results of comparisons of the population median and distribution of theropod SCM2 values for different continents, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Africa	Asia	1803	**0.001112966**	**0.004946516**
Africa	Australasia	188.5	**0.014894926**	**0.033099836**
Africa	Europe	942	0.923692555	0.923692555
Africa	North America	1220	0.23714081	0.297199848
Africa	South America	953	0.608225766	0.640237649
Asia	Australasia	1384	**0.000103602**	**0.000690679**
Asia	Europe	8405	**7.03E-07**	**1.41E-05**
Asia	North America	10982	**0.003757205**	**0.011560632**
Asia	South America	8757	**2.00E-05**	**0.000199881**
Australasia	Europe	106.5	**0.009246147**	**0.023115369**
Australasia	North America	125	**0.001713582**	**0.00685433**
Australasia	South America	94	**0.002661695**	**0.00967889**
Europe	North America	2416.5	0.057959838	0.105381523
Europe	South America	1873.5	0.275386776	0.314727744
North America	South America	3567	0.257423735	0.31202877

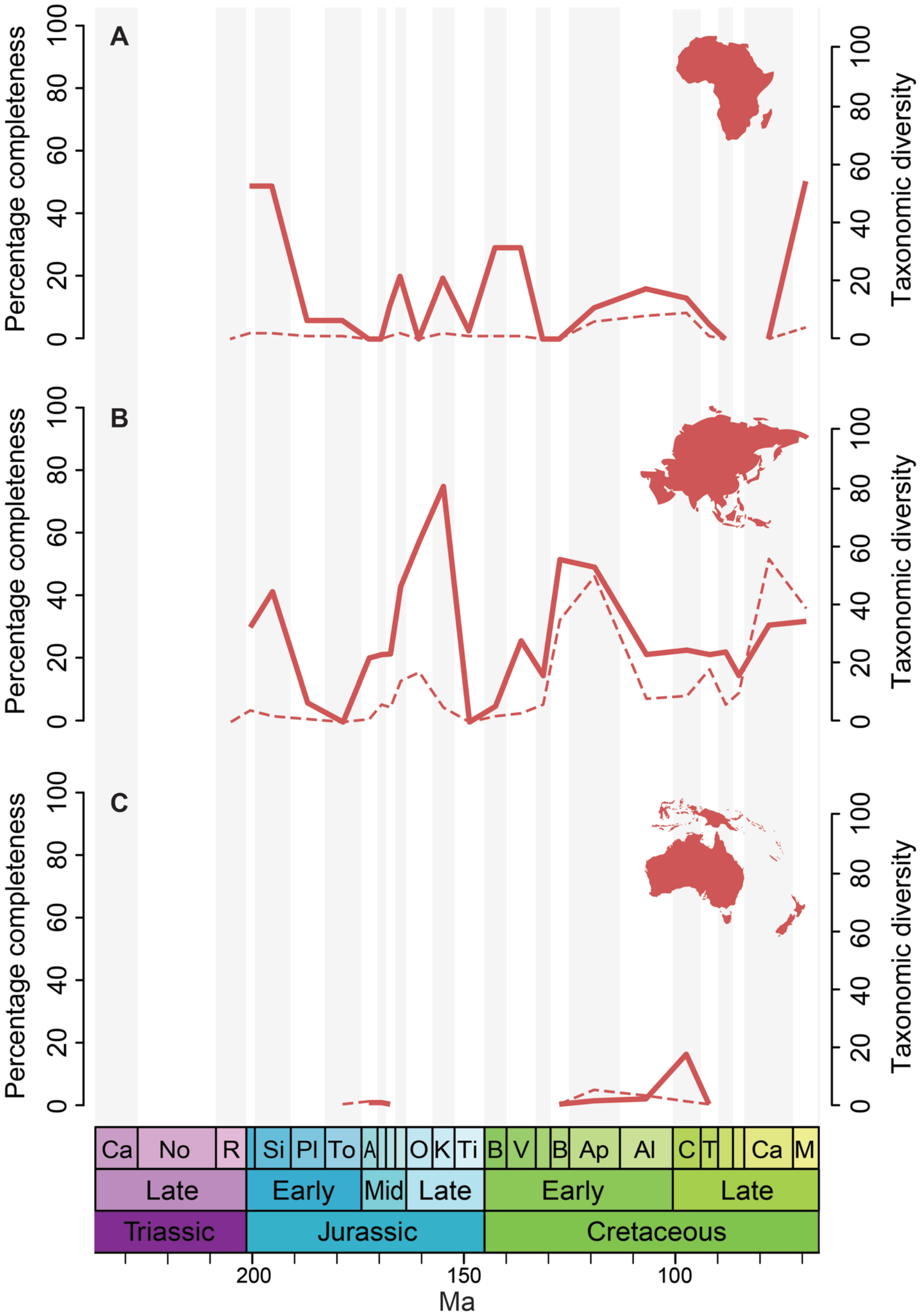


Figure A.7A-C. Changes in mean theropod SCM2 (red line) and raw taxonomic richness (dashed) through time for each individual continent. A, Africa; B, Asia; C, Australasia; Continued on next page.

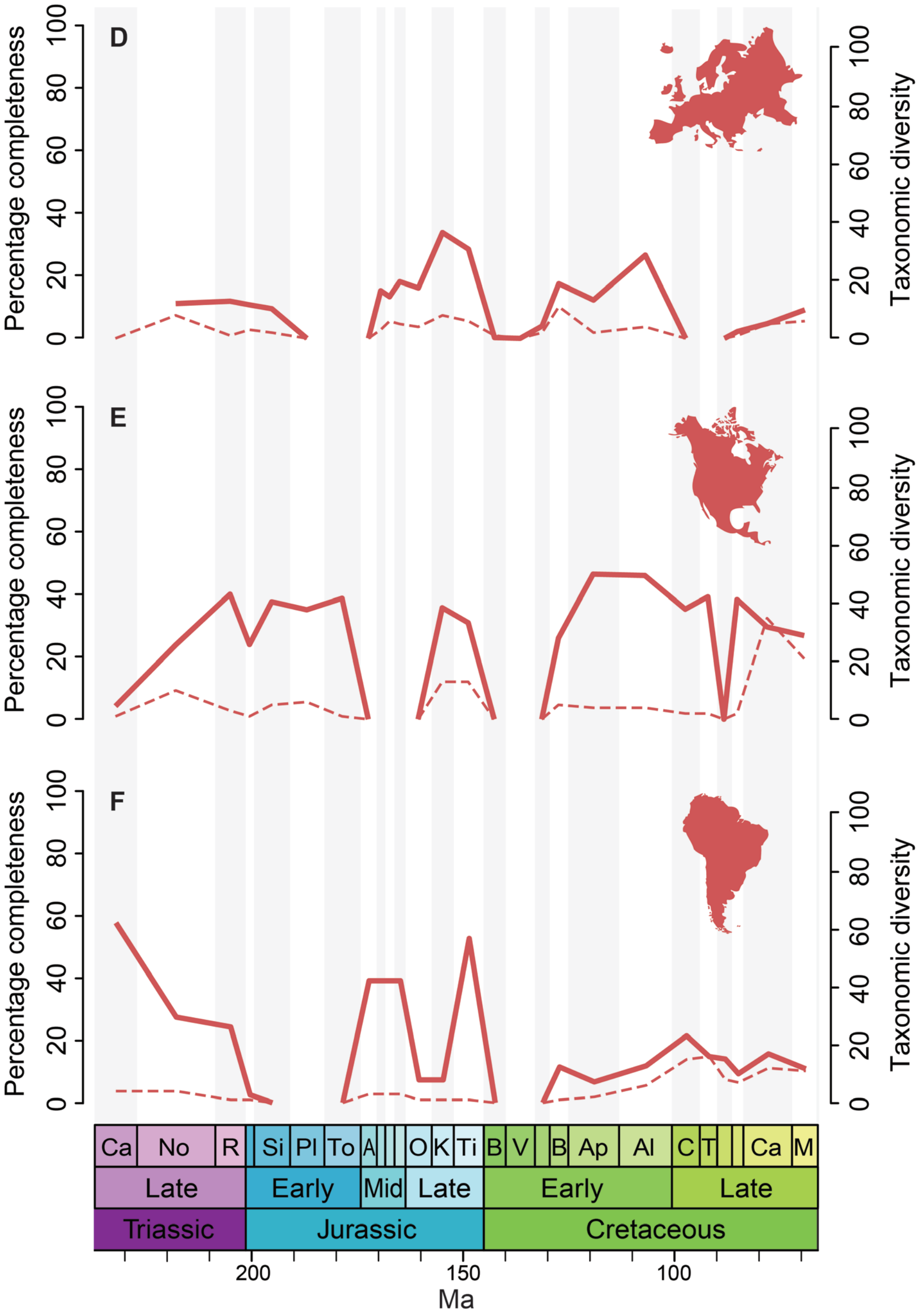


Figure A.7D-F. Changes in mean theropod SCM2 (red line) and raw taxonomic richness (dashed) through time for each individual continent. D, Europe; E, North America; F, South America.

Table A.8. Results of pairwise comparisons between continental theropod time series using GLS. Statistically significant results indicated in bold. Abbreviations: AF, Africa; AS, Asia; AU, Australasia; EU, Europe; NA, North America; SA, South America.

Comparison	Slope	t-value	p-value	R^2
AF SCM2 ~ total SCM2	0.058589	0.0829286	0.9352	0.015926805
AF SCM2 ~ AF diversity	0.2941148	0.995949	0.3375	0.078665575
AS SCM2 ~ total SCM2	1.3131889	5.764073	**<0.0001**	0.626517584
AS SCM2 ~ AS diversity	0.2801762	3.009405	**0.0072**	0.313041285
AU SCM2 ~ total SCM2	-4.016035	-1.577774	0.2127	0.257923825
AU SCM2 ~ AU diversity	-0.3781475	-0.4700368	0.6704	0.195062697
EU SCM2 ~ total SCM2	2.007566	5.537471	**<0.0001**	0.596239448
EU SCM2 ~ EU diversity	0.9881482	3.36564	**0.0039**	0.415965906
NA SCM2 ~ total SCM2	-0.671245	-1.867661	0.0815	0.264829527
NA SCM2 ~ NA diversity	0.1445271	1.400042	0.1818	0.201022601
SA SCM2 ~ total SCM2	-0.0351748	-0.0629054	0.9505	0.000216426
SA SCM2 ~ SA diversity	0.1242996	0.622762	0.5413	0.019848273

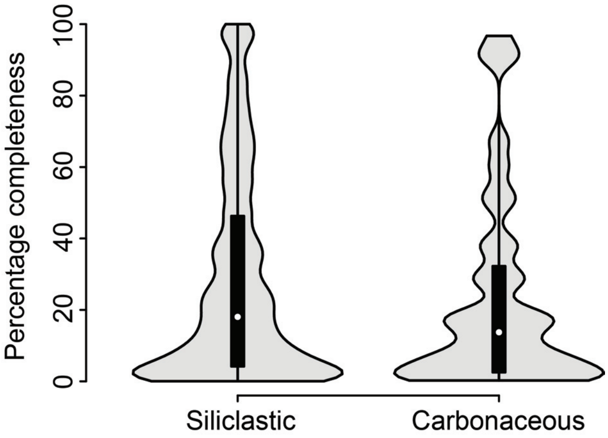


Figure A.8. Distribution of theropod SCM2 scores between siliclastic and carbonaceous depositional settings.

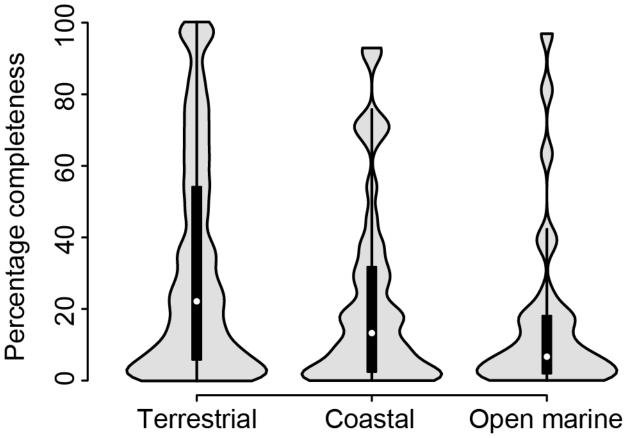


Figure A.9. Distribution of theropod SCM2 scores between terrestrial, coastal and marine depositional settings.

Table A.9. Results of comparisons of the population median and distribution of theropod SCM2 values for different depositional environments, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Aeolian	Alluvial plain	1810.5	0.130164677	0.200253349
Aeolian	Fluvial channel	4338	**0.007499264**	**0.019998036**
Aeolian	Lacustrine	1885.5	0.237759879	0.297199848
Aeolian	Coastal	1013	**0.016104468**	**0.033904143**
Aeolian	Open	800	**0.00075616**	**0.0037808**
Alluvial plain	Fluvial channel	9506	0.108659232	0.177563128
Alluvial plain	Lacustrine	3893	**0.00038472**	**0.002198399**
Alluvial plain	Coastal	2230	0.156539167	0.208718889
Alluvial plain	Open	1776	**0.012722898**	**0.029936231**
Fluvial channel	Lacustrine	7374	**8.13785E-09**	**3.25514E-07**
Fluvial channel	Coastal	4393	0.72111136	0.739601394
Fluvial channel	Open	3469.5	0.153968213	0.208718889
Lacustrine	Coastal	3843	**5.80505E-05**	**0.000464404**
Lacustrine	Open	2950	**4.29839E-06**	**5.73119E-05**
Coastal	Open	770.5	0.343736087	0.381928985

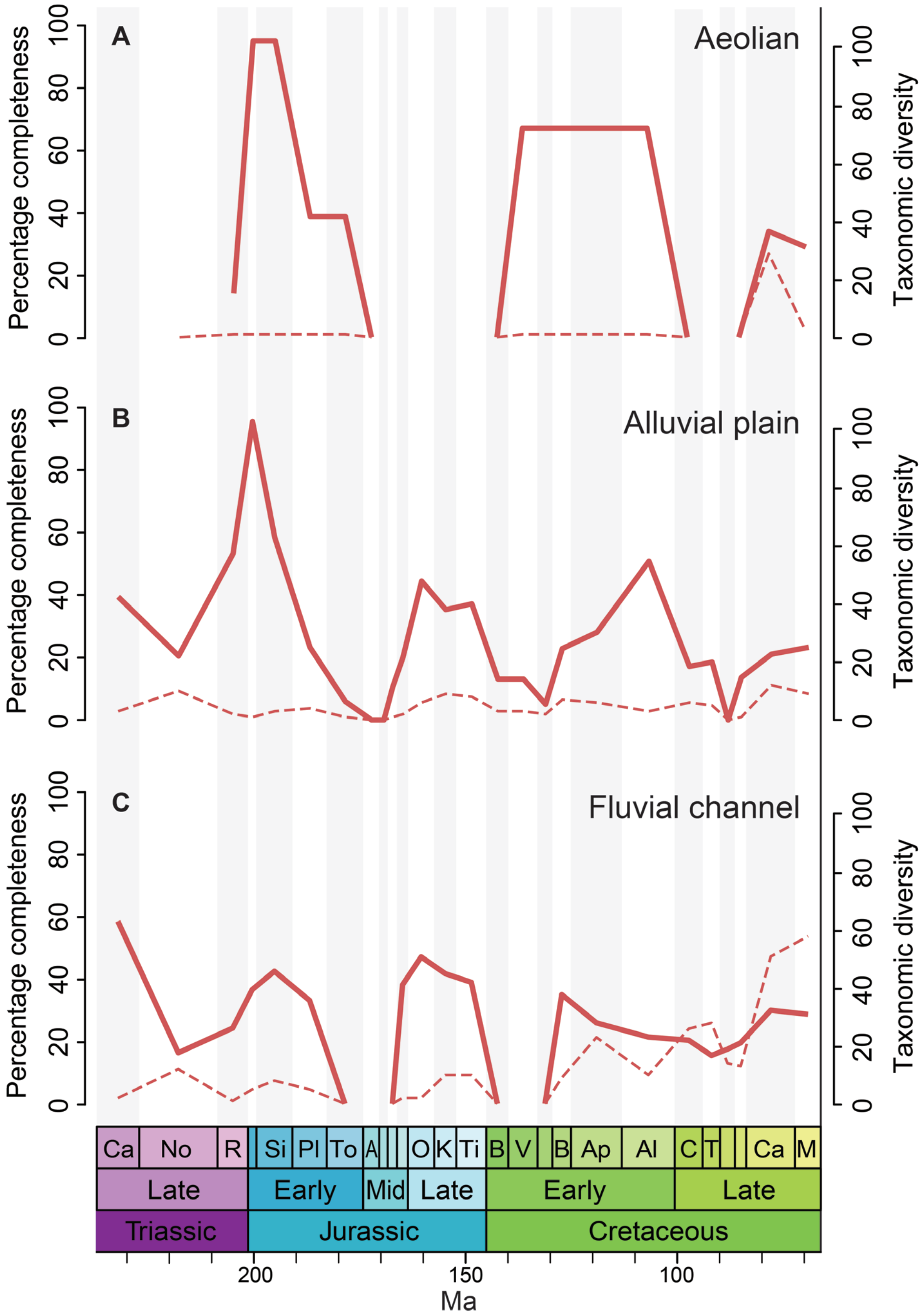


Figure A.10A-C. Changes in mean theropod SCM2 (red line) and raw taxonomic richness (dashed) through time for each individual depositional setting. A, Aeolian; B, Alluvial plain; C, Fluvial channel; Continued on the next page.

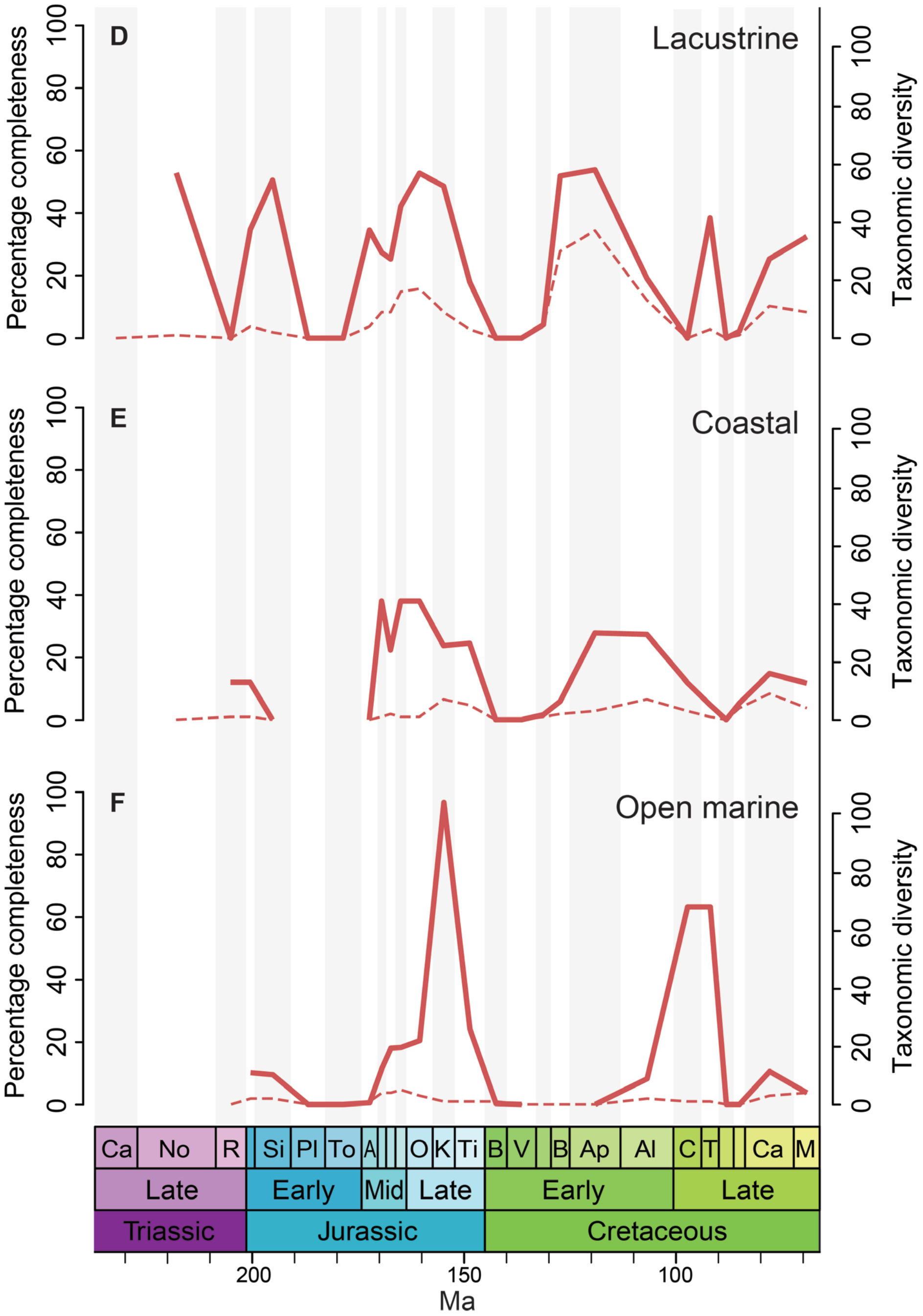


Figure A.10D-F. Changes in mean theropod SCM2 (red line) and raw taxonomic richness (dashed) through time for each individual depositional setting. D, Lacustrine; E, Coastal; F, Open marine.

Table A.10. Results of pairwise comparisons between depositional environment specific theropod time series, using GLS. Statistically significant results indicated in bold. Abbreviations: non-conserv., non-conservation; Lager., Lagerstätten.

Comparison	Slope	t-value	p-value	R^2
Aeolian SCM2 ~ total SCM2	-0.064985	-0.1254846	0.9026	0.04862595
Aeolian SCM2 ~ background SCM2	-0.629243	-1.746876	0.1112	0.2699278
Aeolian SCM2 ~ non-conserv. Lager. SCM2	-0.511236	-1.0853	0.3033	0.1473976
Alluvial plain SCM2 ~ total SCM2	0.8660194	3.49399	**0.0022**	0.49150726
Alluvial plain SCM2 ~ background SCM2	0.6819188	2.309556	**0.0312**	0.3611599
Alluvial plain SCM2 ~ non-conserv. Lager. SCM2	1.052214	3.618959	**0.0016**	0.5065481
Fluvial channel SCM2 ~ total SCM2	0.740656	3.486348	**0.0028**	0.5102999
Fluvial channel SCM2 ~ background SCM2	0.9462467	7.029242	**<0.0001**	0.7916303
Fluvial channel SCM2 ~ non-conserv. Lager. SCM2	1.0818141	7.179392	**<0.0001**	0.7982605
Lacustrine SCM2 ~ total SCM2	1.495019	6.040638	**<0.0001**	0.54831127
Lacustrine SCM2 ~ background SCM2	1.1556026	3.0417022	**0.007**	0.3386886
Lacustrine SCM2 ~ non-conserv. Lager. SCM2	1.355152	3.1566731	**0.0055**	0.3549593
Coastal SCM2 ~ total SCM2	1.562815	3.852518	**0.0016**	0.50533307
Coastal SCM2 ~ background SCM2	1.669258	2.965486	**0.0096**	0.3706199
Coastal SCM2 ~ non-conserv. Lager. SCM2	2.204789	3.909167	**0.0014**	0.5117402
Open marine SCM2 ~ total SCM2	2.226608	2.053852	0.0607	0.25722383
Open marine SCM2 ~ background SCM2	2.251821	1.94869	0.0732	0.2385032
Open marine SCM2 ~ non-conserv. Lager. SCM2	2.344453	1.821041	0.0917	0.2140067

Table A.11. Taxonomic occurrences of each theropod subgroup per Lagerstätte and depositional environment. Occurrences in the depositional settings may be higher than total diversity as some taxa are found in multiple settings. Abbreviations: Concent., Concentration; Conserv., Conservation; div., diversity; Lacust., Lacustrine; Lager., Lagerstätten; SCM2., mean SCM2; Singl., single specimen taxa; Var., Variable; basal Thero., basal Theropoda; Neothero., basal Neotheropoda; Cerato., Ceratosauria; basal Tet., basal Tetanurae; Megalo., Megalosauroidea; Allo., Allosauroidea; Megarap., Megaraptora; Coeluro., basal Coelurosauria; Tyranno., Tyrannosauroidea; Compsog., Comsognathidae; Ornitho., Ornithomimosauria; Theriz., Therizinosauria; Alvarez., Alvarezsauroidea; Ovirap., Oviraptorosauria; Dromaeo., Dromaeosauridae; Trood., Troodontidae; Paraves, non-deinonychosaurian Paraves.

Subgroup	Var.	All taxa	Singl.	Concent. Lager.	Conserv. Lager.	Aeolian	Alluvial plain	Fluvial channel	Lacust.	Coastal	Marine
basal Thero.	div.	12	7	3	0	0	5	8	0	0	0
	% div.	1	0.58	0.25	0.00	0.00	0.42	0.67	0.00	0.00	0.00
	SCM2	31.89	12.04	29.17	0.00	0.00	28.16	32.19	0.00	0.00	0.00
Neothero.	div.	28	14	5	0	3	11	10	5	1	2
	% div.	1	0.50	0.18	0.00	0.11	0.39	0.36	0.18	0.04	0.07
	SCM2	25.54	17.59	58.80	0.00	49.38	32.81	19.22	61.60	11.95	18.11
Cerato.	div.	52	37	10	0	0	11	33	6	7	4
	% div.	1	0.71	0.19	0.00	0.00	0.21	0.63	0.12	0.13	0.08
	SCM2	16.82	11.46	40.76	0.00	0.00	37.17	13.35	46.37	22.26	24.08
Tetanurae	div.	10	5	2	0	0	0	5	5	0	1
	% div.	1	0.50	0.20	0.00	0.00	0.00	0.50	0.50	0.00	0.10
	SCM2	27.8	24.48	21.88	0.00	0.00	0.00	41.61	28.01	0.00	6.66
Megalo.	div.	28	13	6	3	0	4	8	6	5	10
	% div.	1	0.46	0.21	0.11	0.00	0.14	0.29	0.21	0.18	0.36
	SCM2	20.89	17.95	23.43	34.70	0.00	35.46	24.10	22.71	23.85	22.34
Allo.	div.	39	16	4	1	0	9	19	12	6	2
	% div.	1	0.41	0.10	0.03	0.00	0.23	0.49	0.31	0.15	0.05
	SCM2	25.02	19.11	55.48	60.32	0.00	39.82	27.24	33.38	18.11	12.09
Megarap.	div.	12	9	1	0	0	1	8	0	2	1
	% div.	1	0.75	0.08	0.00	0.00	0.08	0.67	0.00	0.17	0.08
	SCM2	11.73	6.79	33.77	0.00	0.00	16.12	11.51	0.00	15.24	2.18
Coeluro.	div.	13	9	4	0	0	5	6	7	0	0
	% div.	1	0.69	0.31	0.00	0.00	0.38	0.46	0.54	0.00	0.00
	SCM2	18.75	25.43	25.15	0.00	0.00	14.44	30.51	16.43	0.00	0.00
Tyranno.	div.	38	20	8	5	1	10	17	9	4	6
	% div.	1	0.53	0.21	0.13	0.03	0.26	0.45	0.24	0.11	0.16
	SCM2	29.78	13.23	51.88	45.03	98.18	27.90	42.39	46.97	27.30	10.32
Comps.	div.	10	6	1	7	0	1	0	5	4	0
	% div.	1	0.60	0.10	0.70	0.00	0.10	0.00	0.50	0.40	0.00
	SCM2	67.87	55.55	23.57	81.10	0.00	23.57	0.00	76.89	67.66	0.00
Ornitho.	div.	28	12	4	3	1	5	13	10	2	0
	% div.	1	0.43	0.14	0.11	0.04	0.18	0.46	0.36	0.07	0.00
	SCM2	35.9	21.42	25.56	28.45	2.46	35.80	50.55	30.51	1.06	0.00
Therizino.	div.	19	12	2	2	1	2	8	5	2	1
	% div.	1	0.63	0.11	0.11	0.05	0.11	0.42	0.26	0.11	0.05
	SCM2	26.91	22.25	38.70	52.67	10.12	9.48	21.86	36.35	5.11	63.28
Alvarez.	div.	21	15	1	0	6	4	9	2	1	0
	% div.	1	0.71	0.05	0.00	0.29	0.19	0.43	0.10	0.05	0.00
	SCM2	20.31	19.74	4.59	0.00	25.30	21.62	10.64	43.86	20.56	0.00
Ovirap.	div.	45	25	3	6	9	3	19	13	3	0
	% div.	1	0.56	0.07	0.13	0.20	0.07	0.42	0.29	0.07	0.00
	SCM2	36.91	30.18	15.21	64.12	48.37	22.04	28.22	49.53	15.42	0.00
Dromaeo.	div.	47	26	10	9	7	13	18	14	3	2
	% div.	1	0.55	0.21	0.19	0.15	0.28	0.38	0.30	0.06	0.04
	SCM2	32.3	28.83	33.69	68.53	35.24	22.91	20.07	62.05	29.71	1.39
Trood.	div.	31	23	2	7	7	3	9	11	2	0
	% div.	1	0.74	0.06	0.23	0.23	0.10	0.29	0.35	0.06	0.00
	SCM2	26.04	24.45	0.20	69.68	31.06	17.70	4.40	47.36	0.18	0.00
Paraves	div.	15	14	1	14	0	0	1	13	1	0
	% div.	1	0.93	0.07	0.93	0.00	0.00	0.07	0.87	0.07	0.00
	SCM2	49.96	46.39	2.23	53.37	0.00	0.00	2.23	56.16	17.09	17.09

Good’s u R function:

```
goodsU <- function(occvec) {
  n <- sum(occvec)
  f1 <- sum(occvec == 1); f2 <- sum(occvec == 2)
  # out <- 1 - (f1 / sum(occvec)) #singleton-only coverage estimator
  out <- 1 - (f1/n) * (((n - 1) * f1) / ((n - 1) * f1 + 2 * f2)) #Chao and Jost
(2012) coverage estimator using singletons and doubletons
  out[is.nan(out) | is.infinite(out)] <- NA
  return(out)
}

#Need a vector of abundance or occurrence counts per stage, e.g:
Carnian_Thero_Occ<-table(table(Carnian_sample$accepted_name))
Carnian_Thero_Occ #=1,1,1,1,1,1,7
goodsU(Carnian_Thero_Occ)
```

JUSTIFICATION FOR PREFERRED THEROPOD SUBGROUPS

We separated taxa into seventeen distinct non-avian theropod subgroups based on recent phylogenetic assessments in order to analyse the in-group differences in the theropod fossil record. These subgroups are: Basal Theropoda, Basal Neotheropoda, Ceratosauria, Basal Tetanurae, Megalosauroidea, Allosauroidea, Megaraptora, Basal Coelurosauria, Tyrannosauroidea, Compsognathidae, Ornithomimosauria, Alvarezsauroidea, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae, and non-deinonychosaurian Paraves. We followed the Hendrickx *et al.* (2015) extensive review of theropod classification as a guide for the overall relationships (see Fig. S1) and designations of most subgroups. Below are short justifications for each group:

Basal Theropoda. Includes Herrerrasauridae and *Caseosaurus crosbyensis*, *Daemonosaurus chauliodus*, *Eodromaeus murphi, Guaibasaurus candelariensis*, *Tawa hallae*. From phylogenetic analyses, a number of authors (Ezcurra 2006; Langer and Benton 2006; Irmis *et al*. 2007; Nesbitt *et al*. 2009b; Ezcurra 2010; Apaldetti *et al*. 2011; Nesbitt 2011; Novas *et al*. 2011; Langer 2014; Baron *et al*. 2017; Baron and Barrett 2017; Parry *et al*. 2017) recently found herrerasaurids, along with other basal theropods, to be placed as basal saurischians outside Theropoda, or basal sauropodomorphs, or even basal dinosaurs outside Saurischia. However, we follow taxonomic classifications and the majority of recent cladistics studies (Gauthier 1986; Juul 1994; Novas 1996; Benton 1999 Benton 2004; Langer and Benton 2006; Nesbitt *et al*. 2009a; Nesbitt *et al*. 2010; Apaldetti *et al*. 2011; Langer *et al*. 2011; Novas *et al*. 2011; Langer 2014; Novas *et al*. 2015; Langer 2017; Müller et al. 2017) and include Herrerasauridae and other basal theropods within Basal Theropoda

Basal Neotheropoda. Includes Coelophysoidea, Dilophosauridae and *Dracoraptor hanigani*, *Liliensternus liliensterni*, *Shuangbaisaurus anlongbaoensis*, *Tachiraptor admirabilis*, and *Velocipes guerichi*. All of the latter are assigned as neotheropods and/or fall stemward of Ceratosauria in recent cladistics analyses (Langer *et al*. 2014; Nesbitt and Ezcurra 2015; Martill *et al*. 2016; Skawiński et al. 2016; Wang *et al*. 2017).

Ceratosauria. Monophyletic group including Ceratosauridae, Noasauridae and Abelisauroidea.

Basal Tetanurae. Includes a number of taxa assigned as tetanurans and which are found stemward of Megalosauroidea and Allosauroidea in cladistics analyses (Benson 2010; Brusatte *et al*. 2010; Gay 2010; Carrano *et al*. 2012; Hendrickx *et al*. 2015; Novas *et al*. 2015; Rauhut and Pol 2017).

Megalosauroidea. Monophyletic group including Megalosauridae, Piatnitzkysauridae and Spinosauridae.

Allosauroidea. Monophyletic group including Allosauridae, Carcharodontosauridae, Metriacanthosauridae and Neovenatoridae.

Megaraptora. We regard Megaraptora as separate too both Allosauroidea and Tyrannosauroidea, too which they have been previously hypothesized to belong (Benson *et al*. 2010; Porfiri *et al*. 2014; Novas *et al*. 2016; Porfiri *et al*. 2018).

Basal Coelurosauria. Includes a number of coelurosaurian taxa that are consistently positioned at the base of Coelurosauria or on the stems of monophyletic coelurosaurian groups in phylogenetic analyses (Rauhut and Xu 2005; Butler and Upchurch 2007; Choiniere *et al.* 2010; Novas *et al*. 2012; Godefroit *et al*. 2013; Choiniere *et al.* 2014; Azuma *et al*. 2016). This subgroup is largely artificial and most likely represents a grade of coelurosaurian forms, but is useful for the inclusion of a number of taxa of uncertain affinities.

Tyrannosauroidea. Monophyletic group including Proceratosauridae and Tyrannosauridae.

Compsognathidae. Monophyletic family.

Ornithomimosauria. Monophyletic group including Ornithomimidae and Deinocheiridae.

Alvarezsauroidea. Monophyletic group including Alvarezsauridae.

Therizinosauria. Monophyletic group including Therizinosauridae.

Oviraptorosauria. Monophyletic group including Caudipterygidae, Caenagnathidae, and Oviraptoridae.

Dromaeosauridae. Monophyletic family.

Troodontidae. Monophyletic family.

Non-deinonychosaurian Paraves. Consists of a grade of bird-like paravians not included in either Dromaeosauridae or Troodontidae. We include anchiornithids, scansoriopterygids and *Caihong juji, Pedopenna daohugouensis, Pneumatoraptor fodori, Serikornis sungei, Xiaotingia zhengi,* and *Yixianosaurus longimanus*. Some of these taxa have been situated within Avialae (Zhang *et al*. 2008; Xu *et al*. 2011; Godefroit *et al*. 2013a), but are found outside Avialae in most recent phylogenetic analyses (Xu and Zhang 2005; Xu *et al*. 2009; Xu *et al*. 2011; Godefroit *et al*. 2013b; O'Connor and Sullivan 2014; Xu *et al*. 2015; Foth and Rauhut 2017; Lefèvre *et al*. 2017; Guo *et al*. 2018; Hu *et al*. 2018), and are all assigned as non-avian theropod taxa.

Indeterminate. A number of taxa included in our dataset have affinities too uncertain to confidently include in any of the above subgroups. Notable taxa are *Bahariasaurus ingens*, *Gualicho shinyae*, *Labocania anomala*, *Ozraptor subotaii* and *Shanyangosaurus niupanggouensis*. These taxa were excluded from analyses of the in-group theropod fossil record.

ADDITIONAL REFERENCES

APALDETTI, C., MARTINEZ, R. N., ALCOBER, O. A. and POL, D. 2011. A new basa sauropodomorph (Dinosauria: Saurischia) from Quebrada del Barro Formatio (Marayes-El Carrizal Basin), northwestern Argentina. PLoS One, 6, e26964.

BENSON, R. B. J. and RADLEY, J. D. 2010. A new large−bodied theropod dinosaur fro the Middle Jurassic of Warwickshire, United Kingdom. Acta Palaeontologic Polonica, 55, 35–42.

BRUSATTE, S. L., BENSON, R. B., CURRIE, P. J. and XIJIN, Z. 2010. The skull o Monolophosaurus jiangi (Dinosauria: Theropoda) and its implications for earl theropod phylogeny and evolution. Zoological Journal of the Linnean Society, 158 573-607.

CARRANO, M. T., BENSON, R. B. J. and SAMPSON, S. D. 2012. The phylogeny o Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology, 10, 211-300

FOTH, C. and RAUHUT, O. W. 2017. Re-evaluation of the Haarlem Archaeopteryx an the radiation of maniraptoran theropod dinosaurs. BMC Evolutionary Biology, 17 236.

GODEFROIT, P., CAU, A., DONG-YU, H., ESCUILLIÉ, F., WENHAO, W. and DYKE, G 2013a. A Jurassic avialan dinosaur from China resolves the early phylogenetic histor of birds. Nature, 498, 359.

GUO, X., XU, L. and JIA, S. 2018. Morphological and Phylogenetic study based on ne materials of Anchiornis huxleyi (dinosauria, theropoda) from Jianchang, Wester Liaoning, China. Acta Geologica Sinica, 92, 1-15.

HENDRICKX, C., HARTMAN, S. C. and MATEUS, O. 2015. An overview of non-avia theropod discoveries and classification. PalArch's Journal of Vertebrate Palaeontology, 12, 1-73.

HU, D., CLARKE, J. A., ELIASON, C. M., QIU, R., LI, Q., SHAWKEY, M. D., ZHAO, C. D'ALBA, L., JIANG, J. and XU, X. 2018. A bony-crested Jurassic dinosaur wit evidence of iridescent plumage highlights complexity in early paravian evolution Nature Communications, 9, 217.

LANGER, M. C., RINCÓN, A. D., RAMEZANI, J., SOLÓRZANO, A. and RAUHUT, O W. 2014. New dinosaur (Theropoda, stem-Averostra) from the earliest Jurassic of th La Quinta formation, Venezuelan Andes. Royal Society Open Science, 1, 140184.

LEFÈVRE, U., CAU, A., CINCOTTA, A., HU, D., CHINSAMY, A., ESCUILLIÉ, F. an GODEFROIT, P. 2017. A new Jurassic theropod from China documents a transitiona step in the macrostructure of feathers. The Science of Nature, 104, 74.

MARTILL, D. M., VIDOVIC, S. U., HOWELLS, C. and NUDDS, J. R. 2016. The oldes Jurassic dinosaur: a basal neotheropod from the Hettangian of Great Britain. PloS One 11, e0145713.

NESBITT, S. J. and EZCURRA, M. D. 2015. The early fossil record of dinosaurs in Nort America: A new neotheropod from the base of the Upper Triassic Dockum Group o Texas. Acta Palaeontologica Polonica, 60, 513-526.

NOVAS, F. E., EZCURRA, M. D., CHATTERJEE, S. and KUTTY, T. S. 2011. Ne dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmara formations of central India. Earth and Environmental Science Transactions of th Royal Society of Edinburgh, 101, 333-349.

O'CONNOR, J. K. and SULLIVAN, C. 2014. Reinterpretation of the Early Cretaceou maniraptoran (Dinosauria: Theropoda) Zhongornis haoae as a scansoriopterygid-lik non-avian, and morphological resemblances between scansoriopterygids and basa oviraptorosaurs. Vertebrata PalAsiatica, 52, 3-30.

RAUHUT, O. W. and POL, D. 2017. A theropod dinosaur from the Late Jurassic Cañadó Calcáreo Formation of Central Patagonia, and the evolution of the theropod tarsus Ameghiniana, 54, 539-566.

SKAWIŃSKI, T., ZIEGLER, M., CZEPIŃSKI, Ł., SZERMAŃSKI, M., TAŁANDA, M., SURMIK, D. and NIEDŹWIEDZKI, G. 2017. A re-evaluation of the historica 'dinosaur' remains from the Middle-Upper Triassic of Poland. Historical Biology, 29 442-472.

WANG, S., STIEGLER, J., AMIOT, R., WANG, X., DU, G. H., CLARK, J. M. and XU, X 2017. Extreme ontogenetic changes in a ceratosaurian theropod. Current Biology, 27 144-148.

XU, X. and ZHANG, F. 2005. A new maniraptoran dinosaur from China with lon feathers on the metatarsus. Naturwissenschaften, 92, 173-177.

XU, X., ZHAO, Q., NORELL, M., SULLIVAN, C., HONE, D., ERICKSON, G., WANG X., HAN, F. and GUO, Y. 2009. A new feathered maniraptoran dinosaur fossil that fill a morphological gap in avian origin. Chinese Science Bulletin, 54, 430-435.

XU, X., YOU, H., DU, K. and HAN, F. 2011. An Archaeopteryx-like theropod from Chin and the origin of Avialae. Nature, 475, 465.

XU, X., ZHENG, X., SULLIVAN, C., WANG, X., XING, L., WANG, Y., ZHANG, X. O'CONNOR, J. K., ZHANG, F. and PAN, Y. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. Nature, 521, 70.

ZHANG, F., ZHOU, Z., XU, X., WANG, X. and SULLIVAN, C. 2008. A bizarre Jurassi maniraptoran from China with elongate ribbon-like feathers. Nature, 455, 1105.

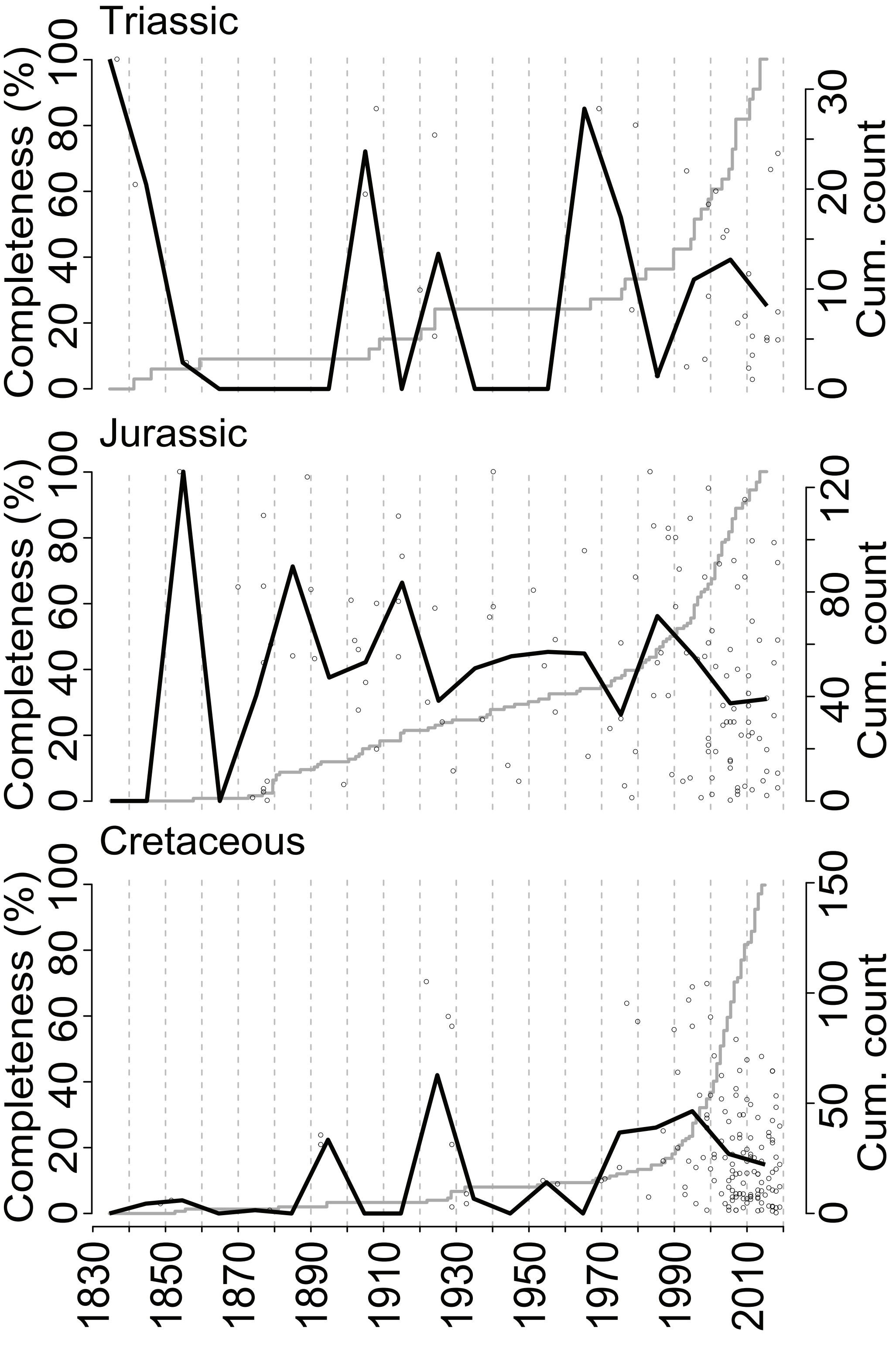


Figure B.1. Historical accumulation and completeness curves for sauropodomorph species for each Mesozoic geological Period. Black line, mean SCM2 score per 10 year bin; grey line, cumulative species count; circles, individual species' SCM2 score in relation to first publication date. Abbreviations: cum. count, cumulative species count.

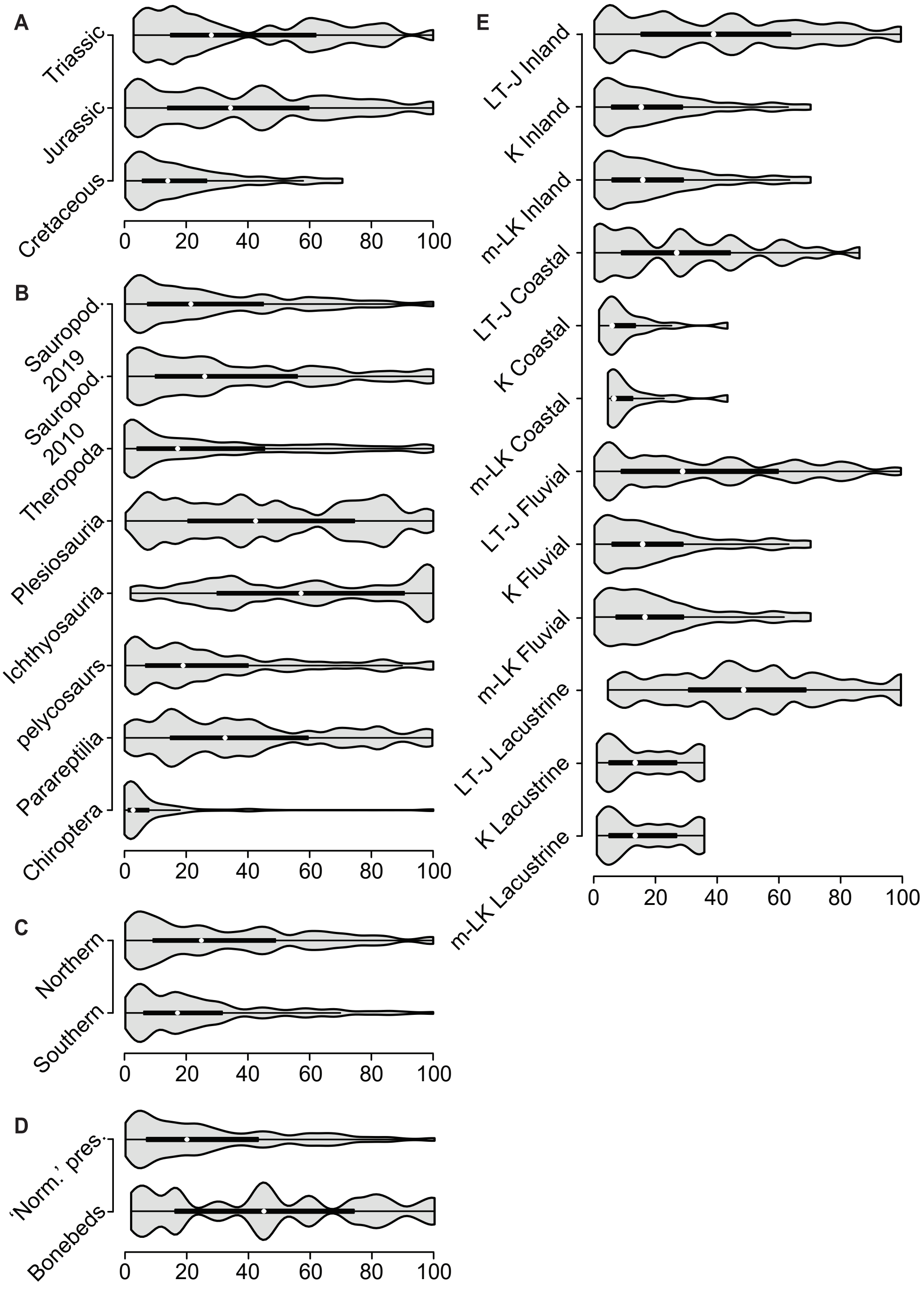


Figure B.2. Distribution of sauropodomorph SCM2 scores between different A, Mesozoic geological periods; B, tetrapod groups, including Mannion and Upchurch (2010a) sauropodomorph data; C, hemispheres; D, depositional regimes, and E, depositional settings of different time bins. Shaded polygon width represents the relative density of species. Abbreviations: Sauropod., Sauropodomorpha; LT, Late Triassic; J, Jurassic; K, Cretaceous; m-LK, 'middle'-Late Cretaceous. Note inland depositional settings includes both the fluvial and lacustrine terrestrial settings, as well as 'others' (aeolian, trap/fills).

Table B.1. Results of comparisons of the population median and distribution of completeness values using Mann-Whitney-Wilcoxon tests. Comparisons between the current sauropodomorph data set and, sauropodomorph data from Mannion and Upchurch (2010), theropods (Cashmore and Butler 2019), plesiosaurs (Tutin and Butler 2017), ichthyosaurs (Cleary *et al.* 2015), synapsid-grade pelycosaurs (Brocklehurst and Fröbisch 2014), parareptiles (Verrière *et al.* 2016), and bats (Brown *et al.* 2019). Statistically significant results indicated in bold. Abbreviations: LT, Late Triassic; J, Jurassic; K, Cretaceous; M&U (2010), Mannion and Upchurch (2010).

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Sauropod.	Sauropod. M&U (2010)	24102.5	0.075199075	0.097758798
LT-J Sauropod.	LT-J Sauropod. M&U (2010)	6877	0.326922929	0.386363462
K Sauropod. SCM2	K Sauropod. M&U (2010)	5346.5	0.065137914	0.094088098
Sauropod.	Theropoda	76375	**0.028394038**	0.052731785
LT Sauropod.	LT Theropoda	649	**0.016466221**	**0.035676812**
LT-J Sauropod.	LT-J Theropoda	11822	**0.004411559**	**0.011726167**
J Sauropod.	J Theropoda	7039.5	0.05202923	0.084547499
K Sauropod.	K Theropoda	23279	0.378850477	0.41042135
Sauropod.	Plesiosauria	11096	**7.87E-09**	**3.41E-08**
Sauropod.	Ichthyosauria	7616.5	**7.65E-15**	**4.97E-14**
Sauropod.	pelycosaurs	14884.5	0.881883669	0.881883669
Sauropod.	Parareptilia	9211.5	**0.004510064**	**0.011726167**
Sauropod.	Chiroptera	110657.5	**1.98E-49**	**2.58E-48**

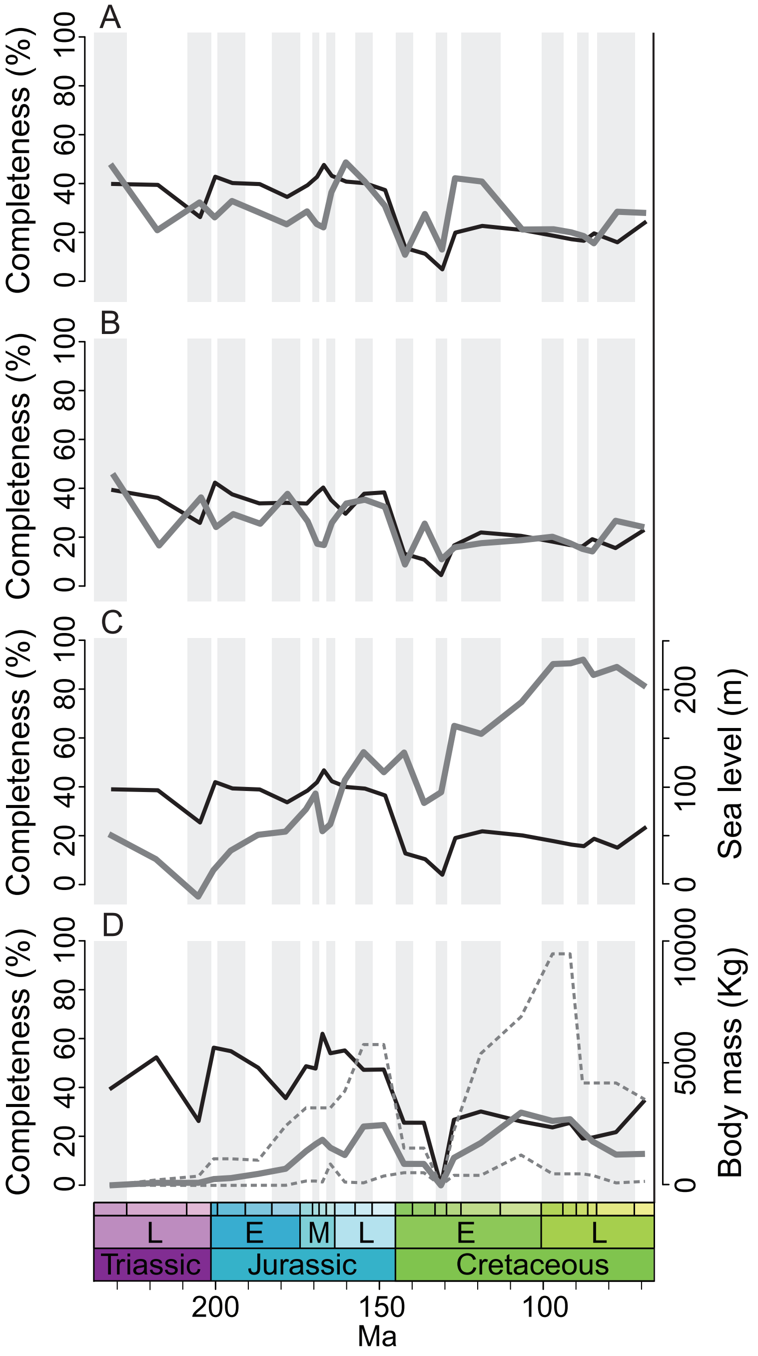


Figure B.3. Changes in mean sauropodomorph completeness through geological time from our current data set in comparison to A, Theropoda (Cashmore and Butler 2019); B, non-conservation Lagerstätten Theropoda (Cashmore and Butler 2019); C, sea level (Butler *et al.* 2010), and D, body mass estimates per stage. Black lines, mean sauropodomorph SCM2; grey lines, comparative variable; Note in D, dashed grey lines are maximum and minimum body mass estimates per stage, while grey line is the mean body mass estimates per stage.

Table B.2. Results of comparisons of the population median and distribution of sauropodomorph completeness values between different continents, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Africa	Asia	1694.5	0.335207394	0.541488868
Africa	Australasia	107	0.871540479	0.95869892
Africa	Europe	977	0.788987406	0.943877694
Africa	North America	690.5	**0.045317424**	0.118958237
Africa	South America	2099.5	0.649370278	0.852298489
Asia	Australasia	242	0.574597132	0.842029628
Asia	Europe	1994	0.234897121	0.411069962
Asia	North America	1454	0.159500262	0.334950551
Asia	South America	4373	5.40E-02	1.26E-01
Australasia	Europe	107	9.59E-01	9.59E-01
Australasia	North America	65.5	0.197606063	0.377247938
Australasia	South America	254	0.601449734	0.842029628
Europe	North America	618	**2.72E-02**	8.15E-02
Europe	South America	1918.5	0.809038023	0.943877694
North America	South America	2445.5	**0.001876903**	**0.007882994**

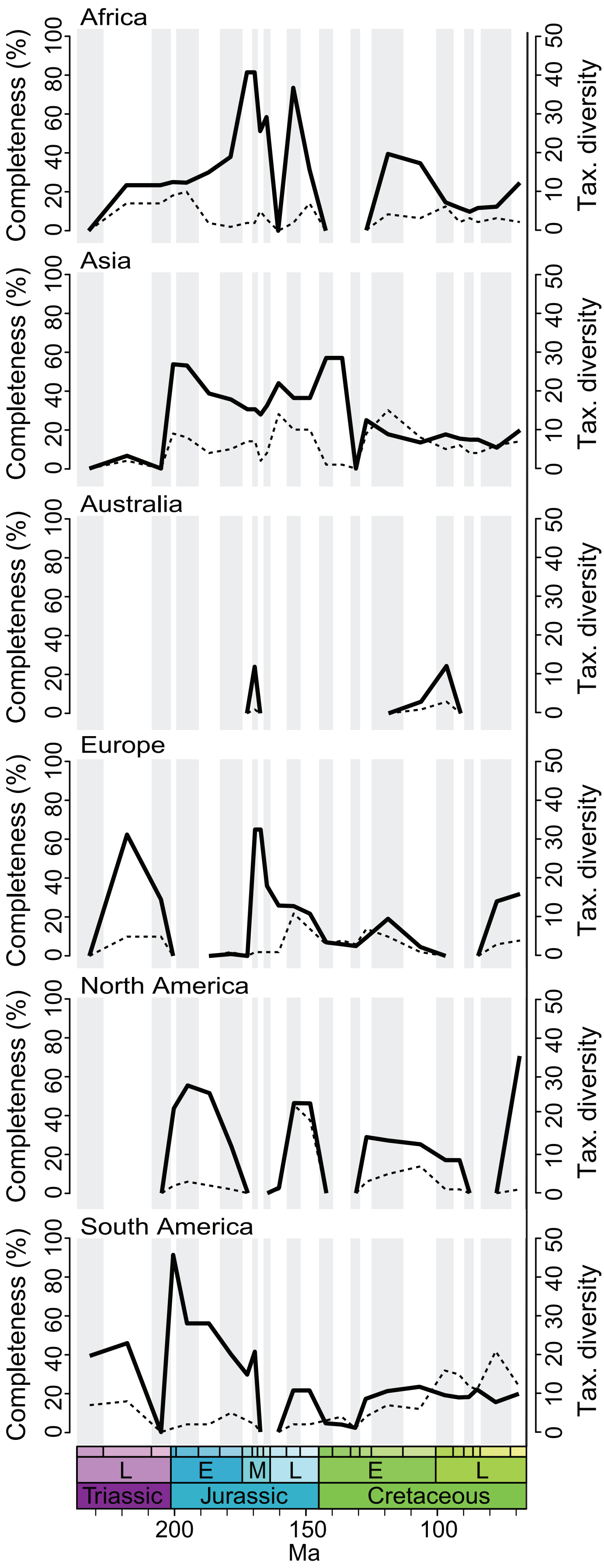


Figure B.4. Changes in mean sauropodomorph completeness and raw diversity through geological time from our current data set for each continent. Abbreviations, Tax. diversity, raw taxonomic diversity.

Table B.3. Presence/absence of valid sauropodomorph species per continent and geological stage. Abbreviations: AF, Africa, AS, Asia; AU, Australasia; EU, Europe; NA, North America; SA, South America; Carn., Carnian; Nor., Norian; Rhaet., Rhaetian; Hett., Hettangian; Sine., Sinemurian; Pliens., Pliensbachian; Toar., Toarcian; Aal., Aalenian; Bajo., Bajocian; Callo., Callovian; Oxf., Oxfordian; Kimm., Kimmeridgian; Tith., Tithonian; Berr, Berriasian; Val., Valanginian; Haut., Hauterivian; Barr., Barremian; Apt., Aptian; Alb., Albian; Ceno., Cenomanian; Turo., Turonian; Coni., Coniacian; Sant., Santonian; Camp., Campanian; Maas., Maastrichtian.

Stage	AF	AS	AU	EU	NA	SA	Total
Carn.	1	0	0	0	0	1	2
Nor.	1	1	0	1	0	1	4
Rhaet.	1	0	0	1	0	0	2
Hett.	1	1	0	0	1	1	4
Sine.	1	1	0	0	1	1	4
Pliens.	1	1	0	0	1	1	4
Toar.	1	1	0	1	1	1	5
Aal.	1	1	0	0	0	1	3
Bajo.	1	1	1	1	0	1	5
Bath.	1	1	0	1	0	0	3
Callo.	1	1	0	1	0	0	3
Oxf.	0	1	0	1	1	0	3
Kimm.	1	1	0	1	1	1	5
Tith.	1	1	0	1	1	1	5
Berr.	0	1	0	1	0	1	3
Val.	0	1	0	1	0	1	3
Haut.	0	0	0	1	0	1	2
Barr.	0	1	0	1	1	1	4
Apt.	1	1	0	1	1	1	5
Alb.	1	1	1	1	1	1	6
Ceno.	1	1	1	0	1	1	5
Turo.	1	1	0	0	1	1	4
Coni.	1	1	0	0	0	1	3
Sant.	1	1	0	0	0	1	3
Camp.	1	1	0	1	0	1	4
Maas.	1	1	0	1	1	1	5
Total	21	23	3	17	13	22	99
%	80.77	88.46	11.54	65.38	50	84.62	63.46

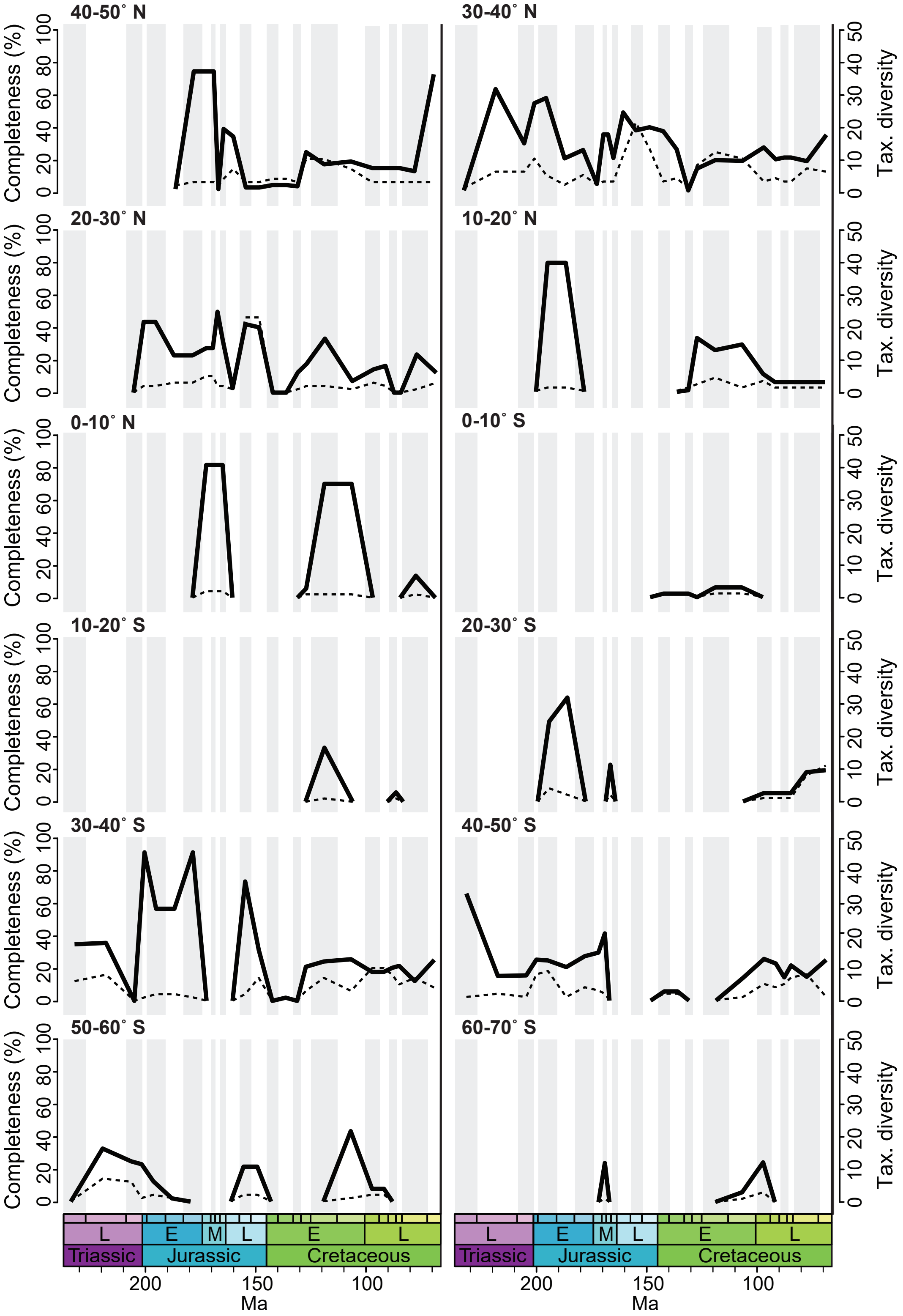


Figure B.5. Changes in mean sauropodomorph completeness and raw diversity through geological time from our current data set for each 10° paleolatitudinal bin. Abbreviations, Tax. diversity, raw taxonomic diversity.

Table B.4. Presence/absence of valid sauropodomorph species per 10° paleolatitudinal bin and geological stage. Abbreviations: Carn., Carnian; Nor., Norian; Rhaet., Rhaetian; Hett., Hettangian; Sine., Sinemurian; Pliens., Pliensbachian; Toar., Toarcian; Aal., Aalenian; Bajo., Bajocian; Callo., Callovian; Oxf., Oxfordian; Kimm., Kimmeridgian; Tith., Tithonian; Berr, Berriasian; Val., Valanginian; Haut., Hauterivian; Barr., Barremian; Apt., Aptian; Alb., Albian; Ceno., Cenomanian; Turo., Turonian; Coni., Coniacian; Sant., Santonian; Camp., Campanian; Maas., Maastrichtian.

Stage	50-60N	40-50N	30-40N	20-30N	10-20N	0-10N	0-10S	10-20S	20-30S	30-40S	40-50S	50-60S	60-70S	Total
Carn.	0	0	0	0	0	0	0	0	0	1	1	0	0	2
Nor.	0	0	1	0	0	0	0	0	0	1	1	1	0	4
Rhaet.	0	0	1	0	0	0	0	0	0	0	1	1	0	3
Hett.	0	0	1	1	0	0	0	0	0	1	1	1	0	5
Sine.	0	0	1	1	1	0	0	0	1	1	1	1	0	7
Pliens.	0	0	1	1	1	0	0	0	1	1	1	1	0	7
Toar.	0	1	1	1	0	0	0	0	0	1	1	0	0	5
Aal.	0	1	1	1	0	1	0	0	0	0	1	0	0	5
Bajo.	0	1	1	1	0	1	0	0	0	0	1	0	1	6
Bath.	0	0	1	1	0	1	0	0	1	0	0	0	0	4
Callo.	0	1	1	1	0	1	0	0	0	0	0	0	0	4
Oxf.	0	1	1	1	0	0	0	0	0	0	0	0	0	3
Kimm.	0	1	1	1	0	0	0	0	0	1	0	1	0	5
Tith.	0	1	1	1	0	0	0	0	0	1	0	1	0	5
Berr.	0	1	1	0	0	0	1	0	0	0	1	0	0	4
Val.	0	1	1	0	0	0	1	0	0	1	1	0	0	5
Haut.	0	1	0	1	1	0	1	0	0	0	0	0	0	4
Barr.	0	1	1	1	1	1	0	0	0	1	0	0	0	6
Apt.	0	1	1	1	1	1	1	1	0	1	0	0	0	8
Alb.	0	1	1	1	1	1	1	0	0	1	1	1	1	10
Ceno.	1	1	1	1	1	0	0	0	1	1	1	1	1	10
Turo.	0	1	1	1	1	0	0	0	1	1	1	1	0	8
Coni.	0	1	1	0	1	0	0	1	1	1	1	0	0	7
Sant.	0	1	1	0	1	0	0	0	1	1	1	0	0	6
Camp.	0	1	1	1	1	1	0	0	1	1	1	0	0	8
Maas.	0	1	1	1	1	0	0	0	1	1	1	0	0	7
Total	1	19	24	19	12	8	5	2	9	18	18	10	3	148
%	3.85	73.08	92.31	73.08	46.15	30.77	19.23	7.69	34.62	69.23	69.23	38.46	11.54	43.79

Table B.5. Results of comparisons of the population median and distribution of sauropodomorph completeness values between different depositional settings, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold. Abbreviations: terrest. Other, non-typical terrestrial deposits; LT, Late Triassic; J, Jurassic; K, Cretaceous; m-LK, 'middle'-Late Cretaceous.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
Fluvial	Lacustrine	4006	**0.000842671**	**0.00189601**
Fluvial	Coastal / Marine	5049	0.157547892	0.18905747
Fluvial	terrest. Other	568	0.378597023	0.400867437
Lacustrine	Coastal / Marine	1732	**0.000522732**	**0.001568197**
Lacustrine	terrest. Other	226.5	0.511695479	0.511695479
Coastal / Marine	terrest. Other	105	0.184252817	0.207284419
Inland	Coastal / Marine	6924.5	0.051595245	0.084428583
LT-J Inland	LT-J Coastal / Marine	1387	0.070326017	0.097374486
K Inland	K Coastal / Marine	818.5	5.96E-02	8.94E-02
m-LK Inland	m-LK Coastal / Marine	646	9.45E-02	1.22E-01
LT-J Fluvial	K Fluvial	6568.5	**0.000189558**	**0.00068241**
LT-J Fluvial	m-LK Fluvial	3379.5	**6.59E-04**	**1.69E-03**
LT-J Lacustrine	K Lacustrine	558.5	**1.58092E-05**	**7.11416E-05**
LT-J Lacustrine	m-LK Lacustrine	81.5	**1.58092E-05**	**7.11416E-05**
LT-J Coastal / Marine	K Coastal / Marine	330	**0.015911764**	**0.031823529**
LT-J Coastal / Marine	m-LK Coastal / Marine	109.5	**0.029817628**	0.053671731
LT-J Inland	K Inland	12600	**2.14339E-09**	**3.8581E-08**
LT-J Inland	m-LK Inland	4950	**1.24154E-08**	**1.11739E-07**

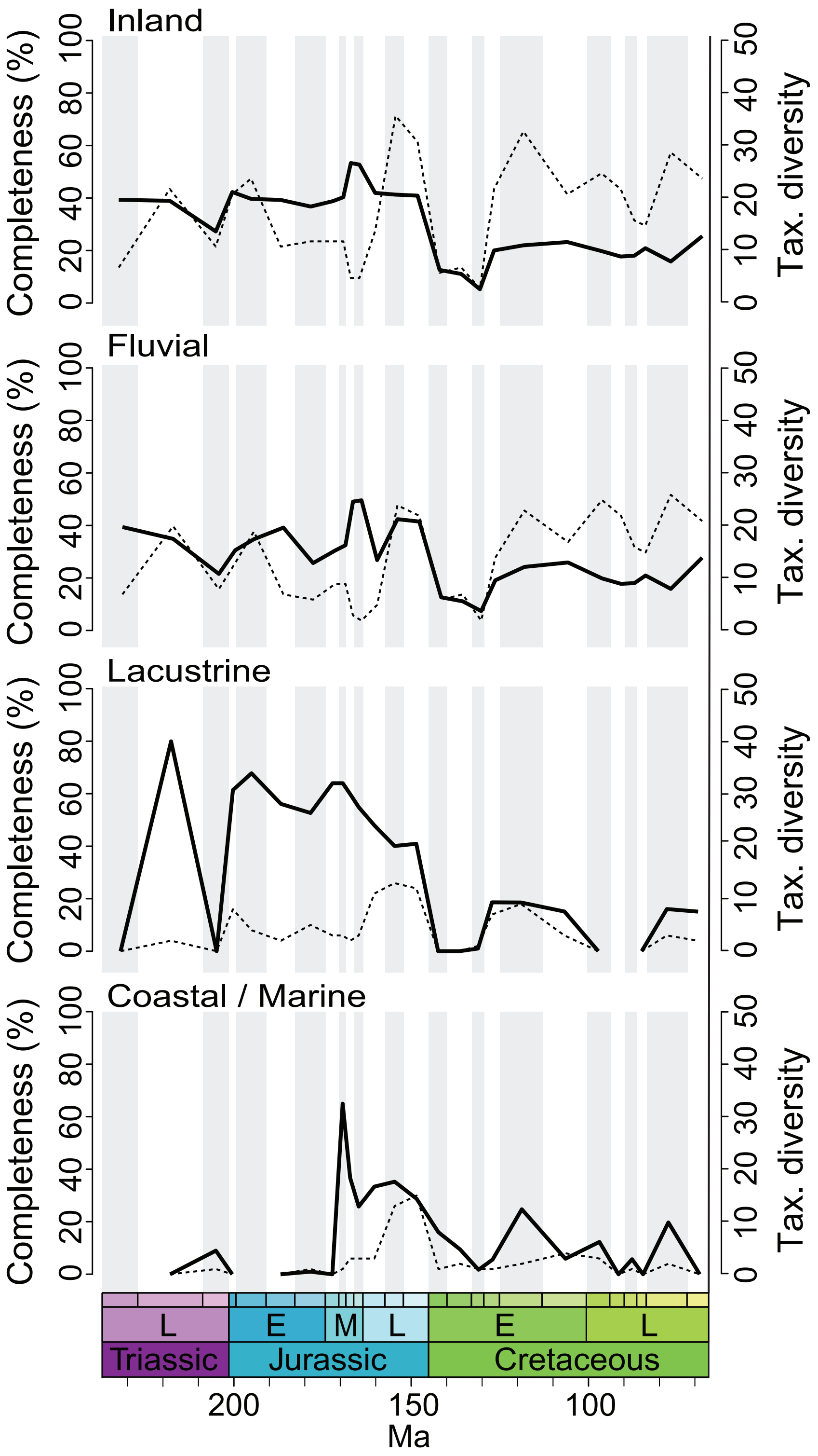


Figure B.6. Changes in mean sauropodomorph completeness and raw diversity through geological time from our current data set for each depositional setting. Abbreviations, Tax. diversity, raw taxonomic diversity. Note inland depositional settings includes both the fluvial and lacustrine terrestrial settings, as well as 'others' (aeolian, trap/fills).

Table B.6. Results of comparisons of the population median and distribution of completeness values between different sauropodomorph subgroups, using Mann-Whitney-Wilcoxon tests. Statistically significant results indicated in bold. Abbreviations: non-neo. Sauropoda, non-neosauropod Sauropoda; n-titano. macro., non-titanosaurian macronarians.

Dataset 1	Dataset 2	Test statistic (W)	p-value	p-value following FDR corrections
non-Sauropoda	non-neo. Sauropoda	2133	**0.064448196**	**0.118155026**
non-Sauropoda	Diplodocoidea	1703	**0.00642062**	**0.014125363**
non-Sauropoda	non-titano. macro.	2035.5	**0.001764632**	**0.006470317**
non-Sauropoda	Titanosauria	3262	**0.00000695**	**0.0000765**
non-neo. Sauropoda	Diplodocoidea	1794	0.229168972	0.280095411
non-neo. Sauropoda	non-titano. macro.	2194	0.075866243	0.119218382
non-neo. Sauropoda	Titanosauria	3531	**0.002487612**	**0.006840933**
Diplodocoidea	non-titano. macro.	1383.5	0.799239355	0.799239355
Diplodocoidea	Titanosauria	2257.5	2.06E-01	2.80E-01
non-titano. macro.	Titanosauria	2528.5	3.81E-01	4.19E-01

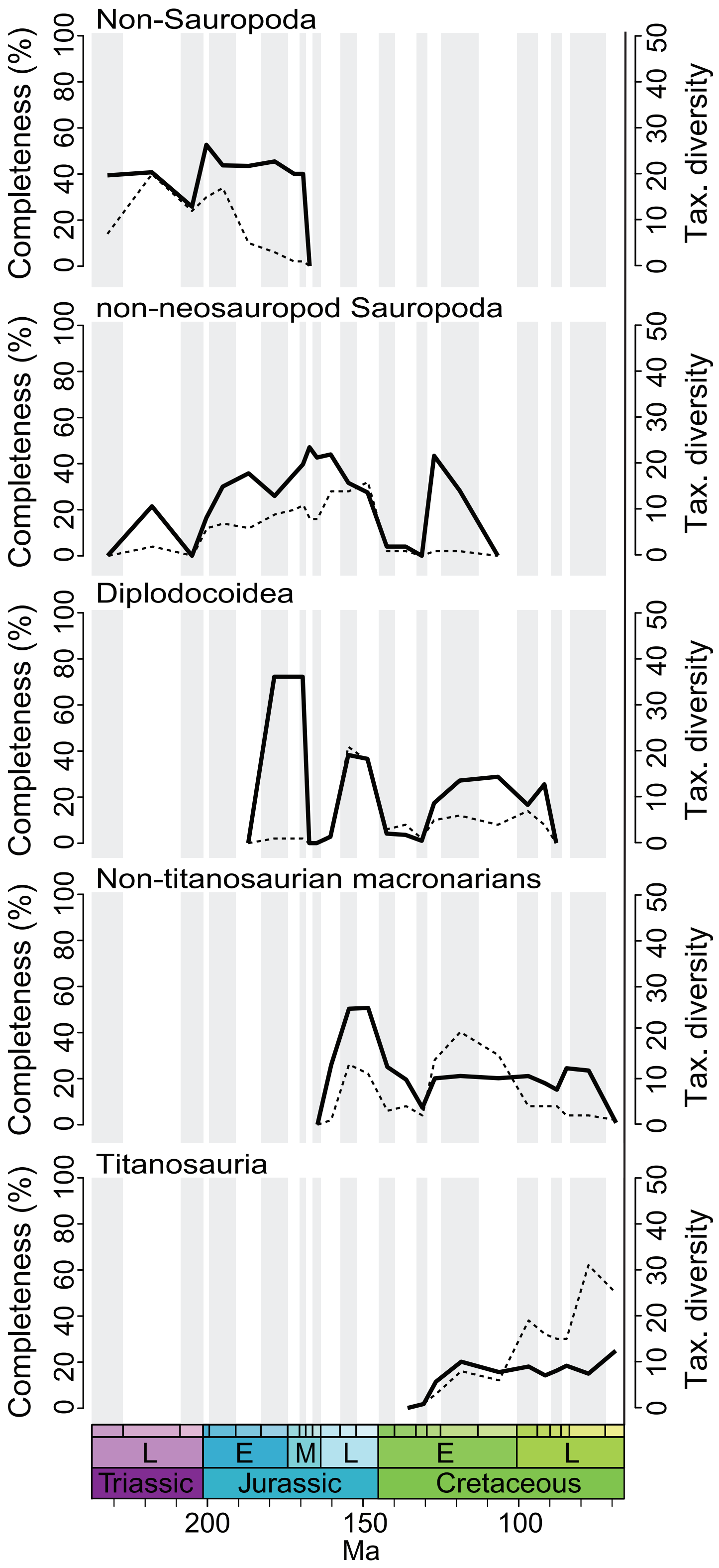
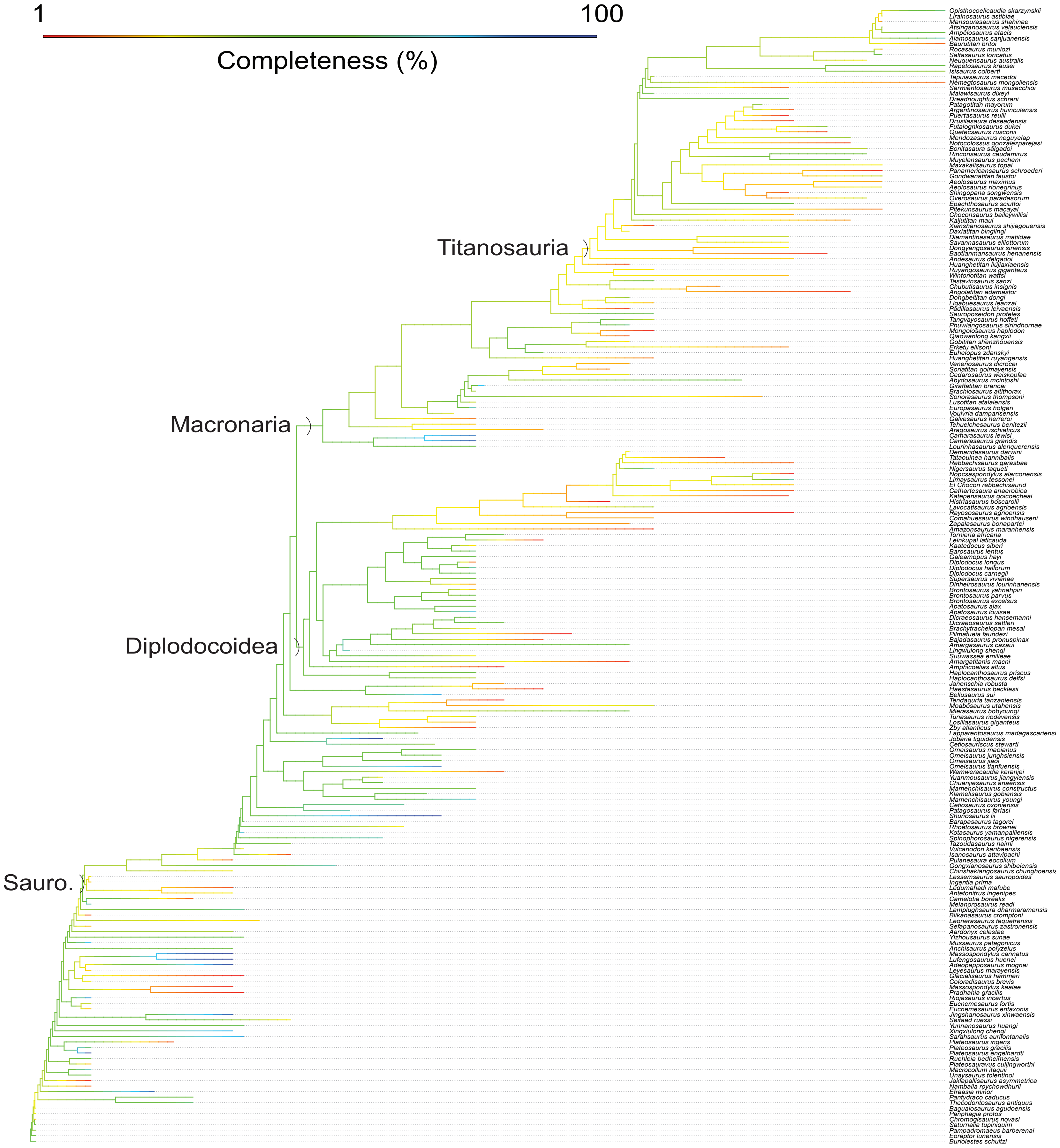


Figure B.7. Changes in mean completeness and raw diversity through geological time from our current data set for each major sauropodomorph subgroup. Abbreviations, Tax. diversity, raw taxonomic diversity.

Figure B.8. Informal supertree depicting sauropodomorph relationships in comparison to SCM2 scores, mapped as a continuous character, and displayed on a red-blue colour spectrum. Red represents low completeness and body size, while blue is high completeness and body size. Abbreviations: Sauro., Sauropoda.



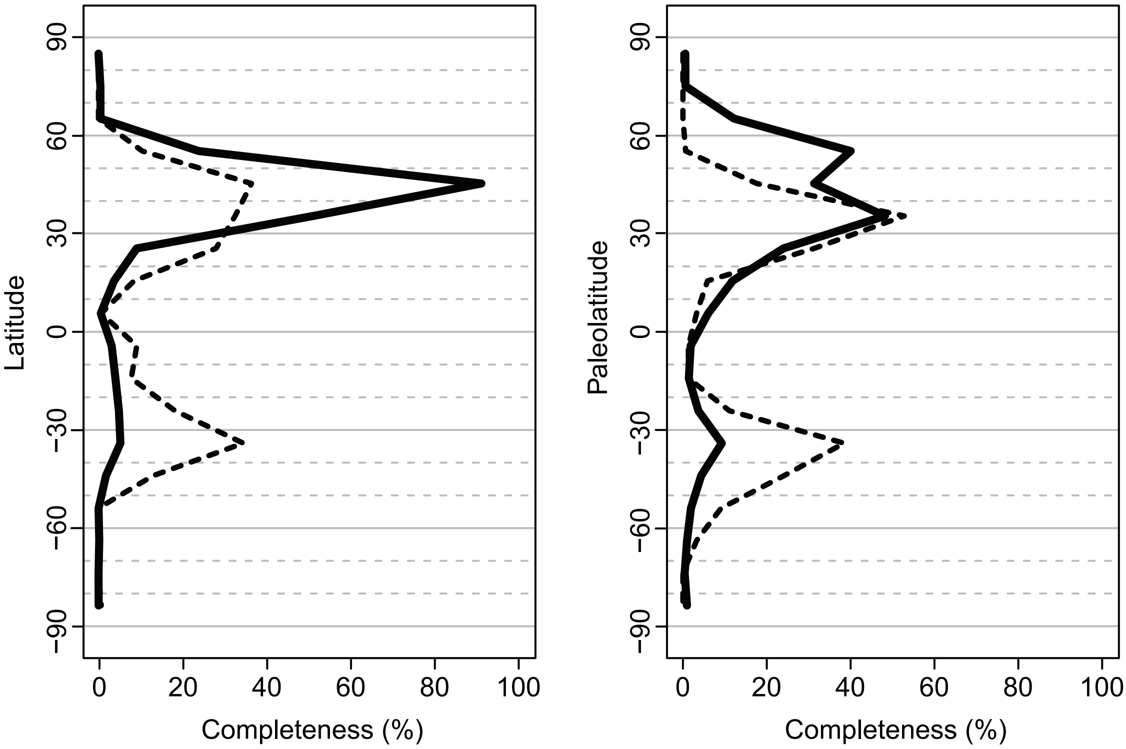


Figure B.9. Relative occurrences of all Carnian-Maastrichtian tetrapod body fossils (black line) and valid sauropodomorph species (dashed line) per modern latitude and paleolatitude.

Table C.1. Relative percentage of occurrences and assigned autapomorphies for each skeletal element per subgroup. 'O' and 'A' denote relative percentage of occurrences and assigned autapomorphies, respectively. Abbreviations: Thero., Theropoda; b.Thero., basal Theropoda; b.Neo., basal Neotheropoda; Cerato., Ceratosauria; b.Tet., basal Tetanurae; Megalo., Megalosauroidea; Allo., Allosauroidea; Megar., Megaraptora; b.Coeluro., basal Coelurosauria; Tyranno., Tyrannosauroidea; Comp., Compsognathidae; Ornitho., Ornithomimosauria; Theriz., Therizinosauria; Alvarez., Alvarezsauroidea; Ovirap., Oviraptorosauria; Dromaeo., Dromaeosauridae; Trood., Troodontidae; Paraves., non-avialan Paraves;

	Thero.		b.Thero.		b.Neo.		Cerato.		b.Tet.		Megalo.		Allo.		Megar.		b.Coeluro.		Tyranno.		Comp.		Ornitho.		Theriz.		Alvarez.		Ovirap.		Dromaeo.		Trood.		Paraves	
Element	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**
Premaxilla	1.7	2.8	1.1	4.5	2.1	4.0	1.8	1.4	1.5	9.3	2.2	4.5	1.4	1.4	0.6	0.0	2.6	2.9	1.9	4.0	1.8	4.1	1.4	1.6	0.4	0.0	0.4	0.0	1.8	5.2	1.5	2.0	1.7	2.0	1.8	2.9
Maxilla	2.2	5.4	2.0	4.5	2.6	9.3	2.0	3.3	2.4	0.0	3.9	8.2	3.0	10.4	1.7	0.0	1.9	1.4	3.0	13.9	1.8	0.0	1.5	3.3	0.9	4.4	1.1	0.0	1.6	2.1	2.0	6.1	2.6	9.9	1.8	8.8
Lacrimal	1.6	1.8	1.1	1.5	1.9	5.3	1.5	1.4	1.8	4.7	0.9	3.0	1.8	1.4	0.6	0.0	1.9	2.9	2.2	4.0	1.8	0.0	1.5	0.8	0.6	2.2	0.9	0.0	1.4	0.3	1.3	1.7	2.2	3.0	1.8	1.5
Nasal	1.5	1.7	1.4	0.0	1.9	1.3	1.4	3.3	1.5	4.7	0.9	2.2	1.7	2.8	0.6	0.0	1.1	0.0	2.0	4.6	1.8	0.0	1.4	0.0	0.9	2.2	0.7	0.0	1.6	1.8	1.1	0.7	1.9	2.0	1.8	1.5
Prefrontal	1.1	0.3	1.1	1.5	1.6	0.0	1.0	0.0	1.2	0.0	0.7	0.0	1.1	0.7	1.1	0.0	0.7	0.0	1.5	1.2	1.6	0.0	1.2	0.0	0.4	0.0	0.9	1.4	0.6	0.0	0.8	0.3	0.6	0.0	1.2	0.0
Frontal	1.9	2.4	0.8	0.0	1.9	0.0	2.1	4.7	1.8	2.3	1.1	0.0	1.9	6.9	1.1	0.0	1.9	0.0	2.0	4.0	1.6	2.0	1.9	0.0	2.1	2.2	1.6	2.2	1.6	1.2	1.9	2.7	3.3	4.0	1.9	0.0
Parietal	1.5	1.2	0.8	0.0	1.8	1.3	1.7	1.9	1.5	0.0	0.9	0.7	1.7	0.0	0.6	0.0	1.1	0.0	1.9	4.0	1.6	2.0	1.4	1.6	0.6	2.2	1.1	0.0	1.5	1.5	1.1	0.3	2.1	2.0	1.8	0.0
Postorbital	1.6	1.6	1.1	1.5	1.8	0.0	1.6	3.3	1.5	0.0	1.1	0.7	2.0	5.6	1.7	0.0	2.2	2.9	2.1	1.7	1.8	2.0	1.4	0.8	0.9	0.0	0.9	0.7	1.7	0.9	1.3	1.0	1.4	2.0	1.6	1.5
Squamosal	1.4	0.6	1.1	1.5	1.7	0.0	1.4	0.0	1.2	2.3	0.8	0.7	1.0	0.7	0.0	0.0	1.9	0.0	1.9	1.7	1.6	2.0	1.3	0.0	0.4	0.0	1.1	0.0	1.4	0.6	1.3	0.7	1.3	0.0	1.5	0.0
Jugal	1.5	1.3	1.4	4.5	1.8	1.3	1.4	0.9	1.5	0.0	1.2	0.7	1.5	1.4	0.0	0.0	1.5	0.0	2.3	2.9	1.8	0.0	1.3	0.8	0.4	1.1	0.9	0.7	1.4	1.2	1.2	2.0	1.9	2.0	1.6	0.0
Quadratojugal	1.4	1.0	1.4	1.5	1.6	0.0	1.1	0.9	1.2	0.0	0.7	0.7	1.3	2.1	0.6	0.0	1.9	2.9	2.0	0.6	1.6	0.0	1.3	2.4	0.2	0.0	0.4	0.0	1.6	1.5	1.2	1.0	1.3	0.0	1.4	0.0
Quadrate	1.6	1.0	1.4	0.0	1.8	1.3	1.5	0.9	1.2	0.0	1.9	0.7	1.6	0.7	1.1	0.0	1.9	2.9	2.0	0.0	1.6	0.0	1.5	0.8	0.6	1.1	1.1	0.7	1.8	2.1	1.2	1.0	1.7	0.0	1.5	0.0
Vomer	0.8	0.0	0.6	0.0	1.0	0.0	0.5	0.0	0.9	0.0	0.6	0.0	0.6	0.0	0.0	0.0	0.7	0.0	0.9	0.0	1.5	0.0	0.6	0.0	0.2	0.0	0.2	0.0	0.7	0.0	0.8	0.0	1.3	0.0	1.2	0.0
Palatine	1.1	0.4	0.6	0.0	1.3	0.0	0.8	0.0	0.9	0.0	0.4	0.0	0.9	0.7	0.0	0.0	1.1	0.0	1.6	3.5	1.5	0.0	0.9	0.8	0.4	0.0	0.7	0.0	1.0	0.0	1.0	0.3	1.4	0.0	1.3	0.0
Pterygoid	1.1	0.2	0.6	0.0	1.3	0.0	0.8	0.0	0.9	0.0	0.4	0.0	1.1	0.0	1.1	0.0	1.5	0.0	1.4	0.0	1.3	0.0	0.8	0.0	0.4	0.0	0.2	0.0	1.3	0.9	1.2	0.0	1.0	1.0	1.3	0.0
Ectopterygoid	1.1	0.3	0.3	0.0	1.3	0.0	0.8	0.0	1.2	0.0	0.4	1.5	1.1	0.0	0.6	0.0	1.5	0.0	1.5	1.2	1.3	0.0	0.9	0.0	0.4	0.0	0.2	0.0	1.1	0.3	1.2	0.0	1.1	1.0	1.4	0.0
Supraoccipital	1.3	0.3	0.8	0.0	1.4	0.0	1.3	0.0	1.5	0.0	0.8	0.0	1.7	1.4	1.1	0.0	0.7	0.0	1.6	0.6	1.5	0.0	1.2	0.8	1.5	1.1	0.7	0.0	1.4	0.3	1.0	0.0	1.6	0.0	1.4	0.0
Otoccipital	1.4	0.5	1.1	1.5	1.4	0.0	1.5	1.4	1.5	0.0	1.1	0.0	1.7	0.7	1.1	0.0	0.7	0.0	1.6	0.0	1.5	0.0	1.2	0.8	1.5	0.0	1.3	0.7	1.6	0.6	1.2	0.7	1.8	0.0	1.3	0.0
Laterosphenoid	1.2	0.2	0.8	0.0	1.2	0.0	1.3	0.0	1.5	0.0	1.1	0.0	1.6	1.4	0.6	0.0	1.1	0.0	1.6	0.0	1.5	0.0	0.9	0.0	1.1	0.0	0.4	0.0	1.1	0.3	1.0	0.0	1.4	0.0	1.3	0.0
Prootic	1.2	0.3	0.8	1.5	1.2	0.0	1.2	0.0	1.5	0.0	0.9	0.0	1.4	0.7	1.1	0.0	0.7	0.0	1.5	0.6	1.5	0.0	0.9	0.0	1.5	0.0	0.4	0.0	1.0	0.3	1.0	0.7	1.4	0.0	1.3	0.0
Basioccipital	1.4	0.7	1.1	1.5	1.5	0.0	1.5	0.9	1.5	0.0	1.1	0.7	1.6	0.0	1.1	0.0	0.7	0.0	1.7	0.6	1.5	0.0	1.1	0.0	1.5	0.0	1.6	2.9	1.5	1.8	1.1	0.0	1.6	0.0	1.5	0.0
Parabasisphenoid	1.4	0.9	1.1	1.5	1.4	1.3	1.5	1.4	1.5	0.0	1.1	0.0	1.6	0.7	1.1	0.0	1.1	0.0	1.6	0.6	1.5	0.0	1.2	0.8	1.3	1.1	1.1	2.2	1.3	0.6	1.1	1.0	1.7	1.0	1.4	0.0
Dentary	2.2	4.1	1.7	3.0	2.0	0.0	1.5	2.3	1.8	2.3	3.4	7.5	1.9	2.8	1.7	0.0	1.9	4.3	2.8	1.7	1.8	0.0	1.4	1.6	2.6	3.3	1.6	1.4	2.5	12.8	2.1	1.7	2.8	2.0	2.0	4.4
Splenial	1.3	0.1	1.1	0.0	1.4	0.0	1.2	0.0	0.9	0.0	0.5	0.7	0.9	0.0	0.0	0.0	1.1	0.0	1.7	1.2	1.6	0.0	1.0	0.0	0.6	0.0	1.1	0.0	1.1	0.0	1.5	0.0	1.4	0.0	1.8	0.0
Coronoid	1.0	0.1	0.6	0.0	1.3	0.0	0.9	0.0	0.9	0.0	0.2	0.0	0.6	0.0	0.6	0.0	0.4	0.0	1.3	0.0	1.5	0.0	0.8	0.0	0.2	1.1	0.0	0.0	0.9	0.6	0.9	0.0	0.8	0.0	1.6	0.0
Prearticular	1.2	0.0	1.1	0.0	1.5	0.0	1.2	0.0	0.9	0.0	0.5	0.0	1.0	0.0	1.1	0.0	0.7	0.0	1.6	0.0	1.5	0.0	1.0	0.0	0.4	0.0	0.4	0.0	1.3	0.0	1.3	0.0	1.1	0.0	1.6	0.0
Surangular	1.5	1.3	1.7	1.5	1.5	0.0	1.0	0.0	1.2	0.0	0.7	0.0	1.3	1.4	0.6	0.0	1.1	1.4	2.3	2.9	1.6	0.0	1.3	0.0	0.9	0.0	1.1	0.7	2.0	3.0	1.3	0.3	1.8	4.0	2.0	2.9
Angular	1.4	0.4	1.7	0.0	1.6	0.0	1.0	0.5	1.2	0.0	0.8	0.0	1.0	0.0	0.6	0.0	1.5	0.0	1.7	0.6	1.6	0.0	1.3	0.0	0.6	0.0	0.9	0.0	1.8	2.1	1.4	0.0	1.4	0.0	2.0	0.0
Articular	1.3	0.6	1.7	0.0	1.5	4.0	0.9	0.0	1.2	0.0	0.4	0.0	1.1	0.7	0.6	0.0	1.5	2.9	1.9	0.6	1.5	0.0	1.1	0.0	0.4	0.0	1.1	0.0	1.6	1.8	1.3	0.0	0.8	0.0	1.5	1.5
Dentition	1.8	4.6	2.0	9.1	2.0	5.3	2.0	3.8	2.4	2.3	3.6	3.0	2.1	0.7	1.1	0.0	2.2	12.9	2.3	5.8	1.8	6.1	0.2	2.4	1.7	7.8	0.4	2.2	0.2	2.4	2.4	7.4	2.4	5.9	1.8	4.4
Cervical vertebrae	2.5	5.4	3.1	3.0	2.5	5.3	3.4	15.5	2.4	2.3	5.3	9.7	2.8	6.9	3.4	0.0	3.0	11.4	2.1	4.0	2.1	6.1	2.3	0.8	4.5	3.3	2.7	8.0	2.2	2.7	2.2	3.4	1.5	2.0	2.0	0.0
Dorsal vertebrae	3.0	4.6	3.1	3.0	2.7	5.3	4.2	3.3	4.2	0.0	7.4	16.4	3.5	11.8	2.8	47.4	2.6	4.3	2.4	0.0	2.5	4.1	2.7	4.1	4.5	5.6	3.3	5.8	2.1	1.8	2.6	2.7	2.3	0.0	2.0	0.0
Sacral vertebrae	2.0	2.2	2.5	0.0	2.4	2.7	2.4	1.4	1.2	0.0	2.5	4.5	2.6	1.4	3.4	36.8	2.2	5.7	1.4	0.6	1.9	2.0	2.1	1.6	2.8	1.1	2.9	2.9	1.7	1.5	1.9	2.4	2.1	1.0	1.5	0.0
Caudal vertebrae	3.3	4.4	3.7	0.0	2.3	4.0	5.3	3.8	3.3	4.7	5.4	2.2	3.7	6.9	3.9	0.0	4.4	11.4	2.5	0.6	2.4	6.1	4.6	6.5	4.5	4.4	3.8	5.8	2.2	4.6	3.0	4.4	2.9	1.0	1.9	5.9
Chevrons	1.7	0.7	1.7	0.0	0.9	1.3	1.9	1.4	1.2	0.0	1.5	0.0	2.6	0.0	2.2	0.0	1.1	0.0	1.5	0.0	1.8	0.0	2.0	0.0	1.1	2.2	1.6	0.0	1.4	0.6	2.2	1.0	1.8	3.0	1.5	1.5
Cervical ribs	1.3	0.2	1.1	0.0	1.5	1.3	1.4	0.0	0.9	2.3	1.2	0.7	1.3	0.7	1.1	0.0	0.4	0.0	1.2	0.0	1.5	0.0	1.2	0.0	1.9	0.0	0.7	0.0	1.4	0.3	1.3	0.0	1.1	0.0	1.3	0.0
Dorsal ribs	2.0	0.1	1.4	0.0	1.3	0.0	2.0	0.0	1.8	0.0	4.0	0.0	1.9	0.0	3.4	0.0	1.1	0.0	2.0	0.6	1.8	0.0	2.2	0.0	2.1	0.0	1.6	0.0	1.9	0.3	1.9	0.0	1.4	1.0	2.2	0.0
Sternal ribs	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Gastralia	1.0	0.0	0.8	0.0	0.7	0.0	0.4	0.0	0.3	0.0	1.3	0.0	0.8	0.0	2.8	0.0	0.4	0.0	1.0	0.0	1.8	0.0	1.2	0.0	0.9	0.0	0.4	0.0	1.0	0.0	1.5	0.0	1.0	0.0	1.5	0.0
Furcula	0.6	0.3	0.3	0.0	0.5	0.0	0.4	0.0	0.3	0.0	0.1	0.0	0.2	0.0	0.6	0.0	0.0	0.0	0.3	0.0	0.7	0.0	0.1	0.8	1.1	0.0	0.0	0.0	1.2	0.0	1.0	1.7	0.8	1.0	1.6	0.0
Scapula	1.9	1.7	2.3	3.0	1.7	1.3	1.9	2.3	2.1	0.0	2.3	1.5	1.9	0.0	1.7	0.0	1.9	0.0	1.7	1.2	1.6	0.0	2.2	2.4	3.0	1.1	2.7	3.6	2.0	2.1	1.9	2.4	1.4	0.0	2.2	1.5
Coracoid	1.7	1.3	2.0	0.0	1.5	0.0	1.6	0.9	1.8	2.3	1.9	0.7	1.2	0.0	2.2	0.0	1.5	0.0	1.4	1.2	1.6	0.0	1.9	2.4	2.4	0.0	2.7	2.2	1.8	0.9	1.7	2.4	1.3	0.0	2.1	8.8
Sternal plate	0.3	0.1	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.9	0.0	1.0	0.6	1.3	0.3	0.1	0.0	0.1	0.0
Humerus	2.0	2.9	1.7	4.5	1.6	1.3	1.7	1.9	2.7	0.0	1.9	1.5	1.4	4.2	4.5	0.0	3.0	1.4	1.4	1.7	2.4	4.1	2.4	1.6	4.3	4.4	2.2	5.1	2.1	3.0	2.4	4.1	1.5	1.0	2.2	7.4
Ulna	1.6	1.4	1.7	3.0	1.4	0.0	0.9	1.4	1.8	0.0	0.9	1.5	0.9	0.7	3.9	0.0	2.6	0.0	1.0	0.0	1.8	4.1	2.2	0.0	2.4	0.0	1.8	0.7	2.0	1.2	2.1	2.7	1.8	1.0	2.2	4.4
Radius	1.6	0.6	1.7	0.0	1.5	0.0	1.1	0.9	1.5	0.0	0.7	2.2	1.0	0.0	1.1	0.0	2.2	0.0	0.9	0.0	1.8	0.0	1.9	0.8	2.4	1.1	1.1	0.0	2.1	0.9	2.2	0.3	1.8	1.0	2.2	1.5
Carpals	0.9	0.6	0.8	7.6	0.7	0.0	0.1	0.5	0.6	0.0	0.2	0.0	0.6	0.0	1.1	0.0	1.1	0.0	0.5	0.6	1.3	4.1	1.1	0.0	1.1	0.0	1.6	0.0	1.3	0.6	1.5	0.7	1.3	0.0	2.0	1.5
Metacarpals	1.8	3.2	1.7	0.0	1.2	0.0	1.2	5.2	2.1	0.0	1.4	0.0	1.2	0.7	2.2	0.0	2.6	1.4	1.1	1.2	1.8	10.2	2.4	8.1	3.0	3.3	2.4	3.6	2.2	4.6	2.2	3.0	1.8	3.0	2.2	4.4
Manual digits	1.9	4.3	1.7	0.0	1.2	0.0	1.0	3.3	1.8	4.7	1.5	0.0	1.5	0.7	4.5	0.0	3.0	2.9	1.2	1.7	1.6	22.4	2.5	8.9	4.5	8.9	2.2	4.3	2.2	5.2	2.7	2.7	1.7	5.9	2.2	11.8
Ilium	2.5	4.1	4.0	3.0	2.8	1.3	2.5	1.9	3.6	7.0	4.0	6.0	2.6	6.3	3.4	15.8	1.5	1.4	2.0	4.6	2.4	6.1	2.1	4.9	3.4	8.9	3.8	5.1	2.4	3.7	2.1	2.7	1.7	2.0	1.7	4.4
Pubis	2.4	3.6	2.8	9.1	3.1	2.7	2.7	3.8	3.3	7.0	2.8	1.5	2.9	1.4	3.4	0.0	3.3	4.3	1.8	1.7	1.9	2.0	2.8	5.7	2.4	8.9	3.1	1.4	2.2	2.1	1.9	6.4	1.7	4.0	1.7	0.0
Ischium	2.1	2.7	2.3	1.5	2.7	2.7	1.7	1.9	2.7	2.3	2.6	3.7	3.1	2.1	1.7	0.0	0.7	1.4	1.9	2.3	2.1	2.0	2.5	1.6	3.0	8.9	2.4	2.2	1.8	1.8	1.7	3.0	1.7	5.0	1.8	2.9
Femur	3.1	3.8	6.2	6.1	3.4	0.0	3.6	1.9	3.0	16.3	3.6	3.0	3.5	4.9	10.6	0.0	2.6	1.4	2.4	4.0	2.4	6.1	3.6	4.1	3.6	1.1	5.1	2.9	2.6	6.1	2.5	3.4	2.4	3.0	2.1	0.0
Tibia	3.2	3.5	4.0	7.6	3.6	14.7	4.5	6.1	3.9	2.3	3.3	2.2	2.9	2.1	3.9	0.0	3.3	4.3	2.4	1.2	3.0	0.0	3.5	2.4	3.4	0.0	5.3	10.1	3.3	1.5	2.5	2.0	2.3	5.9	2.3	0.0
Fibula	2.3	1.2	3.1	1.5	3.0	1.3	2.8	2.3	3.0	0.0	2.0	1.5	2.4	1.4	1.7	0.0	3.0	1.4	2.0	1.2	1.9	0.0	2.9	0.8	1.7	1.1	2.9	1.4	2.0	0.6	1.9	0.7	2.1	0.0	1.6	2.9
Astragalus	1.9	2.0	3.1	4.5	1.9	8.0	2.0	0.5	2.4	9.3	1.1	1.5	1.2	0.7	2.2	0.0	3.3	7.1	1.7	2.3	1.3	0.0	2.5	2.4	1.3	0.0	3.6	2.9	2.1	0.9	1.9	0.7	2.1	5.0	1.5	0.0
Calcaneum	1.5	0.6	2.5	0.0	1.8	4.0	1.7	0.0	1.5	2.3	0.9	0.0	0.9	1.4	0.6	0.0	1.9	0.0	1.1	0.6	1.2	0.0	1.7	0.8	0.4	0.0	2.7	0.0	1.7	0.6	1.8	1.0	1.7	0.0	1.3	1.5
Distal tarsals	0.8	0.6	1.4	0.0	0.7	5.3	0.7	0.0	0.9	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.7	0.0	0.7	0.0	1.3	0.0	0.8	0.8	1.1	0.0	1.8	0.7	1.2	1.2	1.3	1.0	1.0	0.0	0.8	0.0
Metatarsals	3.1	5.4	2.8	1.5	1.8	2.7	3.3	6.1	2.4	7.0	3.9	1.5	3.5	0.7	2.2	0.0	3.0	2.9	2.6	4.0	2.1	2.0	4.0	10.6	3.0	4.4	4.9	10.9	4.0	3.0	2.9	9.5	3.8	9.9	2.3	4.4
Pedal digits	3.0	2.3	2.0	0.0	1.5	0.0	4.0	1.4	2.4	2.3	2.1	2.2	4.4	0.0	2.2	0.0	2.6	0.0	2.2	2.3	1.8	0.0	3.8	8.1	4.3	1.1	5.3	4.3	2.6	0.6	4.5	3.7	3.0	3.0	2.1	5.9
Total no. bones	60	56	58	29	59	27	60	38	58	21	59	34	59	39	52	3	58	25	60	43	58	20	60	36	58	29	57	31	60	52	60	45	59	33	59	25
% total	100	93	97	48	98	45	100	63	97	35	98	57	98	65	87	5	97	42	100	72	97	33	100	60	97	48	95	52	100	87	100	75	98	55	98	42

Table C.2. LoD1 scores for each skeletal element per subgroup (proportioned per subgroup), representing the percentage likelihood of diagnosing a valid species of the subgroup from each element. Abbreviations: Thero., Theropoda; b.Thero., basal Theropoda; b.Neo., basal Neotheropoda; Cerato., Ceratosauria; b.Tet., basal Tetanurae; Megalo., Megalosauroidea; Allo., Allosauroidea; Megar., Megaraptora; b.Coeluro., basal Coelurosauria; Tyranno., Tyrannosauroidea; Comp., Compsognathidae; Ornitho., Ornithomimosauria; Theriz., Therizinosauria; Alvarez., Alvarezsauroidea; Ovirap., Oviraptorosauria; Dromaeo., Dromaeosauridae; Trood., Troodontidae; Paraves., non-avialan Paraves.

Element	Thero.	b.Thero.	b.Neo.	Cerato.	b.Tet.	Megalo.	Allo.	Megar.	b.Coeluro.	Tyranno.	Comp.	Ornitho.	Theriz.	Alvarez.	Ovirap.	Dromaeo.	Trood.	Paraves
Premaxilla	2.1	3.7	3.1	1.0	6.7	3.2	1.0	0.0	2.1	3.4	3.2	1.2	0.0	0.0	4.2	1.5	1.5	2.4
Maxilla	5.5	5.0	9.6	3.3	0.0	8.0	10.4	0.0	1.4	15.6	0.0	3.1	4.5	0.0	2.3	6.2	10.3	9.5
Lacrimal	1.3	1.2	4.0	1.0	3.3	2.1	1.0	0.0	2.1	3.3	0.0	0.6	1.6	0.0	0.2	1.3	2.2	1.2
Nasal	1.2	0.0	0.9	2.3	3.1	1.5	1.9	0.0	0.0	3.6	0.0	0.0	1.6	0.0	1.4	0.5	1.4	1.1
Prefrontal	0.2	0.8	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.6	0.0	0.0	0.0	0.7	0.0	0.2	0.0	0.0
Frontal	2.1	0.0	0.0	3.9	1.9	0.0	5.8	0.0	0.0	3.8	1.8	0.0	1.9	1.7	1.1	2.3	3.4	0.0
Parietal	0.8	0.0	0.9	1.3	0.0	0.5	0.0	0.0	0.0	3.1	1.5	1.1	1.5	0.0	1.1	0.2	1.4	0.0
Postorbital	1.2	1.2	0.0	2.4	0.0	0.5	4.0	0.0	2.1	1.4	1.6	0.6	0.0	0.5	0.7	0.8	1.5	1.2
Squamosal	0.4	1.0	0.0	0.0	1.4	0.4	0.4	0.0	0.0	1.2	1.3	0.0	0.0	0.0	0.4	0.4	0.0	0.0
Jugal	0.9	3.4	0.9	0.6	0.0	0.5	1.0	0.0	0.0	2.2	0.0	0.5	0.8	0.5	0.9	1.4	1.4	0.0
Quadratojugal	0.6	1.0	0.0	0.6	0.0	0.5	1.3	0.0	1.8	0.4	0.0	1.5	0.0	0.0	1.0	0.6	0.0	0.0
Quadrate	0.7	0.0	1.0	0.7	0.0	0.5	0.5	0.0	2.0	0.0	0.0	0.6	0.8	0.5	1.7	0.7	0.0	0.0
Vomer	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Palatine	0.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	1.9	0.0	0.4	0.0	0.0	0.0	0.2	0.0	0.0
Pterygoid	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	0.0
Ectopterygoid	0.1	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.2	0.0	0.5	0.0
Supraoccipital	0.2	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.4	0.0	0.5	0.7	0.0	0.2	0.0	0.0	0.0
Otoccipital	0.3	1.1	0.0	0.9	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.5	0.0	0.4	0.4	0.4	0.0	0.0
Laterosphenoid	0.1	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Prootic	0.1	0.9	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0
Basioccipital	0.4	1.0	0.0	0.6	0.0	0.5	0.0	0.0	0.0	0.4	0.0	0.0	0.0	1.7	1.3	0.0	0.0	0.0
Parabasisphenoid	0.6	1.0	0.8	0.9	0.0	0.0	0.4	0.0	0.0	0.4	0.0	0.5	0.7	1.2	0.4	0.6	0.6	0.0
Dentary	4.0	3.2	0.0	2.3	2.2	7.0	2.7	0.0	4.1	1.9	0.0	1.5	3.3	1.3	13.5	1.7	2.0	4.6
Splenial	0.1	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coronoid	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3	0.0	0.0	0.0
Prearticular	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Surangular	0.9	1.1	0.0	0.0	0.0	0.0	1.0	0.0	1.0	2.2	0.0	0.0	0.0	0.5	2.3	0.2	2.8	2.2
Angular	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
Articular	0.4	0.0	2.4	0.0	0.0	0.0	0.4	0.0	1.6	0.4	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.9
Dentition	3.7	7.9	4.3	3.0	1.8	2.3	0.5	0.0	10.1	5.2	5.1	1.9	6.3	1.6	2.1	6.0	4.9	3.8
Cervical vertebrae	6.2	3.8	6.2	17.5	2.6	10.7	7.8	0.0	12.8	5.2	7.4	0.9	3.9	8.3	3.4	3.9	2.3	0.0
Dorsal vertebrae	6.3	4.5	7.4	4.4	0.0	21.5	15.9	55.7	5.7	0.0	5.8	5.3	7.6	7.2	2.7	3.7	0.0	0.0
Sacral vertebrae	2.0	0.0	2.5	1.3	0.0	3.9	1.3	29.2	5.1	0.6	2.0	1.4	1.0	2.4	1.5	2.2	0.9	0.0
Caudal vertebrae	6.6	0.0	6.0	5.5	6.6	3.2	10.1	0.0	16.6	1.0	9.5	9.2	6.6	7.8	7.3	6.6	1.5	9.3
Chevrons	0.5	0.0	1.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.5	0.8	2.3	1.2
Cervical ribs	0.1	0.0	0.8	0.0	1.3	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Dorsal ribs	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.9	0.0
Sternal ribs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastralia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Furcula	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.4	0.3	0.0
Scapula	1.5	2.9	1.2	2.0	0.0	1.2	0.0	0.0	0.0	1.1	0.0	2.0	1.0	2.9	2.0	2.1	0.0	1.4
Coracoid	1.0	0.0	0.0	0.7	1.7	0.5	0.0	0.0	0.0	1.0	0.0	1.8	0.0	1.5	0.7	1.8	0.0	7.1
Sternal plate	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
Humerus	2.7	4.4	1.2	1.7	0.0	1.3	3.7	0.0	1.3	1.7	3.8	1.4	4.0	4.2	3.0	3.7	0.9	7.0
Ulna	1.0	2.4	0.0	1.0	0.0	1.0	0.5	0.0	0.0	0.0	3.1	0.0	0.0	0.5	1.0	2.0	0.7	3.4
Radius	0.4	0.0	0.0	0.7	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.5	0.8	0.0	0.7	0.2	0.7	1.1
Carpals	0.3	3.5	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.3	1.8	0.0	0.0	0.0	0.3	0.3	0.0	0.7
Metacarpals	2.6	0.0	0.0	4.0	0.0	0.0	0.5	0.0	1.1	1.0	8.5	6.1	2.7	2.6	3.9	2.4	2.4	3.7
Manual digits	3.7	0.0	0.0	2.8	3.8	0.0	0.6	0.0	2.4	1.6	20.0	7.3	7.6	3.4	4.8	2.3	5.2	10.7
Ilium	4.5	3.6	1.5	2.1	7.4	6.3	6.8	15.1	1.5	5.7	7.1	5.1	9.9	5.1	4.4	3.0	2.2	5.2
Pubis	4.0	10.7	3.0	4.0	7.3	1.6	1.5	0.0	4.6	2.1	2.3	5.9	9.8	1.4	2.5	7.1	4.4	0.0
Ischium	2.6	1.6	2.6	1.8	2.2	3.5	2.0	0.0	1.3	2.5	2.1	1.5	8.7	1.9	1.9	3.0	4.9	3.0
Femur	5.4	9.2	0.0	2.6	22.0	4.0	6.7	0.0	2.0	6.3	9.0	5.5	1.6	3.7	9.3	4.8	4.3	0.0
Tibia	5.1	11.7	21.4	8.6	3.2	3.1	2.9	0.0	6.0	1.8	0.0	3.3	0.0	13.3	2.4	2.9	8.7	0.0
Fibula	1.3	1.7	1.4	2.4	0.0	1.5	1.4	0.0	1.4	1.3	0.0	0.8	1.2	1.4	0.7	0.7	0.0	3.2
Astragalus	1.7	4.3	7.1	0.4	7.8	1.2	0.6	0.0	6.1	2.2	0.0	2.0	0.0	2.3	0.9	0.6	4.4	0.0
Calcaneum	0.4	0.0	2.7	0.0	1.5	0.0	0.9	0.0	0.0	0.4	0.0	0.5	0.0	0.0	0.4	0.7	0.0	1.1
Distal tarsals	0.2	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.5	0.4	0.0	0.0
Metatarsals	7.7	2.3	3.8	8.4	9.4	2.0	1.0	0.0	3.9	6.3	3.0	14.1	6.3	13.9	4.6	13.4	14.2	6.6
Pedal digits	3.1	0.0	0.0	1.9	3.0	2.9	0.0	0.0	0.0	3.5	0.0	10.5	1.5	5.4	0.9	5.1	4.1	8.5

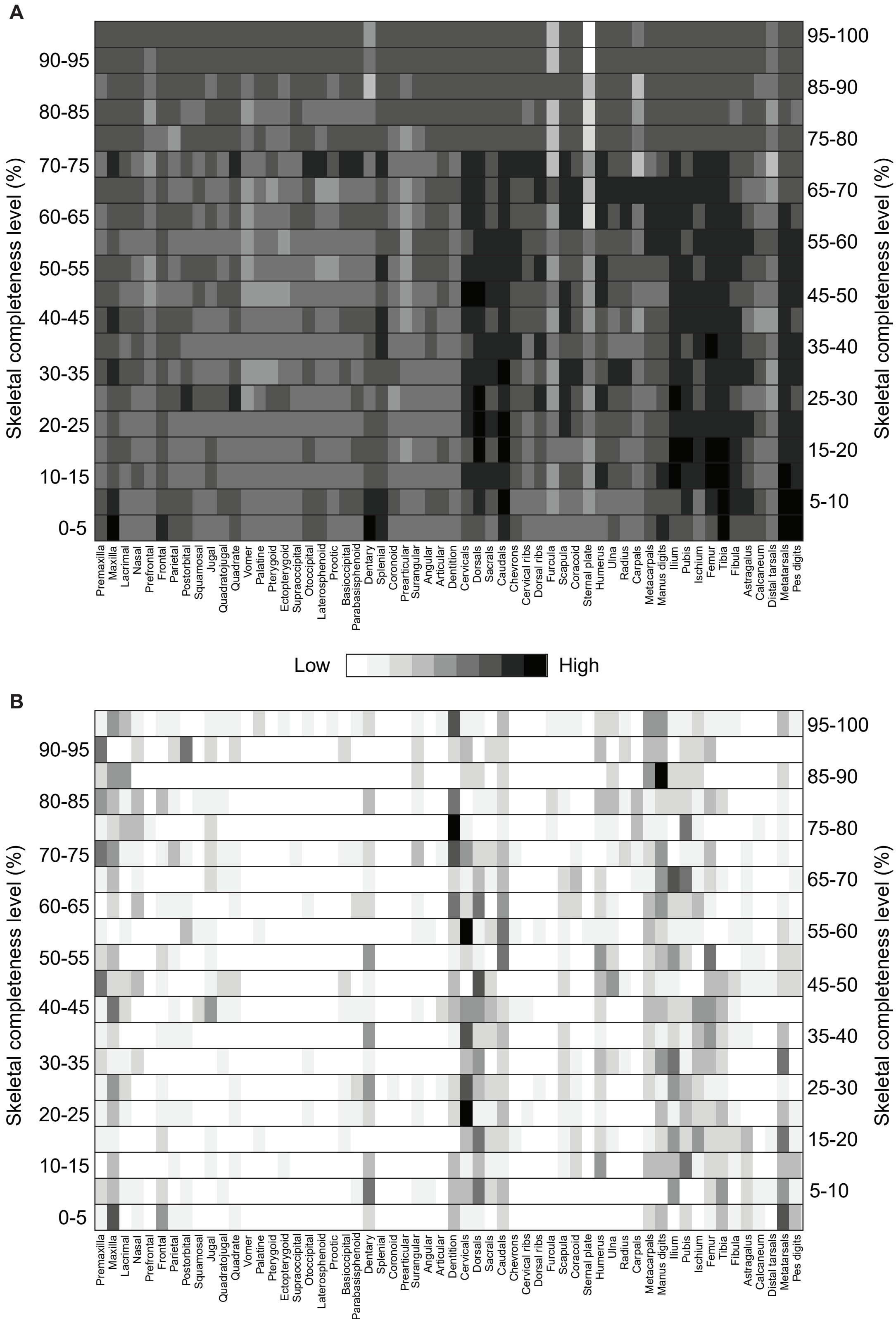


Figure C.1. Taphonomic heat maps representing the relative proportion of, A. skeletal element occurrences, B. assigned autapomorphies, and C. species diagnosed using different skeletal elements, within in each 5% completeness category.

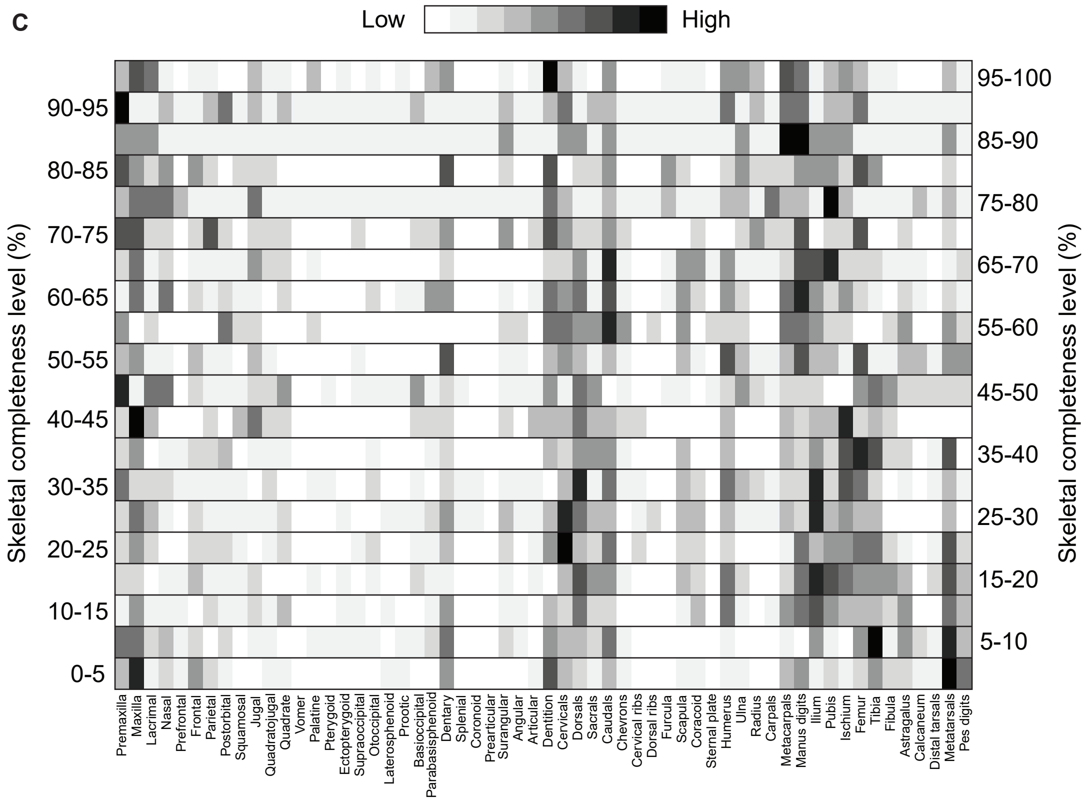


Figure C.1. Continued.

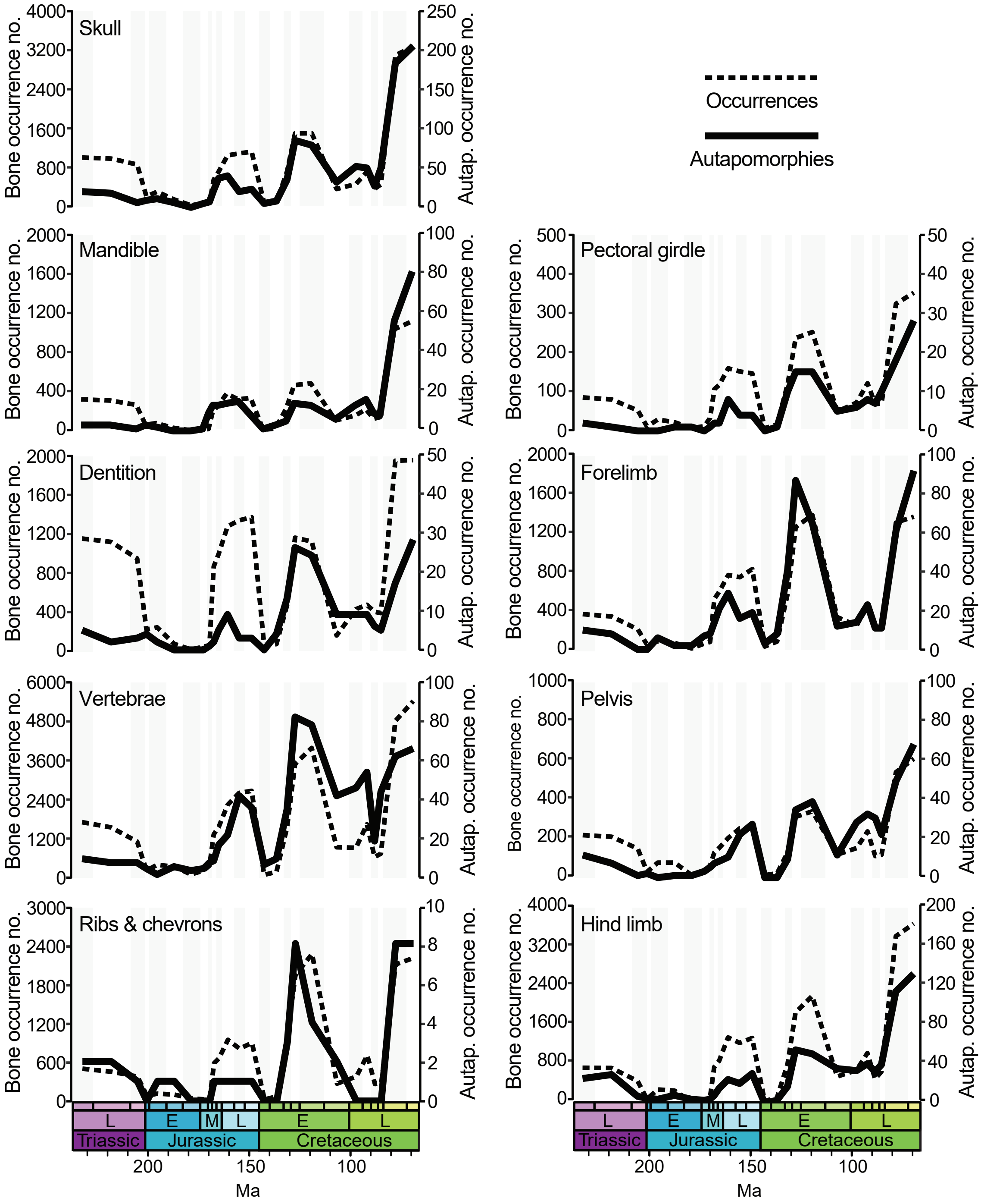


Figure C.2. Changes in the number of bone occurrences and assigned autapomorphies per skeletal region through geological time. Solid line, autapomorphies; dashed line, bone occurrences.

Table C.3. Results of pairwise comparisons between time series representing number of occurrences and assigned autapomorphies per skeletal region, using GLS. Statistically significant results indicated in bold.

Comparison	Slope	t-value	p-value	R^2
skull occ. ~ autap.	0.6334105	6.695472	**0**	0.842374
mandible occ. ~ autap.	0.5283825	3.961667	**0.0007**	0.6286967
teeth occ. ~ autap.	0.2656536	2.3985346	**0.0263**	0.5916064
vertebrae occ. ~ autap.	0.4666922	5.024265	**0**	0.8160124
ribs occ. ~ autap.	0.4127052	2.869596	**0.0124**	0.667496
pectoral girdle occ. ~ autap.	0.6018536	4.747073	**0.0001**	0.7628517
forelimb occ. ~ autap.	0.6893153	8.426785	**0**	0.8369535
pelvic girdle occ. ~ autap.	0.5029377	2.5572383	**0.0184**	0.7090897
hind limb occ. ~ autap.	0.7940638	8.210254	**0**	0.8279392

Table C.4. Theropod-bearing geological formations ranked by LoD1 scores, representing the likelihood of diagnosing the valid species within each.

Rank	Formation	Tax. diversity	mean SCM2	LoD1	LoD1 (%)
1	Yixian	31	63.71	511.23	100.00
2	Nemegt	16	36.61	378.65	74.07
3	Barun Goyot	7	29.98	200.77	39.27
4	Djadokhta	12	44.35	189.52	37.07
5	Cedar Mountain	7	17.48	169.48	33.15
6	Dinosaur Park	12	33.36	155.91	30.50
7	Shishugou	8	48.55	153.60	30.04
8	Morrison	12	38.75	146.20	28.60
9	Bajo de la Carpa	5	12.83	138.75	27.14
10	Portezuelo	6	14.37	129.57	25.34
11	Tiaojishan	9	58.48	112.68	22.04
12	Iren Dabasu	4	33.38	104.27	20.40
13	Huincul	6	18.37	98.67	19.30
14	Jiufotang	6	58.40	93.05	18.20
15	Hell Creek	4	23.35	92.20	18.03
16	Horseshoe Canyon	7	35.18	92.01	18.00
17	Kem Kem	2	30.38	89.16	17.44
18	Ischigualasto	3	63.91	86.81	16.98
19	Aoufous	3	28.47	84.50	16.53
20	Candeleros	5	34.20	82.64	16.17
21	Tendaguru	2	19.43	78.22	15.30
22	Bayan Mandahu (Wulansuhai)	7	16.06	74.57	14.59
23	Cloverly	3	60.78	73.19	14.32
24	Qiupa	4	32.02	70.68	13.82
25	Oldman	5	58.41	67.69	13.24
26	Baharije	1	45.31	63.10	12.34
27	Aïn el Guettar	1	45.31	63.10	12.34
28	Toqui	1	52.65	62.66	12.26
29	Antlers	2	74.81	61.91	12.11
30	Wessex	3	18.94	59.49	11.64
31	Maevarano	3	67.10	58.12	11.37
32	Kaiparowits	3	24.19	58.02	11.35
33	Chinle	4	42.87	55.15	10.79
34	Rio Paraná	1	23.39	52.53	10.28
35	Elrhaz	5	10.58	50.63	9.90
36	Baynshire	4	29.27	48.38	9.46
37	La Huerguina	2	43.98	47.77	9.34
38	Baharije	3	18.51	47.45	9.28
39	Taynton Limestone	1	37.85	47.28	9.25
40	Sharp's Hill	1	37.85	47.28	9.25
41	Forest Marble	1	37.85	47.28	9.25
42	Cotswold Slate	1	37.85	47.28	9.25
43	Coral Rag	1	37.85	47.28	9.25
44	Stanford	1	37.85	47.28	9.25
45	Kitadani	2	38.70	46.58	9.11
46	Sebes	1	34.73	46.53	9.10
47	Twin Mountain	1	71.43	41.73	8.16
48	Majiacun	2	13.13	39.11	7.65
49	Cañadón Asfalto	3	39.12	35.66	6.97
50	Klettgau	1	44.61	35.44	6.93
51	Los Colorados	2	14.04	35.28	6.90
52	Upper	1	29.66	34.59	6.77
53	Prince Creek	2	4.86	34.52	6.75
54	Judith River	2	52.61	34.42	6.73
55	Two Medicine	1	29.73	33.30	6.51
56	Xingezhuang	2	2.64	32.96	6.45
57	Echkar	4	6.32	32.73	6.40
58	Kayenta	3	45.92	32.32	6.32
59	Allen	2	15.99	31.21	6.10

Table C.4. Continued.

Rank	Formation	Tax. diversity	mean SCM2	LoD1
60	Lianmugin	3	3.59	30.83
61	Bayingobi	2	44.68	30.13
62	Baynshire	2	19.52	29.79
63	Weald Clay	1	32.92	28.51
64	Papo Seco	1	32.92	28.51
65	Grès supérieurs	1	15.55	28.47
66	Moreno Hill	2	19.61	28.44
67	Santana	4	11.20	28.37
68	Zhutian	1	65.27	27.80
69	Lower Argiles Rutilantes	1	6.10	27.43
70	Ulansuhai	3	38.30	27.22
71	Ifezouane	2	7.46	27.16
72	Solnhofen	2	91.84	25.78
73	Fruitland	2	64.41	24.26
74	Calcaires de Caen	2	13.74	22.68
75	Bajo Barreal	1	23.57	22.65
76	Sao Khua	4	8.33	22.00
77	Wahweap	1	10.71	21.95
78	Moon-Airel	1	11.95	21.07
79	Tiourarén	2	17.35	20.78
80	Oxford Clay	2	29.29	20.54
81	Arundel Clay	1	78.20	20.18
82	Javkhlant	1	13.57	19.76
83	Ornatenton	1	5.17	19.69
84	New Egypt	1	10.79	19.68
85	Lameta	2	30.12	19.66
86	Pingling	1	19.55	19.27
87	Cerro Barcino	2	12.94	19.03
88	Kirtland	1	31.40	18.82
89	Ukureyskaya	1	3.43	18.67
90	La Colonia	1	71.13	18.58
91	Packard Shale	1	0.83	18.20
92	Shaximiao	4	39.30	18.06
93	Kimmeridge Clay	1	24.08	17.97
94	Pietraroja	1	67.47	17.87
95	Pari Aike	2	1.91	17.42
96	Minhe	1	98.26	17.17
97	Dabrazhin	1	98.26	17.17
98	Zouyun	1	98.26	17.17
99	Xinlong	1	7.98	16.72
100	Sables verts	1	6.25	16.01
101	Cooper Canyon	1	1.63	15.78
102	Kirkwood	1	29.12	15.73
103	Haifanggou	1	69.62	15.60
104	Camarillas	1	6.69	15.56
105	Lufeng	3	38.12	15.21
106	La Quinta	1	2.54	15.19
107	Cañadón Calcáreo	1	7.31	14.55
108	Arcillas de Morella	1	14.41	14.48
109	Anacleto	3	23.20	14.08
110	Ambolafotsy	1	4.71	13.89
111	Saltrio	1	4.88	13.35

Table C.4. Continued.

Rank	Formation	Tax. diversity	mean SCM2	LoD1
112	Sierra Barrosa	1	25.74	13.34
113	Tropic Shale	1	63.28	13.32
114	Gaogou	1	34.35	13.15
115	Santa Maria	1	38.97	13.15
116	Painten	1	92.76	12.65
117	Snow Hill Island	1	1.26	11.95
118	Denver	1	4.71	11.61
119	Ferris	1	4.71	11.61
120	Los Blanquitos	1	2.55	11.54
121	Ojo Alamo	1	2.84	11.54
122	White Limestone	1	6.78	11.35
123	Elliot	2	48.80	11.30
124	Adamantina	1	6.16	10.61
125	Khukhteeg (Barunbayaskaya)	1	56.97	10.46
126	Lourinha	2	18.14	10.41
127	phosphates'	1	0.15	10.34
128	Rögling	1	96.71	10.17
129	Chinle	1	15.60	9.90
130	Colorado City	1	15.60	9.90
131	Bull Canyon	1	15.60	9.90
132	Lecho	1	1.09	9.68
133	Aïn el Guettar	1	14.73	9.19
134	São José do Rio Preto	1	0.58	9.12
135	Wapiti	1	0.62	8.99
136	La Bocana Roja	1	2.19	8.69
137	Bissekty	2	5.55	8.45
138	Caturrita	1	57.35	8.12
139	Blue Lias	1	18.74	7.74
140	Haoling (Mangchuan)	1	14.54	7.73
141	Farta Pao	1	33.23	7.73
142	Quebrada del Barro	1	24.28	7.61
143	Demopolis	1	18.40	7.46
144	Navajo Sandstone	1	38.77	7.26
145	Scollard	1	97.14	7.21
146	Öösh	1	0.72	7.12
147	Forest Sandstone	1	95.23	6.19
148	Nyamandhlovu Sandstones	1	95.23	6.19
149	Alcobaca	1	5.81	5.87
150	La Posa	1	2.54	5.83
151	Vitoria	1	2.54	5.83
152	Upper Inferior Oolite	1	1.09	5.37
153	Hanson	1	21.84	5.14
154	Fengjiahe	1	6.08	4.69
155	Winton	1	18.39	4.67
156	Menefee	1	2.76	4.49
157	Alcantara	1	0.11	4.12
158	Colalura Sandstone	1	0.54	3.80
159	Chipping Norton Limestone	1	6.66	3.73
160	Eumeralla	1	2.60	3.73
161	Tecovas	1	4.23	2.93
162	Middle Inferior Oolite	1	6.92	2.58
163	Csehba´nya	1	2.23	2.01

Table C.5. LoD1, LoD2, and taxonomic composition, of theropod-bearing quarries of the Morrison Formation, as defined by Maidment and Muxworthy (*in press*).

Quarry	Systems Tract	LoD1	LoD1 (%)	LoD2	LoD2 (%)	Species	Genera	Indet.
Delfs Quarry, Garden Park (CMNH)	STA2	NA	NA	NA	NA	0	0	1
Meyer Site 1, Garden Park	STA2	9.81	6.49	NA	NA	0	1	0
Meyer Site 2, Garden Park	STA2	NA	NA	2.95	1.17	0	1	0
Section 19 Mine (stope 4303)	STA2	9.81	6.49	14.00	5.53	0	1	0
Blue Mesa Quarry	STB3	9.81	6.49	NA	NA	0	1	0
Bollan Quarry, Rabbit Valley	STB3	9.81	6.49	4.56	1.80	0	1	0
Dinosaur Beach (CURE)	STB3	9.81	6.49	4.33	1.71	0	1	0
Felch Quarry 1, Garden Park (YPM) (=Marsh-Felch Quarry)	STB3	66.30	43.87	201.70	79.76	3	0	1
Felch Quarry 2, Garden Park (YPM)	STB3	9.81	6.49	NA	NA	0	1	0
Kessler's Quarry, Garden Park	STB3	9.81	6.49	NA	NA	0	1	0
Northern Dinosaur Beach (CURE)	STB3	9.81	6.49	9.12	3.60	0	2	0
Valley of Death 5	STB3	NA	NA	NA	NA	0	0	1
Brush Creek, Yale College Scientific Party	STB4	9.81	6.49	4.56	1.80	0	1	0
Cactus Park Quarry 3A (CU-Denver)	STB4	9.81	6.49	NA	NA	0	1	0
Calico Gulch Dinosaur Quarry	STB4	9.81	6.49	4.33	1.71	0	1	1
Cleveland-Lloyd Dinosaur Quarry	STB4	85.83	56.79	252.90	100.00	5	1	2
Deweese Quarry, Green Acres (DMNH)	STB4	NA	NA	4.56	1.80	0	0	1
Dinosaur National Monument Quarry (CM)	STB4	21.92	14.51	113.03	44.69	2	2	0
Dry Mesa Quarry [BYU]	STB4	26.01	17.21	188.77	74.64	1	3	7
Eriksen Ceratosaurus, FPA	STB4	8.32	5.51	68.74	27.18	1	0	0
Green River Dinosaur Quarry	STB4	9.81	6.49	12.48	4.93	0	1	0
Hanksville-Burpee Quarry	STB4	9.81	6.49	NA	NA	0	1	0
Holt Quarry	STB4	9.81	6.49	11.65	4.61	0	1	0
Jones Hole Quarry	STB4	9.81	6.49	NA	NA	0	1	0
Lakes Quarry 1, Morrison (YPM)	STB4	9.81	6.49	NA	NA	0	1	0
Lakes Quarry 10, Morrison (YPM)	STB4	9.81	6.49	NA	NA	0	1	0
Lakes Quarry 5, Morrison (YPM)	STB4	9.81	6.49	8.06	3.19	0	1	0
Lindsey Quarry (DMNH)	STB4	9.81	6.49	NA	NA	1	0	0
Main Callison Quarry	STB4	NA	NA	NA	NA	0	0	2
McConnell I	STB4	9.81	6.49	4.56	1.80	0	1	0
McElmo Canyon	STB4	14.94	9.88	44.84	17.73	1	0	0
Mother's Day Quarry	STB4	9.81	6.49	9.12	3.60	0	1	1
Mygatt-Moore Quarry, lower mudstone	STB4	18.13	12.00	83.98	33.21	2	0	1
Nielsen Gulch (DNM)	STB4	12.12	8.02	27.16	10.74	1	0	0
NMMNH L-3285 vertebrate site	STB4	9.81	6.49	NA	NA	0	1	0
NMMNH L-555, San Ysidro Camarasaurus Quarry	STB4	9.81	6.49	4.56	1.80	0	1	0
NMMNH locality L-344	STB4	NA	NA	NA	NA	0	0	1
Peterson Quarry, NMMNH L-3282	STB4	NA	NA	31.49	12.45	0	0	3
Potter Creek Quarry	STB4	NA	NA	4.56	1.80	0	0	1
Rabbit Valley Iguanodon	STB4	9.81	6.49	NA	NA	0	1	0
Small's Quarry, Garden Park	STB4	NA	NA	3.50	1.38	0	0	2
Stovall's Pit 5, Kenton (OMNH)	STB4	9.81	6.49	NA	NA	0	1	0
Stovall's Pit 6, Kenton (OMNH)	STB4	9.81	6.49	NA	NA	0	1	0
Stovall's Pit 8, Kenton (OMNH)	STB4	NA	NA	NA	NA	0	0	1
Suwanee Peak	STB4	9.81	6.49	NA	NA	0	1	0
Upper Strickland Creek Quarry	STB4	9.81	6.49	13.31	5.26	0	1	1
Uravan Locality (BYU) (Scheetz quarry)	STB4	NA	NA	4.56	1.80	0	0	1
Big Al site (MOR M-106)	STC5	9.81	6.49	98.94	39.12	1	0	0
Cope Quarry I, Cope's Nipple	STC5	9.81	6.49	8.61	3.40	1	0	0
Cope Quarry II, Cope's Nipple	STC5	9.81	6.49	3.78	1.49	1	0	0
Cope Quarry III, Cope's Nipple	STC5	9.81	6.49	16.71	6.61	1	0	0
Dana Quarry	STC5	15.84	10.48	98.43	38.92	0	5	0
DNM 315, Dinosaur National Monument	STC5	NA	NA	4.56	1.80	0	0	0
Howe-Stephens Quarry	STC5	9.81	6.49	98.94	39.12	0	1	0
Howe Quarry	STC5	9.81	6.49	9.12	3.60	1	0	1
Howe Quarry 2	STC5	9.81	6.49	4.56	1.80	0	1	0
Hups Quarry, MWC Loc. 197	STC5	9.81	6.49	NA	NA	0	1	0
Meilyn Quarry, Flat Top Anticline	STC5	19.62	12.98	33.75	13.34	0	2	0
OMNH Quarry 1, Kenton (OMNH V92)	STC5	18.22	12.05	85.13	33.66	2	0	1
Poison Creek Quarry (MSM)	STC5	9.81	6.49	13.63	5.39	0	2	0
Quarry 13, Como Bluff (YPM)	STC5	57.98	38.36	56.81	22.46	1	1	0
Quarry 1A, Como Bluff (YPM)	STC5	9.81	6.49	8.29	3.28	0	2	0
Rainbow Park (DNM 94)	STC5	9.81	6.49	9.12	3.60	0	1	1
Rainbow Park microsite (DNM 96)	STC5	9.81	6.49	9.12	3.60	0	1	1
Red Canyon Ranch	STC5	9.81	6.49	104.79	41.43	0	2	1
AMNH Stego 99 Quarry	STC6	NA	NA	4.56	1.80	0	0	1
Bertha Quarry	STC6	9.81	6.49	4.56	1.80	0	1	0
Bone Cabin Quarry (AMNH)	STC6	47.77	31.61	224.26	88.68	3	1	0
Bone Cabin Quarry West (BCQ West)	STC6	21.48	14.21	133.20	52.67	2	1	0
BS Quarry + S Quarry, Warm Springs Ranch	STC6	9.81	6.49	9.12	3.60	0	1	1
Freezeout Hills Quarry 6	STC6	19.98	13.22	15.24	6.03	1	1	0
Fuller's 351 (SDSM V351)	STC6	9.81	6.49	12.11	4.79	0	1	1
Hatch Ranch, Piedmont Butte	STC6	9.81	6.49	4.56	1.80	0	1	0
Jimbo Quarry (2A) (PROXY)	STC6	NA	NA	83.33	32.95	1	0	0
KU Camarasaurus Quarry	STC6	NA	NA	NA	NA	0	0	0
Little Houston Quarry, Main Quarry (SDSM V9138)	STC6	9.81	6.49	47.19	18.66	0	1	0
Little Houston Quarry, Mammal Quarry (SDSM V941)	STC6	NA	NA	32.64	12.91	0	0	1
Louise Quarry	STC6	19.98	13.22	0.28	0.11	1	1	0
Mile 175 (SDSM V931)	STC6	NA	NA	4.56	1.80	0	0	1
Nail Quarry	STC6	19.98	13.22	54.19	21.43	1	1	0
Ninemile Hill	STC6	9.81	6.49	4.56	1.80	0	1	0
Quarry 1-1/2, Como Bluff (YPM)	STC6	9.81	6.49	NA	NA	1	0	0
Quarry 1, Como Bluff (YPM)	STC6	9.81	6.49	34.39	13.60	1	0	0
Quarry 12, Como Bluff (YPM)	STC6	51.09	33.80	52.62	20.81	3	2	2
Quarry 14, Como Bluff (YPM)	STC6	9.81	6.49	33.98	13.44	1	0	0
Quarry 3, Como Bluff (YPM)	STC6	9.81	6.49	30.94	12.23	1	0	0
Quarry 4, Como Bluff (YPM)	STC6	9.81	6.49	NA	NA	1	0	0
Quarry 5, Como Bluff (YPM)	STC6	NA	NA	NA	NA	0	0	1

Table C.5. Continued.

Quarry	SystTract	LoD1	LoD1 (%)	LoD2	LoD2 (%)	Species	Genera	Indet.
Quarry 8, Como Bluff (YPM)	STC6	57.98	38.36	NA	NA	1	1	0
Quarry 9, Como Bluff (YPM)	STC6	100.00	66.17	61.79	24.43	5	2	1
RB Quarry, Warm Springs Ranch	STC6	9.81	6.49	4.56	1.80	0	1	0
Red Fork Powder River Quarry B	STC6	9.81	6.49	4.37	1.73	0	1	0
Something Interesting Quarry (SI), unit 1	STC6	NA	NA	4.56	1.80	0	0	1
Wonderland Quarry (SDSM V9141)	STC6	9.81	6.49	14.04	5.55	0	1	2
Zane Quarry, Sheep Creek	STC6	NA	NA	4.70	1.86	0	0	1
5 km west of Exeter	Unknown strat. location	9.81	6.49	NA	NA	0	1	0
Acoma Site	Unknown strat. location	9.81	6.49	NA	NA	0	1	0
Alameda Parkway dinosaur site	Unknown strat. location	NA	NA	NA	NA	0	0	1
Aurora Quarry 3 (AMNH)	Unknown strat. location	9.81	6.49	49.95	19.75	1	0	0
Bobcat Pit	Unknown strat. location	9.81	6.49	NA	NA	0	1	2
Carnegie Quarry N, Sheep Creek	Unknown strat. location	9.81	6.49	22.84	9.03	1	0	0
Ceratosaurus Pond, FPA	Unknown strat. location	NA	NA	4.56	1.80	0	1	0
CO-49, Dino Cove	Unknown strat. location	NA	NA	NA	NA	0	0	0
Como Bluff (AMNH 222)	Unknown strat. location	9.81	6.49	4.56	1.80	0	1	0
DNM 375, Dinosaur National Monument	Unknown strat. location	NA	NA	NA	NA	0	0	1
DNM Allosaurus Quarry	Unknown strat. location	15.84	10.48	99.40	39.30	1	0	0
Fossil Ridge, FPA	Unknown strat. location	9.81	6.49	4.56	1.80	0	1	0
Fox Mesa (USNM)	Unknown strat. location	NA	NA	NA	NA	0	0	1
FPA General Site (LACM)	Unknown strat. location	NA	NA	NA	NA	0	0	2
Freeze Out Mtns. Kansas Univ. Expedition	Unknown strat. location	9.81	6.49	27.35	10.81	1	0	0
Green Acres (general)	Unknown strat. location	NA	NA	NA	NA	0	0	1
Hinkle Site (BYU)	Unknown strat. location	9.81	6.49	58.89	23.28	1	0	0
Howe-Scott Quarry	Unknown strat. location	NA	NA	4.56	1.80	0	0	1
Kings View Quarry, Fruita	Unknown strat. location	NA	NA	NA	NA	0	0	1
Lynn Quarry	Unknown strat. location	9.81	6.49	NA	NA	0	1	0
Middle Park (USNM 218)	Unknown strat. location	9.81	6.49	4.37	1.73	1	0	0
Mill Canyon Quarry (BYU)	Unknown strat. location	9.81	6.49	20.12	7.96	0	1	0
Montezuma Canyon	Unknown strat. location	9.81	6.49	3.50	1.38	0	1	0
NMMNH Loc. 363 (PROXY)	Unknown strat. location	NA	NA	7.27	2.88	0	0	1
Parking Lot, FPA	Unknown strat. location	NA	NA	NA	NA	0	0	1
Picketwire Canyonlands (upper)	Unknown strat. location	9.81	6.49	NA	NA	0	1	0
Poison Creek Quarry 1 (=Sheridan College Quarry 1)	Unknown strat. location	9.81	6.49	4.70	1.86	0	1	0
Poison Creek Quarry 2 (=Sheridan College Quarry 2)	Unknown strat. location	NA	NA	4.56	1.80	0	0	1
Poison Creek Quarry 3 (=Sheridan College Quarry 3)	Unknown strat. location	9.81	6.49	NA	NA	0	1	0
Quarry 9, Pit A (AMNH/YPM)	Unknown strat. location	NA	NA	NA	NA	0	0	1
Quarry 9, producing layer (AMNH-YPM)	Unknown strat. location	NA	NA	NA	NA	0	0	1
Quarry C, Como Bluff (YPM)	Unknown strat. location	9.81	6.49	23.85	9.43	0	1	0
Quarry D, Como Bluff (YPM)	Unknown strat. location	9.81	6.49	14.18	5.61	0	1	0
Quarry R (AMNH)	Unknown strat. location	9.81	6.49	32.04	12.67	0	1	0
Red Mountain	Unknown strat. location	NA	NA	NA	NA	0	0	0
Tom's Place Quarry	Unknown strat. location	NA	NA	NA	NA	0	0	1
Traildust Theropod Quarry	Unknown strat. location	9.81	6.49	NA	NA	1	0	0
Warm Springs Ranch tracksite, unit 1	Unknown strat. location	NA	NA	4.56	1.80	0	0	1
Willow Springs Quarry	Unknown strat. location	9.81	6.49	30.48	12.05	0	1	0
Young locality, Delta (MW 122.1)	Unknown strat. location	NA	NA	4.56	1.80	0	0	1

SCORING SPECIMEN COMPLETENESS – METHODOLOGY

The skeletal completeness scores assigned to taxa are based on the completeness of individual bones from each of their specimens. Each bones' completeness was judged from figures and text information in the literature and scored from 0-100%. We regarded 'completeness' to be how much of an original element was missing, and did not judge based on the relative quality of the preservation, e.g. weathering, compression, distortion. For example, bones that were fully complete but had some surface weathering, would still be assigned 100%, whereas a bone sliced in half but with perfect surface preservation would be assigned 50%. Most individual bones were rigidly scored as either 0%, 25%, 50%, 75%, or 100% complete, though some elements were scored less rigidly if the case required it.

Continuous elements

For most bones in the skull, the pectoral and pelvic girdles, and the fore- and hindlimbs, completeness is simply assessed based on a singular discrete element. However, the number of teeth, vertebrae, ribs, carpals and tarsals, and manual and pedal phalanges of each digit vary depending on the tetrapod group or even individual species. Completeness of these continuous skeletal series was calculated based on the completeness of the individual elements in proportion to the total numbe supposedly present within the series. The total number of individual bones for each series were derived from the literature (see Supporting data, "Cont. element references" datasheets). If specific information pertaining to the individual taxon was unavailable then the number of elements from a closely related taxon or a typical number seen in a representative clade were used. Each individual bone (e.g. one caudal verterbra) was still judged on its completeness, but each series (e.g. caudal vertebrae) were only scored as complete if the entire contents of that series were present.

Untypical specimens

Preservation in the fossil record is highly variable so completeness scoring had to be relatively flexible. Flattened, distorted specimens were treated and scored exactly like well-preserved three-dimensional specimens. If preservation of certain specimens only allowed a particular side or portion of a bone to be seen (e.g. covered by sediment or obscured by another bone), we scored completeness based on the likelihood of the remainder of the non-visible portions being present in the rock. Bones were assigned 50% if they were obscured with no visible indication of presence but a strong likelihood of presence. This scenario occurred numerous times with the skulls of flattened conservation Lagerstätten specimens - individual skull bones are very likely present but difficult to distinguish from one another.

Non-existent elements

Certain bones that made up the skeleton of some taxa were never present in life in others (e.g. manual phalange V-1 in theropod dinosaurs). These bones were disregarded in the scoring of taxa for which this applied. To accommodate these 'missing' elements, altered skeletal body proportions were used to calculate completeness scores, whereby the skeletal proportion of the 'missing' element was allocated to another localised element.