Palaeontology The Palaeontological Association www.palass.org

[Palaeontology, 2020, pp. 1–28]

TEN MORE YEARS OF DISCOVERY: REVISITING THE QUALITY OF THE SAUROPODOMORPH DINOSAUR FOSSIL RECORD

by DANIEL D. CASHMORE[1], PHILIP D. MANNION[2], PAUL UPCHURCH[2] *and* RICHARD J. BUTLER[1]

[1]School of Geography, Earth & Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK; ddcashmore13@gmail.com
[2]Department of Earth Sciences, University College London, Gower Street, London, WC1E 6BT, UK

Typescript received 16 January 2020; accepted in revised form 17 April 2020

Abstract: Spatiotemporal changes in fossil specimen completeness can bias our understanding of a group's evolutionary history. The quality of the sauropodomorph fossil record was assessed a decade ago, but the number of valid species has since increased by 60%, and 17% of the taxa from that study have since undergone taxonomic revision. Here, we assess how 10 years of additional research has changed our outlook on the group's fossil record. We quantified the completeness of all 307 sauropodomorph species currently considered valid using the skeletal completeness metric, which calculates the proportion of a complete skeleton preserved for each taxon. Taxonomic and stratigraphic age revisions, rather than new species, are the drivers of the most significant differences between the current results and those of the previous assessment. No statistical differences appeared when we use our new dataset to generate temporal completeness curves based solely on taxa known in 2009 or 1999. We now observe a severe drop in mean completeness values across the Jurassic–Cretaceous boundary that never recovers to pre-Cretaceous levels. Explaining this pattern is difficult, as we find no convincing evidence that it is related to environmental preferences or body size changes. Instead, it might result from: (1) reduction of terrestrial fossil preservation space due to sea level rise; (2) ecological specificities and relatively high diagnosability of Cretaceous species; and/or (3) increased sampling of newly explored sites with many previously unknown taxa. Revisiting patterns in this manner allows us to test the longevity of conclusions made in previous quantitative studies.

Key words: Sauropodomorpha, fossil record, skeletal, completeness, sampling bias, body size.

SAUROPODOMORPHS were a successful, global clade of predominantly quadrupedal herbivorous dinosaurs that dominated many Mesozoic terrestrial ecosystems from the Late Triassic until their extinction at the end of the Cretaceous (Upchurch *et al.* 2004). Macroevolutionary patterns in sauropodomorphs have received substantial attention (e.g. Upchurch 1995; Sereno 1997, 1999; Carrano 2006; Lloyd *et al.* 2008; Benson *et al.* 2014, 2018; Sakamoto *et al.* 2016; Benson 2018), with many studies identifying several potential peaks and troughs in their diversity through time (Barrett & Upchurch 2005; Upchurch & Barrett 2005; Barrett *et al.* 2009; Benson & Mannion 2011; Lloyd 2011; Mannion *et al.* 2011; Upchurch *et al.* 2011; Starrfelt & Liow 2016; Tennant *et al.* 2018). However, whether these patterns reflect genuine diversity dynamics, rather than artefacts of an imperfect fossil record, remains uncertain.

Fossils are inconsistently preserved between different time periods, geographical localities, environmental settings, and taxonomic groups, leaving many gaps in the record (Newell 1959; Foote & Raup 1996; Kidwell & Holland 2002). To add to this, spatial and temporal sampling of the fossil record is highly uneven due in part to collector bias. Interpretations about the evolutionary patterns of a taxonomic group must therefore consider the incompleteness of the fossil record and sampling variation. In the last three decades, much research has focused on the impact of these limitations on our interpretations. Studies focused on sampling have attempted to identify areas of collector bias and to account for their influence on our understanding of macroevolutionary changes (e.g. Alroy 2000, 2010; Alroy *et al.* 2001; Hunter & Donovan 2005; Tarver *et al.* 2007; Wagner & Marcot 2013; Close *et al.* 2017; Lehmann *et al.* 2019). Many assessments of the

doi: 10.1111/pala.12496

incompleteness of the fossil record have focused on the relative proportions of species or species ranges represented in the fossil record (e.g. Dingus 1984; Benton & Storrs 1994, 1996; Foote & Raup 1996; Foote & Sepkoski 1999; Benton *et al.* 2000; Smith 2001, 2007; Teeling *et al.* 2005; Upchurch & Barrett 2005; Cooper *et al.* 2006; Eiting & Gunnell 2009; O'Connor *et al.* 2011). Recently, however, a number of studies have concentrated on the variation in information content provided by fossil specimens of a group (e.g. Benton *et al.* 2004; Fountaine *et al.* 2005; Smith 2007; Dyke *et al.* 2009; Benton 2010; Beardmore *et al.* 2012). Mannion & Upchurch (2010*a*) refined these latter approaches by developing two metrics that quantify the completeness of individual specimens and species in more detail and with greater accuracy. These metrics are the skeletal completeness metric, which measures the absolute proportion of the skeleton that is preserved for a species, and the character completeness metric, which measures the proportion of phylogenetically informative characters preserved. In this scenario, a high-quality fossil record would be one that contains many species known from highly complete material. Calculating such metrics enables meaningful comparisons to be drawn between various sampling biases that could influence the record of a group, such as the number of fossil-bearing localities, variable geographical and/or temporal sampling, or potential palaeobiological biases, including palaeoenvironmental preferences or species body sizes. These metrics have since been used in numerous studies quantifying the completeness of several tetrapod groups (Brocklehurst *et al.* 2012; Walther & Fröbisch 2013; Brocklehurst & Fröbisch 2014; Cleary *et al.* 2015; Dean *et al.* 2016; Verrière *et al.* 2016; Davies *et al.* 2017; Tutin & Butler 2017; Driscoll *et al.* 2019; Brown *et al.* 2019; Cashmore & Butler 2019; Mannion *et al.* 2019*a*; Lukic-Walther *et al.* 2019).

In their original exploration of these metrics, Mannion & Upchurch (2010*a*) quantified the completeness of the sauropodomorph fossil record. They identified a number of biases acting upon this record, including a negative relationship between completeness and sea level through time, a positive correlation between completeness and taxonomic ('raw') 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 by Mannion & Upchurch (2010*a*) have undergone taxonomic revision, and the number of valid sauropodomorph species has increased by 60% (see Cashmore *et al.* 2020).

New discoveries and research can have a strong impact on 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 10 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 & Benton 1987; Sepkoski 1993; Benton & Storrs 1994; Weishampel 1996; Alroy 2000; Tarver *et al.* 2011; Brocklehurst *et al.* 2012; Ksepka & Boyd 2012; Nicholson *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 palaeobiological and palaeoecological influences on the sauropodomorph fossil record by statistically comparing completeness between depositional environments, taxonomic subgroups and body sizes. 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 probably influences the preservation potential of fossils (Nicholson 1996; Cooper *et al.* 2006; Noto 2011; Brown *et al.* 2013; Cleary *et al.* 2015; Benson 2018), and ultimately our understanding of the fossil 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 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.

METHODOLOGY

Completeness metrics

Mannion & Upchurch (2010*a*) proposed two different versions of 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 only used the SCM2 metric in this study because it examines all of the available information for each species and is more appropriate than arbitrarily nominating a 'most important' specimen (Mannion & Upchurch 2010*a*; Brocklehurst *et al.* 2012; Brocklehurst & Fröbisch 2014).

The character completeness metric (CCM) is not considered in this study as this approach will form part of an independent and comprehensive study of dinosaur CCM following on from Bell *et al.* (2013).

Mannion & Upchurch (2010*a*) 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 & Fröbisch 2014; Cleary *et al.* 2015; Verrière *et al.* 2016; Cashmore & Butler 2019) to more precisely estimate the skeletal proportions of different tetrapod groups. Here we continue to use the proportions defined by Mannion & Upchurch (2010*a*) to ensure comparability with this earlier work, but we partially modified them to score element completeness on a finer scale (see Cashmore *et al.* 2020, datasheet 5).

Data

We present a new dataset of 307 sauropodomorph species. This comprises all species currently considered to be 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. Of the species in our dataset, 192 were present in some form in Mannion & Upchurch (2010*a*). Skeletal completeness scores of 138 of these taxa were extracted from Mannion & Upchurch (2010*a*). The completeness of the remaining 54 species had to be rescored because they were either only previously included within generic-level completeness scores (26 species) or have undergone taxonomic revision (28 species) since the publication of Mannion & Upchurch (2010*a*), resulting in revised specimen lists. We also calculated the skeletal completeness of 115 additional species, including newly described and recently revised species (see Cashmore *et al.* 2020, datasheet 2).

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. References and data sources for each species and specimen are provided in Cashmore *et al.* (2020). 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 to 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 (Cashmore *et al.* 2020).

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 Macronaria and Titanosauria. We also gathered geographical information for each taxon from the Paleobiology Database (PBDB; https://paleobiodb.org), including the present-day hemisphere and continent, and the present-day latitude and palaeolatitudinal coordinates for each taxon's holotype locality, to assess the varying spatial completeness of the sauropodomorph fossil record. The major continental regions 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 present-day continents (i.e. Asia and Africa respectively), as analyses were concerned with bias associated with present-day 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. All 307 sauropodomorph taxa were included in these non-phylogenetic analyses, unless key information was not available, such as a lack of known depositional environment.

To test whether a phylogenetic signal is present in sauropodomorph completeness, an informal supertree, comprising 207 species, was constructed in Mesquite (v. 3.6; Maddison & Maddison 2018), based on an existing supertree (Benson *et al.* 2018) updated via a number of recently published phylogenetic hypotheses (Carballido *et al.* 2017; Tschopp & 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.* 2018*a*, *b*; Pretto *et al.* 2018; Sallam *et al.* 2018; Simón *et al.* 2018; Xu *et al.* 2018; Zhang *et al.* 2018, 2019; Filippi *et al.* 2019; Gallina *et al.* 2019; Mannion *et al.* 2019*b*). The positions of some taxa (e.g. *Atlasaurus*) were highly unstable between analyses, and so were excluded. Several topologies (e.g. Gorscak & 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 both the `cal3TimePaleoPhy()` function in the package `paleotree` (Bapst 2012; Bapst & Wagner 2019) and `Hedman.tree.dates()` function (Lloyd *et al.* 2016) based on methods described in Hedman (2010). The cal3 method requires representative birth, extinction and sampling rates for the taxonomic group in question, and we used the rates previously calculated for all dinosaurs in Lloyd *et al.* (2016). Inclusion of at least five outgroup taxa is necessary to confidently date nodes in the Hedman method (Hedman 2010). We selected nine outgroups, including representatives of Theropoda, Ornithischia, and non-dinosaurian Dinosauromorpha. Prior to performing both dating methods we randomly resolved all polytomies in the supertree using 20 tree randomizations. After time-scaling each of these resolved trees, we randomly selected one individual tree per dating method for use in statistical analyses.

We also collected body mass estimates of 140 species from Benson *et al.* (2018). Using the methods presented in that study we calculated 13 additional species body mass estimates, and also added three estimates from other literature sources (see Cashmore *et al.* 2020, datasheet 6). These data were used to test the potential relationship between sauropodomorph body size and skeletal completeness. To assess the relationship within 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.

Geological time series. Mean SCM2 scores per geological stage-level time bin were used to examine temporal fluctuations in completeness from the Carnian to the Maastrichtian (237–66 Ma). Stage-level time bins were chosen as it is the stratigraphic level used in the majority of previous studies, for most sampling proxy data, and because most species stratigraphic data are not well constrained to finer levels. Stage ages were determined from Walker *et al.* (2018). Taxa that were present over multiple geological stages, or that have an uncertain stratigraphic age, were included in each stage in which they potentially were present. The most up-to-date stratigraphic ages of each species were gathered from the literature (see Cashmore *et al.* 2020, datasheet 6). The ages of the Chinese Middle–Upper 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. It should be noted that stratigraphic age resolution of 156/307 (51%) sauropodomorph species in our dataset exceeds one geological stage. This may have the effect of smoothing the temporal SCM2 curve by increasing the similarities in completeness values for adjacent time bins. 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. We further assembled three geological time series of the maximum, minimum and mean body mass estimates per geological stage.

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 separately partitioned this data by present-day 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.

Analyses

Temporal correlations. The mean sauropodomorph SCM2 curve through historical time was statistically compared to decadal midpoints to test for a significant trend in the completeness of discoveries. 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 & Upchurch (2010*a*), and to each historical decade SCM2 time series based on removing taxa unavailable (not yet discovered or described) at the time. We tested the correlation between SCM2 and changes in taxonomic 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 midpoints to test for a temporal trend as well as with fluctuations in sea level (data derived from Haq *et al.* 1987, transformed by Butler *et al.* 2010), which may partially control terrestrial fossil preservation. To identify shared or diverging completeness signals, the sauropodomorph SCM2 time series was also compared with the records of other Mesozoic tetrapod groups for which skeletal completeness studies have been performed, that is plesiosaurs (Tutin & Butler 2017), ichthyosaurs (Cleary *et al.* 2015), and theropod dinosaurs (Cashmore & Butler 2019), and groups for which character completeness studies have been performed, that is avialans (Brocklehurst *et al.* 2012), pterosaurs (Dean *et al.* 2016), and crocodylomorphs (Mannion *et al.* 2019*a*). 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 dataset and the older dates used for some of these other tetrapod groups based on PBDB data. This is unfortunately difficult to overcome without extensive revision of the data, but we believe the analyses we have performed are still valid and informative. In addition to pairwise comparisons, we originally performed multivariate regressions in an attempt to explain the new sauropodomorph SCM2 time series. However, no significant explanatory models were recovered, and therefore we excluded the results of these multivariate analyses from further discussion.

Non-temporal comparisons. A variety of comparisons of median and distribution of SCM2 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 known from multiple specimens occurs in more than one of these subsets, its SCM2 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 & Fröbisch 2014), ichthyosaurs (Cleary *et al.* 2015), parareptiles (Verrière *et al.* 2016), plesiosaurs (Tutin & Butler 2017), bats (Brown *et al.* 2019), and theropod dinosaurs (Cashmore & Butler 2019).

SCM2 values for individual species were also used to statistically test for phylogenetic completeness signals, and for comparisons with the present-day and palaeolatitudinal coordinates of their type specimens, as well as their body mass estimates, when available. Body mass estimates were first compared to completeness using a simple linear pairwise correlation, as there is strong evidence for greater preservation potential of larger non-avian dinosaur species (e.g. Brown *et al.* 2013; Benson 2018). However, it is possible that there is an optimal body size that could aid specimen completeness, and this optimum might not lie at either the small or the gigantic ends of the body size spectrum. It might be expected that most preserved fossil species are of ‘intermediate’ sizes, as very small taxa with delicate skeletons are susceptible to taphonomic loss (Von Endt & Ortner 1984; Behrensmeyer *et al.* 2003; Soligo & Andrews 2005; Carrano 2006; Muñoz-Durán & Van Valkenburgh 2006; Brown *et al.* 2013; Gardner *et al.* 2016; Benson 2018), and very large taxa might be prone to greater skeletal fragmentation (Yeshurun *et al.* 2007; Bandeira *et al.* 2018). With this in mind, a relationship between body size and completeness for sauropodomorphs could be non-linear; therefore, we also tested for a non-linear relationship between the two variables. Furthermore, species’ body mass estimates were compared to SCM2 scores whilst taking into account their phylogenetic relationships, in order to assess whether a relationship between completeness and body size is independent of phylogeny.

Statistical tests. All statistical analyses were performed in R (R Core Team 2019). Time series plots were produced using the package `ggplot2` (Wickham 2016), non-temporal completeness distributions plots were produced with the package `vioplot` (Adler & Kelly 2019), and phylogenetic trees with visually mapped continuous characters were produced using the function `contMap()` in the package `phytools` (Revell 2012, 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 2019) was also 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 & Hochberg 1995) adjustments were used to reduce the likelihood of acquiring type I statistical errors (‘false positives’) 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

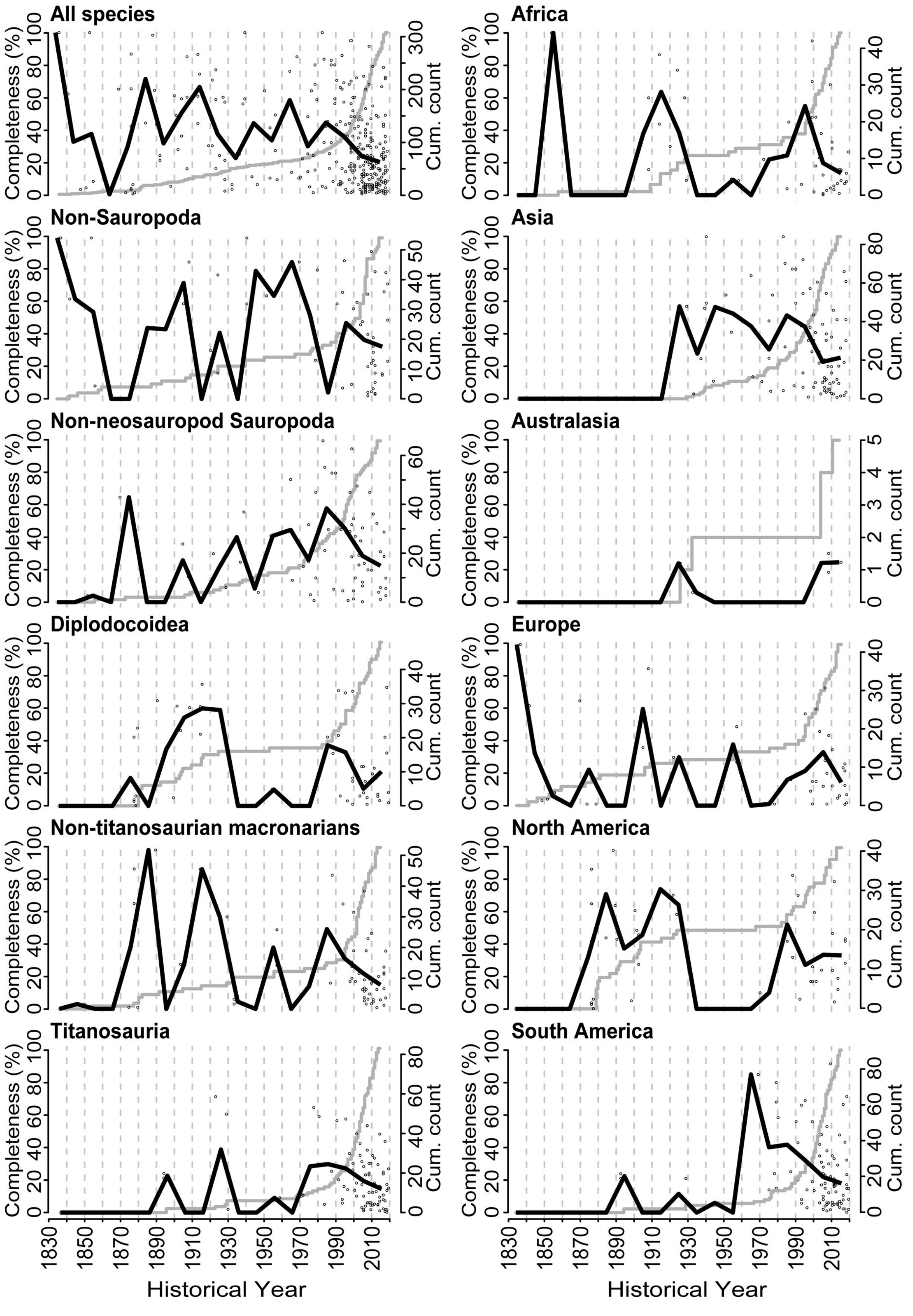
All species
Non-Sauropoda
Non-neosauropod Sauropoda
Diplodocoidea
Non-titanosaurian macronarians
Titanosauria
Africa
Asia
Australasia
Europe
North America
South America
Completeness (%)
0 20 40 60 80 100
Cum. count
0 100 200 300
0 10 20 30 40 50
0 20 40 60
0 10 20 30 40
0 10 20 30 40 50
0 20 40 60 80
0 10 20 30 40
0 20 40 60 80
0 1 2 3 4 5
0 10 20 30 40
0 10 20 30 40
0 20 40 60 80
1830 1850 1870 1890 1910 1930 1950 1970 1990 2010
Historical Year
1830 1850 1870 1890 1910 1930 1950 1970 1990 2010
Historical Year

FIG. 1. Historical accumulation and completeness curves for all sauropodomorph species, each major subgroup, and each continent. Black lines, mean SCM2 score per 10 year bin; grey lines, cumulative species count; circles, individual species' SCM2 score in relation to first publication date. *Abbreviations*: cum. count, cumulative species count.

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 2012, 2019) was used to test if sauropodomorph 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 generalized least squares (PGLS) linear regression with maximum likelihood methods were also 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; Paradis & Schliep 2019) was used, and for the latter we applied the `pgls()` function in the R package `caper` (Orme *et al.* 2018).

RESULTS

Historical sampling changes

Species accumulation and changes in historical completeness. As Mannion & Upchurch (2010*a*) previously showed, the number of identified sauropodomorph species rose steadily through historical time up to the last years of the twentieth century, when discoveries began to rise exponentially (Fig. 1) (Tennant *et al.* 2018). This trend continued into the early twenty-first century and has not abated in the last decade, with the rate of discovery increasing further (an average of 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. 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. 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 (Cashmore *et al.* 2020, fig. S1), 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 nineteenth century and the first half of the twentieth century. By contrast, there has been a statistically significant ($R^2 = 0.25$, $p = 0.04$) 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. 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. 1).

Changes to geological completeness and diversity curves through historical time. Time series based on our new dataset of mean sauropodomorph SCM2 values change drastically throughout research time (Fig. 2). Prior to the twenty-first century, each time series shows large fluctuations per stage, with swings from low to high mean completeness that are indicative 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 SCM2 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. 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).

By contrast, a significant difference was recovered between the current SCM2 curve and that presented in Mannion & Upchurch (2010*a*). 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 & Upchurch (2010*a*) curve (Fig. 2). The Mannion & Upchurch (2010*a*) curve is also significantly different to the pre-2010 curve derived from our data ($R^2 = 0.45$; $p = 0.38$) (Fig. 2).

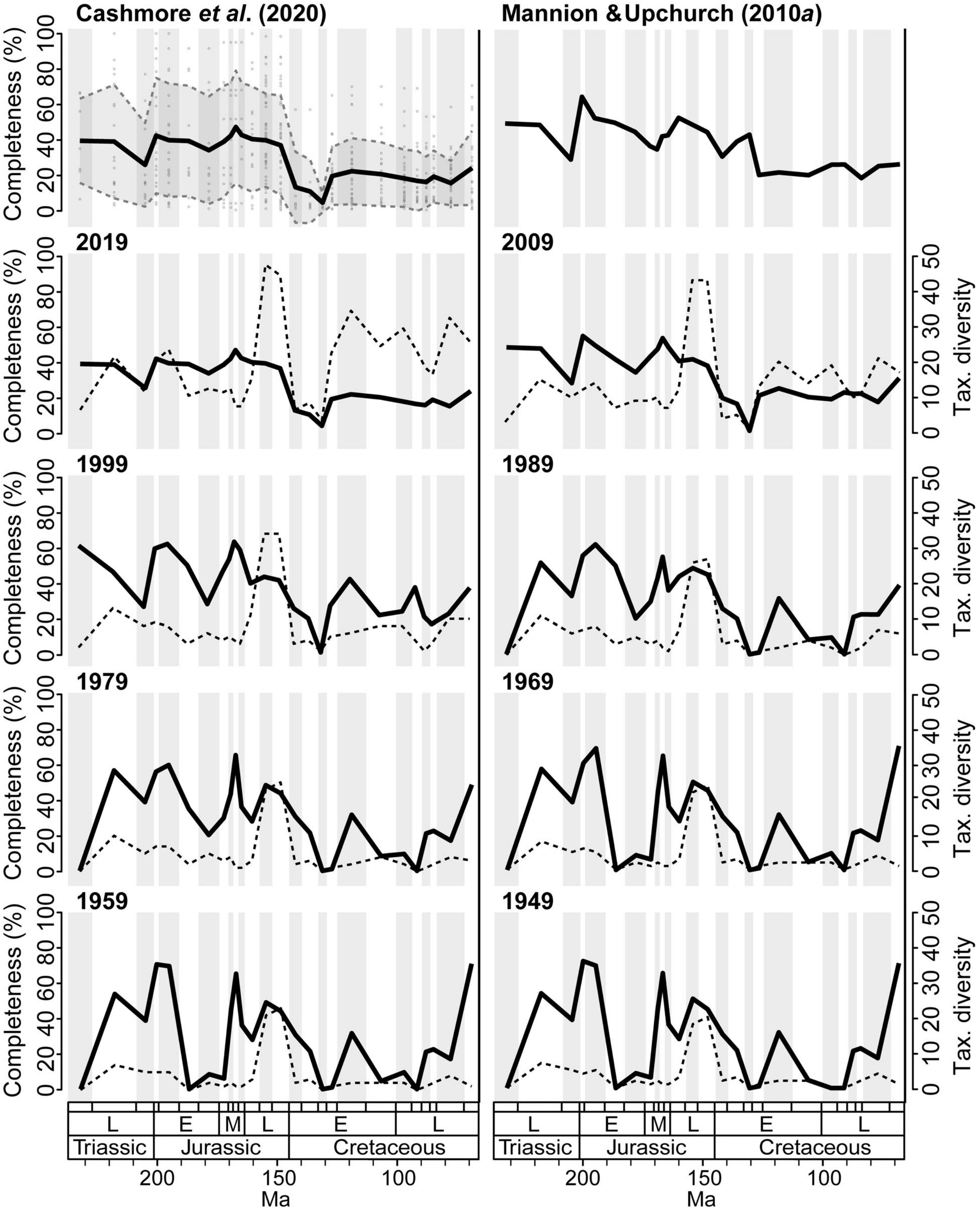

FIG. 2. Changes in mean sauropodomorph completeness through geological time from our current data set, from Mannion & Upchurch (2010*a*), and partitioned by available data per research decade based on our current data set, with raw diversity changes for comparison. Black lines, mean SCM2; grey polygon 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.

TABLE 1. Results of pairwise comparisons of the current sauropodomorph SCM2 and raw diversity time series in relation to past iterations using GLS.

Comparison	Slope	t-value	p-value	R^2
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	8.189470	**<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

Statistically significant results indicated in bold. *Abbreviations*: M&U (2010), Mannion & Upchurch (2010*a*); no LJ, removed Late Jurassic stages. Unless specifically stated, ‘SCM2’ and ‘diversity’ refers to the current sauropodomorph data.

Conversely, taxonomic 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. 2). With a spate of research and discoveries in predominantly Lower 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 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).

Current understanding of the sauropodomorph fossil record

Sauropodomorph completeness through geological time. Mean sauropodomorph SCM2 (Fig. 2) ranges between 4% and 48% throughout the stages of the Mesozoic, with minor peaks in the Hettangian, Bajocian and Maastrichtian, and notable lows in the Rhaetian, Valanginian and Hauterivian (Fig. 2). The most striking observation is that mean completeness noticeably drops across the Jurassic–Cretaceous (J/K) boundary, and never recovers to pre-Cretaceous levels. There is no significant trend in sauropodomorph completeness through time ($R^2 = 0.51$; $p = 0.09$). The Triassic and Jurassic exhibit relatively wide standard deviations, whereas this is narrower in the Cretaceous (Fig. 2). Mann–Whitney–Wilcoxon tests show that there is no significant difference between the distributions of Triassic and Jurassic ($W = 2104$, $p = 0.92$) SCM2 values, but there are strongly significant differences between distributions for the Triassic and Cretaceous ($W = 3474.5$, $p = 0.0002$), Jurassic and Cretaceous ($W = 13122$, $p = 1.32 \times 10^{-8}$), and Triassic–Jurassic and Cretaceous ($W = 16518.5$, $p = 1.02 \times 10^{-9}$) (Cashmore *et al.* 2020, fig. S2A).

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, Berriasian and Valanginian, and at its lowest in the Hauterivian (Fig. 2). There is no statistically significant trend in raw diversity changes through time ($R^2 = 0.18$; $p = 0.12$), but there is a strong, significant positive correlation between temporal fluctuations in sauropodomorph SCM2 and raw species diversity (Table 2) although this is not clear in observation (Fig. 2). This correlation is non-significant when assessed for the Triassic–Jurassic and Jurassic intervals alone (even when Late Jurassic stages are removed), but is still retained in the Cretaceous (Table 2).

Comparisons with other tetrapod fossil records. Sauropodomorph species SCM2 values range from just above 0% to 100%, with a median value of 21.5%, which is statistically similar to pelycosaur-grade synapsids, but significantly different to all other previously assessed groups (Cashmore *et al.* 2020, table S1, fig. S2B). The non-temporal distribution of sauropodomorph SCM2 values has remained statistically unchanged since Mannion & Upchurch (2010*a*) (Cashmore *et al.* 2020, table S1, fig. S2B). We also recovered the statistically significant higher completeness distribution of sauropodomorphs in comparison to theropods found by Cashmore & Butler (2019), but note that the significant difference is lost not only when using Cretaceous data alone, but also with just Jurassic data (Cashmore *et al.* 2020, table S1).

There is no significant correlation between sauropodomorph SCM2 and that of either marine reptile group examined (ichthyosaurs and plesiosaurs) through time (Table 2). Unlike Cashmore & Butler (2019), the sauropodomorph and theropod SCM2 time series are now significantly correlated when either including or excluding conservation Lagerstätten (Table 2; Cashmore *et al.* 2020, fig. S3A–B). However, the sauropodomorph and theropod Triassic–Jurassic data are no longer significantly correlated, and the Jurassic and Cretaceous data are not significantly correlated when considered separately, but there is a positive correlation when the Jurassic and Cretaceous data series are combined (Table 2).

Geographical completeness. The northern hemisphere has significantly more species at higher completeness levels in comparison to its southern counterpart (W = 13248; p = 0.02). However, this significant difference is lost after accounting for false discovery (adj. p = 0.06) (Cashmore *et al.* 2020, fig. S2C). 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). The palaeolatitudinal bin with the highest species diversity in both hemispheres is 30–40°. Mean SCM2 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 SCM2, respectively (Fig. 3).

The SCM2 distributions of each continent are all statistically similar to one another (Fig. 4A; Cashmore *et al.* 2020, table S2), 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 (Fig. 4A; Cashmore *et al.* 2020, table S2). 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 recognized, its distribution is still not significantly different to the other continents.

No contemporary continental or palaeolatitudinal time series has species present in all time bins. 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 3 stages (Cashmore *et al.* 2020, table S3, fig. S4). 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, whereas 10–20° S appears only in 2 stages. The high palaeolatitudes of 60–70° S are represented only in 3 stages, whereas 50–60° N appears in only one stage (Cashmore *et al.* 2020, table S4, fig. S5). 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 stage specific palaeolatitudinal bins represented, respectively (Cashmore *et al.* 2020, table S4, fig. S5), and species present only in Asia, South America and Europe (Cashmore *et al.* 2020, table S3, fig. S4). 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 (Cashmore *et al.* 2020, tables S3, S4). 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 (Cashmore *et al.* 2020, table S4, fig. S5). The only stage represented in every continent is the Albian, which is also known from nearly all palaeolatitudinal bins except 50–60° N, 10–20° S, and 20–30° S (Cashmore *et al.* 2020, tables S3, S4).

TABLE 2. Results of pairwise comparisons of current sauropodomorph SCM2 and raw diversity, body mass, other Mesozoic tetrapods, and sea level time series using GLS.

Comparison	Slope	t-value	p-value	R^2
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 Theropod SCM2	−0.038116	−0.337635	0.7434	0.155188796
J–K SCM2 ~ J–K Theropod SCM2	0.5777531	3.703968	**0.0013**	0.67416404
K SCM2 ~ K 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-cons. SCM2	−0.127089	−0.771550	0.4553	0.04479128
K non-cons. SCM2 ~ K Theropod non-cons. SCM2	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	−0.020780	−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

Statistically significant results indicated in bold. *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.

As noted above, the prominent drop in completeness across the 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 (Cashmore *et al.* 2020, fig. S4), which corresponds to peaks seen in 20–30° N and 30–40° N palaeolatitudinal bins (Cashmore *et al.* 2020, fig. S5). 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 (Cashmore *et al.* 2020, fig. S4). 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 (Cashmore *et al.* 2020, fig. S5).

Environmental completeness. By contrast with the results of Mannion & Upchurch (2010*a*), we find no correlation between sauropodomorph SCM2 and changes in sea level throughout the entire Mesozoic, but we find a positive correlation for the Cretaceous when considered alone (Table 2; Cashmore *et al.* 2020, fig. S3C). However, excluding the first three stages of the Cretaceous results in a significant negative correlation between sea level and SCM2 for the later Cretaceous (Table 2; Cashmore *et al.* 2020, fig. S3C). Although we find contrasting results to those of Mannion & Upchurch (2010*a*), this is not because of differing statistical tests used, as we recover the significant negative relationship ($R^2 = 0.52$; $p = 0.01$) they found for the entirety of the time series when comparing their previous mean SCM2 time series to sea level fluctuations using the GLS regression applied in this study.

Sauropodomorph species known from concentration Lagerstätten ('bonebeds' such as found in the Upper Jurassic Morrison and Tendaguru formations of North America and Tanzania, respectively) are on average significantly more complete than species known from non-Lagerstätten deposits ($W = 2701.5$, $p = 0.002$) (Cashmore *et al.* 2020, fig. S2D). There is no significant difference in

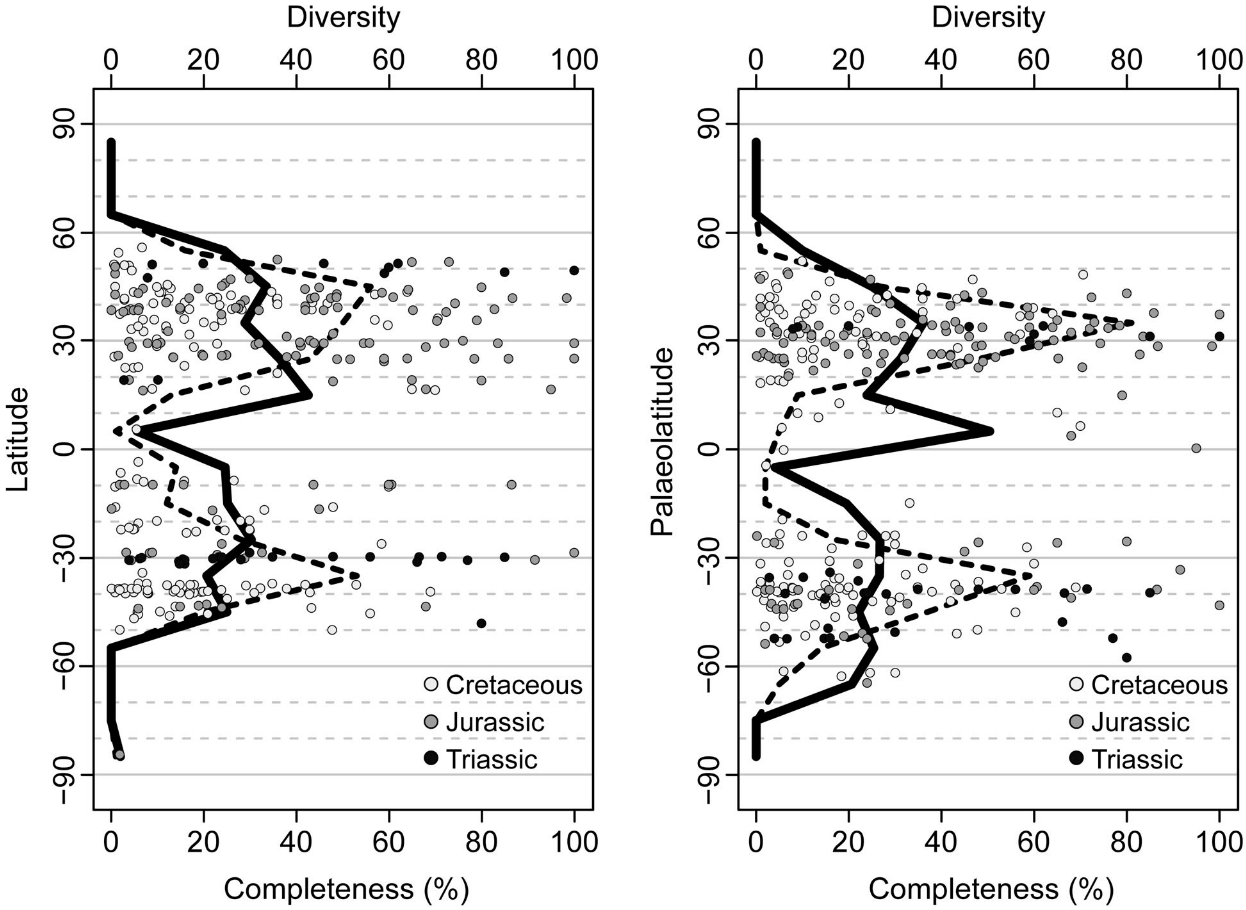

FIG. 3. Scatter distribution of SCM2 values in relation to present-day latitudinal and palaeolatitudinal coordinates. Point shades correspond to Mesozoic geological periods. Black lines, mean specimen completeness, and, dashed lines, raw taxonomic diversity per 10° latitudinal bin.

the distribution of SCM2 values between inland and coastal/marine deposits (Fig. 4B), even when separated between Triassic–Jurassic and Cretaceous species (Cashmore *et al.* 2020, table S5, fig. S2E). Species known from lacustrine deposits are significantly more complete than those from fluvial or coastal/marine settings (Fig. 4B; Cashmore *et al.* 2020, table S5). In all inland, coastal, fluvial and lacustrine deposits, the non-temporal distribution of SCM2 values is statistically much higher in the Triassic–Jurassic than the Cretaceous (Cashmore *et al.* 2020, table S5, fig. S2E). Temporal fluctuations in SCM2 for species found in fluvial, lacustrine or coastal environments each show a drop across the J/K boundary that fails to recover pre-Cretaceous levels (Cashmore *et al.* 2020, fig. S6).

Taxonomic and biological completeness. Different sauropodomorph groups have contrasting levels of completeness. Non-sauropod sauropodomorph skeletons are most commonly discovered at higher levels of completeness in comparison to sauropods, with a non-temporal distribution of SCM2 scores which is significantly different to all other subgroups, except non-neosauropod sauropods (Fig. 4C; Cashmore *et al.* 2020, table S6). The latter has a distribution of SCM2 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 Macronaria, and Titanosauria), all have distributions that are not significantly different from one another (Fig. 4C; Cashmore *et al.* 2020, table S6). Geological time series show consistently high completeness for non-sauropods, while non-neosauropod sauropods, diplodocoids and non-titanosaurian macronarians all exhibit greater fluctuations in completeness, with prominent peaks in the Late Jurassic, and lows in the earliest Cretaceous. Furthermore, titanosaur completeness gradually rises to moderate levels, along with diversity, throughout the ‘middle’–Late Cretaceous (Cashmore *et al.* 2020, fig. S7).

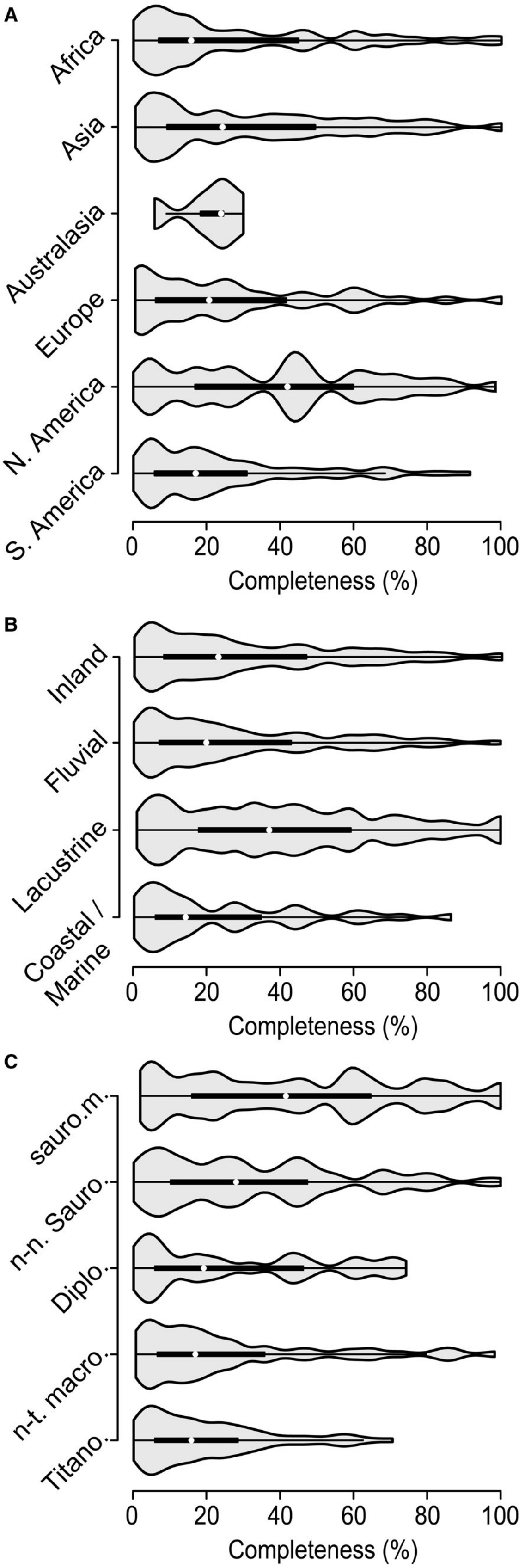

FIG. 4. Distribution of sauropodomorph SCM2 scores between different A, continents; B, depositional settings; C, sauropodomorph subgroups. Shaded polygon width represents the relative density of species. *Abbreviations*: sauro.m, non-Sauropoda; n-n. Sauro., non-neosauropod Sauropoda; Diplo., Diplodocoidea; 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).

Our sauropodomorph supertree, with SCM2 mapped on as a continuous character, can be seen in Figure S8 (Cashmore *et al.* 2020). 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, and Rebbachisauridae, which tend to have low levels of completeness. We detect a very strongly significant phylogenetic signal for skeletal completeness for all sauropodomorphs ($\lambda = 0.81$; $p = 2.4 \times 10^{-5}$), and a weaker, but significant signal, in just Sauropoda ($\lambda = 0.55$; $p = 2.1 \times 10^{-12}$) using the cal3 time-scaled supertree. However, using the Hedman time-scaling method, we detect no significant phylogenetic signal for all sauropodomorphs ($\lambda = 0.13$; $p = 0.13$), but a strongly significant signal in just Sauropoda ($\lambda = 0.64$; $p = 1.55 \times 10^{-10}$).

Figure 5 displays the relationship between species’ body mass estimates and SCM2, 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 (the basal sauropodomorph *Chromogisaurus novasi*) known from relatively small body size and relatively low completeness. We find a very weakly significant negative linear relationship between SCM2 and body size for all species ($R^2 = 0.03$; $p = 0.04$), but no relationship for solely the Triassic ($R^2 = 0.13$; $p = 0.30$), Jurassic ($R^2 = 0.03$; $p = 0.16$), or Cretaceous ($R^2 = 0.01$; $p = 0.60$) 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 6 shows the reduced composite phylogenetic tree with SCM2 and body mass estimations mapped as continuous characters. Phylogenetic independent contrasts reveal no significant relationship between SCM2 and body mass estimates for all Sauropodomorpha (cal3:

$R^2 = 0.007$, $p = 0.34$; Hedman: $R^2 = 0.03$, $p = 0.07$), or solely Sauropoda (cal3: $R^2 = 0.0003$, $p = 0.87$; Hedman: $R^2 = 0.01$, $p = 0.26$), using either the cal3 or Hedman time-scaling methods. Similar results were also found in PGLS tests for all sauropodomorph species (cal3: $R^2 = 0.004$, $p = 0.80$; Hedman: $R^2 = 0.008$, $p = 0.31$), as well as solely Sauropoda (cal3: $R^2 = 0.02$, $p = 0.18$; Hedman: $R^2 = 0.02$, $p = 0.15$).

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 gradual decline until the end-Cretaceous (Cashmore *et al.* 2020, fig. S3D). Time series correlations between mean, maximum and minimum body mass estimates and mean SCM2 per time bin reveal no significant correlations for mean and maximum estimates, but a significant positive correlation with minimum estimates (Table 2).

DISCUSSION

Changes in our understanding of the sauropodomorph fossil record

As Mannion & Upchurch (2010*a*) showed, the number of identified sauropodomorph species has risen exponentially 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 recognized 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. 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).

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. 2). The downward trend in mean completeness through historical time, also recorded in the mosasaur fossil record (Driscoll *et al.* 2019), 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 are more thoroughly sampled, more species are potentially identified from a wider range of completeness scores, and therefore a stage is more likely 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

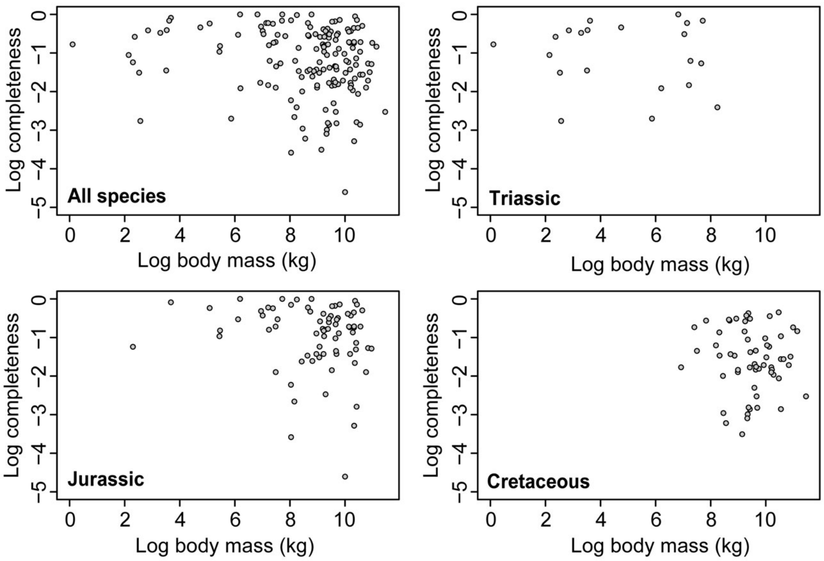

FIG. 5. Scatter distribution of sauropodomorph SCM2 values in relation to logged body mass estimates, and separated for each Mesozoic geological period.

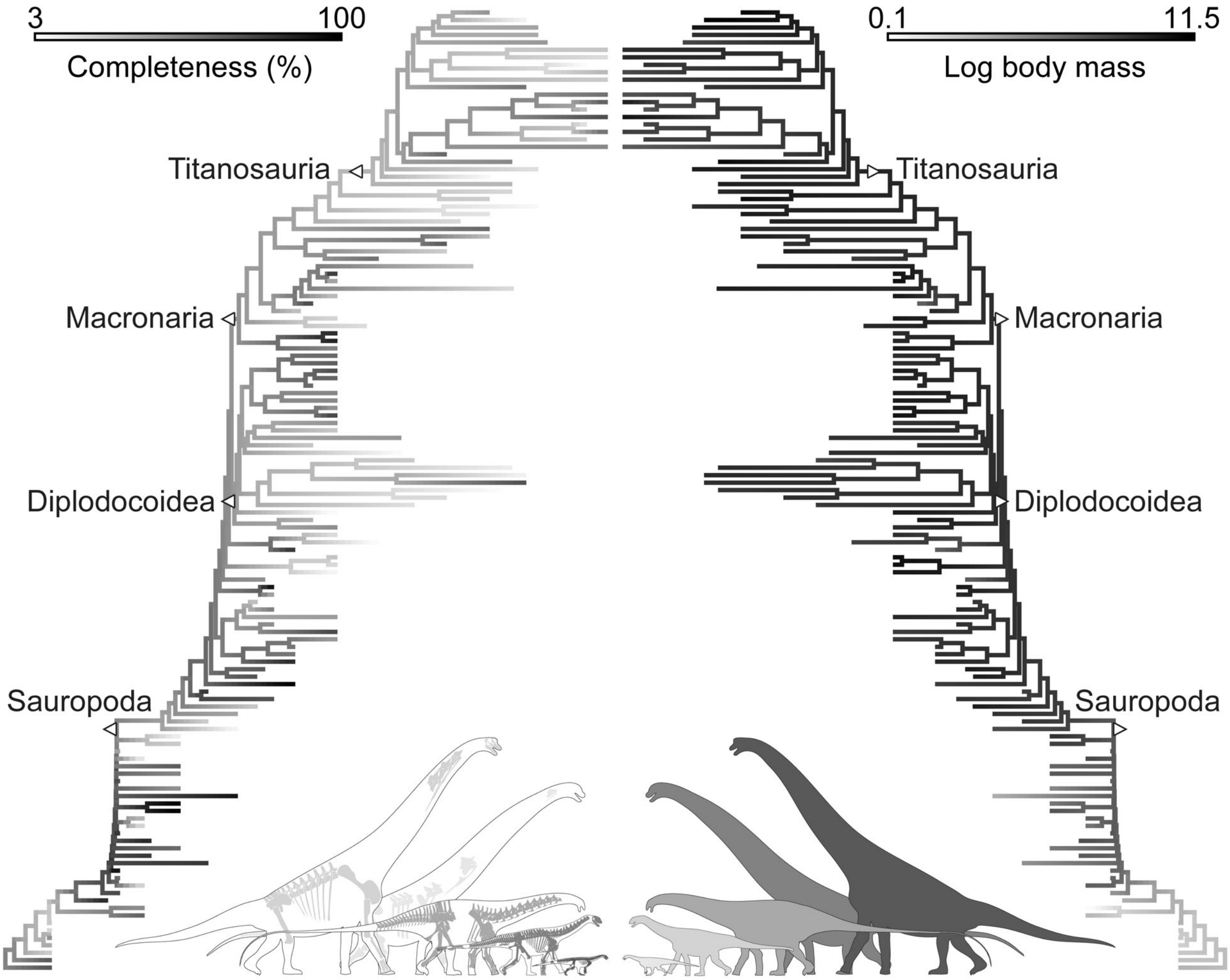

FIG. 6. Composite trees depicting sauropodomorph relationships with SCM2 scores, and logged body mass estimates, mapped on as continuous characters, and displayed on a greyscale spectrum. Lighter shades represent lower completeness and body size, while darker shades represent higher completeness and body size. Time-scaled using the Hedman method (Hedman 2010; Lloyd *et al.* 2016). Silhouettes used were created by S. Hartman (http://phylopic.org/; CC BY-SA 3.0). From the foreground to background, silhouettes represent *Riojasaurus incertus*, *Shunosaurus lii*, *Brontosaurus excelsus, Brachiosaurus altithorax* and *Dreadnoughtus schrani*. *Abbreviation*: Sauro., Sauropoda.

relatively little change in the overall structure of the completeness time series (Table 1; Fig. 2), it is probable that we are beginning to see an accurate representation of the changes in quality of the sauropodomorph record through geological time (cf. Sepkoski 1993; Alroy 2000). We predict that additional future discoveries will have comparatively minor impacts on these completeness patterns.

By contrast, the lack of correlation between the current or pre-2010 SCM2 curve and that presented in Mannion & Upchurch (2010*a*) requires explanation (Table 1; Fig. 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 & Upchurch (2010*a*) 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). Brocklehurst *et al.* (2012) also found changes in the temporal completeness patterns of Mesozoic birds over an 8-year research period, but attributed them to differences in the nature of the metrics used in the separate studies, rather than new discoveries or taxonomic revisions.

Temporal changes in the raw diversity time series exhibit considerably larger fluctuations in comparison to time series from previous decades (Fig. 2). Like Tennant *et al.*

(2018), 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. 2; Cashmore *et al.* 2020, fig. S1). The significant correlations between the current curve and pre-90s historical time series 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, which both began early in the history of dinosaur study. Therefore, our understanding of sauropodomorph diversity fluctuations outside of the Late Jurassic has significantly changed in recent decades and may yet change with additional findings (Tarver *et al.* 2011; Jouve *et al.* 2017; Tennant *et al.* 2018).

Impact of changes on understanding of 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. 2). This correlation persists after 10 years of discovery, as well as numerous taxonomic and stratigraphic revisions (Mannion & Upchurch 2010*a*). 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 probably 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, or we are over-splitting isolated specimens into new species and inflating the record (see below). It is likely that the steep increase in Cretaceous discoveries in the last 20 years (Cashmore *et al.* 2020, fig. S1), especially of often incomplete South American titanosaurs (Fig. 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.* 2010; Starrfelt & Liow 2016; Tennant *et al.* 2016*a*, *b*). This was partially contended by Mannion & Upchurch (2010*a*) because they noted a coincident drop in sauropodomorph completeness. This J/K decline has also been previously recognized in the theropod fossil record (Cashmore & Butler 2019), and notable drops in completeness can be seen in the crocodylomorph (Mannion *et al.* 2019*a*), 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. There are probably strong preservation issues impacting evolutionary interpretations during this interval, especially considering the limited number of continents sampled in the earliest Cretaceous (Tennant *et al.* 2017) (Cashmore *et al.* 2020, table S3).

After the severe drop at the J/K boundary, sauropodomorph mean completeness remains low throughout the earliest Cretaceous, and never obtains pre-Cretaceous highs (Fig. 2). This shows a clear temporal segregation in the levels of completeness, which is corroborated by the statistically significant difference in the range of SCM2 values between the periods (Cashmore *et al.* 2020, fig. S2A). 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.

Explaining the current completeness of the sauropodomorph record

Comparative signals. 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 megabias, most likely 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 (Cashmore *et al.* 2020, fig. S3B). A drop in completeness across the J/K boundary and moderate latest Cretaceous completeness values are features also shared in the CCM records of Mesozoic birds, pterosaurs (see Cashmore & Butler 2019 for further discussion), and the recently studied terrestrial crocodylomorphs (Mannion *et al.* 2019*a*) (though the latter possesses a very gradual J/K decline in comparison to those other groups). 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 SCM2 values are significantly higher than those of theropods (Cashmore *et al.* 2020, table S1, fig. S2B), which could reflect significant preservational differences between the two groups, derived from palaeobiological or palaeoecological distinctions. Sauropodomorphs were mostly gregarious herbivores (Upchurch *et al.* 2004; Myers & Fiorillo 2009), potentially enhancing their preservation potential in comparison to theropods (see Cashmore & Butler (2019) for further discussion). It has also been argued that sauropods are overrepresented in the Morrison Formation, partially because a small population of adults (Engelmann *et al.* 2004; Farlow *et al.* 2010) had a broad resource base, and would travel long distances to access resources as the dry seasons took hold (Engelmann *et al.* 2004). This might have enabled sauropods to live in multiple environments, and therefore increased their chances of entering the fossil record through a variety of preservational modes.

Geographical sampling bias. Although the northern hemisphere has a significantly more complete distribution of non-temporal sauropodomorph SCM2 values than its southern counterpart (Cashmore *et al.* 2020, fig. S2C), sampling in each hemisphere is relatively even (Fig. 3), and therefore the well-established historical focus of palaeontological research in the northern mid-latitudes is not that apparent. However, this pattern is mostly due to Cretaceous occurrences, probably related to the huge growth in South American finds in recent decades (Fig. 1) and potentially because stratigraphically younger outcrops are more likely to survive geological processes.

The statistically similar non-temporal distributions of SCM2 values between most continents (Cashmore *et al.* 2020, table S2) suggests a generality of preservational influences and similar global sampling effort. North America is unique for its combination of high mean completeness scores (Fig. 4A) and temporally patchy record (Cashmore *et al.* 2020, fig. S4) (Tennant *et al.* 2018), probably resulting from historical research interest, fortunate preservation regimes (e.g. Morrison Formation), and discontinuous continental deposition due to palaeoepicontinental seas (Chiarenza *et al.* 2019). A heightened research interest in the last 30 years (Fig. 1) can explain the drastic increase in South American (especially Cretaceous) sauropodomorph finds (e.g. Jesus Faria *et al.* 2015; Pretto *et al.* 2018). This also suggests that South American discoveries are far from finished (Tennant *et al.* 2018), and therefore the continent's current diversity and completeness curves might not be representative of its wealth of potential information. However, 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. 2). Tennant *et al.* (2018) noted that the 'middle'–Late Cretaceous sauropodomorph record in Africa, Asia, and South America have seen volatile changes in subsampled diversity and sampling coverage estimation from 1991 to 2015 due to taxonomic revision and new discoveries. Continents such as these, and hopefully also 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 palaeolatitudinal time series has a continuous fossil record for the entirety of sauropodomorph history (Cashmore *et al.* 2020, fig. S4, S5), and they only show mildly similar patterns to the global record, 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*a*). The Late Jurassic peak in raw diversity is primarily the result of finds from North America (Cashmore *et al.* 2020, fig. S4), indicating that our understanding of the diversity changes of this period is heavily influenced by one continent. 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*a*) and, as we demonstrate, regional records have exhibited strong changes through historical time (Fig. 1).

An almost complete absence of sauropodomorph finds at high present-day and palaeolatitudes (> 60° N and > 70° S), 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). This could represent either geographically limited sampling opportunities, indicating a significant spatial bias, or the genuine rarity of sauropodomorphs at such latitudes in the Mesozoic (Nesbitt *et al.* 2009; Whiteside *et al.* 2011; Mannion *et al.* 2012; Poropat *et al.* 2016). To test this, we downloaded all non-marine body fossil occurrences of Carnian–Maastrichtian tetrapods from the PBDB and compared it to the latitudinal and palaeolatitudinal distributions of sauropodomorphs (Cashmore *et al.* 2020, fig. S9). A strong positive correlation is found ($R^2 = 0.82$; $p = 0.0002$) between the palaeolatitudinal distributions; however, this only occurs when the 50–60° N bin is excluded, as it contains just a single 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 (Cashmore *et al.* 2020, fig. S9). The near-absence of sauropodomorphs from palaeolatitudes higher than 50° demonstrates some degree of climatic and ecological control on their distribution (Mannion *et al.* 2012; Poropat *et al.* 2016), and therefore the quality of their fossil record. However, the significant similarity for the remainder of the distributions suggests that gross under-sampling is the main driver behind the limited sauropodomorph occurrences at higher and more equatorial latitudes. This might partially be controlled by historical research interest, but probably has more to do with climate dynamics, vegetation cover, subsequent erosion, and working conditions in present-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). However, a lack of consistently exposed fossiliferous localities in high and low latitudes, because of extensive ice cover and vegetation overgrowth respectively, will greatly reduce the chances of successful discoveries. Although there might be a wealth of unsampled data at these latitudes, given that species have been found (e.g. *Glacialisaurus hammeri* from Antarctica (Smith & Pol 2007) and *Padillasaurus leivaensis* from Colombia (Carballido *et al.* 2015)), they need a great deal of effort to access and are much less 'profitable' than mid-latitudinal localities.

Palaeoenvironmental bias. Sea level highstands and lowstands have both been argued to hinder and aid terrestrial tetrapod fossil preservation (Weishampel & Horner 1987; Haubold 1990; Hunt *et al.* 1994; Hedges *et al.* 1996; Sereno 1997; Smith 2001; Chiarenza *et al.* 2019) within different time bins, although no statistically significant relationship has yet to be found (Fara 2002; Butler *et al.* 2010). We find the positive correlation found between sauropodomorph completeness and sea level fluctuations in the Cretaceous is probably driven by outliers in the Berriasian, Valanginian and Hauterivian (Cashmore *et al.* 2020, fig. S3C). The substantial sea level regression (Haq *et al.* 1987) could possibly explain the concurrent drop in mean completeness if we consider non-titanosaur sauropodomorphs mostly inhabited erosion-prone coastal environments (Mannion & Upchurch 2010*b*) during the interval. A titanosaur environmental preference change to more inland settings (with possibly lower levels of preservation potential) in the latter half of the Early Cretaceous, along with terrestrial environmental contraction due to higher sea levels, has been suggested to partially explain the poor-quality preservation for Cretaceous sauropodomorphs (Mannion & Upchurch 2010*b*). The statistically significant negative correlation (Table 2) for sea level and completeness for the majority of the Cretaceous favours the negative impact of rising sea levels on the Cretaceous sauropodomorph fossil record. However, lower quantity and quality of sauropodomorph fossils in inland settings are not supported by our data. There is no significant difference between the completeness of species from coastal and inland deposits within any interval (Cashmore *et al.* 2020, table S5, fig. S2E), and on average, species found from Cretaceous coastal, inland, fluvial and lacustrine deposits do not maintain the level of completeness of their Triassic–Jurassic equivalents (Cashmore *et al.* 2020, table S5, fig. S2E). This indicates a lack of statistical evidence to suggest that Cretaceous sauropodomorph completeness was significantly reduced by an environmental preference shift, or the expansion or contraction of one or more depositional environment. However, Mannion & Upchurch (2011) found that the total number of inland deposits decreased in North America and Europe during the middle 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.

Taxonomic and biological bias. A number of studies have documented taphonomic size bias influencing preservation of tetrapod fossils on local scales (Behrensmeyer *et al.* 2003; Soligo & Andrews 2005; Muñoz-Durán & Van Valkenburgh 2006; González Riga & Astini 2007; Brown *et al.* 2013; Zanno & Makovicky 2013), and others have noticed connections between completeness and body size (Cleary *et al.* 2015; Gardner *et al.* 2016; Driscoll *et al.* 2019). However, we might not expect to detect similar taphonomic biases for adult sauropodomorphs given that they were much larger than most terrestrial tetrapods (Benson *et al.* 2018) and sauropods in particular, had body sizes (ranging from one to tens of tonnes) above previously proposed taphonomic thresholds (Brown *et al.* 2013).

The overall body size-completeness scatterplot (Fig. 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 weakly significant negative linear correlation between body mass and SCM2 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. 6). The very weakly significant positive temporal relationship between mean SCM2 and minimum body size (Cashmore *et al.* 2020, fig. S3D) might suggest the smallest body sizes of a population have an influence on the level of completeness in a 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 described above, and the low explanatory power of the correlation and the lack of relationship between completeness and the mean and maximum body mass estimates suggest that 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 is probably not hampered by size related taphonomic controls.

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. The lack of a significant phylogenetic signal for all taxa in the Hedman dated tree demonstrates the strong impact of the dating methodology on results, but suggests the signal in Sauropoda is trustworthy and more likely to be biologically significant. However, this signal only demonstrates that there is a recognizable pattern to the sauropodomorph fossil record, and does not necessarily imply any underlying process (Blomberg & Garland 2002).

The non-temporal distributions of SCM2 scores of sauropodomorph subgroups have changed little in comparison to one another over the last 10 years. Mannion & Upchurch (2010*a*) 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 (Fig. 4C; Cashmore *et al.* 2020, table S6). The Cretaceous produces considerably less complete sauropodomorph skeletons on average than preceding time intervals (Cashmore *et al.* 2020, fig. S2A), and a large component of that pattern is the consistently low completeness scores for titanosaurs (Fig. 4; Cashmore *et al.* 2020, fig. S7), which dominated many Cretaceous terrestrial faunas (56% of Cretaceous sauropodomorphs in our dataset), 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 Upper Triassic of western Europe (Sander 1992) and Upper Jurassic of the western USA (Carpenter 2013), and productive formations in the Middle–Upper Jurassic of China (Li *et al.* 2011), whereas there are no equivalent Cretaceous deposits preserving titanosaurs. González Riga & 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 Upper Cretaceous Patagonian deposits.

As well as unfortunate preservation regimes, there might be more subtle biological and ecological influences upon the relatively poor Cretaceous sauropodomorph record. 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 & Klein 2005; Griebeler *et al.* 2013; Hofmann & Sander 2014), and ecological and environmental interactions (Barrett & 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.* 2012). 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 & 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. Higher ecological specificity (Bonaparte & Coria 1993; Sander *et al.* 2008, 2011; Griebeler & Werner 2011; Klein *et al.* 2012) could also have precluded some titanosaur species from consistent preservation in active depositional settings. By contrast, non-sauropod sauropodomorphs are regarded as having high ecological diversity, varying diets (McPhee *et al.* 2017; Müller & 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.

Human bias. It is possible that researchers might 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 (Polly & Head 2004; Soligo & Andrews 2005; Bell *et al.* 2010; Mannion & Upchurch 2010*a*; Zeder & Pilaar 2010; Hendy 2011; Carrasco 2013). As Mannion & Upchurch (2010*a*) 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 & Upchurch 2010*a*). Though the relative diagnosability of individual sauropodomorph bones and subgroups has not yet been quantified, we can make some generalizations as to the usefulness of different skeletal sections.

In sauropods (especially eusauropods) for example, the presacral vertebrae are extremely character-rich, primarily relating to complex laminae (e.g. Upchurch *et al.* 2004). 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 the vertebral series of the latter constitute higher numbers of more robust individual vertebrae, which might 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 are distinctly procoelous (Otero *et al.* 2011) and often the most common elements found in sauropod-bearing assemblages are caudal vertebrae and limbs (e.g. Winkler *et al.* 2000; González Riga & 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 (e.g. presacral vertebrae). Although we have not quantified it here, future studies could attempt to understand the connection between element-specific preservation biases, skeletal completeness, and recognition of diagnostic traits by identifying which bones are used to characterize species in published diagnoses in combination with element-specific presence data, such as that presented in Cashmore *et al.* (2020).

On the other hand, there is the possibility that researchers have artificially oversplit Cretaceous species because of the isolated nature of remains (Mannion & Upchurch 2010*a*), 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. 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.

Specimen collection bias, fieldwork collection preferences and museum practice could also potentially influence the signals documented in completeness studies, including the current one. For example, there are known historical collection biases towards the acquisition of adult ceratopsian dinosaur skulls in some North American localities (Goodwin & Horner 2010), and a preference for dinosaur fossil collection from particular lithologies in the Hell Creek Formation (Lyson & Longrich 2010). 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. Like most previous studies of completeness, we have been unable to incorporate unpublished museum material. When such material is included in other macroevolutionary studies, significant changes have been noted (e.g. Marshall *et al.* 2018). The assembly of this ‘dark’ data, and an informed understanding of sauropodomorph fossil collection practices, is beyond the scope of this study, but may provide a useful avenue for future research. Nevertheless, these precise issues highlight the importance of retrospective studies like the one presented here. Our study, and historical studies like it, act to test whether previous conclusions are robust to the impact of new data, and help palaeontologists recognize the influence of new discoveries and research on our evolutionary understanding of the fossil record.

CONCLUSION

We reassess the quality of the fossil record for a tetrapod group in a retrospective manner. Through the consistent use of a simple metric to quantify the completeness of fossil specimens, it is possible to keep a detailed 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 10 years, are as follows:

1. Research findings change through historical time and are currently changing rapidly. Ten years of discoveries and revisions to existing taxa since Mannion & Upchurch's (2010*a*) initial assessment of the completeness of the sauropodomorph fossil record has led to a 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.
2. 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 substantially change further in the next decades.
3. 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 drop in completeness in the Cretaceous.
4. These consistencies suggest that our current understanding of sauropodomorph diversity changes might be influenced by the completeness of the sauropodomorph fossil specimens, as well as temporal and spatial sampling, especially in the Cretaceous. Sauropodomorphs show 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. Although most of these similarities result from the lower quality fossil record in the earliest Cretaceous, geological processes acting upon all Mesozoic terrestrial deposits might 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 strongly influenced the completeness of discoveries at the global scale, and therefore has not negatively influenced our understanding of sauropodomorph macroevolution.
5. 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 substantially impacted the quality of their record. The much lower Cretaceous completeness could, however, be related to sea level fluctuations and their 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 recognizable remains of more morphologically distinct derived forms, enabling consistent species identification from less complete material.
6. 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.

Acknowledgements. This research was funded by the European Union's Horizon 2020 research and innovation programme under grant agreement 637483 (ERC Starting Grant TERRA to RJB). PDM's contribution was supported by a Royal Society University Research Fellowship (UF160216). This is Paleobiology Database official publication number 367. We thank Pedro Godoy and Roger Close for their invaluable methodological assistance. We would further like to thank Neil Brocklehurst and Daniel Driscoll for their helpful reviews which improved the manuscript.

DATA ARCHIVING STATEMENT

Data for this study, including the completeness database and supplementary figures and tables, are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6hdr7sqxb
Paleobiology Database data downloads used in this study are available in the PBDB Data Archive: https://doi.org/10.13021/07xa-0m52 (archive ID 364: Sauropodomorpha occurrences); https://doi.org/10.13021/bbn5-7s28 (archive ID 365: Carnian–Maastrichtian Tetrapoda occurrences).

Editor. Roger Benson

REFERENCES

ADLER, D. and KELLY, S. T. 2019. vioplot: Violin plot. R package v. 0.3.4. https://github.com/TomKellyGenetics/vioplot

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

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

—— 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.

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.

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. 2012. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology & Evolution*, **3**, 803–807.

—— and WAGNER, P. J. 2019. paleotree: Paleontological and Phylogenetic Analyses of Evolution. R package v. 3.3.0. https://cran.r-project.org/package=paleotree

BARRETT, P. M. and UPCHURCH, P. 2005. Sauropod diversity through time: possible macroevolutionary and palaeoecological implications. 125–156. *In* CURRY-ROGERS, K. A. and WILSON, J. A. (eds). *The sauropods: Evolution and paleobiology*. University of California Press, 358 pp.

—— McGOWAN, A. J. and PAGE, V. 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society B*, **276**, 2667–2674.

BARTOŃ, K. 2019. MuMIn: Multi-model inference. R package v. 1.43.15. https://cran.r-project.org/package=MuMIn

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., 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, 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 & Abstracts*, 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. 2018. Dinosaur macroevolution and macroecology. *Annual Review of Ecology, Evolution, and Systematics*, **49**, 379–408.

—— and MANNION, P. D. 2011. Multi-variate models are essential for understanding vertebrate diversification in deep time. *Biology Letters*, **8**, 127–130.

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

—— 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.

—— 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.

—— 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. 2008. Fossil quality and naming dinosaurs. *Biology Letters*, **4**, 729–732.

—— 2010. Naming dinosaur species: the performance of prolific authors. *Journal of Vertebrate Paleontology*, **30**, 1478–1485.

—— and STORRS, G. W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology*, **22**, 111–114.

—— —— 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, 316 pp.

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

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

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

BONAPARTE, J. F. and CORIA, R. A. 1993. A new and huge titanosaur sauropod from the Rio Limay Formation (Albian-Cenomanian) of Neuquen Province, Argentina. *Ameghiniana*, **30**, 271–282.

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.

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.

—— 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. and BUTLER, R. J. 2019. Quantifying the completeness of the chiropteran fossil record. *Palaeontology*, **62**, 757–776.

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 B*, **278**, 1165–1170.

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., PARRA RUGE, M. L., PADILLA BERNAL, S., PÁRAMO-FONSECA, M. E. and ETAVO-SERNA, F. 2015. A new Early Cretaceous brachiosaurid (Dinosauria, Neosauropoda) from northwestern Gondwana (Villa de Leiva, Colombia). *Journal of Vertebrate Paleontology*, **35**, e980505.

—— —— 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*, **284**, 20171219.

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. and WIBLE, J. R. (eds). *Amniote paleobiology*. University of Chicago Press, 547 pp.

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

CASHMORE, D. D. and BUTLER, R. J. 2019. Skeletal completeness of the non-avian theropod dinosaur fossil record. *Palaeontology*, **62**, 951–981.

—— MANNION, P. D., UPCHURCH, P. and BUTLER, R. J. 2020. Data from: Ten more years of discovery: revisiting the quality of the sauropodomorph dinosaur fossil record. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.6hdr7sqxb

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.

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.

—— 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 & 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.

—— —— and CLAUSS M. 2013. Ecological interactions in dinosaur communities: influences of small offspring and complex ontogenetic life histories. *PLoS One*, **8**, e77110.

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.

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.

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. 2019. The mosasaur fossil record through the lens of fossil completeness. *Palaeontology*, **62**, 51–75.

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.

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

ENGELMANN, G. F., CHURE, D. J. and FIORILLO, A. R. 2004. The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation. *Sedimentary Geology*, **167**, 297–308.

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

FARLOW, J. O., COROIAN, I. D. and FOSTER, J. R. 2010. Giants on the landscape: modelling the abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA). *Historical Biology*, **22**, 403–429.

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.

—— and SEPKOSKI, J. J. Jr 1999. Absolute measures of the completeness of the fossil record. *Nature*, **398**, 415–417.

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 B*, **272**, 289–294.

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.

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.

—— 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. 551–563. *In* RYAN, M. J., CHINNERY-ALLGEIER, B. J. and EBERTH, D. A. (eds). *New perspectives on horned dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Indiana University Press, 567 pp.

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. 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, 331 pp.

—— 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.

HAQ, B., HARDENBOL, J. and VAIL, P. R. 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, **235**, 1156–1167.

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.

HEDMAN, M. M. 2010. Constraints on clade ages from fossil outgroups. *Paleobiology*, **36**, 16–31.

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, 600 pp.

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.

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

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.

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.

KIDWELL, S. M. and HOLLAND, S. M. 2002. The quality of the fossil record: implications for evolutionary analyses. *Annual Review of Ecology & 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.

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.

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.

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.

—— 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*, **275**, 2483–2490.

—— 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.

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*, **278**, 1158–1164.

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

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

—— —— 2010*b*. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology*, **36** (2), 253–282.

—— —— 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.

—— —— 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.

—— 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 & Biogeography*, **21**, 898–908.

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

—— UPCHURCH, P., SCHWARZ, D. and WINGS, O. 2019*b*. 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.

MARSOLA, J. C., FERREIRA, G. S., LANGER, M. C., BUTTON, D. J. and BUTLER, R. J. 2019. Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. *Palaeontology*, **62**, 473–482.

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, Short Papers*. Occasional Paper of the Tyrrell Museum of Palaeontology, Alberta, vol. **3**, 239 pp.

McNAMARA, M. E., ORR, P. J., ALCALÁ, L., ANADÓN, P. and PEÑALVER, E. 2012. 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.

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.

—— 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.

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

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*, published online 8 March. https://doi.org/10.1080/08912963.2019.1587754

—— LANGER, M. C., BRONZATI, M., PACHECO, C. P., CABREIRA, S. F. and DIAS-DA-SILVA, S. 2018*a*. 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.

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

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

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.

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. 600 pp.

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.

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 v. 1.0.1. https://cran.r-project.org/package=caper

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.

—— 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.

PARADIS, E. and SCHLIEP, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**, 526–528.

—— 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 v. 5.3. https://cran.r-project.org/package=ape

PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D., HEISTERKAMP, S., WILLIGEN, B. V. and R CORE TEAM 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package v. 3.1-142. https://cran.r-project.org/package=nlme

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, 270 pp.

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., 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.

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

—— 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology*, **2**, 289–297.

R CORE TEAM 2019. R: a language and environment for statistical computing. v. 3.6.1. R Foundation for Statistical Computing. https://www.r-project.org

REVELL, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology & Evolution*, **3**, 217–223.

—— 2019. phytools: Phylogenetic Tools for Comparative Biology (and Other Things). R package v. 0.6-60. https://cran.r-project.org/package=phytools

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.

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.

—— 2013. An evolutionary cascade model for sauropod dinosaur gigantism-overview, update and tests. *PLoS One*, **8**, e78573.

—— and CLAUSS, M. 2008. Sauropod gigantism. *Science*, **322**, 200–201.

—— and KLEIN, N. 2005. Developmental plasticity in the life history of a prosauropod dinosaur. *Science*, **310**, 1800–1802.

—— 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.

—— 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.

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 & Planetary Sciences*, **25**, 435–489.

—— 1999. The evolution of dinosaurs. *Science*, **284**, 2137–2147.

SIMÓN, E., SALGADO, L. and CALVO, J. O. 2018. 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 B*, **356**, 351–367.

—— 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.

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*, **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.

—— 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*, **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.

TENNANT, J. P., MANNION, P. D. and UPCHURCH, P. 2016*a*. Environmental drivers of crocodyliform extinction across the Jurassic/Cretaceous transition. *Proceedings of the Royal Society B*, **283**, 20152840.

—— —— —— 2016*b*. Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nature Communications* **7**, 12737.

—— —— —— SUTTON, M. D. and PRICE, G. D. 2017. Biotic and environmental dynamics through the Late Jurassic-Early Cretaceous transition: evidence for protracted faunal and ecological turnover. *Biological Reviews*, **92**, 776–814.

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

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

—— —— 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.

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

—— 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, 349 pp.

—— —— and DODSON P. 2004. Sauropoda. 259–322. *In* WEISCHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). *Dinosauria*. 2nd edn. University of California Press, 861 pp.

—— 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 pp.

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. 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 & 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.

WEISHAMPEL, 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.

—— 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.

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.

WICKHAM, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer, 260 pp.

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., 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*, **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.

—— 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*, **303**, 759–771.