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Spatiotemporal variation in completeness of the early cynodont fossil record and its implications for mammalian evolutionary history

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RRH: CYNODONT FOSSIL RECORD
LRH: VARNHAM ET AL.

ABSTRACT

Mammals are the only surviving group of Cynodontia, a synapsid clade that first appears in the fossil record in the late Permian, ~260 million years ago. Here, using three metrics that capture skeletal completeness, we quantify the quality of the early cynodont fossil record in time and space to evaluate the impact of sampling and preservational biases on our understanding of the group's evolutionary history. There is no consistent global sampling signal for early cynodonts. Completeness of the cynodont fossil record increases across the Permian/Triassic boundary, peaking in the Early–early Late Triassic. This peak is dominated by specimens from southern Africa and South America, where a highly seasonal climate likely favoured preservation. Completeness is generally lower thereafter, correlated with a shift from a Gondwanan to a predominantly Laurasian fossil record. Phylogenetic and stratigraphic congruence in early cynodonts is high, although their fossil record exhibits less skeletal completeness overall than other tetrapod clades, including the contemporaneous anomodont synapsids. This discrepancy could be due to differences in the diagnosability of their fossils, especially for small-bodied species. Establishing the timing and assembly of derived ('mammalian') anatomical features in Cynodontia is obscured by sampling. Two of the major nodes at which acquisition of mammalian features is concentrated (Cynodontia and

Mammaliamorpha) suffer from lengthy intervals of poor sampling prior to becoming abundant parts of tetrapod faunas. Low completeness in these intervals limits our ability to determine when certain ‘key’ mammalian characteristics evolved, or to identify the selective pressures that might have driven their origins.

Keywords: Cynodontia; diversity; mammals; sampling bias; Synapsida.

INTRODUCTION

Permo-Triassic terrestrial fossil assemblages, such as those documented in the Karoo Basin in southern Africa and Paraná Basin in South America, preserve evidence of complex ecosystems made up of a diverse array of vertebrate groups (e.g. Langer et al. 2007; Schultz et al. 2020; Smith et al. 2020). These assemblages include various diapsids and temnospondyls (e.g. Damiani 2004; Langer 2005), but are most renowned for their extensive record of therapsid synapsids (e.g. Fröbisch 2014; Viglietti et al. 2016; Abdala et al. 2020). Over the course of the Permian, therapsids diversified to fill a wide range of dietary and environmental niches (Kemp 2005; Angielczyk and Kammerer 2018). However, following the Permian/Triassic (P/T) mass extinction, around 251.9 million years ago (Ma), only a small fraction of the once diverse therapsid lineage survived (Botha and Smith 2006). Of the surviving therapsids, cynodonts were the most successful, and their descendants, the mammals, represent the only extant synapsid group (Hopson and Kitching 2001).

The earliest known cynodonts appear in the Wuchiapingian (early late Permian) of South Africa, but are rare and incompletely known components of the fauna (Botha et al. 2007; Kammerer 2016). Much more abundant and often exceptionally preserved cynodont fossils are found in Triassic deposits, particularly in southern Africa and South America. This Gondwanan record provides an important window into the acquisition of mammalian characteristics along the mammal stem (e.g. Bonaparte et al. 2005; Rodrigues et al. 2013; Crompton et al. 2017; Jones et al. 2018). In Laurasia, cynodonts are present by the Changhsingian (latest Permian; Ivakhnenko 2013) and also become more species-rich and widespread in the Triassic, with fossils found at sites across Europe, Asia, and North America (e.g. Godefroit and Battail 1997; Sues 2001; Gao et al. 2010).

Despite a global distribution, rich fossil record, and extensive study, prominent gaps in our knowledge of early cynodont evolution remain. These gaps limit our understanding of macroevolutionary trends within Cynodontia, such as response to mass extinctions and the timing and drivers of radiations, and can be attributed in large part to incomplete sampling. Sampling biases have long been recognized as a major factor obscuring our reading of the fossil record (e.g. Raup 1972; Allison and Briggs 1993; Alroy 2010) and encompass both human-mediated (e.g. worker effort) and natural (e.g. area of exposed outcrop) factors. To address these biases and try to mitigate their effects on our interpretations of prehistory, attempts have been made to assess the completeness of the fossil record, with most focusing on particular clades as case studies (e.g. Alba et al. 2001; Fountaine et al. 2005; Eiting and Gunnell 2009; Beardmore et al. 2012). Mannion and Upchurch (2010) developed two methods that quantified the completeness of individual skeletons to obtain a pair of completeness metrics for each species. They then used these metrics to evaluate trends in completeness across sauropodomorph dinosaurs through time (see also Cashmore et al. 2020). These approaches have since been applied to a number of additional taxonomic groups, namely non-avian theropods (Cashmore and Butler 2019), Mesozoic birds (Brocklehurst et al. 2012), pterosaurs (Dean et al. 2016), crocodylomorphs (Mannion et al. 2019), ichthyosaurs (Cleary et al. 2015), plesiosaurs (Tutin and Butler 2017), parareptilian tetrapods (Verrière et al. 2016), and several synapsid groups. The latter include pelycosaurs (Brocklehurst and Fröbisch, 2014), anomodonts (Walther and Fröbisch 2013), non-mammaliaform cynodonts (Lukic-Walther et al. 2019), eutherian mammals (Davies et al. 2017), and bats (Brown et al. 2019).

Lukic-Walther et al. (2019) examined global patterns of non-mammaliaform cynodont completeness across geological time using phylogenetically informative characters. In addition to general temporal patterns, they also studied phylogenetic diversity and body size as related to the cynodont record through time. The results of their analyses did not support a trend of decreasing preservation potential, indicating that progressive cynodont decline following the Middle Triassic is a genuine aspect of their evolutionary history and not just a sampling artefact. However, Lukic-Walther et al. (2019) did not address potential spatial variation in cynodont completeness, which is a major concern given the apparent ‘Gondwanocentrism’ of the Permo-Triassic cynodont record (Abdala and Ribeiro 2010).

Some aspects of the temporal patterns analyzed by Lukic-Walther et al. (2019) are also worth re-examining in further detail. Gondwanan cynodont species diversity appears to have increased between the late Permian and the Early Triassic, with continued high diversity through to the Late Triassic, when the diversity of non-mammaliaform members of Cynodontia seems to have declined. Although these observed patterns have been shown not to result from a decrease in preservational potential, there are additional sampling biases that could be obscuring genuine macroevolutionary signal in the data.

Here, non-mammaliaform cynodont completeness is quantified in a number of additional ways and examined spatially as well as temporally, to evaluate how regional patterns contribute to any global signal. The completeness of the early cynodont record is also compared with that of other taxonomic groups to assess whether there are common preservational patterns, especially as regards other synapsids. Finally, we discuss how the completeness of the group's fossil record might impact our interpretation of early cynodont evolution and timing of the acquisition of mammalian characters.

MATERIALS AND METHODS

Dataset

We compiled a dataset of 126 species of non-mammaliaform cynodonts (i.e. cynodonts outside of the subclade Mammaliaformes *sensu* Rowe 1988) currently considered to be valid. Fossils of non-mammaliaform cynodonts have been found globally, and are known in deposits ranging from the late Permian (e.g. Sues and Munk 1996; Ivakhnenko 2012; Abdala et al. 2019) to the Early Cretaceous (e.g. Lopatin and Agadjanian 2008; Matsuoka et al. 2016). Only taxa based on body fossils were included; ichnotaxa were not analyzed. Although ichnites can provide important complements to the body fossil record in determining geographic and stratigraphic ranges of major tetrapod clades (e.g. Marchetti et al. 2017), their effective '0% completeness' and the difficulty in assigning ichnotaxa to specific trackmakers makes them unsuited for this type of analysis. Our dataset is based on data presented in Lukic-Walther et al. (2019), augmented with a comprehensive review of the recent literature. Mammaliaforms were excluded from the analysis in order to focus on the fossil record outside of the major Mesozoic mammal radiations (which have a predominantly dental record; Kielan-Jaworowska et al. 2004), examining effects of this record on the timing and assembly of mammal-like features.

Data on the stratigraphic age and geographic location (including present-day- and palaeo-coordinates) of occurrences of each cynodont species were compiled from the literature and The Paleobiology Database (www.paleobiodb.org). We used a conservative approach to stratigraphic ages when there is some uncertainty; for example, the Manda Formation in Tanzania is generally considered to be Middle Triassic (Anisian–Ladinian) but might be Carnian (e.g. Ottone et al. 2014; Wynd et al. 2017); as such, occurrences from this stratigraphic unit are assigned to the Middle–early Late Triassic. In addition to newly described species and some revisions to stratigraphic ages, one notable difference from the dataset of Lukic-Walther et al. (2019) pertains to our treatment of *Oligokyphus* from the Early Jurassic of the UK (Kühne 1956). Whereas those authors considered the co-occurring species *O. major* and *O. minor* as distinct taxa, with each represented by limited skeletal remains, here we follow Hopson and Kitching (1972; see also Sues 1985) in regarding the latter species as a junior synonym of the former. As a consequence, material that could not previously be unequivocally assigned to either species has now all been included in *O. major*, greatly increasing the completeness score for this taxon. The dataset is up-to-date as of the 25th of June, 2020 and is available in Varnham et al. (2020).

The body size of each cynodont species was estimated to evaluate whether sampling and preservation bias varied between different size classes. Previous studies have shown that tooth dimensions are good proxies for overall body size in mammals (e.g. Creighton 1980), and that approach is used here for their cynodont outgroups. Each species was assigned to a size category based on the average anteroposterior length of their postcanines, using k-means clustering to identify discrete body size clusters (Wang and Song 2011). The optimal number of clusters was four using the Elbow method (Wang and Song 2011), with tooth size ranges of: (1) 0–2.8 mm; (2) >2.8–5.0 mm; (3) >5.0–8.0 mm; and (4) >8.0 mm. This analysis was carried out using RStudio version 1.2.5019 (R Core Team 2019; RStudio Team 2019).

Completeness metrics

Using the approach proposed by Mannion and Upchurch (2010), a Skeletal Completeness Metric (SCM) was calculated for each species. This was achieved by dividing the cynodont skeleton into body regions, each of which was assigned a percentage based on approximations of how much of the skeleton is accounted for by that region (Figure 1). Within each region, individual elements were also assigned a percentage (Table 1). Absence of an element resulted in a score of zero, whereas it received 50% of its weighted score if some part of that element was preserved. There is variation in the numbers of vertebrae, carpal elements, and phalanges amongst cynodonts, making it difficult to determine the completeness of a partial skeleton. As such, for species in which these areas are incompletely preserved, the total possible number of these elements was estimated based on the anatomy of the most closely related species in which the relevant region of the skeleton is completely preserved. We calculated this metric based on all known specimens of each species, which is equivalent to SCM2 in Mannion and Upchurch (2010), hereafter referred to as SCM for simplicity.

A second completeness metric, proposed by Beardmore et al. (2012), was also used. Here, the cynodont skeleton was divided into six regions (skull, vertebrae and ribs, pectoral girdle, forelimbs, pelvic girdle, hindlimbs) and the completeness of each region was scored using a semi-qualitative scale from 0 to 4, with 0 being entirely absent and 4 being complete. In the current study, regions of specimens were scored as: (i) zero if the region was absent; (ii) 1 if ≤25% complete; (iii) 2 if 26–50% complete; (iv) 3 if 51–75% complete; and (v) 4 if ≥76% complete. Values for each region were then summed and divided by the total possible score (in this case, 24) and multiplied by 100 to give a percentage completeness score. Following Cleary et al. (2015), we refer to this metric as Beardmore's Skeletal Completeness Metric (BSCM).

Mannion and Upchurch (2010) also proposed a Character Completeness Metric (CCM). The CCM follows the same principles as the SCM, but the percentages assigned to each region are instead a measure of the amount of phylogenetically informative data preserved within each region. CCM values can be calculated from the average percentage of characters attributed to each region of the skeleton from published phylogenies of the clade. Here, CCM values for cynodont species were obtained from Lukic-Walther et al. (2019), excluding those for *Oligokyphus major* (see above).

Data series and spatiotemporal bins

A mean average completeness value of cynodont scores and associated standard deviations was calculated for each metric in each spatiotemporal bin. Where fossil occurrences have poor stratigraphic age resolution and could not be assigned to a single time bin, their full stratigraphic uncertainty was used as their temporal range. Observed ('face value') diversity was also calculated by summing the number of valid species within each spatiotemporal bin. Two different time binning strategies were used. Firstly, we used standard stratigraphic stages based on the 2018 version (v. 5.0) of the geological time scale presented by Cohen et al. (2013). As such, species were assigned to a full stage (e.g. Carnian), even if they could be dated more precisely (e.g. early Carnian). However, the durations of each stage are highly variable; for example, the Induan spans less than one million years (251.9–251.2 Ma), whereas the Norian spans 18.5 million years (227–208.5 Ma). Longer intervals might preserve a greater number of species purely as a result of there being a longer time for fossil accumulation, such that stage-level binning causes time-averaging of non-contemporaneous species. Therefore, a second set of time bins with approximately equal durations was used (e.g. see Benson et al. 2016), combining several short stages whilst maintaining important stratigraphic boundaries (Table 2).

Temporal fluctuations in cynodont completeness (using all three metrics) and observed diversity were reconstructed at the global level for both time-binning strategies. By contrast, we limited our spatial reconstructions of completeness and observed diversity to stage-level bins. In these reconstructions, we evaluated completeness (using only SCM) and observed diversity in five palaeocontinents (Africa + Indo-Madagascar, Asia, Europe, North America, and South America; note that Antarctica and Australasia were excluded due to the limited amount of non-mammaliaform cynodont remains found in the former and total absence in the latter), Laurasia (comprising specimens from Asia, Europe, and North America) and Gondwana (consisting of specimens from Africa, Antarctica, India, Madagascar, and South America), as well as within 10° palaeolatitudinal bands.

Comparisons with other clades

The completeness metrics calculated for cynodonts were compared with contemporaneous clades for which completeness data exists. Comparisons were made with terrestrial taxa, comprising anomodonts (Walther and Fröbisch 2013), parareptilian tetrapods (Verrière et al. 2016), Mesozoic birds (Brocklehurst et al. 2012), pterosaurs (Dean et al. 2016), pelycosaurian-grade synapsids (Brocklehurst and Fröbisch 2014), non-avian theropods (Cashmore and Butler 2019), and sauropodomorphs (Cashmore et al. 2020), as well as marine taxa, consisting of plesiosaurs (Tutin and Butler 2017) and ichthyosaurs (Cleary et al. 2015). Comparisons were also made with two non-contemporaneous mammalian clades: eutherians (Davies et al. 2017) and bats (Brown et al. 2019). In all cases, the spread of data (i.e. distribution of completeness values) for each of these groups was compared with that of non-mammaliaform cynodonts. Where there is substantial temporal overlap, comparisons of completeness were also evaluated through geological time.

Stratigraphic and phylogenetic congruence

There are several methods for testing the congruence between phylogeny and stratigraphy, although all of them are biased by parameters that are not distributed uniformly through time, such as tree size, average ghost length duration, and speciation rates (O'Connor et al. 2011). Here, we applied four widely used metrics for assessing congruence: (1) the stratigraphic consistency index (SCI) (Huelsenbeck 1994); (2) the relative completeness index (RCI) (Benton and Storrs 1994); (3) the gap excess ratio (GER) (Wills 1999); and (4) the Manhattan stratigraphic measure (MSM*) (Pol and Norell 2001; Siddall 1998). We constructed an informal supertree based on Lukic-Walther et al. (2019) and recent topologies and taxonomic studies (Hopson and Kitching 2001; Sidor and Smith 2004; Matsuoka et al. 2016; Pavanatto et al. 2018; Sidor and Hopson 2018; Abdala et al. 2019; Hendrickx et al. 2019; Wallace et al. 2019; Mocke et al. 2020). This supertree includes 93 non-mammaliaform cynodont species.

Analyses

Spatiotemporal bins with zero value data were excluded prior to analysis. All spatial- and time-series data were log-transformed, and generalised differencing was applied to remove the effects of trend and autocorrelation, using a function written by Lloyd (2008). Three statistical tests were used to assess the degree of spatiotemporal correlation between the completeness metrics (SCM, CCM, and BSCM [including those of comparative clades]) and diversity. Spearman's rank correlation coefficient and Kendall's tau coefficient are non-parametric tests that measure the ordinal association of two variables. Pearson's correlation coefficient is a parametric test that measures the strength of the linear correlation between two variables. Non-temporal pairwise comparisons were conducted using the non-parametric Mann-Whitney U test. Congruence between stratigraphic and phylogenetic data was evaluated using the R packages ape v.5.3 (Paradis and Schliep 2019) and strap v.1.4 (Bell and Lloyd 2015), using the StrapPhyloCongruence function. All analyses were implemented in the R programming language (R Core Team 2019), using RStudio version 1.2.5019 (RStudio Team 2019).

RESULTS

Comparisons of completeness metrics and diversity for cynodonts

All SCM, BSCM, and CCM metrics for non-mammaliaform cynodonts have a statistically significant positive correlation through time and space with one another (Table 3). This is the case under both binning schemes, although the correlation is weaker when using stage-level bins. The strongest correlation is consistently between SCM and BSCM, whereas the weakest correlation is between BSCM and CCM.

There is no statistically significant relationship between observed diversity and any of the completeness metrics spatially (Table 3), but some significant relationships are present temporally. Using stage-level bins, there is a significant positive correlation between observed diversity and CCM using Spearman's rank correlation coefficient, and with BSCM using Kendall's tau coefficient. Using the 'equal'-length time bins, a significant positive correlation between observed diversity and CCM is found in all three tests, with BSCM using Kendall's tau coefficient and Pearson's correlation coefficient, and with SCM using Pearson's correlation coefficient (Table 3).

Global patterns in completeness and diversity

The mean average SCM for all 126 cynodont species is 18%, with completeness values for each species ranging from 1% to 99% (Figure 2). The Permian has the highest mean SCM (23%: 9 species in total) of the four geological periods under study, whereas the Cretaceous is characterised by the lowest mean SCM (1%: 3 species) (Figure 3). Although the Triassic records the greatest number of cynodonts (88 species), including the most completely known species (*Thrinaxodon liorhinus* at 99%), it also has the largest range of SCM values and a mean SCM of only 18%. 26 species are known from the Jurassic, which has a mean SCM of 19%.

Temporal patterns of global completeness and observed diversity using 'equal'-length time bins do not differ significantly from those at stage-level (Figure 2); as such, the following focuses on results based on the latter analyses. The mean SCM and CCM values are relatively high in the Wuchiapingian (23% and 41%, respectively) and Changhsingian (20% and 32%, respectively), whereas the mean BSCM is substantially lower (9% in the Wuchiapingian and 4% in the Changhsingian). Mean SCM, CCM and BSCM values increase across the P/T boundary. Observed diversity is consistently low throughout the late Permian and Early Triassic, followed by a rapid increase during the Anisian (early Middle Triassic) and peaking during the Ladinian–Carnian (late Middle–early Late Triassic; reaching 49 species). The mean averages of the three completeness metrics each show an overall decline during the Triassic, reaching a minimum in the Rhaetian. Following the Carnian, observed cynodont diversity declines, remaining low throughout the successive stages (Figure 2), with the exception of a relatively small spike in the number of species (5) in the Oxfordian (early Late Jurassic). There is an increase in mean completeness values in the Early Jurassic, but completeness is relatively low throughout the remainder of the Mesozoic. Both the SCM (46%) and BSCM (42%) peak during the Pliensbachian (Early Jurassic), whereas the CCM attains its highest value (52%) in the Anisian.

Regional patterns in completeness and diversity

The mean SCM of non-mammaliaform cynodont species from Gondwana is higher (24%: 74 species) than that of species from Laurasia (11%: 55 species). Laurasian species have been found in time intervals ranging from the late Permian to the Early Cretaceous, whereas no Gondwanan species have been recorded from later than the Early Jurassic (Figure 4).

Within each of the five smaller palaeocontinents under consideration, Africa + Indo-Madagascar has the highest mean SCM (27%: 39 species) and the greatest range of SCM values (1–99%), with early cynodont species represented in every stage between the Wuchiapingian and Sinemurian, inclusive (Figures 5 and 6). South America has the second highest mean SCM at 24% (38 species between the Anisian and Pliensbachian). The range of SCM values from South America is similar to that of Africa (1–92%). The mean SCM of cynodonts from Asia is 12% (19 species between the Olenekian and Valanginian) and that of North America is 15% (10 species between the Carnian and Pliensbachian). The greatest temporal range is observed in the European palaeocontinental record, which spans the Wuchiapingian to the Aptian (based on the occurrence of *Xenocretosuchus sibiricus* in present-day Russia [Tatarinov and Matchenko 1999], here binned into the European palaeocontinental region for analytical purposes. Although Russia spans the European and

Asian continents, the majority of non-mammaliaform cynodont fossils have been found in European Russia, with *Xenocretosuchus* from Siberia being one of the few exceptions. If *Xenocretosuchus* is excluded, the youngest European record is Bathonian [*Stereognathus ooliticus* from the UK]). Although it has the temporally most extensive non-mammaliform cynodont record, the mean European SCM is the lowest of all the palaeocontinents (9%: 26 species).

Palaeolatitudinal patterns in completeness and diversity

The southernmost palaeolatitudinal bands (71–80˚S and 81–90˚S) have the highest mean completeness at 99%, but this is due to a single occurrence of *Thrinaxodon liorhinus* (Colbert and Kitching 1977) within each palaeolatitudinal band (Figure 7). The palaeolatitudinal band of 11–20° N has the highest mean SCM of the Northern Hemisphere at 42% (4 species), resulting from highly complete specimens of *Kayentatherium wellesi* (Kermack 1982; Sues 1986). All other northern palaeolatitudinal bands have a mean SCM of <13%. The palaeolatitudinal bands of 51–60˚N and 61–70˚N have the lowest mean SCM at 1% (1 species). All Southern Hemisphere palaeolatitudinal bands have a mean SCM of >17%.

Body size variation in completeness and diversity

The smallest cynodont species (based on a postcanine length of 0–2.8 mm) have the lowest mean SCM (11%: 52 species), with values ranging between 1% and 99% (Figure 8). Their observed diversity is highest during the Middle–Late Triassic (Figure 9), peaking during the Ladinian and Norian. Species with a postcanine length of >2.8–5.0 mm have a mean SCM of 21% (41 species) and are present from the Wuchiapingian to the Aptian, peaking in diversity during the Carnian. Species with a postcanine length of >5.0–8.0 mm have a mean SCM of 26% (18 species) and are also found mostly between the Middle–Late Triassic. The largest cynodont species (postcanine length >8.0 mm) have the highest mean SCM of 28% (15 species), peaking in diversity during the Carnian.

Comparisons with other clades

There is no significant temporal correlation between cynodont completeness metrics and those of ichthyosaurs, plesiosaurs, anomodonts, parareptilian tetrapods, sauropodomorphs, or non-avian theropods (Table 4). However, there is a statistically significant correlation between the completeness of cynodonts and that of pterosaurs.

Regarding non-temporal comparisons, the results from the Mann-Whitney U tests demonstrate that the mean SCM (and BSCM) value for cynodonts is significantly lower than that of ichthyosaurs, parareptilian tetrapods, plesiosaurs, pelycosaurian-grade synapsids, non-avian theropods, and sauropodomorphs (Table 5; Figure 10A). Similarly, the mean CCM value of cynodonts is significantly lower than that of anomodonts, parareptilian tetrapods, plesiosaurs, and eutherians (Table 5; Figure 10B). In particular, the CCM values for anomodonts and parareptilian tetrapods are substantially greater. Although the mean SCM of cynodonts is significantly higher than that for bats, the reverse is true for the CCM.

Stratigraphic and phylogenetic congruence

High SCI and GER values suggest that that the early cynodont supertree has a better stratigraphic fit than would be expected by chance (Table 6). By contrast, the RCI value is equivocal, whereas the MSM* value indicates little congruence (Table 6).

DISCUSSION

Geological and environmental constraints on the early cynodont fossil record

Our results clearly demonstrate that there is no consistent global sampling signal for the non-mammaliaform cynodont fossil record, with most time intervals dominated by fossils from a relatively narrow spatial range. This accords with recent evaluations of the completeness of other terrestrial vertebrate groups (Mannion et al. 2019; Cashmore et al. 2020), as well as the broader sampling regime of the fossil record (e.g. Benson et al. 2016; Close et al. 2020).

All completeness metrics for cynodonts display a large increase across the P/T boundary (Figure 2). Two of the six Induan (earliest Triassic) species are among the most completely known early cynodonts (*Thrinaxodon liorhinus* and *Galesaurus planiceps,* with an

SCM of 99% and 96%, respectively), underlying this spike in completeness. By contrast, parareptilian tetrapods (Verrière et al. 2016) and anomodonts (Walther and Fröbisch 2013) show no substantial change in completeness across the P/T boundary. All three of these tetrapod groups survived the P/T mass extinction and are commonly found within the Beaufort Group of the Karoo Basin in South Africa, which provides a near-continuous, high-quality record of vertebrate faunas from the middle Permian to Middle Triassic. Unlike cynodonts, however, parareptiles and anomodonts also have an extensive Permian record. Thus, although these groups also exhibit high completeness in the Early Triassic, it constitutes continuation of an existing pattern rather than a notable spike.

During the Early–Middle Triassic, the cynodont record is dominated by species within the smaller cynodont size classes (i.e. those with a postcanine length ≤8 mm; see Figure 9), and their completeness is relatively high (Figure 2). Species at this time are found in high abundance mostly at palaeolatitudes of 40–70˚S (Figures 9 and 11) within the Beaufort Group in South Africa and the Puesto Viejo and Rosario do Sul groups of South America. These stratigraphic units consist of banded shales, mudstones, and fine-grained sandstones, indicative of low energy fluvial and floodplain depositional environments (e.g. Smith et al. 1993; Zerfass et al. 2003; Ottone et al. 2014). Badgley (1986) also noted that low energy fluvial environments have the potential to preserve a high proportion of small-bodied taxa, even if remains are mostly scattered and disarticulated. The Early–Middle Triassic climate of these high palaeolatitude Gondwanan regions was also highly seasonal, with periods of sustained aridification and reduced precipitation, interspersed by intense sporadic flooding (Dubiel et al. 1991; Smith et al. 1993; Zerfass et al. 2003; Pires et al. 2005; Pace et al. 2007). Highly variable climatic conditions have the potential to preserve concentrated fossil deposits of relatively complete individuals due to the aggregation of species in drought conditions (Smith 1993; Viglietti et al. 2013), reduced chemical weathering (Behrensmeyer 1978), or through mummification via windblown dust (Smith and Botha-Brink 2014). Furthermore, extreme flash floods can also preserve highly complete specimens through rapid burial and flooding of dens/burrows, as has been observed in some cynodonts (e.g. Smith 1993; Fernandez et al. 2013). It has also been suggested that both the synapsids (e.g. cynodonts) and archosauromorphs that survived the P/T extinction were well adapted to these stressful climatic conditions, allowing them to thrive, which might explain the relatively high cynodont diversity in the Early Triassic (Smith and Botha-Brink 2014) (Figures 2, 4 and 5).

On a global scale, values for all three cynodont completeness metrics decline from the Ladinian onwards, reaching a minimum in the Rhaetian (Figures 2, 4A). By contrast, observed diversity increases until the Carnian, declining in the Norian and thereafter. This contrasting trend of diversity and completeness was also noted by Lukic-Walther et al. (2019). They suggested that the reduction in completeness (using CCM in their case) throughout the latter half of the Triassic could be due to either a change in taxonomic practice (i.e. naming species based on poorly preserved fragmentary material) and/or a shift in cynodont body size evolution, potentially altering the preservation potential of the group. Behrensmeyer (1978) proposed that the rate of degradative taphonomic processes should operate more rapidly on smaller-bodied taxa as they have a higher surface area to volume ratio, providing a potential explanation as to why small cynodont taxa tend to have lower completeness values than their larger-bodied counterparts (Figures 8 and 9). Furthermore, global climate became increasingly humid from the Ladinian onwards (Zerfass et al. 2003; Tanner 2018), which might have led to increased weathering rates and elevated soil acidity. Humid conditions would thus affect the rate at which organic material corrodes on the surface (Behrensmeyer 1978; Fernández-Jalvo et al. 2010), and this might have severely impacted the completeness of skeletons of small taxa. Furthermore, taphonomic processes might vary between different sized taxa (Badgley 1986), with species <60 kg more commonly found as isolated remains (likely the case for cynodonts, see Figure 9), and larger taxa more often found as articulated skeletons (Brown et al. 2013). This might explain why the skeletons of larger-bodied taxa (e.g. sauropodomorphs) from the same deposits as cynodonts retain relatively high completeness during the Late Triassic (Mannion and Upchurch 2010; Cashmore et al. 2020). Collection techniques might also affect completeness values for Late Triassic and Early Jurassic taxa. For example, Lukic-Walther et al. (2019) noted that the Late Triassic record is characterised by intensive sieving and screen-washing sampling techniques, which is especially characteristic of collections from Rhaetian deposits. This method typically yields disarticulated and incomplete material, and indeed several Late Triassic cynodonts have been discovered this way (e.g. Sues et al. 1994; Godefroit 1999; Datta et al. 2004*;* Sulej et al. 2020). Therefore, genuine declines in diversity, a trend towards smaller body size, and a change in collection techniques likely all contribute to the Late Triassic decline in cynodont completeness.

Despite the apparent reduced number of rich tetrapod-bearing formations in the Early Jurassic relative to other Paleozoic and Mesozoic epochs (Benton et al. 2013), notably high completeness values have been observed at this time for sauropodomorphs (Mannion and Upchurch 2010), pterosaurs (Dean et al. 2016), ichthyosaurs (Cleary et al. 2015), and plesiosaurs (Tutin and Butler 2017). A small number of Early Jurassic formations have yielded exceptionally preserved specimens of these taxa, such as the upper Elliot Formation in South Africa for sauropodomorphs (e.g. McPhee et al. 2017) and the Blue Lias Formation in the UK for pterosaurs, plesiosaurs, and ichthyosaurs (e.g. Owen 1870). By contrast, there is no equivalent peak in cynodont completeness at this time. The majority of Jurassic and Cretaceous cynodont species are Laurasian and exhibit a lower completeness than their earlier Gondwanan counterparts (Figure 6). This low Laurasian completeness might partly result from certain environmental conditions during the Jurassic; for example, European localities that have yielded several cynodont remains are characterised by high humidity (Ruffell et al. 2002; Sellwood and Valdes 2008; Bougeault et al. 2017). The global peak in completeness during the Pliensbachian results from almost complete skeletons of the tritylodontid *Kayentatherium wellesi* (SCM of 92%) in the USA (Sues 1986), and the extensive number of disarticulated remains attributed to *Oligokyphus major* (SCM of 75%) from fissure fill deposits in the UK (Kühne 1956). These two taxa make up 50% of known Pliensbachian non-mammaliaform cynodont diversity (Figure 2). By contrast, the majority of European taxa have completeness values below 2%, composed mostly of isolated dental fragments, e.g. from the Gres à Avicula Formation in France (Godefroit and Battail 1997; Sigogneau-Russell 1983). Low completeness values throughout the remainder of the Mesozoic likely reflect genuine declines in diversity and abundance of non-mammaliaform cynodonts (Ruta et al. 2013; Lukic-Walther et al. 2019), reducing the likelihood of their preservation. Their reduced diversity might have resulted from increased competition, as their decline coincides with the emergence and diversification of Mammaliaformes, including morganucodontids and multituberculates (Newham et al. 2014).

Stratigraphic congruence of early cynodont evolutionary relationships

Despite low completeness for early cynodonts relative to most other clades, SCI (77%) and GER (85%) are high (Table 6), suggesting the group's phylogeny is generally stratigraphically congruent. By way of comparison, the values of SCI and GER for pelycosaurs are 54% and 58%, respectively (Brocklehurst and Fröbisch 2014). The high SCI and GER values of cynodonts contrast with their low MSM* values (22%). It has been observed that tetrapods in general have a lower MSM* (<50%) than plants, fishes, or echinoderms, but higher than arthropods and molluscs (O'Connor and Wills 2016). MSM* has been found to be heavily biased by tree size and shape (Siddall 1998), more so than SCI and GER, and it does not correlate strongly with other metrics (O'Connor and Wills 2016). Furthermore, MSM* is negatively correlated with the number of taxa included within the tree (O'Connor and Wills 2016), which might explain why the value for cynodonts is low given the relatively high number of taxa used here. Whereas the SCI, GER, and MSM* are more strictly measures of congruence, the RCI is better characterised as a measure of the completeness of the fossil record, defined as the ratio of the sum of observed ranges of taxa to the sum of the ghost ranges of taxa (Benton and Storrs 1994). The RCI score for cynodonts (45%) is lower than those of the SCI and GER. Lower RCI values can result from inaccurate phylogenies and/or a poor fossil record (Wagner 2000). However, given that the SCI and GER scores are higher than for other clades, this suggests that the congruence between phylogeny and stratigraphy for cynodonts is no worse than for other clades, and likely better. As such, we interpret the lower RCI value to more likely reflect a poor fossil record, as is further supported by the low completeness values relative to other clades (Figure 10).

The impact of diagnosability on fossil record completeness

Several authors have commented that the completeness of the fossil record potentially influences diversity reconstructions of any given clade (e.g. Benton et al. 2004; Eiting and Gunnell 2009; Mannion and Upchurch 2010; Brocklehurst et al. 2012; Brocklehurst and Fröbisch 2014). A spatiotemporal bin containing multiple complete skeletons might be expected to have high diversity, because such specimens should be more confidently assigned to species level given the increased opportunity to preserve and therefore identify autapomorphies (Mannion and Upchurch 2010). This appears to be the case for Mesozoic birds and pterosaurs, which are both characterised by a positive correlation between diversity and completeness (CCM in both cases), with a substantial proportion of their fossil records known from Lagerstätten (Brocklehurst et al. 2012; Dean et al. 2016). The fossil record of bats is also highly dependent on Lagerstätten (Brown et al. 2019), with a higher average CCM than cynodonts, but a significantly lower mean average SCM (Table 5). Whereas the low SCM of bats might be explained by rapid taphonomic degradation and disarticulation as a result of their small and fragile skeletons (e.g. Behrensmeyer 1978; Badgley 1986), their higher CCM could be because even disarticulated postcranial remains of bats are more phylogenetically informative relative to those of cynodonts. For example, postcranial characters account for approximately 50% of the total character completeness score in bats (Brown et al. 2019), compared to just over 10% in cynodonts (Lukic-Walther et al. 2019).

A positive correlation between cynodont diversity and CCM in some of our analyses (Table 3), but no correlation with SCM, could be explained by differences in diagnosability of fossil remains between this group and other tetrapod clades. Several cynodont species are known only from teeth and dental fragments, but cynodont dentition is often highly diagnostic (e.g. the gomphodont dentition exhibited in Cynognathia), making it easier to confidently assign incomplete material to lower taxonomic levels. Consequently, cynodont phylogenetic matrices are biased towards cranial and dental characteristics, resulting in a fossil record which might have low skeletal completeness relative to character completeness and diversity. The phylogenetic matrices of parareptilian tetrapods and anomodonts are also dominated by cranial characteristics (Walther and Fröbisch 2013), but members of these groups are generally more difficult to identify to lower taxonomic levels (i.e. genus or species) based on very limited material (e.g. isolated teeth), so that fewer nominal taxa used in phylogenetic analyses for those groups are known from fragments alone. Temporal pairwise comparisons show no significant correlation between the CCM of cynodonts and parareptilian tetrapods or anomodonts. This lack of correlation might be because both anomodonts and parareptilian tetrapods were genuinely much more abundant than cynodonts during the late Permian (Nicolas and Rubidge 2010; Fröbisch 2014; MacDougall et al. 2019), thereby increasing their preservation potential.

Similarly, a spatiotemporal bin dominated by highly incomplete specimens might be expected to have low observed diversity, due to a lack of preserved autapomorphies, meaning specimens can only be confidently assigned to higher taxonomic levels (Mannion and Upchurch 2010). However, Brocklehurst and Fröbisch (2014) recovered a significant negative correlation between completeness and diversity for pelycosaurs. This is most readily explained whereby multiple fragmentary specimens of the same species have been misdiagnosed as separate taxa, thus resulting in an overly-inflated diversity estimate

(Mannion and Upchurch 2010; Brocklehurst et al. 2012; Brocklehurst and Fröbisch 2014). It is possible that this issue is much more pervasive in groups with relatively low diagnosability.

Uncertainty in the timing of mammalian character acquisition

The origin of mammals from Triassic cynodonts is often cited as one of the best-documented macroevolutionary transitions in the fossil record (e.g. Hopson 1987), and we do not dispute this characterization. With that said, however, there is clear variation in the completeness of the cynodont record, and accordingly some sections of this transition are better understood than others. The spatiotemporal gaps in the cynodont record have particular influence on our understanding of the timing and sequence of acquisition of mammalian characters, and thus interpretations of selective forces shaping cynodont evolution.

Despite the low diversity of late Permian cynodonts, their completeness is relatively high (Figure 2), owing mostly to cranial material. Even these earliest known cynodonts already display a number of mammal-like cranial features related to increased efficiency of masticatory processing (Figure 12). One such feature is a shallow fossa on the coronoid process of the dentary paired with a flared zygomatic arch, placing the coronoid process near the middle of the temporal fenestra (Rubidge and Sidor 2001). This placement is widely observed across late Permian cynodonts, including *Dvinia*, *Procynosuchus, Charassognathus*, and *Abdalodon* (Hopson 1987; Kammerer 2016), and has been taken as evidence for the differentiation of the plesiomorphically unipartite adductor mandibulae into the more mammalian condition of the temporalis and masseter muscles (Barghusen 1968). Several late Permian cynodonts also show development of a secondary palate (Figure 12a), although it is incomplete in most taxa (e.g. *Procynosuchus*; Kemp 1979). A complete secondary palate is first observed at the node containing the Early Triassic *Thrinaxodon* and latest Permian *Nanictosaurus* (Pusch et al. 2019), indicating an origin of this morphology shortly before the P/T boundary.

The time of origin of the complete bony secondary palate and extension of the masseter onto the base of the dentary can be determined with a high degree of confidence, given that these characters appear during the peak of cynodont completeness in the late Permian–Early Triassic (Figures 2, 12). Similarly, there is robust support for the initial appearance of derived features characterizing the major cynodont subclade Eucynodontia in the Early or early Middle Triassic. In general (and perhaps unsurprisingly), many of the canonical exemplars used to illustrate the transitional series in cynodont evolution (e.g. Hopson 1987; Hopson and Kitching 2001; Rubidge and Sidor 2001) hail from the best-sampled, most complete, and most species-rich segment of non-mammaliaform cynodont history, such that we can have reasonable confidence that the suite of increasingly derived 'mammalian' features characterizing taxa such as *Procynosuchus*, *Thrinaxodon*, *Lumkuia*, and *Probainognathus* evolved close to the first appearances of these taxa in the fossil record.

By contrast, it is much more difficult to establish the time of origin for the mammal-like features (including those cited above) seen in the very earliest cynodonts. Cynodonts are unique among the major therapsid subclades in lacking a middle Permian (Guadalupian) record, although recent phylogenetic analyses indicate they must have originated by that time (Huttenlocker 2009). The ghost lineage between presumed cynodont origins (at some point in the middle Permian) and their first appearance in the late Permian record hinders our understanding of the assembly of mammalian characters. Did these characters appear rapidly, as part of coordinated changes in the masticatory system, or by gradual, stepwise addition? Our results indicate that additional sampling, at either localities or size classes beyond those currently sampled, will be necessary to address this question. Known Permian cynodont species are almost entirely restricted to high southern palaeotitudes in southern Africa (Figure 5), with substantially rarer records from lower northern palaeolatitudes (Figure 7), and the possibility that early cynodont diversification was occurring outside this handful of sampled basins must be considered.

Although the latest Permian and Early Triassic record accords reasonable confidence regarding the assembly of mammal-like cranial features in cynodonts, the postcranial signal is less clear. The earliest Triassic cynodont fossils are among the most complete known from any time bin, e.g. *Galesaurus planiceps* and *Thrinaxodon liorhinus* from South Africa. The nearly-complete postcrania of these species illustrate a number of derived features, demonstrating a differentiated vertebral column, reduced lumbar ribs, and a more mammalian structure of the manus (Jenkins 1971; Butler et al. 2019: Figure 12b). However, because of the low completeness of postcranial remains from the late Permian (Figure 2), it is difficult to confirm these features as novel to the Early Triassic (and thus possibly related to selective forces associated with ecological change across the P/T boundary). In particular, the lack of known postcrania in the earliest cynodonts (charassognathids) and later Permian relatives of *Galesaurus* and *Thrinaxodon* (e.g. *Cynosaurus* and *Nanictosaurus*) makes it difficult to reconstruct the origins of these morphologies; they probably evolved in the Permian (based on phylogenetic bracketing), but the sequence and timing of origin is unknown. Until more complete postcranial remains of cynodonts are discovered from the late Permian, this will remain unresolved.

Eucynodontia is made up of two subclades, Cynognathia and Probainognathia (Hopson and Kitching, 2001), both of which are found globally in the Triassic. Even the earliest-known eucynodonts (from the latest Early or earliest Middle Triassic) are clearly identifiable as belonging to one of these subclades, and in the case of the most 'basal' cynognathian (*Cynognathus* itself), show a circum-Gondwanan distribution. Although eucynodonts may well have been part of a rapid burst of post-extinction Triassic diversification also observed in coeval diapsid reptiles, the extensive geographic range of an already highly-specialized taxon like *Cynognathus* suggests that there is a missing record for the earliest phase of eucynodont evolution. Whether this is best attributed to temporal (i.e. greater separation between the *Lystrosaurus* and *Cynognathus* Assemblage Zones than usually thought; see Ottone et al. 2014) or geographic (i.e. eucynodonts originating outside of the well-sampled Gondwana basins; see Gao et al. 2010 for possible evidence of this) gaps is currently uncertain.

A final problem, comparable to the origins of Cynodontia and to a lesser extent Eucynodontia, concerns the early evolution of Mammaliamorpha, the clade containing mammaliaforms and their near-outgroups such as brasilodontids and tritylodontids (Kemp 1983; Liu and Olsen 2010; Martinelli 2016). In terms of cranial and postcranial morphology, these groups share many similarities with early Mammaliaformes (Figure 12), particularly regarding the loss of a postorbital bar, an expanded dentary, and highly modified dentition (Lucas and Luo 1993; Kemp 2005; Sullivan et al. 2013; Martinelli 2016; Martinelli et al. 2017; Guignard et al. 2019) (Figure 12c-f). The majority of 'basal' (i.e. non-mammaliaform) mammaliamorph diversity and their greatest skeletal completeness is found in the Jurassic; yet, based on phylogenetic relationships, its various subclades must have diverged by the Carnian, leaving extensive ghost lineages in the Late Triassic. The timing and assembly of the highly derived morphologies characteristic of groups such as the rodent-like tritylodontids is essentially unknown; the record seems biased against this group, as the relevant time intervals (late Middle and early Late Triassic) otherwise involve peaks in cynodont richness. Definite tritylodontids do not appear in the record until the latest Triassic (terminal Rhaetian), their record is almost exclusively Laurasian (with *Tritylodon* itself being a notable outlier), and it exhibits extremely low completeness (Figures 4–7).

The poor Triassic record of tritylodontids and other early mammaliamorphs impedes our understanding of the adaptive origins and initial function of several notable mammalian postcranial characters, such as epipubic bones (Fourie 1963; Parrington 1978). Epipubic bones in extant mammals are best known in marsupials, where they support the pouch; in the absence of a broader sample, it would be tempting to infer that they evolved for that purpose. However, the presence of epipubic bones in the pouchless, oviparous monotremes and numerous other fossil mammals (e.g. 'basal' eutherians, Novacek et al. 1997; multituberculates, Kielan-Jaworowska 1969), indicates that this is not the case, and their function in extant marsupials has likely been co-opted (Reilly and White, 2003; Reilly et al. 2009; White, 1989). Critical to interpretation of the initial acquisition of epipubic bones is their function in tritylodontids, the first cynodont group in which they appear. Unfortunately, the low completeness of the Late Triassic–Early Jurassic cynodont fossil record makes it hard to determine how and why such synapomorphic traits evolved.

CONCLUSIONS

Completeness of the non-mammaliaform cynodont fossil record is highest between the late Permian and the early Late Triassic. This early record is dominated by species from southern Africa and South America. During this time, these continents experienced highly variable climates, alternating between arid and monsoonal conditions, both of which can favour the preservation of skeletons. Completeness decreases from the Norian (middle Late Triassic) onwards, which might be a result of a genuine decline in non-mammaliaform cynodont diversity and abundance, combined with a shift in body size evolution. However, this also likely reflects the negative effect of increasingly humid conditions on fossil preservation, especially with the shift from a Gondwanan to a predominantly Laurasian fossil record from the Jurassic onwards.

The incompleteness of the early cynodont fossil record has implications for our understanding of the timing of the acquisition of mammal-like characteristics. For example, characters like complex, multicusped dentition, a masseteric fossa on the dentary, and development of a secondary palate are present in even the earliest cynodonts; we cannot tell when these characters first appeared, in what sequence they evolved, or infer the selective pressures that may have favoured their evolution, due to the poor Permian fossil record for the group. Similar issues cloud our understanding of the origins of several major cynodont subclades as well. Early members of Tritylodontidae, one of the cynodont subclades thought to be most closely related to mammaliaforms, first appear in the Late Triassic fossil record, but are already highly apomorphic and exhibit derived mammal-like features, such as an expanded dentary and the presence of epipubic bones. It is probable that these characters originated earlier in the Triassic, but poor sampling of postcranial elements, particularly at small body size, has obscured this record. Increased scope and geographic breadth of P/T microvertebrate sampling may ameliorate such issues, but the historical dominance of dental elements in such samples means that substantial uncertainty concerning the evolution in mammalian postcrania is likely to remain.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://datadryad.org/stash/share/el5_BWNNdRxPSz8GLC3rP03AUgIGKZuIINAU1om3HzY

REFERENCES

ABDALA, F. and RIBEIRO, A. M. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida: Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **286**, 202-217.

ABDALA, F., GAETANO, L. C., SMITH, R. M. H., and RUBIDGE, B. S. 2019. A new large cynodont from the Late Permian (Lopingian) of the South African Karoo Basin and its phylogenetic significance. *Zoological Journal of the Linnean Society*, **186**, 983-1005.

ABDALA, F., GAETANO, L. C., MARTINELLI, A. G., SOARES, M. B., HANCOX, P. J. and RUBIDGE, B. S. 2020. Non-mammaliaform cynodonts from western Gondwana and the significance of Argentinean forms in enhancing understanding of the group. *Journal of South American Earth Sciences,* **104**, 102884.

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

ALLISON, P. A. and BRIGGS, D. E. G. 1993. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology,* **21**, 65-68.

ALROY, J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology,* **53**, 1211-1235.

ANGIELCZYK, K. D. and KAMMERER, C. F. 2018. Non-mammalian synapsids: the deep roots of the mammalian family tree. In Asher, R. and Zachos, F. (eds). *Handbook of Zoology: Mammalia*. DeGruyter, Berlin, 117-198.

BADGLEY, C. 1986. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology,* **12**, 119-142.

BARGHUSEN, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor musculature. *Postilla,* **166**, 1-49.

BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T. and FURRER, H. 2012. Float or sink: modelling the taphonomic pathway of marine crocodiles (Mesoeucrocodylia, Thalattosuchia) during the death-burial interval. *Palaeobiodiversity and Palaeoenvironments,* **92**, 83-98.

BEHRENSMEYER, A. K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology,* **4**, 150-162.

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

BELL, M. A. and LLOYD, G. T. 2015. strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology,* **58**, 379-389.

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

BENTON, M. J., RUTA, M., DUNHILL, A. M. and SAKAMOTO, M. 2013. The first half of tetrapod evolution, sampling proxies, and the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **372**, 18-41.

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

BONAPARTE, J. F., MARTINELLI, A. G. and SCHULTZ, C. L. 2005. New information on Brasilodon and Brasilitherium (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia*, **8**, 25–46.

BOTHA, J. and SMITH, R. M. H. 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* **45**, 502-514.

BOTHA, J., ABDALA, F. and SMITH, R. 2007. The oldest cynodont: new clues on the origin and early diversification of the cynodontian. *Zoological Journal of the Linnean Society,* **149**, 477-492.

BOUGEAULT, C., PELLENARD, P., DECONINCK, J. –F., HESSELBO, S. P., DOMMERGUES, J. –L., BRUNEAU, L., COCQUEREZ, T., LAFFONT, R., HURET, E. and THIBAULT, N. 2017. Climatic and palaeoceanographic changes during the Pliensbachian (Early Jurassic) inferred from clay mineralogy and stable isotope (C-O) geochemistry (NW Europe). *Global and Planetary Change,* **149**, 139-152.

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

BROCKLEHURST, N., UPCHURCH, P., MANNION, P. D. and O'CONNOR, J. 2012. The Completeness of the Fossil Record of Mesozoic Birds: Implications for Early Avian Evolution. *PLoS ONE,* **7**, e39056.

BROWN, C. M., EVANS, D. C., CAMPIONE, N. E., O'BRIEN, L. J. and EBERTH, D. A. 2013. Evidence for size bias in the Dinosaur Park Formation (Campanian, Alberta), a model for

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 bat fossil record. *Palaeontology,* **62**, 757-776.

BUTLER, E., ABDALA, F. and BOTHA-BRINK, J. 2019. Postcranial morphology of the Early Triassic epicynodont *Galesaurus planiceps* (Owen) from the Karoo Basin, South Africa. *Papers in Palaeontology,* **5**, 1-32.

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

COHEN, K. M., FINNEY, S. and GIBBARD, P. L. 2012. International Chronostratigraphic Chat: International Commission on Stratigraphy. www.stratigraphy.org.

COLBERT, E. H. and KITCHING, J. W.. 1977. Triassic Cynodont Reptiles From Antarctica. *American Museum Novitates,* **2611**, 1-30

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. J., ALROY, J., CARRANO, M. T., CLEARY, T. J., DUNNE, E. M., MANNION, P. D., UHEN, M. D., and BUTLER, R. J. 2020. The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling biases. *Proceedings of the Royal Society B* 287: 20200372.

CREIGHTON, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. *Journal of Zoology,* **191**, 435-443.

CROMPTON, A. W., OWERKOWICZ, T., BHULLAR, B. –A. S. and MUSINSKY, C. 2017. Structure of the nasal region of non-mammalian cynodonts and mammaliaforms: Speculations on the evolution of mammalian endothermy. *Journal of Vertebrate Palaeontology,* **37**, e1269116.

DAMIANI, R. J. 2004. Temnospondyls of the Beaufort Group (Karoo Basin) of South Africa and their Biostratigraphy. *Gondwana Research,* **7**, 165-173.

DATTA, P. M., DAS, D. P. and LUO, Z. –X. 2004. A Late Triassic dromatheriid (Synapsida: Cynodontia) from India. *Annals of the Carnegie Museum,* **73**, 72-84.

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

EITING, T. P. and GUNNELL, G. F. 2009. Global Completeness of the Bat Fossil Record. *Journal of Mammalian Evolution,* **16**, 151-173.

FERNANDEZ, V., ABDALA, F., CARLSON, K. J., COOK, D. C., RUBIDGE, B. S., YATES, A. and TAFFOREAU, P. 2013. Synchrotron reveals Early Triassic odd couple: Injured amphibian and aestivating therapsid share burrow. *PLoS ONE,* **8**, e64978.

FERNÁNDEZ-JALVO, Y., ANDREWS, P., PESQUERO, D., SMITH, C., MARÍN-MONFORT, D., SÁNCHEZ, B., GEIGL, Q. –M. and ALONSO, A. 2010. Early bone diagenesis in temperate environments: Part 1: Surface features and histology. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **288**, 62-81.

FOUNTAINE, T. M. R., 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.

FOURIE, S. 1963. A new Tritylodontid from the Cave Sandstone of South Africa. *Nature*, **198**, 201.

FRÖBISCH, J. 2014. Chapter 18: Synapsid Diversity and the Rock Record in the Permian-Triassic Beaufort Group (Karoo Supergroup), South Africa. *In* KAMMERER, C. F., ANGIELCZYK, K. D. and FRÖBISCH, J. (eds). Early Evolutionary History of the Synapsida. *Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht, pp. 305-319.

GAO, K.-Q., FOX, R. C., ZHOU, C.-F. and LI, D.-Q. 2010. A new nonmammalian eucynodont (Synapsida: Therapsida) from the Triassic of northern Gansu Province, China, and its biostratigraphic and biogeographic implications. *American Museum Novitates*, **3685**, 1-25.

GODEFROIT, P. and BATTAIL, B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas* **19**, 567-631.

GODEFROIT, P. 1999. New traversodontid (Therapsida: Cynodontia) teeth from the Upper Triassic of Habay-la-Vielle (southern Belgium). *Paläontologische Zeitschrift,* **73**, 385-394.

GUIGNARD, M. L., MARTINELLI, A. G. and SOARES, M. B. 2019. The postcranial anatomy of *Brasilodon quadrangularis* and the acquisition of mammaliaform traits among non-mammaliaform cynodonts. *Plos One*, **14**, e0216672.

HENDRICKX, C., ABDALA, F. and CHOINIERE, J. N. 2019. A proposed terminology for the dentition of gomphodont cynodonts and dental morphology in Diademodontidae and Trirachodontidae. *PeerJ*, **7**: e6752.

HOPSON, J. A. 1987. The mammal-like reptiles: a study of transitional fossils. *The American Biology Teacher*, **49**, 16-26.

HOPSON, J. A. and KITCHING, J. W. 1972. A revised classification of cynodonts (Reptilia: Therapsida). *Palaeontologia africana* **14**, 71-85.

HOPSON, J. A. and KITCHING, J. W. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology*, **156**, 5-35.

HUELSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology*, **20**, 470-483.

HUTTENLOCKER, A. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society*, **157**, 865-891.

IVAKHNENKO, M. F. 2012. Permian Cynodontia (Theromorpha) of Eastern Europe. *Paleontological Journal,* **46**, 199-207.

IVAKHNENKO, M. F. 2013. Cranial morphology of *Dvinia prima* Amalitzky (Cynodontia, Theromorpha). *Paleontological Journal*, **47**, 210-222.

JENKINS, F. A. 1971. The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History,* **36**, 1-28.

JONES, K. E., ANGIELCYZK, K. D., POLLY, P. D., HEAD, J. J., FERNANDEZ, V., LUNGMUS, J. K., TULGA, S. and PIERCE, S. E. 2018. Fossils reveal the complex evolutionary history of the mammalian regionalised spine. *Science,* **361**, 1249-1252.

KAMMERER, C. F. 2016. A new taxon of cynodont from the *Tropidostoma* Assemblage Zone (upper Permian) of South Africa, and the early evolution of Cynodontia. *Papers in Palaeontology,* **2**, 387-397.

KEMP, T. S. 1979. The primitive cynodont *Procynosuchus*: Functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **285**, 72-122.

KEMP, T. S. 1983. The relationships of mammals. *Zoological Journal of the Linnean Society,* **77**, 353-384.

KEMP, T. S. 2005. The Origin and Evolution of Mammals. Oxford University Press, Oxford.

KERMACK, D. M. Kermack. 1982. A new tritylodontid from the Kayenta formation of Arizona. *Zoological Journal of the Linnean Society* **76**, 1-17

KIELEN-JAWOROWSKA, Z. 1969. Discovery of a Multituberculate Marsupial Bone. *Nature,* **222**, 1091-1092.

KIELAN-JAWOROWSKA, Z., CIFELLI, R. L. and LUO, Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. Columbia University Press, New York.

KÜHNE, D. G. 1956. The Liassic therapsid *Oligokyphus*. *British Museum (Natural History),* London.

LANGER, M. C. 2005. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences* **19**, 205-218.

LANGER, M. C., RIBEIRO, A. M., SCHULTZ, C. L. and FERIGOLO, J. 2007. The continental tetrapod-bearing Triassic of south Brazil. *In* LUCAS, S. G. and SPIELMAN, J. A. (eds). The global Triassic. *New Mexico Museum of Natural History and Science Bulletin* **41,** 201-218.

LIU, J. and OLSEN, P. 2010. The phylogenetic relationships of Eucynodontia (Amniota: Synapsida). *Journal of Mammalian Evolution,* **17**, 151-176.

LLOYD, G. T. 2008. Generalized differencing of time series. http://www.graemetlloyd.com/methgd.html

LOPATIN, A. V. and AGADJANIAN, A. K. 2008. A Tritylodont (Tritylodontidae, Synapsida) from the Mesozoic of Yakutia. *Doklady Biological Sciences,* **419**, 107-110.

LUCAS, S. G. and LUO, Z. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. *Journal of Vertebrate Paleontology,* **13**, 309-334.

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

MACDOUGALL, M. J., BROCKLEHURST, N. and FRÖBISCH, J. 2019. Species richness and disparity of parareptiles across the end-Permian mass extinction. *Proceedings of the Royal Society B,* **286**: 20182572.

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

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

MARCHETTI, L., VOIGT, S. and KLEIN, H. 2017. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). *Historical Biology*, **31**, 748-783.

MARTINELLI, A. G., SOARES, M. B. and SCHWANKE, C. 2016. Two new cynodonts (Therapsida) from the Middle-Early Late Triassic of Brazil and comments on the South American probainognathians. *PLoS ONE,* **11**, 0162945.

MARTINELLI, A. G., ELTINK, E., DA-ROSA, A. A. S. and LANGER, M. C. 2017. A new cynodont from the Santa Maria formation, south Brazil, improves Late Triassic probainognathian diversity. *Papers in Palaeontology,* **3**, 401-423.

MATSUOKA, H., KUSUHASHI, N., and CORFE, I. J. 2016. A new Early Cretaceous tritylodontid (Synapsida, Cynodontia, Mammaliamorpha) from the Kuwajima Formation (Tetori Group) of central Japan. *Journal of Vertebrate Paleontology*, **36**, e1112289.

MCPHEE B. W., BORDY, E. M., SCISCIO, L. and CHONIERE, 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.

MOCKE, H. B., GAETANO, L. C. and ABDALA, F. 2020. A new species of the carnivorous cynodont *Chiniquodon* (Cynodontia, Chiniquodontidae) from the Namibian Triassic*. Journal of Vertebrate Paleontology,* **39:** e1754231.

NEWHAM, E., BENSON, R., UPCHURCH, P. and GOSWAMI, A. 2014. Mesozoic mammaliaform diversity: The effect of sampling corrections on reconstructions of evolutionary dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **412**, 32-44.

NICOLAS, M. and RUBIDGE, B. S. 2010. Changes in Permo-Triassic terrestrial tetrapod ecological representation in the Beaufort Group (Karoo Supergroup) of South Africa. *Lethaia,* **43**, 45-59.

NOVACEK, M. J., ROUGIER, G. W., WIBLE, J. R., MCKENNA, M. C., DASHZEVEG, D. and HOROVITZ, I. 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature,* **389**, 483-486.

O'CONNOR, A. and WILLS, M. A. 2016. Measuring stratigraphic congruence across trees, higher taxa, and time. *Systematic Biology,* **65**, 792-811.

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.

OTTONE, E. G., MONTI, M., MARSICANO, C. A., DE LA FEUNTE, M. S., NAIPAUER, M., ARMSTRONG, R. and MANCUSO, A. 2014. A new Late Triassic age for the Puesto Viejo Group (San Rafael depocenter, Argentina): SHRIMP U—Pb zircon dating and biostratigraphic correlations across southern Gondwana. *Journal of South American Earth Sciences,* **56**, 186-189.

OWEN, R. 1870. Monograph of the Fossil Reptilia of the Liassic Formations. *Palaeontographical Society Monographs,* **27**, 41-81.

PACE, D. W., GASTALDO, R. A. and NEVELING, J. 2009. Early Triassic aggradational and degradational landscapes of the Karoo Basin and evidence for climate oscillation following the P-Tr event. *Journal of Sedimentary Research,* **79**, 316-331.

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

PARRINGTON, F. R. 1978. A further account of Triassic mammals. *Philosophical Transactions of the Royal Society,* **282**, 177-204.

PAVANATTO, A. E. B., PRETTO, F. A., KERBER, L., MÜLLER, R. T., DA-ROSA, A. A. S., DIAS-DA-SILVA, S. D. 2018. A new Upper Triassic cynodont-bearing fossiliferous site from southern Brazil, with taphonomic remarks and description of a new traversodontid taxon. *Journal of South American Earth Sciences*, **88**, 179-196.

POL, D. and NORELL, M. A. 2001. Comments on the Manhattan stratigraphic measure. *Cladistics,* **17**, 285-289.

PUSCH, L. C., KAMMERER, C. F. and FRÖBISCH, J. 2019. Cranial anatomy of the early cynodont *Galesaurus planiceps* and the origin of mammalian endocranial characters. *Journal of Anatomy*, **234**, 592-621.

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

REILLY, S. M. and WHITE, T. D. 2003. Hypaxial Motor Patterns and the Function of Epipubic Bones in Primitive Mammals. *Science,* **299**, 400-402.

REILLY, S. M., MCELROY, E. J. and WHITE, T. D. 2009. Abdominal muscle function in ventilation and locomotion in new world opossums and basal eutherians: Breathing and running with and without epipubic bones. *Journal of Morphology,* **270**, 1014-1028.

RODRIGUES, P. G., RUF, I. and SCHULTZ, C. L. 2013. Digital Reconstruction of the Otic Region and Inner Ear of the Non-Mammalian Cynodont *Brasilitherium riograndensis* (Late Triassic, Brazil) and Its Relevance to the Evolution of the Mammalian Ear. *Journal of Mammalian Evolution,* **20**, 291-307.

ROWE, T. 1988. Definition, Diagnosis, and Origin of Mammalia. *Journal of Vertebrate Paleontology,* **8**, 241-264.

R CORE TEAM. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

RUBIDGE, B. S. and SIDOR, C. A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics,* **32**, 449-480.

RUFFELL, A., MCKINLEY, J. M. and WORDEN, R. H. 2002. Comparison of clay mineral stratigraphy to other proxy palaeoclimate indicators in the Mesozoic of NW Europe. *Philosophical Transactions of the Royal Society A,* **360**, 675-693.

RUTA, M., BOTHA-BRINK, J., MITCHELL, S. A. and BENTON, M. J. 2013. The radiation of cynodonts and the ground plan of mammalian morphological diversity. *Proceedings of the Royal Society B,* **280**, 20131865.

SCHULTZ, C. L., MARTINELLI, A. G., SOARES, M. B., PINHEIRO, F. L., KERBER, L., HORN, B. L. D., PRETTO, F. A., MÜLLER, R. T. and MELO, T. P. 2020. Triassic faunal successions of the Paraná Basin, southern Brazil. *Journal of South American Earth Sciences,* **104**, 102846.

SELLWOOD, B. W. and VALDES, P. J. 2008. Jurassic Climates. *Proceedings of the Geologists' Association,* **119**, 5-17.

SIDDALL, M. E. 1998. Stratigraphic fit to phylogenies: A proposed solution. *Cladistics,* **14**, 201-208.

SIDOR, C. A. and SMITH, R. M. H. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* **47**, 535-556.

SIDOR, C. A. and HOPSON, J. A. 2018. *Cricodon metabolus* (Cynodontia: Gomphodontia) from the Triassic Ntawere Formation of northeastern Zambia: patterns of tooth replacement and a systematic review of the Trirachodontidae. *Journal of Vertebrate Paleontology*. **37** (supplement), 39-64.

SIGOGNEAU-RUSSELL, D. 1983. Nouveaux taxons de mammifères rhétiens. *Acta Palaeontologica Polonica* **28**, 233-249.

SMITH, R. AND BOTHA, J. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. *Comptus Rendes Palevol,* **4**, 636-636.

SMITH, R. M. H. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the Southwestern Karoo Basin of South Africa. *PALAIOS,* **8**, 45-67.

SMITH, R. M. H. and BOTHA-BRINK, J. 2014. Anatomy of a mass extinction: Sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **396**, 99-118.

SMITH, R. M. H., ERIKSSON, P. G. and BOTHA, W. J. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of Southern Africa. *Journal of African Earth Sciences (and the Middle East),* **16**, 143-169.

SMITH, R. M. H., RUBIDGE, B. S., DAY, M. O. and BOTHA, J. 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. *South African Journal of Geology* **123**, 131-140.

SUES, H.-D. 1985. First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. *Journal of Vertebrate Paleontology* **5**, 328-335.

SUES, H.-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology* **151**, 217-268.

SUES, H. –D., OLSEN, P. E. and KROEHLER, P. A. 1994. Small tetrapods from the Upper Triassic of the Richmond basin (Newark Supergroup), Virginia. In Fraser, N. C. and Sues, H. –D. (eds). *In the Shadow of the Dinoaurs*. Cambridge University Press, 161-170.

SUES, H. –D. and MUNK, W. 1996. A remarkable assemblage of terrestrial tetrapods from the Zechstein (Upper Permian: Tatarian) near Korbach (northwestern Hesse). *Palaeontologische Zeitschrift,* **70**, 213-223.

SUES, H. –D. 2001. On *Microconodon,* a Late Triassic cynodont from the Newark Supergroup of Eastern North America. *Bulletin of the Museum of Comparative Zoology,* **156**, 37-48.

SULEJ, T., NIEDŹWIEDZKI, G., TAŁANDA, M., DRÓŻDŻ, D. and HARA, E. 2020. A new early Late Triassic non-mammaliaform eucynodont from Poland. *Historical Biology,* **32**, 80-92.

SULLIVAN, C., LIU, J., ROBERTS, E. M., HUANG, T. D., YANG, C. and ZHONG, S. 2013. Pelvic morphology of a tritylodontid (Synapsida: Eucynodontia) from the Lower Jurassic of China, and some functional and phylogenetic implications. *Comptes Rendus Palevol,* **12**, 505-518.

TANNER, L. H. 2018. Climates of the Late Triassic: Perspectives, Proxies and Problems. In: TANNER, L. (ed). The Late Triassic World. *Topics in Geobiology*, **46**. Springer, Cham, 59-90.

TATARINOV, L. P. and MATCHENKO, E. N. 1999. A find of an aberrant tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo Region. *Paleontological Journal*, **33**, 422-428.

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**, 563-573.

VARNHAM, G. L., MANNION, P. D. and KAMMERER, C. F. 2020. Data from: Completeness of the early cynodont fossil record and its influence on interpretations of the timing of acquisition of mammalian characteristics. *Dryad Digital Repository*. https://datadryad.org/stash/share/el5_BWNNdRxPSz8GLC3rP03AUgIGKZuIINAU1om3HzY

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.

VIGLIETTI, P. A., SMITH, R. M. H. and COMPTON, J. S. 2013. Origin and palaeoenvironmental significance of *Lystrosaurus* bonebeds in the earliest Triassic Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **392**, 9-21.

VIGLIETTI, P. A., SMITH, R. M. H., ANGIELCZYK, K. D., KAMMERER, C. F., FRÖBISCH, J. and RUBIDGE, B. S. 2016. The *Daptocephalus* Assemblage Zone (Lopingian), South Africa: A proposed biostratigraphy based on a new compilation of stratigraphic ranges. *Journal of African Earth Sciences* **113**, 153-164.

WAGNER, P. J. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology,* **49**, 463-479.

WALLACE, R. V. S., MARTÍNEZ, R. and ROWE, T. 2019. First record of a basal mammaliamorph from the early Late Triassic Ischigualasto Formation of Argentina. *PLoS ONE* **14**: e0218791.

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

WANG, G. and SONG, M. 2011. Ckmeans.1d.dp: optimal *k*-means clustering in one dimension by dynamic programming. *The R Journal,* **3**, 29-33.

WHITE, T. D. 1989. An analysis of epipubic bone function in mammals using scaling theory. *Journal of Theoretical Biology,* **139**, 343-357.

WILLS, M. A. 1999. Congruence between phylogeny and stratigraphy: Randomization tests and the gap excess ratio. *Systematic Biology,* **48**, 559-580.

WYND, B. M., PEECOCK, B. R., WHITNEY, M. R., SIDOR, C. A. 2017. The first occurrence of *Cynognathus crateronotus* (Cynodontia: Cynognathia) in Tanzania and Zambia, with implications for the age and biostratigraphic correlation of Triassic strata in southern Pangea. *Journal of Vertebrate Paleontology,* **37**, 228-239.

ZERFASS, H., LAVINA, E. L., SCHULTZ, C. L., GARCIA, A. J. V., FACCINI. U. F. and CHEMALE, F. 2003. Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: contribution to Southwestern Gondwana palaeogeorgaphy and palaeoclimate. *Sedimentary Geology,* **161**, 85-105.

FIGURES

FIGURE 1. Skeletal outline of a representative early cynodont, *Thrinaxodon liorhinus* (modified from Kemp 2005: fig. 3.50b), highlighting the body regions used to partition the skeleton. These regions of the skeleton were further subdivided into individual elements (see Table 1) to calculate the Skeletal Completeness Metric (SCM).

FIGURE 2. Global patterns of number of species, mean SCM, mean CCM, and mean BSCM of early cynodonts through time: A, using stage-level time bins; and B, using 'equal'-length time intervals. In each case, the grey bars illustrate the time intervals used. The grey points represent all SCM values for each species known for each stage. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 3. Box-and-whisker plots showing the distribution of early cynodont SCM values for each time period. The median average completeness value is shown by the horizontal black bar in each plot.

FIGURE 4. Number of early cynodont species and mean SCM through time in: A, Laurasia; and B, Gondwana. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 5. Number of early cynodont species and mean SCM through time in each palaeocontinent. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 6. Box-and-whisker plot showing the distribution of early cynodont SCM values for each palaeocontinent.

FIGURE 7. Number of early cynodont species and mean SCM through time at different palaeolatitudes. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 8. Box-and-whisker plot showing the distribution of early cynodont SCM values for each body size cluster based on anteroposterior lengths of postcanine teeth.

FIGURE 9. Number of early cynodont species for each body size cluster through time. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 10. Box-and-whisker plots showing the distribution of completeness data for several vertebrae groups: A, comparison of SCM data for cynodonts, pelycosaurs, parareptiles, bats, sauropodomorphs, non-avian theropods, plesiosaurs, and ichthyosaurs; B, comparison of CCM data for cynodonts, anomodonts, pelycosaurs, parareptiles, eutherians, Mesozoic birds, pterosaurs, and plesiosaurs. Silhouette images of representatives from each group were obtained from Phylopic (http.//phylopic.org) under: Public Domain license (https://creativecommons.org/publicdomain/zero/1.0/) with credit to Christine Axon (http://phylopic.org/image/94fda119-5435-4246-ad23-20b15f3bcb8d/), Steven Traver (http://phylopic.org/image/b02c8c23-4263-436a-9a3a-068fc851dbb7/ and http://phylopic.org/image/31e41454-b7b3-4c17-8e71-bd3ab4bca376/), Tasman Dixon (http://phylopic.org/image/b348100c-7ba8-410d-90df-963064987089/), Yan Wong (http://phylopic.org/image/18bfd2fc-f184-4c3a-b511-796aafcc70f6/), Scott Hartman (http://phylopic.org/image/ba6426aa-337e-4a90-8cdb-c6daac83d819/) and Dann Pigdon

(http://phylopic.org/image/74fce2bf-3fc0-497b-9083-b6f600a697fe/); Attribution-ShareAlike 3.0 Unported license (https://creativecommons.org/licenses/by-sa/3.0/) with no changes made with credit to Dmitry Bogdanov (http://phylopic.org/image/1f3e74df-30e6-422b-9ce2-db7df199f11d/); and Attribution 3.0 Unported license with no changes made (https://creativecommons.org/licenses/by/3.0/) with credit to Mathew Wedel (http://phylopic.org/image/7a99b167-b719-4233-946c-addf3ef1c06c/) and Gareth Monger (http://phylopic.org/image/f0c8064a-eefa-45ab-b3f2-6ea6fb7d17b3/ and http://phylopic.org/image/02651c35-768e-4570-9bad-90cac6911b52/).

FIGURE 11. Global palaeogeographic reconstructions illustrating the distribution of cynodont species included within this study (black dots) for the: A, Lopingian, (reconstructed at 256 Ma); B, Early Triassic (249 Ma); C, Middle Triassic (242 Ma); D, Late Triassic (219 Ma); E, Early Jurassic (187 Ma); F, Middle Jurassic (168 Ma); G, Late Jurassic (154 Ma); and H, Early Cretaceous (122 Ma). Reconstructions from the Paleobiology Database (https://paleobiodb.org/navigator/).

FIGURE 12. A time-scaled phylogenetic tree of early Cynodontia. The observed stratigraphic ranges of each species are colour-coded by palaeocontinent. The underlying stacked area graph represents the relative contribution of each paleocontinent to the completeness of the cynodont record in each stratigraphic stage. The appearances of notable mammalian-like features in the fossil record are also depicted: a, reduced lumbar ribs and differentiation of the vertebral column as exhibited by *Thrinaxodon*; b, an expanded secondary palate as exhibited by *Thrinaxodon*; c, enlargement of the dentary and expansion of the coronoid process displayed by *Lumkuia*; d, gomphodont dentition and advanced dental occlusion exhibited by *Massetognathus*; e, tritylodont dentition seen in *Oligokyphus*; f, a reduced number of skull bones and loss of postorbital bar illustrated by *Kayentatherium*. All anatomical illustrations are modified from Kemp (2005). Light grey shading represents stages.

TABLES

Table 1. Percentage contributions of each region of the cynodont skeleton to calculation of the Skeletal Completeness Metric.

Region	**Percentage %**
Skull	**25**
Skull	24
Teeth/Complete dentition	1
Vertebrae + Ribs	**43**
Cervical	5
Dorsal	15
Sacral	5
Ribs	10
Caudal	8
Pectoral Girdle	**6**
Forelimbs	**10**
Humerus	3
Radius	2
Ulna	2
Carpals	1
Metacarpals	1
Phalanges	1
Pelvic Girdle	**6**
Ilium	2
Ischium	2
Pubis	2

Hindlimb	**10**
Femur	3
Tibia	2
Fibula	2
Tarsals	1
Metatarsals	1
Phalanges	1

The percentages attributed to each region and the subdivisions within each region used to calculate the SCM.

Table 2. ‘Equal’-length time bins.

Start Date of Time Bin (Ma)	Stages Included
259	Wuchiapingian, Changhsingian
252.3	Induan, Olenekian, Anisian
242	Ladinian
235	Carnian
221.5	Norian
205.6	Rhaetian
201.6	Hettangian, Sinemurian
189.6	Pliensbachian
183	Toarcian, Aalenian
171.6	Bajocian, Bathonian

164.7	Callovian, Oxfordian
155.7	Kimmeridgian, Tithonian
145.5	Berriasian, Valanginian
136.4	Hauterivian, Barremian
125.45	Aptian

Start dates for time bins with approximately "equal-length" intervals, and the stages included within that interval.

Table 3. Correlation test results for early cynodont diversity and completeness comparisons across time and space

Test	S	p-value	rho	T	p-value	Tau	t	p-value	Cor
Div/SCM	668	0.079	0.414	111	0.080	0.298	1.286	0.216	0.298
Div/BSCM	656	0.071	0.425	117	0.029*	0.368	1.899	0.075	0.418
Div/CCM	580	0.034	0.491	113	0.058	0.322	1.512	0.149	0.344
SCM/BSCM	120	2.20×10^{-16}*	0.895	149	9.03×10^{-07}*	0.743	9.515	3.19×10^{-08}*	0.918
SCM/CCM	344	0.001*	0.698	129	0.002*	0.509	3.248	0.005*	0.619
CCM/BSCM	426	0.005*	0.626	121	0.013*	0.415	2.794	0.012*	0.561
Div/SCM new time bins	222	0.064	0.512	63	0.062	0.385	2.488	0.029*	0.583

Div/BSCM new time bins	226	0.069	0.503	62	0.079	0.363	2.431	0.032*	0.574
Div/CCM new time bins	150	0.011*	0.670	68	0.014*	0.495	3.044	0.010*	0.660
SCM/BSCM new time bins	22	2.20×10^{-16}*	0.952	84	1.51×10^{-06}*	0.846	12.274	3.76×10^{-08}*	0.962
SCM/CCM new time bins	134	0.006*	0.705	70	0.007*	0.538	3.427	0.005*	0.703
CCM/BSCM new time bins	156	0.013*	0.657	67	0.019*	0.473	2.807	0.016*	0.630
Lat:Div/SCM	236	0.588	0.175	36	0.737	0.091	0.166	0.872	0.052
Lat:Div/BSCM	340	0.558	-0.189	28	0.545	-0.152	-1.089	0.302	-0.326
Lat:Div/CCM	166	0.177	0.420	42	0.250	0.273	1.933	0.082	0.521
Lat:BSCM/SCM	44	0.001*	0.846	56	0.001*	0.697	6.126	1.12×10^{-04}*	0.889
Lat:BSCM/CCM	112	0.040*	0.608	50	0.021*	0.515	1.875	0.090	0.510
Lat:CCM/SCM	26	2.20×10^{-16}*	0.909	58	2.40×10^{-04}*	0.758	3.528	0.005*	0.745

Statistical comparisons between completeness (SCM, CCM and BSCM) and diversity through time (using stages and the intervals described in Table 2) and across space (at 10˚ palaeolatitudinal bins) using Spearman's rank correlation coefficient, Kendall's Tau coefficient, and Pearson's correlation coefficient. Asterisks indicate statistically significant results, using a *p*-value=0.05 as the cut-off.

Table 4. Correlation test results from temporal pairwise comparisons of completeness of tetrapod clades

Test	**S**	**p-value**	**rho**
Cynodont/Ichthyosaur SCM	408	0.7270	0.1032967
Cynodont/Ichthyosaur BSCM	314	0.2806	0.3098901
Cynodont/Plesiosaur SCM	118	0.9816	0.01666667
Cynodont/Plesiosaur CCM	52	0.3556	-0.4857143
Cynodont/Sauropodomorph SCM	230	0.2166	0.3681319
Cynodont/Parareptile SCM	58	0.9635	-0.03571429
Cynodont/Parareptile CCM	80	0.3536	-0.4285714
Cynodont/Pterosaur CCM	34	0.03687*	0.7166667
Cynodont/Amonodont CCM	52	0.3599	0.3809524
Cynodont/Theropod SCM	250	0.2973	0.3131868

Cynodont completeness metrics (SCM, CCM and BSCM) were compared to those of other contemporaneous clades including ichthyosaurs, plesiosaurs, sauropodomorphs, parareptilian tetrapods, pterosaurs, anomodonts, and non-avian theropods using Spearman's correlation coefficient. Data was log-transformed and subject to generalised differencing prior to analysis. Asterisks indicate statistically significant results at p-value=0.5.

Table 5. Correlation test results of non-temporal comparisons of completeness of tetrapod clades

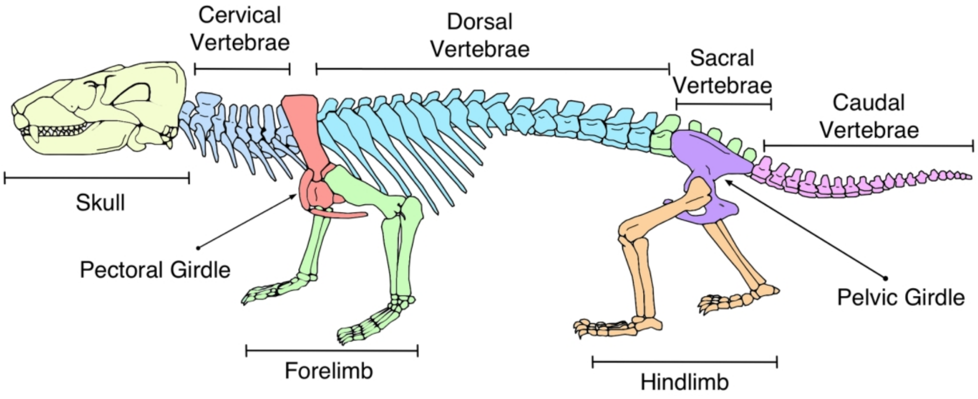
Test	W	p-value
Cynodont CCM/Anomodont CCM	9342	2.20 x 10^{-16}*
Cynodont SCM/ Ichthyosaur SCM	2078.5	2.20 x 10^{-16}*
Cynodont BSCM/Ichthyosaur BSCM	122.5	2.20 x 10^{-16}*
Cynodont CCM/ Parareptilian tetrapods CCM	2294	1.09 x 10^{-06}*
Cynodont SCM/ Parareptilian tetrapods SCM	2564.5	3.26 x 10^{-08}*
Cynodont CCM/Pelycosaur CCM	13581	0.565
Cynodont SCM/Pelycosaur SCM	11598	4.24 x 10^{-07}*
Cynodont CCM/Plesiosaur CCM	4026	2.90 x 10^{05}*
Cynodont SCM/Plesiosaur SCM	2963	3.92 x 10^{-15}*
Cynodont CCM/Pterosaur CCM	8654	0.069
Cynodont SCM/ Sauropodomorph SCM	13600	1.21 x 10-^{06}*
Cynodont CCM/ Eutherian CCM	46725	2.20 x 10^{-16}*
Cynodont SCM/ Bat SCM	19396	1.40 x 10^{-10}*
Cynodont BSCM/ Bat BSCM	46863	2.20 x 10^{-16}*
Cynodont CCM/ Bat CCM	21711	0.0131*
Cynodont SCM/ Theropod SCM	19385	5.30 x 10^{-05}*
Cynodont CCM/ Mesozoic bird CCM	6321	0.3812

Cynodont completeness metrics (SCM, CCM and BSCM) were compared to other clades, including values that do not overlap with cynodonts temporally using the Mann-Whitney U test. Clades included ichthyosaurs, plesiosaurs, sauropodomorphs, parareptilian tetrapods, pterosaurs, anomodonts, pelycosaurian-grade synapsids, eutherians, bats and non-avian theropods. Asterisks indicate statistically significant results at p-value=0.5.

Table 6. Stratigraphic and phylogenetic congruence test results

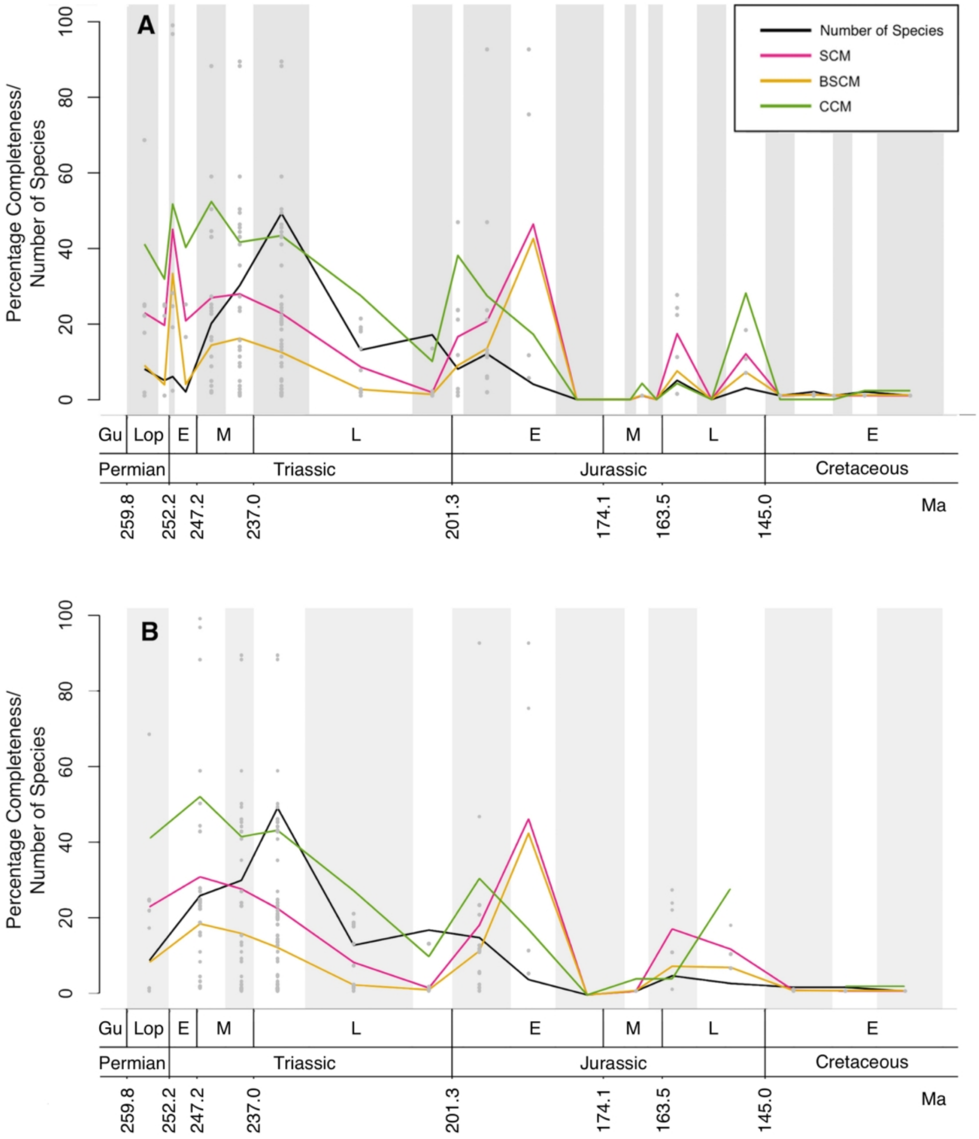
Metric	**Value**	**Estimated p-value**
SCI	0.765432	<0.000001
RCI	44.93839	<0.000001
GER	0.845810	<0.000001
MSM*	0.222069	<0.000001

Values of SCI, RCI, GER, and MSM* and their estimated p-values from the stratigraphic congruence analyses using the phylogenetic supertree.



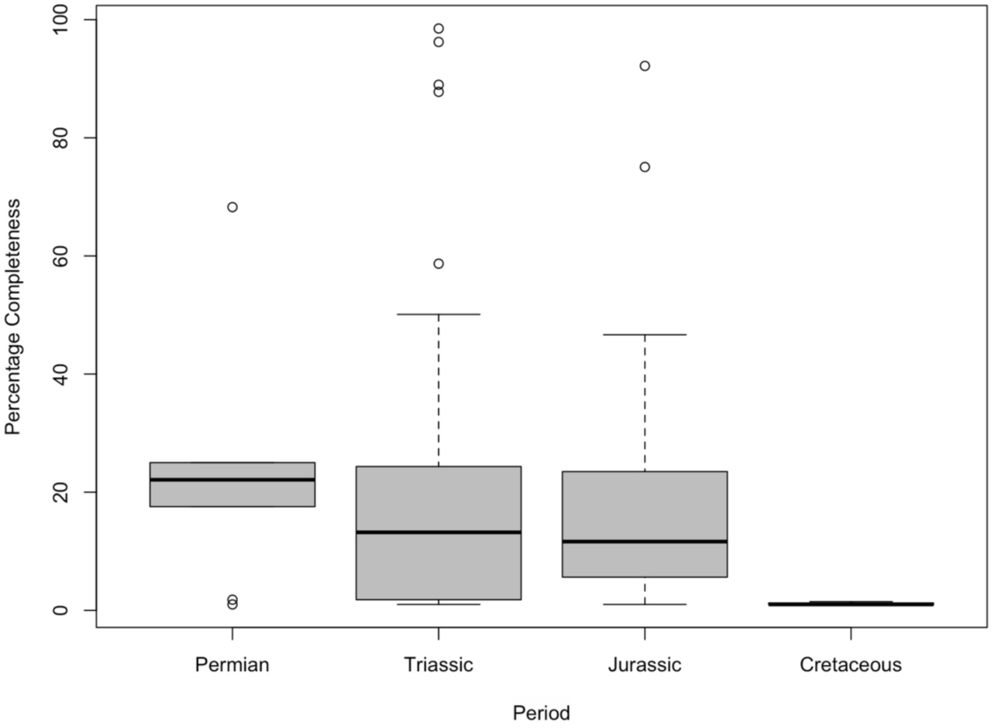
Skeletal outline of a representative early cynodont, Thrinaxodon liorhinus (modified from Kemp 2005: fig. 3.50b), highlighting the body regions used to partition the skeleton. These regions of the skeleton were further subdivided into individual elements (see Table 1) to calculate the Skeletal Completeness Metric (SCM).

160x67mm (300 x 300 DPI)



Global patterns of number of species, mean SCM, mean CCM, and mean BSCM of early cynodonts through time: A, using stage-level time bins; and B, using ‘equal’-length time intervals. In each case, the grey bars illustrate the time intervals used. The grey points represent all SCM values for each species known for each stage. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

165x192mm (300 x 300 DPI)



Box-and-whisker plots showing the distribution of early cynodont SCM values for each time period. The median average completeness value is shown by the horizontal black bar in each plot.

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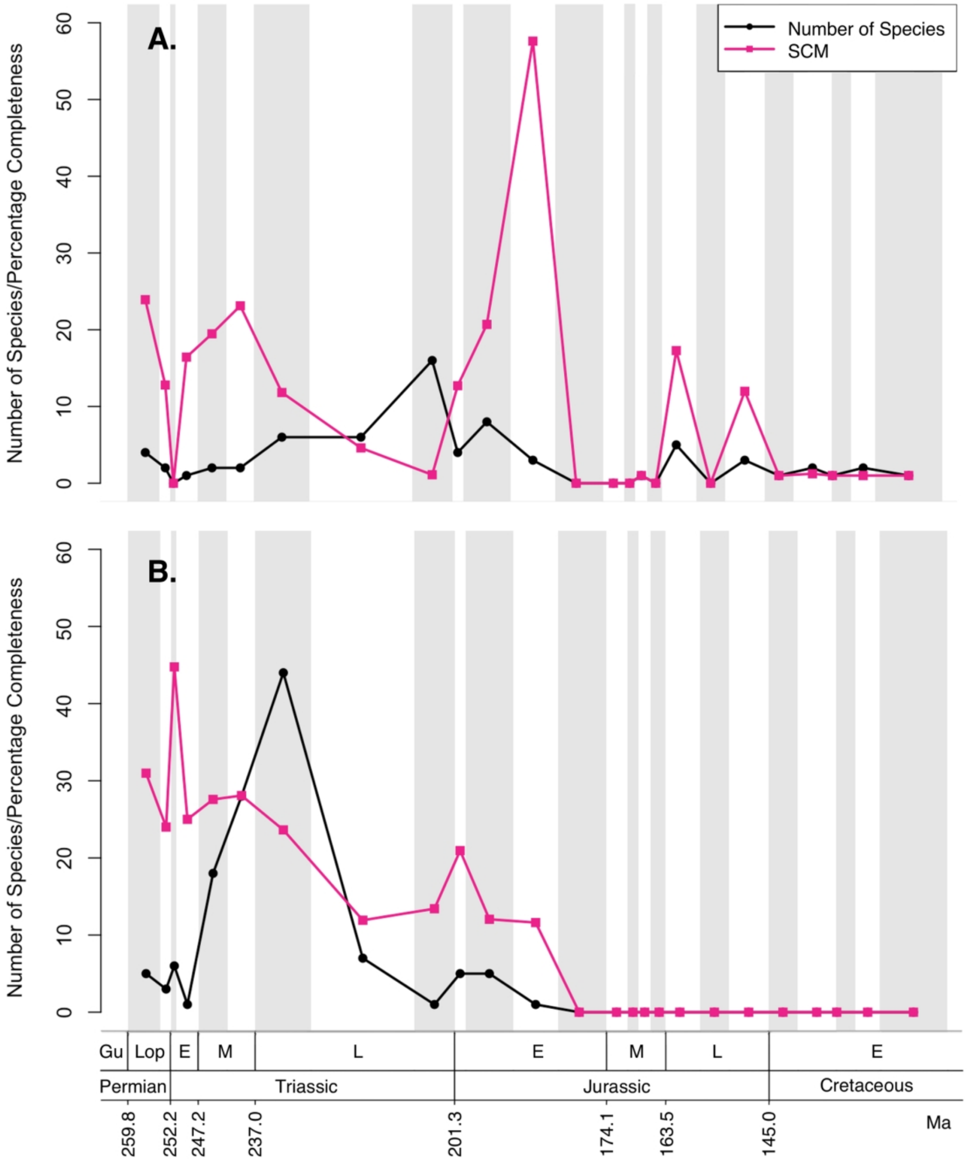
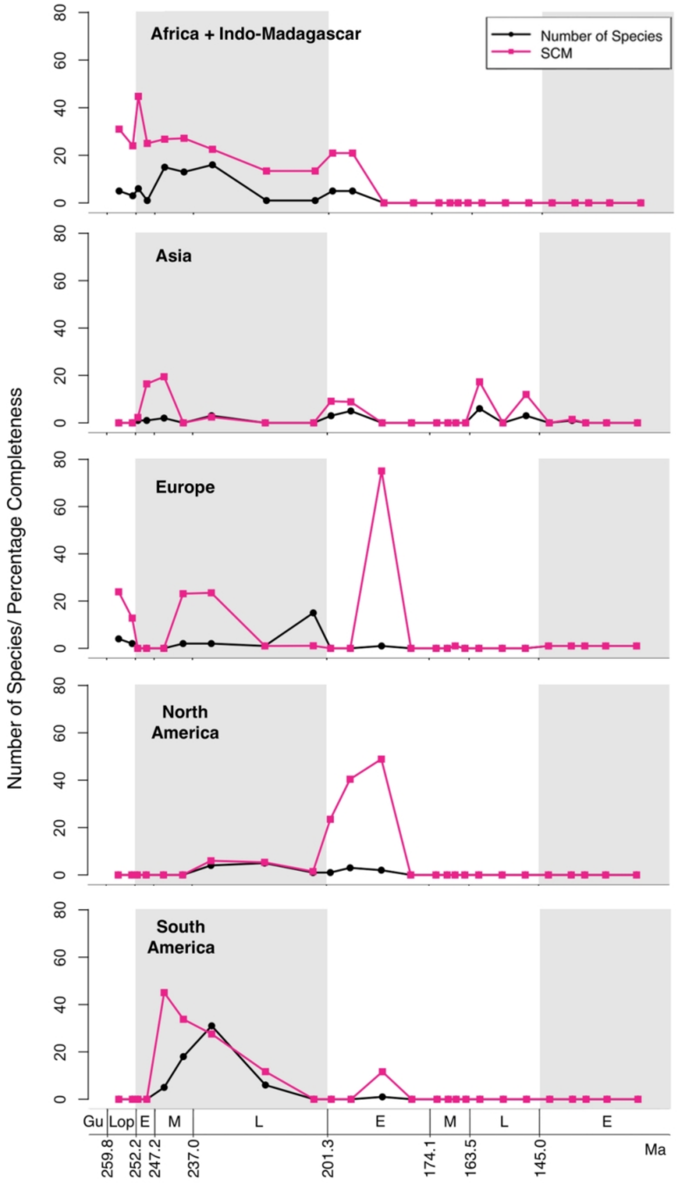


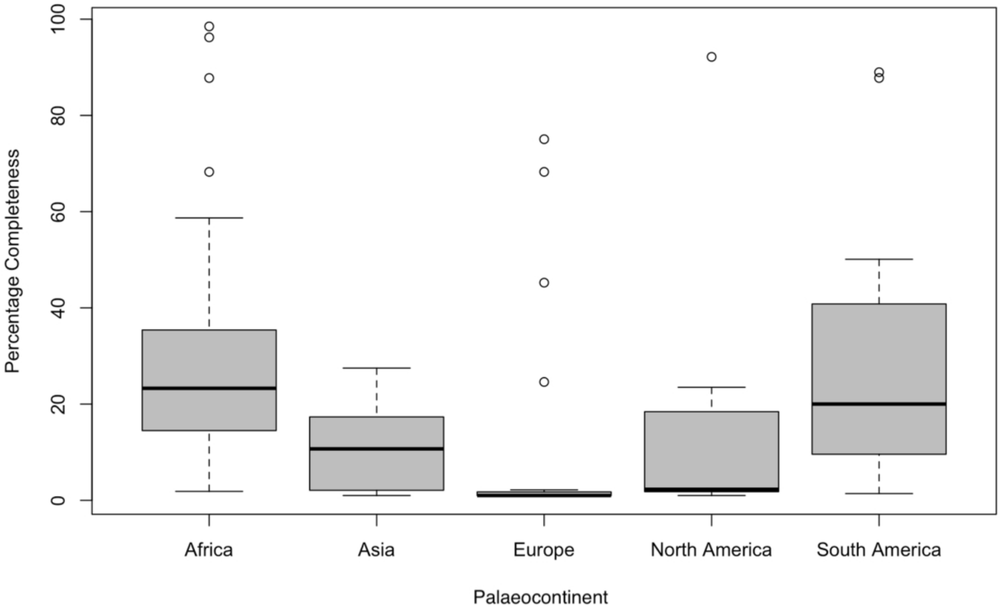
Number of early cynodont species and mean SCM through time in: A, Laurasia; and B, Gondwana. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

165x193mm (300 x 300 DPI)



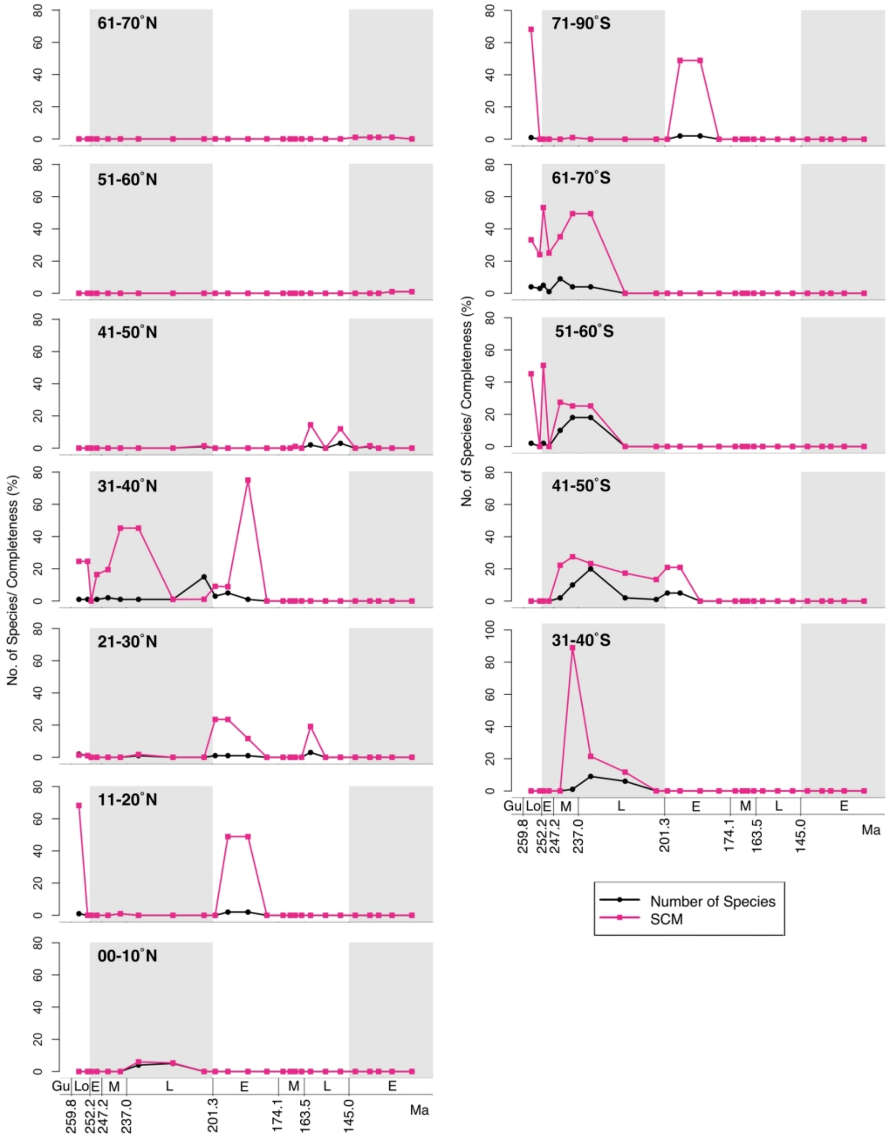
Number of early cynodont species and mean SCM through time in each palaeocontinent. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

87x144mm (300 x 300 DPI)



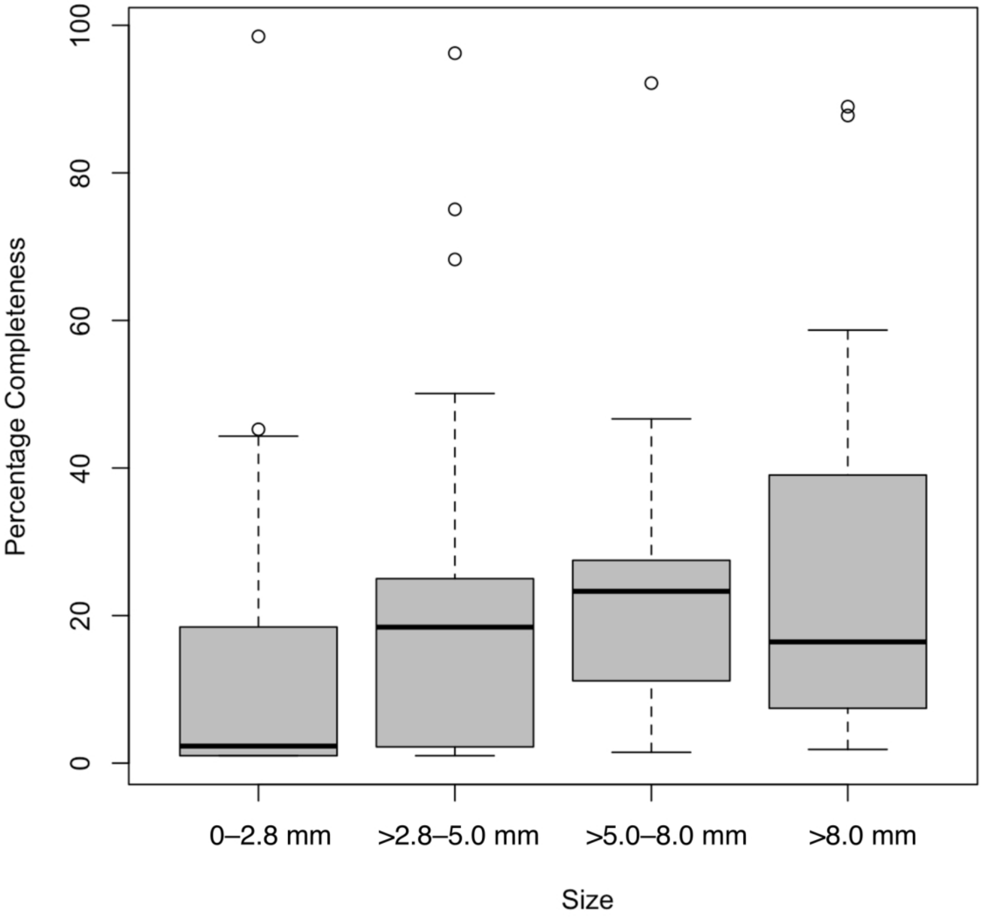
Box-and-whisker plot showing the distribution of early cynodont SCM values for each palaeocontinent.

165x100mm (300 x 300 DPI)



Number of early cynodont species and mean SCM through time at different palaeolatitudes. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

173x220mm (300 x 300 DPI)



Box-and-whisker plot showing the distribution of early cynodont SCM values for each body size cluster based on anteroposterior lengths of postcanine teeth.

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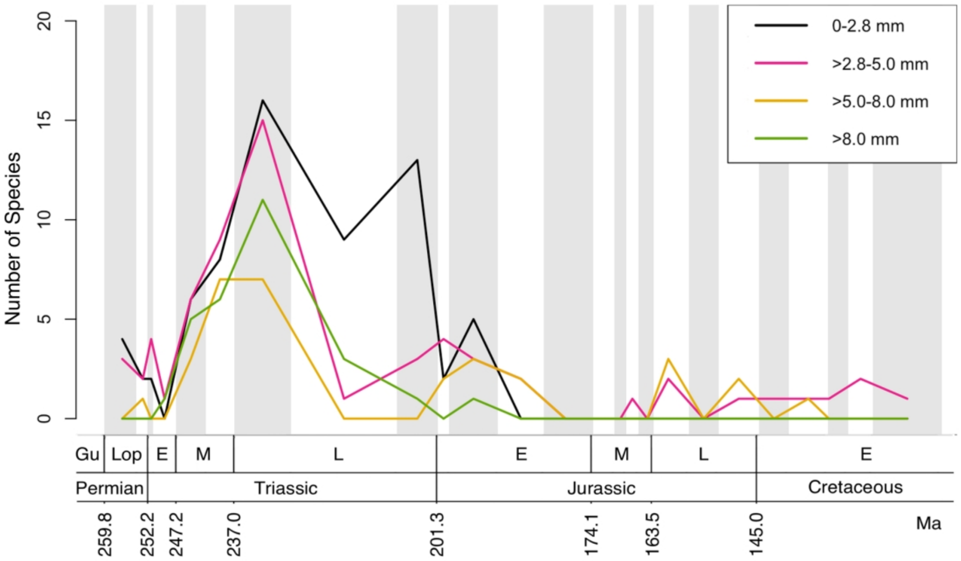
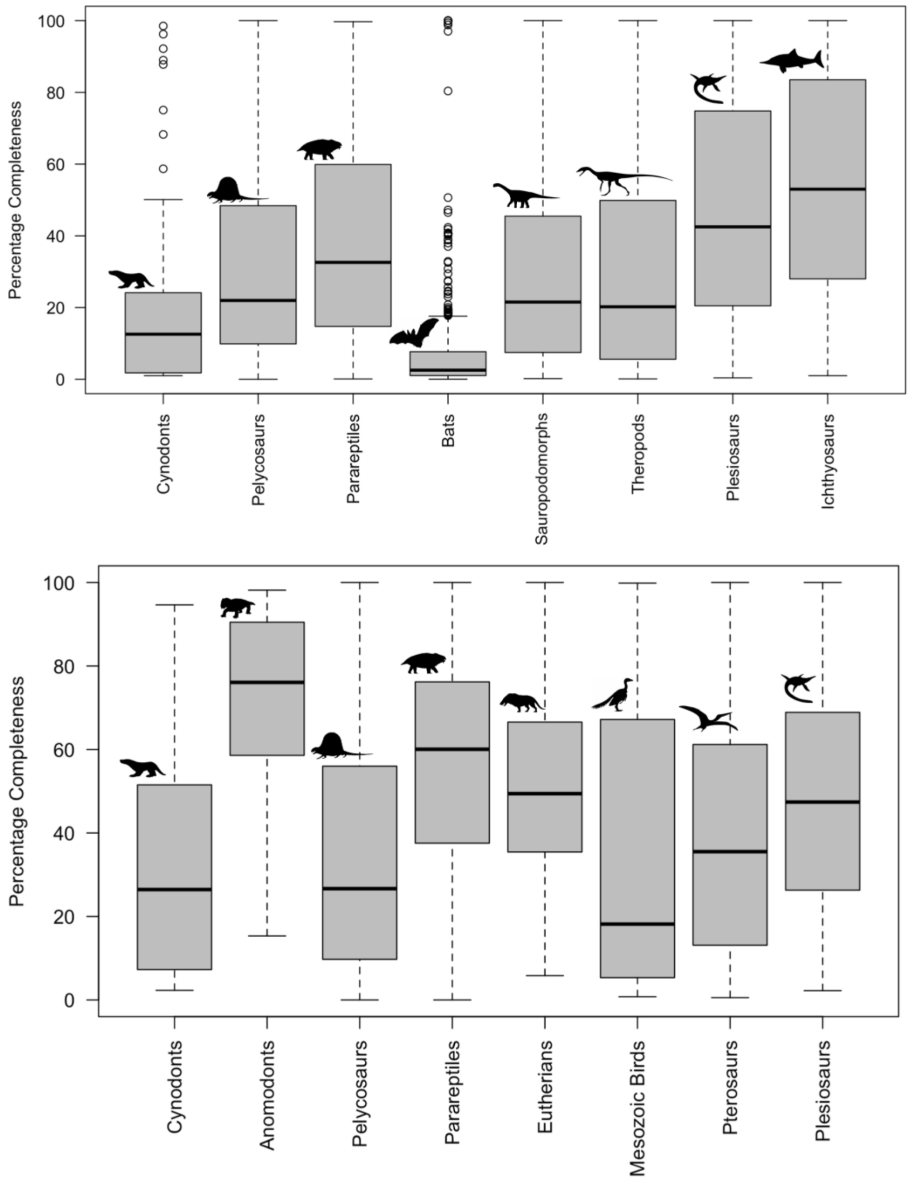


Number of early cynodont species for each body size cluster through time. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

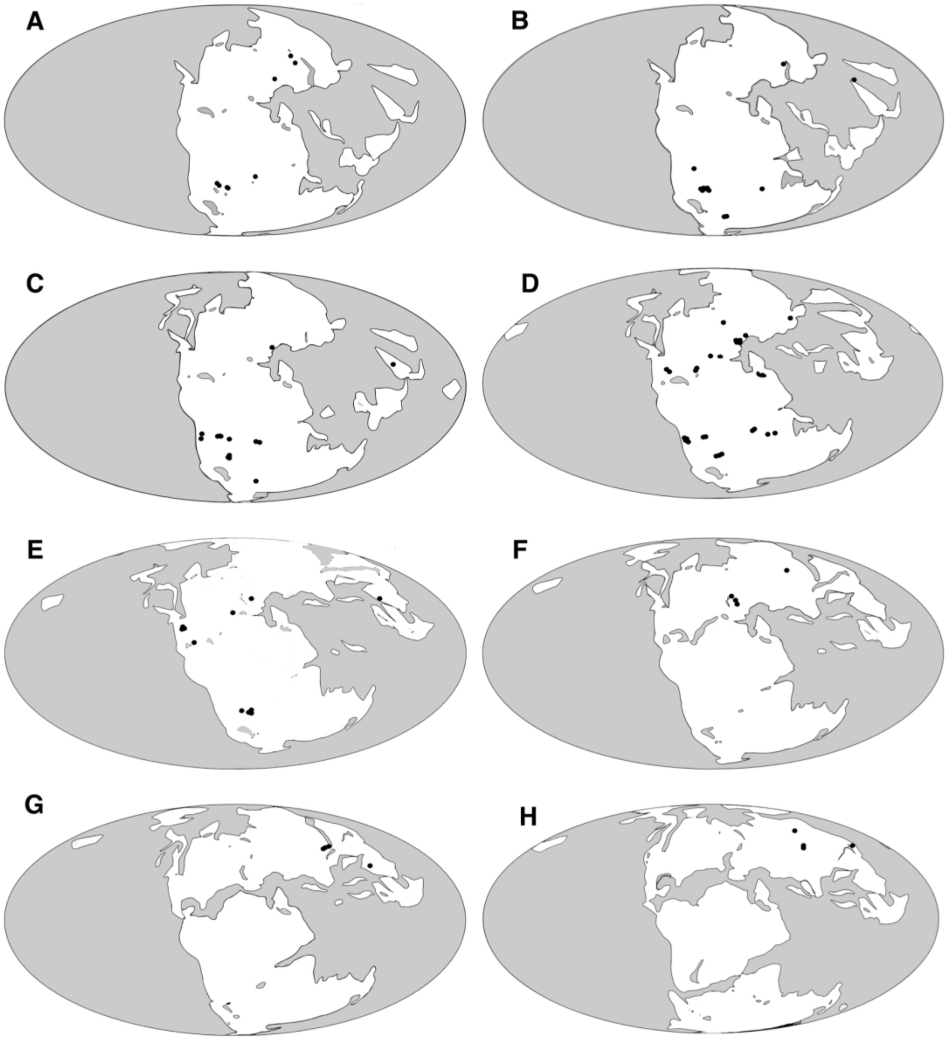
165x103mm (300 x 300 DPI)



Box-and-whisker plots showing the distribution of completeness data for several vertebrae groups: A, comparison of SCM data for cynodonts, pelycosaurs, parareptiles, bats, sauropodomorphs, non-avian theropods, plesiosaurs, and ichthyosaurs; B, comparison of CCM data for cynodonts, anomodonts, pelycosaurs, parareptiles, eutherians, Mesozoic birds, pterosaurs, and plesiosaurs. Silhouette images of representatives from each group were obtained from Phylopic (http.//phylopic.org) under: Public Domain license (https://creativecommons.org/publicdomain/zero/1.0/) with credit to Christine Axon (http://phylopic.org/image/94fda119-5435-4246-ad23-20b15f3bcb8d/), Steven Traver (http://phylopic.org/image/b02c8c23-4263-436a-9a3a-068fc851dbb7/ and http://phylopic.org/image/31e41454-b7b3-4c17-8e71-bd3ab4bca376/), Tasman Dixon (http://phylopic.org/image/b348100c-7ba8-410d-90df-963064987089/), Yan Wong (http://phylopic.org/image/18bfd2fc-f184-4c3a-b511-796aafcc70f6/), Scott Hartman (http://phylopic.org/image/ba6426aa-337e-4a90-8cdb-c6daac83d819/) and Dann Pigdon (http://phylopic.org/image/74fce2bf-3fc0-497b-9083-b6f600a697fe/); Attribution-ShareAlike 3.0 Unported license (https://creativecommons.org/licenses/by-sa/3.0/) with no changes made with credit to Dmitry

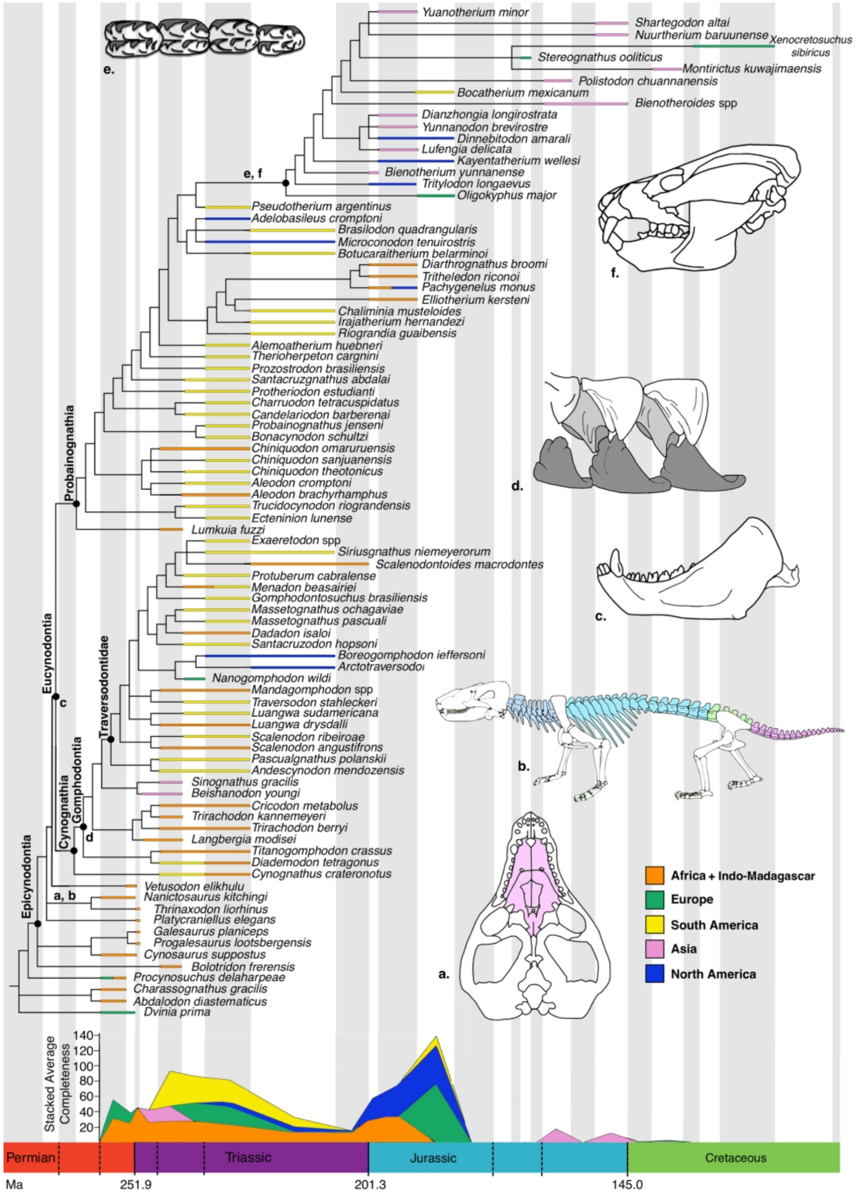
Bogdanov (http://phylopic.org/image/1f3e74df-30e6-422b-9ce2-db7df199f11d/); and Attribution 3.0 Unported license with no changes made (https://creativecommons.org/licenses/by/3.0/) with credit to Mathew Wedel (http://phylopic.org/image/7a99b167-b719-4233-946c-addf3ef1c06c/) and Gareth Monger (http://phylopic.org/image/f0c8064a-eefa-45ab-b3f2-6ea6fb7d17b3/ and http://phylopic.org/image/02651c35-768e-4570-9bad-90cac6911b52/).

165x211mm (300 x 300 DPI)



Global palaeogeographic reconstructions illustrating the distribution of cynodont species included within this study (black dots) for the: A, Lopingian, (reconstructed at 256 Ma); B, Early Triassic (249 Ma); C, Middle Triassic (242 Ma); D, Late Triassic (219 Ma); E, Early Jurassic (187 Ma); F, Middle Jurassic (168 Ma); G, Late Jurassic (154 Ma); and H, Early Cretaceous (122 Ma). Reconstructions from the Paleobiology Database (https://paleobiodb.org/navigator/).

165x180mm (300 x 300 DPI)



A time-scaled phylogenetic tree of early Cynodontia. The observed stratigraphic ranges of each species are colour-coded by palaeocontinent. The underlying stacked area graph represents the relative contribution of each paleocontinent to the completeness of the cynodont record in each stratigraphic stage. The appearances of notable mammalian-like features in the fossil record are also depicted: a, reduced lumbar ribs and differentiation of the vertebral column as exhibited by Thrinaxodon; b, an expanded secondary palate as exhibited by Thrinaxodon; c, enlargement of the dentary and expansion of the coronoid process displayed by Lumkuia; d, gomphodont dentition and advanced dental occlusion exhibited by Massetognathus; e, tritylodont dentition seen in Oligokyphus; f, a reduced number of skull bones and loss of postorbital bar illustrated by Kayentatherium. All anatomical illustrations are modified from Kemp (2005). Light grey shading represents stages.

165x233mm (300 x 300 DPI)

Response to reviewer comments

Technical comments

Fig. 5:

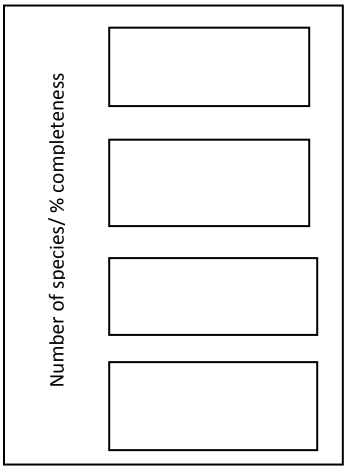
- The text on this figure is still too small when it is viewed at single column width. We could almost fit the figure to two-thirds page width (110 mm wide) but even then the axis labels are slightly too small (the numbers should be ok at that size). Please increase the size of the text on the vertical axis labels.

- ***We have increased the size of text on the vertical axis.***

- Could I also suggest that adjusting the vertical axis might give you a little more space; none of the plotted SCM values go above 80% so the graphs could all be adjusted to only show a scale of 0–80, which could reduce the total height and allow it to be set a little larger.

- ***There is now only one axis label and the axes have been reduced to 80%.***

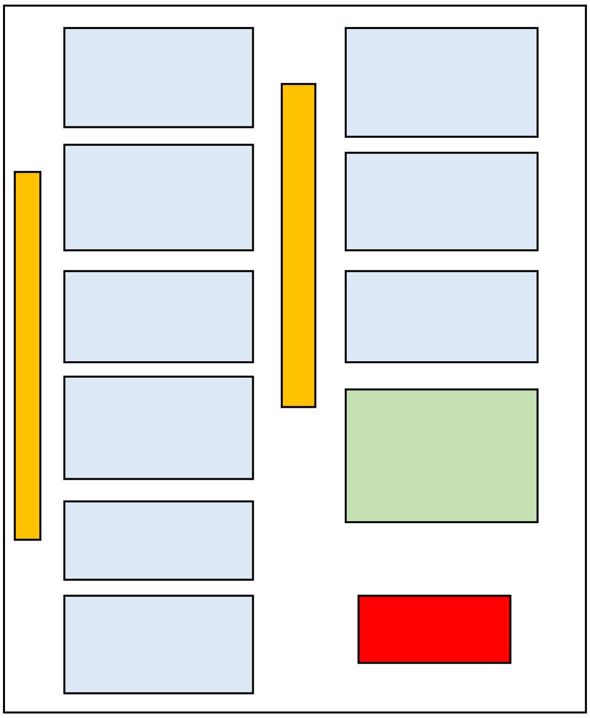
- As all of the vertical axis labels are the same (and it is quite a long label) one solution might be to have a single label centred across all plots, something like:



- Please note that we would also need a higher resolution original file (not scaled up from the version you have already supplied).

- ***The layout is now as above and the image provided is 600dpi.***

Figure 7 is also tricky. It is too tall to fit at the full page width. The text on the horizontal axis labels is still too small even at full page width. Unfortunately, the 31–40 deg S plot has one value at over 80% but I’d suggest seeing what it looks like if you remove the top of most plots so that the scale only goes to 80. As the one plot that the 100 marker is needed is at the bottom, and the bottom of the two columns isn’t aligned anyway, this might look ok. I’ve tried to sketch approximately what I mean on the next page (with the blue plots all identical, the green one slightly bigger, the red box is the legend and the orange ones are the common vertical axis labels):



- ***The layout of figure 7 is now as above, and the font size of the horizontal axis has been increased.***

Figure 12 is much better but the text is still too small. The design is too tall to fit at full page width and as currently presented could only be set to about 151 mm wide on the pdf page. I'd recommend moving the stacked area graph to a separate figure. Features a, b and c could be moved up slightly to reduce the height as far as possible, bringing the time scale as close to the bottom of the tree as possible. Can even more of the Artinskian be shaved off at the left hand side as it doesn't feature in the tree? The top of the figure can also be cropped slightly more closely – anything to change the aspect ratio to make it relatively wider.

- ***As discussed through email, Figure 12 has been trimmed. The stacked area graph and time scale have also been compressed, with the supporting figures a, b and c moved upwards to reduce the height of the image.***

<u>Referees' Comments to Author:</u>

<u>Referee: 1</u>

Comments to the Author
This paper represents a thorough analysis of the completeness of the cynodont fossil record. This is an issue that has been discussed in a previous paper, but the authors do expand on this with new analyses and offer new perspectives. In particular the addition of the spatial perspective is novel and interesting. The paper is methodologically sound (barring one issue that I'll discuss below) and the results are interesting, so I would recommend for publication with moderate revisions.

The methodological issue I want to highlight is the analysis of body size. The authors divide the cynodonts into five discrete size classes. While this is not in itself a problem, the authors don't provide any reason for choosing the particular size classes they do, and the boundaries between the classes seem extremely arbitrary. To a certain extent this is always the case when you discretise a continuous trait (there have to be boundaries somewhere, meaning that there will always be instances where two taxa very similar in size fall into different size classes), but in this case they seem more arbitrary than is desirable. They are not evenly spaced, either in terms of absolute range (e.g. increase by 30mm each class), multiples of increase (e.g. times 3 each class) or orders of magnitude. For example, the small size class (skull length 30-90mm) will contain everything from a dormouse-sized animal up to something the size of a European wild cat, a great diversity of forms, with the upper boundary 3 times higher than the lower. While the medium has the same absolute range (90-150), the range in terms of multiples is much smaller (upper boundary is only about 1.5 times higher than the lower), the log-transformed range (which would represent consistency in terms of orders of magnitude) is less than about half the amount (about 0.48 vs 0.2), and the range of forms considerably smaller (say, wild cat to fox). Then the large category is inconsistent with regards to the absolute range (a range of 50 rather than 60), and considerably smaller in terms of both multiples and orders of magnitude.

I would suggest a better way of doing this would be to identify concentrations of species within the range of sizes, using clustering methods like K means clustering. That way the boundaries between the clusters would represent sizes where there are lower concentrations of taxa, minimising instances where cynodonts of very similar size fall into separate classes from each other). Alternatively, if you prefer to define the boundaries yourself, do so with consistent ranges of log transformed skull lengths; this will make the percentage increases in body size between each size class additive and will reduce instances like I highlighted above where one category includes everything from a dormouse to a wild cat and the next ranges from wildcat to fox.

- ***K means clustering has now been used to identify discrete body size clusters, into which each species could be assigned. This was based on the average anteroposterior lengths of the postcanine teeth for each species, which has previously been shown to be a good proxy for body size in mammals (and was originally used for some of our taxa). Our relative body size estimates are largely consistent with our original dataset. The optimal number of clusters was four using the Elbow method for K means clustering. This has been added to the MS and the body size patterns re-analysed – this does not differ notably from our original results.***

Finally some more minor quibbles:

The time bins of more equal length, created by combining some stages; I found it a bit weird that you acknowledge they are not exactly equal but them refer to them as “equal”, in inverted commas. I know you do just need something to call them, but maybe don’t call them equal when they are not? Bin set A vs bin set B?

- ***This has been left as ‘equal’ in keeping with how previous authors have described these temporal intervals e.g. see Benson et al. 2016. We feel that by using the quotes, it’s clear that they aren’t actually equal.***

Worth noting why Antarctica is not mentioned in the continental bins, when it is included as a location making up Gondwana (I assume it’s because there isn’t enough of a sample to include it as a continental bin?)

- ***The exclusion of Antarctica as a separate palaeocontinent for analysis has now been justified in the text based on a lack of cynodont material that can be confidently assigned to species level.***

Page 13, first paragraph, sentence “Both parareptilian tetrapods (Verrière et al. 2016) and anomodonts (Walther and Fröbisch 2013) show no significant change in completeness across the P/T boundary.” – in a paper primarily based around quantitative methods, I would be very careful in using the word ‘significant’, and would reserve it for instances where you have results from a statistical test. Where you havn’t actually done a test, use something like “substantial”.

- ***Significant has been replaced with substantial.***

Page 17, second paragraph, sentence “This lack of correlation might be because both anomodonts and parareptilian tetrapods were genuinely much more abundant that cynodonts…” – should be “…than cynodonts…”

- ***This typo has been fixed.***

Neil Brocklehurst

Referee: 2

Comments to the Author
This is a thorough, analytically solid and well-written analysis of fossil record completeness for non-mammalian cynodonts, a major group of late Palaeozoic and Mesozoic tetrapods. It is well worth publishing in Palaeontology, and I have only very minor comments.

1. It would be worth providing some additional justification in the introduction for focusing on a paraphyletic assemblage of taxa - why is the exclusion of mammaliamorphs from the analysis justified? I'm not suggesting you include them, just that you make it a bit clearer why they are excluded.

- ***This has now been explained in the Dataset section of the methods: we chose to focus on the cynodont fossil record outside of the major Mesozoic mammaliaform radiations in order to examine the effects of this record on the timing and assembly of mammalian characteristics***

2. It would be worth discussing/mentioning the role of collection techniques on completeness, particularly in the context of the low values in the Rhaetian. The Rhaetian record, which is dominated by European taxa, differs from much of the preceding Triassic and Permian in that it is dominated by fossils collected through screenwashing techniques, which will by its very nature lead to disarticulated material with low completeness metrics.

- ***A section addressing the potential effects of a shift in collection techniques (i.e. emphasis on screen washing for Late Triassic sediments) and how this might affect the completeness of the cynodont fossil record has now been incorporated into the discussion.***

3. I was puzzled by the final section of the discussion 'Implications for early mammalian evolution'. It really appears to be a general review of non-mammalian cynodont evolution, and much of it bears little relation to the rest of the paper. I couldn't quite understand why it was there. I would suggest that this section should be substantially condensed, focusing on just aspects that relate to your data/results, or even completely omitted.

- ***This discussion section has been substantially condensed. The section previously titled "Implications for early mammalian evolution" has been edited to focus more on the uncertainty in the timing of mammalian character acquisition and assembly. We think that this is a novel aspect of our paper that has not been considered in previous treatments of fossil record bias. We hope that our revised text is now more clearly tied to our Results.***

4. A couple of minor typos - on page 12 you say that mean SCM for cynodonts is lower than for bats, but this is incorrect and contradicted by your data. Also, the URL for the Paleobiology Database is paleobiodb.org.

- ***Bats have been removed from this list on Page 12, and the correct URL for the Paleobiology Database is now on page 5.***

5. Seems slightly odd not to cite the Cashmore et al. (2020) study of sauropodomorphs in the introduction, although it does receive citations later on.

- ***This reference has been added to the introduction. We would like to note that its exclusion was because this section started by introducing the method, which was initially applied to sauropodomorphs, and then outlined the other taxonomic groups to which it had been applied. As such, the re-analysis of sauropodomorphs by Cashmore et al. (2020) was a slightly awkward fit in this context.***

Richard Butler

Referee: 3

Comments to the Author

Dear authors,

In general it is a nice paper but there are several points that should be improved. In the Pdf file, I include several comments. The ms lacks several important references, most of the south American non-mammaliaform cynodonts are calibrated with outdated ages, the used of the term mammal-like features is inaccurate (in fact they are mammalian features), the use of non-mammalian cynodont term should be clarified (Does it include mammaliaformes or not? Which it the definition used for Mammalia?), and particularly the discussion on the "acquisition of mammalian characteristics" as stated in the title is mostly incomplete, highlighting a few issues in classical taxa (eg., thrinaxodontids, trytilodontids) using in many case as main references the Book of Kemp (2005). I'm not saying it is a bad reference but it is a resume and several works were published about that, especially on South American cynodonts, in the last years. Also, for summarize mammalian features in non-mammaliform cynodonts one of the chapter of Kielan-Jaworoswa et al. 2004 (Book, Mammal from the age of dinosaurs) is considerably more detailed (although, also outdated in some points). The lack of discussion of mammalian features in probainognathians like Brasilodon, Riograndia, Therioherpeton, Prozostrodon, Pseudotherium is really painful because these specimens include good material, including skull and postcranium, published in relevant journals (JVP, PlosOne, Papers in Palaeontology, Acta Palaeont. Polonica, etc), in the last 3-4 years. To my opinions, it should be addressed. If not, the title should be changed because the acquisition of mammalian features is really incomplete. For example, some of these papers that are lacking for these discussions (ages and acquisition of mammalian features):

Bonaparte, J.F. and Barberena M.C. 2001. On two advanced carnivorous cynodonts from the Late Triassic of Southern Brazil. Bulletin of the Museum of Comparative Zoology, 156, 59–80.

Bonaparte, J.F., Martinelli, A.G. and Schultz C.L. 2005. New information on Brasilodon and Brasilitherium (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. Revista Brasileira de Paleontologia, 8, 25–46.

Guignard, M.L., Martinelli, A.G. and Soares, M.B. 2019a. Reassessment of the postcranial anatomy of Prozostrodon brasiliensis and implications for postural evolution of non-mammaliaform cynodonts. Journal of Vertebrate Paleontology, 38, e1511570-2.

Guidnard, M.L., Martinelli, A.G. and Soares, M.B. 2019b. Postcranial anatomy of Riograndia guaibensis (Cynodontia: Ictidosauria). Geobios, 53, 9–21. Doi:10.1016/j.geobios.2019.02.006

Guignard, M.L., Martinelli, A.G. and Soares, M.B. 2019c. The postcranial anatomy of Brasilodon quadrangularis and the acquisition of mammaliaform traits among non-mammaliaform cynodonts. Plos One, 14(5), e0216672.

Langer, M.C., Ramezani, J. and Da Rosa, A.A.S. 2018. U-Pb age constraints on dinosaur rise from south Brazil. Gondwana Research, 57, 133–140.

Martinelli, A.G. and Rougier, GW. 2007. On Chaliminia musteloides Bonaparte (Cynodontia, Tritheledontidae) and the phylogeny of the Ictidosauria. Journal of Vertebrate Paleontology, 27, 442–460.

Martinelli, A.G., Eltink, E., Da-Rosa, Á.A.S. and Langer, M.C. 2017a. A new cynodont (Therapsida) from the Hyperodapedon Assemblage Zone (upper Carnian-Norian) of southern Brazil improves the Late Triassic probainognathian diversity. Papers in Palaeontology, 3, 401–423.

Martinelli, A.G., Kammerer, C.F., Melo, T.P., Paes Neto, V.D., Ribeiro, A.M., Da-Rosa, Á.A.S., Schultz, C.L. and Soares, M.B. 2017b. The African cynodont Aleodon (Cynodontia, Probainognathia) in the Triassic of southern Brazil and its biostratigraphic significance. Plos One, 12, e0177948.

Martinelli, A.G., Soares, M.B., Oliveira, T.V, Rodrigues, P.G. and Schultz, C.L. 2017c. The Triassic eucynodont Candelariodon barberenai revisited and the early diversity of stem prozostrodontians. Acta Palaeontologica Polonica, 62, 527–542.

Rodrigues, P.G., Ruf, I. and Schultz, C.L. 2013. Digital reconstruction of the otic region and inner ear of the non-mammalian cynodont Brasilitherium riograndensis (Late Triassic, Brazil) and its relevance to the evolution of the mammalian ear. Journal of Mammalian Evolution, 20, 291–307.

Rodrigues, P.G., Ruf, I. and Schultz, C.L. 2014. Study of a digital cranial endocast of the non-mammaliaform cynodont Brasilitherium riograndensis (Later Triassic, Brazil) and its relevance to the evolution of the mammalian brain. Paläontologische Zeitschrift, 88, 329–352.

Wallace, R.V.S., Martínez, R. and Rowe, T. 2019. First record of a basal mammaliamorph from the early Late Triassic Ischigualasto Formation of Argentina. Plos One, 14(8), e0218791.

Wible, J.R. 1991. Origin of Mammalia: the craniodental evidence reexamined. Journal of Vertebrate Paleontology, 11, 1–28.

I hope these comments improve the ms.

Best wishes,

Agustin Martinelli

- ***The definition of non-mammalian cynodonts has been clarified in the introduction as including all cynodonts outside of Mammaliaformes and we have now referred to them as non-mammaliaform cynodonts throughout the text.***
- ***The ages used throughout (and reported in our dataset, which the Referee could not access) represent the most recent literature, including papers that were published in the weeks leading up to our initial submission. There are a few typos in the text, most notably in which we have said Middle Triassic when we should have said Middle Triassic–early Late Triassic, which we suspect account for most of these (understandably) perceived issues. The other issue might come from the fact that the smallest time bins used in our analyses are stage-level. As such, a species that comes from an early Carnian deposit is analysed as a Carnian species and this is also how the stratigraphic ranges of such species are shown in Fig. 12. Finally, we opted to take a conservative view on the ages of many stratigraphic units. For example, the Manda Formation is generally regarded as Middle Triassic in the literature, but might well be Carnian based on the available data; as such, it is treated as Middle Triassic–Carnian in our analyses. We have tried to better clarify these issues in the text, as well as in the caption to Fig. 12.***
- ***In places where Kemp 2005 has been used as a reference we have added "e.g." alongside other references to illustrate that these are exemplar references.***
- ***We have now incorporated more details about the South American taxa in our Discussion. The final section of the discussion has been edited to focus more on the uncertainty in the timing of acquisition and assembly of mammal-like characteristics (see also comments to Reviewer 2).***

Martinelli comments pdf:

Page 2: "they are in fact mammalian features"

- ***This sentence has been deleted.***

Page 2: "i think that the South American peak of diversity is by Late Triassic (Carnian-Norian). Please, consider in the data set the radiometric ages for Ischigualasto Villa Union Basin and Parana Basin, published since 2016."

- ***The original sentence in our abstract is clearly about completeness, not diversity. However, it should have extended into the early Late Triassic (i.e. Carnian). It has been changed from 'Early–Middle Triassic' to 'Early–early Late Triassic' to accommodate this, and was a mistake in the text and not a reflection of the stratigraphic ages used for taxa in our***

analyses – as explained above, we had already incorporated the latest literature in terms of ages.

Page 2: “is it really true for South America. Is it true for the Triassic?!”

- ***Our results show that the early cynodont fossil record was less complete relative to most other tetrapod clades that were included in the analysis. These comparisons were both temporal and non-temporal and the data used for these analyses were at the global level, and not restricted to a certain time interval (e.g. only Triassic overlaps of occurrences of cynodonts and other tetrapods) or palaeocontinent (e.g. only South American occurrences of cynodonts and other tetrapods). As such, although we can’t say with certainty that it’s true for South America, we can say that it’s true of the Triassic and of early cynodonts in general. We have also added in the word ‘overall’ between ‘complete’ and ‘relative’ to emphasise that this a broad pattern.***

Page 4: “add Schultz et al., 2020 JSAES https://doi.org/10.1016/j.jsames.2020.102846”

- ***Added***

Page 4: “add Abdala et al., 2020 https://doi.org/10.1016/j.jsames.2020.102884”

- ***Added***

Pgae 5: “early-mid LATE TRIASSIC?? the time calibrations of n-m cynodont in Abdala and Ribeiro 2010 are old, most cynodont fauna from south america, for example, are now early to late carnian...”

- ***This was an error and should have said early Late Triassic. The Abdala and Ribeiro study showed diversity to peak until (and including) the Carnian, and so this should be early Late Triassic, but not early-mid Late Triassic.***

Page 6: “age for some taxa are not right in that data base, so is that also a bias?”

- ***The ages for each formation in which specimens were found were revised prior to analysis using the literature, with the PBDB used as a starting point. We are confident that the ages used in our study represent the latest literature, taking a conservative view of age constraints. Given that the reviewer could not access the database, we assume this misunderstanding comes from several typos in the text (see earlier responses) which are now fixed.***

Page 6: “i was not able to access to this dataset to check ages, etc...”

- ***We are unsure of the issues with Dryad, as stated in the email.***

Page 9: “I think it is important to define the definition used ir order to understand the real scope of the paper. At some point i thought that the ms include early mammaliaforms, as morganucodontids, docodonts, etc, which accordinly to most recent autors are not included in MAMMALIA. So, if it is not the case, i suggest to change non-mammalian to non-mammaliaforms and detail at some point of the text which term do you used over another, based on who. I suggest to use Mammalaiformes rather than Mammalia which has a definition based on monotrmes and therians."

Page 10: "non-mammaliaform"

- ***We have now revised the text accordingly with regards to this issue (see also earlier response to Referee 2's comment).***

Page 11: "other part of the MS you said that the peak is middle Triassic, and ther middle-late Triassic, which for me is more correct than previous statements"

- ***As noted before, this was an error earlier – throughout it should be Middle–early Late Triassic.***

Page 13: "i'm not sure how pertinent this comparison is because the temporal range of pterosaurs and cynodonts is little overlapped"

- ***The overlap in fossil occurrences of the two groups span from the Norian to the Aptian, which is a temporal range of almost 100 million years, which was a greater length of time compared to other groups e.g. parareptiles (~50 Myr) and plesiosaurs (~80 Myr). As such, we consider it pertinent.***

Page 15: ", whcih reduce the possibility to find them in faunal associations (collection biases)"

- ***A section has been added to the discussion detailing the potential effects of collection practices on the completeness metrics of non-mammalian cynodonts during the Late Triassic, e.g. screen-washing techniques.***

Page 16: "again, you should chose which term use; it is the first time you use mammalaiforms. Also Multitiberculates are considered MAMMALIA by most authors, so using non-mammalian cynodonts it is including morganucodontids but not multituberculates."

- ***The definition of non-mammalian cynodonts has been clarified in the introduction as "all cynodonts outside of Mammaliaformes".***

Page 21: "add more references, as for example, works of Crompton on traversodontid teeth"; "several authors work on these issues…"***;*** "add Hopson and Kitchiing 2001"; "it is a very simplified view, as you said cynognathus is carnivorous, perhaps diademodon was omnivorous and so on... On the other hand early probainognathians can be insectivorans, carnivorans, omnivorans...(e.g., Martinelli et al 2017 Candelariodon review Acta Palaeontologica polonica)."

- ***This section has been deleted in shifting the focus of this section of the discussion towards understanding the uncertainty in the timings of mammalian character assembly. As such, although we otherwise fully agree with the reviewer's above four comments, these are no longer pertinent to our MS (though the Hopson reference is now included).***

Page 21: "add Martinelli et al. 2017 Aleomoatherim Papers in Palaeontologia"

- ***This reference has been added.***

Page 21: “early mammaliaforms”

- ***Changed to early Mammaliaformes.***

Page 21: “i'm not sure what it means? it refers to the fact that the postdenary bones are smaller compared to other groups?”

- ***This has been reworded to clarify that we mean an expanded dentary.***

Page 22: “There are several mammalian features of brasilodontids, or closely related forms not mencioned, even in the postcranium. I think it is necessary an extra parragraph on it!”

- ***We have incorporated additional comments on this group.***

Page 22: “late Late Triassic”

- ***Middle–early Late Triassic has been added here instead because the data shows that the completeness declines immediately following the Carnian.***

Page 56: “several of the taxa are placed as of similar age but it is not the case. For example, Alemoatherium, therioherpeton, przosotrodon and charruodon are younger than most other basal probainognathians. Chaliminia is younger than irajatherium and riograndisa,”
“several of the taxa are placed as of similar age but it is not the case. For example, the traversodontids dom Santcruzodon to protuberum are older than Exaeretidon sps”

- ***Temporally, stages were the smallest scale time intervals used for analysis; therefore, if species were found in “early Carnian” age rocks, they were considered to have been present throughout the Carnian in our analyses. Our figure also therefore reflects this. This has now been clarified in the methods section, as well as the figure caption. As commented upon earlier, these ages reflect the latest literature.***

Spatiotemporal variation in completeness of the early cynodont fossil record and its implications for mammalian evolutionary history

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RRH: CYNODONT FOSSIL RECORD
LRH: VARNHAM ET AL.

ABSTRACT

Mammals are the only surviving group of Cynodontia, a synapsid clade that first appears in the fossil record in the late Permian, ~260 million years ago. Here, using three metrics that capture skeletal completeness, we quantify the quality of the early cynodont fossil record in time and space to evaluate the impact of sampling and preservational biases on our understanding of the group's evolutionary history. There is no consistent global sampling signal for early cynodonts. Completeness of the cynodont fossil record increases across the Permian/Triassic boundary, peaking in the Early–early Late Triassic. This peak is dominated by specimens from southern Africa and South America, where a highly seasonal climate likely favoured preservation. Completeness is generally lower thereafter, correlated with a shift from a Gondwanan to a predominantly Laurasian fossil record. Phylogenetic and stratigraphic congruence in early cynodonts is high, although their fossil record exhibits less skeletal completeness overall than other tetrapod clades, including the contemporaneous anomodont synapsids. This discrepancy could be due to differences in the diagnosability of their fossils, especially for small-bodied species. Establishing the timing and assembly of derived ('mammalian') anatomical features in Cynodontia is obscured by sampling. Two of the major nodes at which acquisition of mammalian features is concentrated (Cynodontia and

Mammaliamorpha) suffer from lengthy intervals of poor sampling prior to becoming abundant parts of tetrapod faunas. Low completeness in these intervals limits our ability to determine when certain ‘key’ mammalian characteristics evolved, or to identify the selective pressures that might have driven their origins.

Keywords: Cynodontia; diversity; mammals; sampling bias; Synapsida.

INTRODUCTION

Permo-Triassic terrestrial fossil assemblages, such as those documented in the Karoo Basin in southern Africa and Paraná Basin in South America, preserve evidence of complex ecosystems made up of a diverse array of vertebrate groups (e.g. Langer et al. 2007; Schultz et al. 2020; Smith et al. 2020). These assemblages include various diapsids and temnospondyls (e.g. Damiani 2004; Langer 2005), but are most renowned for their extensive record of therapsid synapsids (e.g. Fröbisch 2014; Viglietti et al. 2016; Abdala et al. 2020). Over the course of the Permian, therapsids diversified to fill a wide range of dietary and environmental niches (Kemp 2005; Angielczyk and Kammerer 2018). However, following the Permian/Triassic (P/T) mass extinction, around 251.9 million years ago (Ma), only a small fraction of the once diverse therapsid lineage survived (Botha and Smith 2006). Of the surviving therapsids, cynodonts were the most successful, and their descendants, the mammals, represent the only extant synapsid group (Hopson and Kitching 2001).

The earliest known cynodonts appear in the Wuchiapingian (early late Permian) of South Africa, but are rare and incompletely known components of the fauna (Botha et al. 2007; Kammerer 2016). Much more abundant and often exceptionally preserved cynodont fossils are found in Triassic deposits, particularly in southern Africa and South America. This Gondwanan record provides an important window into the acquisition of mammalian characteristics along the mammal stem (e.g. Bonaparte et al. 2005; Rodrigues et al. 2013; Crompton et al. 2017; Jones et al. 2018). In Laurasia, cynodonts are present by the Changhsingian (latest Permian; Ivakhnenko 2013) and also become more species-rich and widespread in the Triassic, with fossils found at sites across Europe, Asia, and North America (e.g. Godefroit and Battail 1997; Sues 2001; Gao et al. 2010).

Despite a global distribution, rich fossil record, and extensive study, prominent gaps in our knowledge of early cynodont evolution remain. These gaps limit our understanding of macroevolutionary trends within Cynodontia, such as response to mass extinctions and the timing and drivers of radiations, and can be attributed in large part to incomplete sampling. Sampling biases have long been recognized as a major factor obscuring our reading of the fossil record (e.g. Raup 1972; Allison and Briggs 1993; Alroy 2010) and encompass both human-mediated (e.g. worker effort) and natural (e.g. area of exposed outcrop) factors. To address these biases and try to mitigate their effects on our interpretations of prehistory, attempts have been made to assess the completeness of the fossil record, with most focusing on particular clades as case studies (e.g. Alba et al. 2001; Fountaine et al. 2005; Eiting and Gunnell 2009; Beardmore et al. 2012). Mannion and Upchurch (2010) developed two methods that quantified the completeness of individual skeletons to obtain a pair of completeness metrics for each species. They then used these metrics to evaluate trends in completeness across sauropodomorph dinosaurs through time (see also Cashmore et al. 2020). These approaches have since been applied to a number of additional taxonomic groups, namely non-avian theropods (Cashmore and Butler 2019), Mesozoic birds (Brocklehurst et al. 2012), pterosaurs (Dean et al. 2016), crocodylomorphs (Mannion et al. 2019), ichthyosaurs (Cleary et al. 2015), plesiosaurs (Tutin and Butler 2017), parareptilian tetrapods (Verrière et al. 2016), and several synapsid groups. The latter include pelycosaurs (Brocklehurst and Fröbisch, 2014), anomodonts (Walther and Fröbisch 2013), non-mammaliaform cynodonts (Lukic-Walther et al. 2019), eutherian mammals (Davies et al. 2017), and bats (Brown et al. 2019).

Lukic-Walther et al. (2019) examined global patterns of non-mammaliaform cynodont completeness across geological time using phylogenetically informative characters. In addition to general temporal patterns, they also studied phylogenetic diversity and body size as related to the cynodont record through time. The results of their analyses did not support a trend of decreasing preservation potential, indicating that progressive cynodont decline following the Middle Triassic is a genuine aspect of their evolutionary history and not just a sampling artefact. However, Lukic-Walther et al. (2019) did not address potential spatial variation in cynodont completeness, which is a major concern given the apparent ‘Gondwanocentrism’ of the Permo-Triassic cynodont record (Abdala and Ribeiro 2010).

Some aspects of the temporal patterns analyzed by Lukic-Walther et al. (2019) are also worth re-examining in further detail. Gondwanan cynodont species diversity appears to have increased between the late Permian and the Early Triassic, with continued high diversity through to the Late Triassic, when the diversity of non-mammaliaform members of Cynodontia seems to have declined. Although these observed patterns have been shown not to result from a decrease in preservational potential, there are additional sampling biases that could be obscuring genuine macroevolutionary signal in the data.

Here, non-mammaliaform cynodont completeness is quantified in a number of additional ways and examined spatially as well as temporally, to evaluate how regional patterns contribute to any global signal. The completeness of the early cynodont record is also compared with that of other taxonomic groups to assess whether there are common preservational patterns, especially as regards other synapsids. Finally, we discuss how the completeness of the group's fossil record might impact our interpretation of early cynodont evolution and timing of the acquisition of mammalian characters.

MATERIALS AND METHODS

Dataset

We compiled a dataset of 126 species of non-mammaliaform cynodonts (i.e. cynodonts outside of the subclade Mammaliaformes *sensu* Rowe 1988) currently considered to be valid. Fossils of non-mammaliaform cynodonts have been found globally, and are known in deposits ranging from the late Permian (e.g. Sues and Munk 1996; Ivakhnenko 2012; Abdala et al. 2019) to the Early Cretaceous (e.g. Lopatin and Agadjanian 2008; Matsuoka et al. 2016). Only taxa based on body fossils were included; ichnotaxa were not analyzed. Although ichnites can provide important complements to the body fossil record in determining geographic and stratigraphic ranges of major tetrapod clades (e.g. Marchetti et al. 2017), their effective '0% completeness' and the difficulty in assigning ichnotaxa to specific trackmakers makes them unsuited for this type of analysis. Our dataset is based on data presented in Lukic-Walther et al. (2019), augmented with a comprehensive review of the recent literature. Mammaliaforms were excluded from the analysis in order to focus on the fossil record outside of the major Mesozoic mammal radiations (which have a predominantly dental record; Kielan-Jaworowska et al. 2004), examining effects of this record on the timing and assembly of mammal-like features.

Data on the stratigraphic age and geographic location (including present-day- and palaeo-coordinates) of occurrences of each cynodont species were compiled from the literature and The Paleobiology Database (www.paleobiodb.org). We used a conservative approach to stratigraphic ages when there is some uncertainty; for example, the Manda Formation in Tanzania is generally considered to be Middle Triassic (Anisian–Ladinian) but might be Carnian (e.g. Ottone et al. 2014; Wynd et al. 2017); as such, occurrences from this stratigraphic unit are assigned to the Middle–early Late Triassic. In addition to newly described species and some revisions to stratigraphic ages, one notable difference from the dataset of Lukic-Walther et al. (2019) pertains to our treatment of *Oligokyphus* from the Early Jurassic of the UK (Kühne 1956). Whereas those authors considered the co-occurring species *O*. *major* and *O*. *minor* as distinct taxa, with each represented by limited skeletal remains, here we follow Hopson and Kitching (1972; see also Sues 1985) in regarding the latter species as a junior synonym of the former. As a consequence, material that could not previously be unequivocally assigned to either species has now all been included in *O*. *major*, greatly increasing the completeness score for this taxon. The dataset is up-to-date as of the 25th of June, 2020 and is available in Varnham et al. (2020).

The body size of each cynodont species was estimated to evaluate whether sampling and preservation bias varied between different size classes. Previous studies have shown that tooth dimensions are good proxies for overall body size in mammals (e.g. Creighton 1980), and that approach is used here for their cynodont outgroups. Each species was assigned to a size category based on the average anteroposterior length of their postcanines, using k-means clustering to identify discrete body size clusters (Wang and Song 2011). The optimal number of clusters was four using the Elbow method (Wang and Song 2011), with tooth size ranges of: (1) 0–2.8 mm; (2) >2.8–5.0 mm; (3) >5.0–8.0 mm; and (4) >8.0 mm. This analysis was carried out using RStudio version 1.2.5019 (R Core Team 2019; RStudio Team 2019).

Completeness metrics

Using the approach proposed by Mannion and Upchurch (2010), a Skeletal Completeness Metric (SCM) was calculated for each species. This was achieved by dividing the cynodont skeleton into body regions, each of which was assigned a percentage based on approximations of how much of the skeleton is accounted for by that region (Figure 1). Within each region, individual elements were also assigned a percentage (Table 1). Absence of an element resulted in a score of zero, whereas it received 50% of its weighted score if some part of that element was preserved. There is variation in the numbers of vertebrae, carpal elements, and phalanges amongst cynodonts, making it difficult to determine the completeness of a partial skeleton. As such, for species in which these areas are incompletely preserved, the total possible number of these elements was estimated based on the anatomy of the most closely related species in which the relevant region of the skeleton is completely preserved. We calculated this metric based on all known specimens of each species, which is equivalent to SCM2 in Mannion and Upchurch (2010), hereafter referred to as SCM for simplicity.

A second completeness metric, proposed by Beardmore et al. (2012), was also used. Here, the cynodont skeleton was divided into six regions (skull, vertebrae and ribs, pectoral girdle, forelimbs, pelvic girdle, hindlimbs) and the completeness of each region was scored using a semi-qualitative scale from 0 to 4, with 0 being entirely absent and 4 being complete. In the current study, regions of specimens were scored as: (i) zero if the region was absent; (ii) 1 if ≤25% complete; (iii) 2 if 26–50% complete; (iv) 3 if 51–75% complete; and (v) 4 if ≥76% complete. Values for each region were then summed and divided by the total possible score (in this case, 24) and multiplied by 100 to give a percentage completeness score. Following Cleary et al. (2015), we refer to this metric as Beardmore's Skeletal Completeness Metric (BSCM).

Mannion and Upchurch (2010) also proposed a Character Completeness Metric (CCM). The CCM follows the same principles as the SCM, but the percentages assigned to each region are instead a measure of the amount of phylogenetically informative data preserved within each region. CCM values can be calculated from the average percentage of characters attributed to each region of the skeleton from published phylogenies of the clade. Here, CCM values for cynodont species were obtained from Lukic-Walther et al. (2019), excluding those for *Oligokyphus major* (see above).

Data series and spatiotemporal bins

A mean average completeness value of cynodont scores and associated standard deviations was calculated for each metric in each spatiotemporal bin. Where fossil occurrences have poor stratigraphic age resolution and could not be assigned to a single time bin, their full stratigraphic uncertainty was used as their temporal range. Observed ('face value') diversity was also calculated by summing the number of valid species within each spatiotemporal bin. Two different time binning strategies were used. Firstly, we used standard stratigraphic stages based on the 2018 version (v. 5.0) of the geological time scale presented by Cohen et al. (2013). As such, species were assigned to a full stage (e.g. Carnian), even if they could be dated more precisely (e.g. early Carnian). However, the durations of each stage are highly variable; for example, the Induan spans less than one million years (251.9–251.2 Ma), whereas the Norian spans 18.5 million years (227–208.5 Ma). Longer intervals might preserve a greater number of species purely as a result of there being a longer time for fossil accumulation, such that stage-level binning causes time-averaging of non-contemporaneous species. Therefore, a second set of time bins with approximately equal durations was used (e.g. see Benson et al. 2016), combining several short stages whilst maintaining important stratigraphic boundaries (Table 2).

Temporal fluctuations in cynodont completeness (using all three metrics) and observed diversity were reconstructed at the global level for both time-binning strategies. By contrast, we limited our spatial reconstructions of completeness and observed diversity to stage-level bins. In these reconstructions, we evaluated completeness (using only SCM) and observed diversity in five palaeocontinents (Africa + Indo-Madagascar, Asia, Europe, North America, and South America; note that Antarctica and Australasia were excluded due to the limited amount of non-mammaliaform cynodont remains found in the former and total absence in the latter), Laurasia (comprising specimens from Asia, Europe, and North America) and Gondwana (consisting of specimens from Africa, Antarctica, India, Madagascar, and South America), as well as within 10° palaeolatitudinal bands.

Comparisons with other clades

The completeness metrics calculated for cynodonts were compared with contemporaneous clades for which completeness data exists. Comparisons were made with terrestrial taxa, comprising anomodonts (Walther and Fröbisch 2013), parareptilian tetrapods (Verrière et al. 2016), Mesozoic birds (Brocklehurst et al. 2012), pterosaurs (Dean et al. 2016), pelycosaurian-grade synapsids (Brocklehurst and Fröbisch 2014), non-avian theropods (Cashmore and Butler 2019), and sauropodomorphs (Cashmore et al. 2020), as well as marine taxa, consisting of plesiosaurs (Tutin and Butler 2017) and ichthyosaurs (Cleary et al. 2015). Comparisons were also made with two non-contemporaneous mammalian clades: eutherians (Davies et al. 2017) and bats (Brown et al. 2019). In all cases, the spread of data (i.e. distribution of completeness values) for each of these groups was compared with that of non-mammaliaform cynodonts. Where there is substantial temporal overlap, comparisons of completeness were also evaluated through geological time.

Stratigraphic and phylogenetic congruence

There are several methods for testing the congruence between phylogeny and stratigraphy, although all of them are biased by parameters that are not distributed uniformly through time, such as tree size, average ghost length duration, and speciation rates (O'Connor et al. 2011). Here, we applied four widely used metrics for assessing congruence: (1) the stratigraphic consistency index (SCI) (Huelsenbeck 1994); (2) the relative completeness index (RCI) (Benton and Storrs 1994); (3) the gap excess ratio (GER) (Wills 1999); and (4) the Manhattan stratigraphic measure (MSM*) (Pol and Norell 2001; Siddall 1998). We constructed an informal supertree based on Lukic-Walther et al. (2019) and recent topologies and taxonomic studies (Hopson and Kitching 2001; Sidor and Smith 2004; Matsuoka et al. 2016; Pavanatto et al. 2018; Sidor and Hopson 2018; Abdala et al. 2019; Hendrickx et al. 2019; Wallace et al. 2019; Mocke et al. 2020). This supertree includes 93 non-mammaliaform cynodont species.

Analyses

Spatiotemporal bins with zero value data were excluded prior to analysis. All spatial- and time-series data were log-transformed, and generalised differencing was applied to remove the effects of trend and autocorrelation, using a function written by Lloyd (2008). Three statistical tests were used to assess the degree of spatiotemporal correlation between the completeness metrics (SCM, CCM, and BSCM [including those of comparative clades]) and diversity. Spearman's rank correlation coefficient and Kendall's tau coefficient are non-parametric tests that measure the ordinal association of two variables. Pearson's correlation coefficient is a parametric test that measures the strength of the linear correlation between two variables. Non-temporal pairwise comparisons were conducted using the non-parametric Mann-Whitney U test. Congruence between stratigraphic and phylogenetic data was evaluated using the R packages ape v.5.3 (Paradis and Schliep 2019) and strap v.1.4 (Bell and Lloyd 2015), using the StrapPhyloCongruence function. All analyses were implemented in the R programming language (R Core Team 2019), using RStudio version 1.2.5019 (RStudio Team 2019).

RESULTS

Comparisons of completeness metrics and diversity for cynodonts

All SCM, BSCM, and CCM metrics for non-mammaliaform cynodonts have a statistically significant positive correlation through time and space with one another (Table 3). This is the case under both binning schemes, although the correlation is weaker when using stage-level bins. The strongest correlation is consistently between SCM and BSCM, whereas the weakest correlation is between BSCM and CCM.

There is no statistically significant relationship between observed diversity and any of the completeness metrics spatially (Table 3), but some significant relationships are present temporally. Using stage-level bins, there is a significant positive correlation between observed diversity and CCM using Spearman's rank correlation coefficient, and with BSCM using Kendall's tau coefficient. Using the 'equal'-length time bins, a significant positive correlation between observed diversity and CCM is found in all three tests, with BSCM using Kendall's tau coefficient and Pearson's correlation coefficient, and with SCM using Pearson's correlation coefficient (Table 3).

Global patterns in completeness and diversity

The mean average SCM for all 126 cynodont species is 18%, with completeness values for each species ranging from 1% to 99% (Figure 2). The Permian has the highest mean SCM (23%: 9 species in total) of the four geological periods under study, whereas the Cretaceous is characterised by the lowest mean SCM (1%: 3 species) (Figure 3). Although the Triassic records the greatest number of cynodonts (88 species), including the most completely known species (*Thrinaxodon liorhinus* at 99%), it also has the largest range of SCM values and a mean SCM of only 18%. 26 species are known from the Jurassic, which has a mean SCM of 19%.

Temporal patterns of global completeness and observed diversity using 'equal'-length time bins do not differ significantly from those at stage-level (Figure 2); as such, the following focuses on results based on the latter analyses. The mean SCM and CCM values are relatively high in the Wuchiapingian (23% and 41%, respectively) and Changhsingian (20% and 32%, respectively), whereas the mean BSCM is substantially lower (9% in the Wuchiapingian and 4% in the Changhsingian). Mean SCM, CCM and BSCM values increase across the P/T boundary. Observed diversity is consistently low throughout the late Permian and Early Triassic, followed by a rapid increase during the Anisian (early Middle Triassic) and peaking during the Ladinian–Carnian (late Middle–early Late Triassic; reaching 49 species). The mean averages of the three completeness metrics each show an overall decline during the Triassic, reaching a minimum in the Rhaetian. Following the Carnian, observed cynodont diversity declines, remaining low throughout the successive stages (Figure 2), with the exception of a relatively small spike in the number of species (5) in the Oxfordian (early Late Jurassic). There is an increase in mean completeness values in the Early Jurassic, but completeness is relatively low throughout the remainder of the Mesozoic. Both the SCM (46%) and BSCM (42%) peak during the Pliensbachian (Early Jurassic), whereas the CCM attains its highest value (52%) in the Anisian.

Regional patterns in completeness and diversity

The mean SCM of non-mammaliaform cynodont species from Gondwana is higher (24%: 74 species) than that of species from Laurasia (11%: 55 species). Laurasian species have been found in time intervals ranging from the late Permian to the Early Cretaceous, whereas no Gondwanan species have been recorded from later than the Early Jurassic (Figure 4).

Within each of the five smaller palaeocontinents under consideration, Africa + Indo-Madagascar has the highest mean SCM (27%: 39 species) and the greatest range of SCM values (1–99%), with early cynodont species represented in every stage between the Wuchiapingian and Sinemurian, inclusive (Figures 5 and 6). South America has the second highest mean SCM at 24% (38 species between the Anisian and Pliensbachian). The range of SCM values from South America is similar to that of Africa (1–92%). The mean SCM of cynodonts from Asia is 12% (19 species between the Olenekian and Valanginian) and that of North America is 15% (10 species between the Carnian and Pliensbachian). The greatest temporal range is observed in the European palaeocontinental record, which spans the Wuchiapingian to the Aptian (based on the occurrence of *Xenocretosuchus sibiricus* in present-day Russia [Tatarinov and Matchenko 1999], here binned into the European palaeocontinental region for analytical purposes. Although Russia spans the European and

Asian continents, the majority of non-mammaliaform cynodont fossils have been found in European Russia, with *Xenocretosuchus* from Siberia being one of the few exceptions. If *Xenocretosuchus* is excluded, the youngest European record is Bathonian [*Stereognathus ooliticus* from the UK]). Although it has the temporally most extensive non-mammaliform cynodont record, the mean European SCM is the lowest of all the palaeocontinents (9%: 26 species).

Palaeolatitudinal patterns in completeness and diversity

The southernmost palaeolatitudinal bands (71–80˚S and 81–90˚S) have the highest mean completeness at 99%, but this is due to a single occurrence of *Thrinaxodon liorhinus* (Colbert and Kitching 1977) within each palaeolatitudinal band (Figure 7). The palaeolatitudinal band of 11–20° N has the highest mean SCM of the Northern Hemisphere at 42% (4 species), resulting from highly complete specimens of *Kayentatherium wellesi* (Kermack 1982; Sues 1986). All other northern palaeolatitudinal bands have a mean SCM of <13%. The palaeolatitudinal bands of 51–60˚N and 61–70˚N have the lowest mean SCM at 1% (1 species). All Southern Hemisphere palaeolatitudinal bands have a mean SCM of >17%.

Body size variation in completeness and diversity

The smallest cynodont species (based on a postcanine length of 0–2.8 mm) have the lowest mean SCM (11%: 52 species), with values ranging between 1% and 99% (Figure 8). Their observed diversity is highest during the Middle–Late Triassic (Figure 9), peaking during the Ladinian and Norian. Species with a postcanine length of >2.8–5.0 mm have a mean SCM of 21% (41 species) and are present from the Wuchiapingian to the Aptian, peaking in diversity during the Carnian. Species with a postcanine length of >5.0–8.0 mm have a mean SCM of 26% (18 species) and are also found mostly between the Middle–Late Triassic. The largest cynodont species (postcanine length >8.0 mm) have the highest mean SCM of 28% (15 species), peaking in diversity during the Carnian.

Comparisons with other clades

There is no significant temporal correlation between cynodont completeness metrics and those of ichthyosaurs, plesiosaurs, anomodonts, parareptilian tetrapods, sauropodomorphs, or non-avian theropods (Table 4). However, there is a statistically significant correlation between the completeness of cynodonts and that of pterosaurs.

Regarding non-temporal comparisons, the results from the Mann-Whitney U tests demonstrate that the mean SCM (and BSCM) value for cynodonts is significantly lower than that of ichthyosaurs, parareptilian tetrapods, plesiosaurs, pelycosaurian-grade synapsids, non-avian theropods, and sauropodomorphs (Table 5; Figure 10A). Similarly, the mean CCM value of cynodonts is significantly lower than that of anomodonts, parareptilian tetrapods, plesiosaurs, and eutherians (Table 5; Figure 10B). In particular, the CCM values for anomodonts and parareptilian tetrapods are substantially greater. Although the mean SCM of cynodonts is significantly higher than that for bats, the reverse is true for the CCM.

Stratigraphic and phylogenetic congruence

High SCI and GER values suggest that that the early cynodont supertree has a better stratigraphic fit than would be expected by chance (Table 6). By contrast, the RCI value is equivocal, whereas the MSM* value indicates little congruence (Table 6).

DISCUSSION

Geological and environmental constraints on the early cynodont fossil record

Our results clearly demonstrate that there is no consistent global sampling signal for the non-mammaliaform cynodont fossil record, with most time intervals dominated by fossils from a relatively narrow spatial range. This accords with recent evaluations of the completeness of other terrestrial vertebrate groups (Mannion et al. 2019; Cashmore et al. 2020), as well as the broader sampling regime of the fossil record (e.g. Benson et al. 2016; Close et al. 2020).

All completeness metrics for cynodonts display a large increase across the P/T boundary (Figure 2). Two of the six Induan (earliest Triassic) species are among the most completely known early cynodonts (*Thrinaxodon liorhinus* and *Galesaurus planiceps,* with an

SCM of 99% and 96%, respectively), underlying this spike in completeness. By contrast, parareptilian tetrapods (Verrière et al. 2016) and anomodonts (Walther and Fröbisch 2013) show no substantial change in completeness across the P/T boundary. All three of these tetrapod groups survived the P/T mass extinction and are commonly found within the Beaufort Group of the Karoo Basin in South Africa, which provides a near-continuous, high-quality record of vertebrate faunas from the middle Permian to Middle Triassic. Unlike cynodonts, however, parareptiles and anomodonts also have an extensive Permian record. Thus, although these groups also exhibit high completeness in the Early Triassic, it constitutes continuation of an existing pattern rather than a notable spike.

During the Early–Middle Triassic, the cynodont record is dominated by species within the smaller cynodont size classes (i.e. those with a postcanine length ≤8 mm; see Figure 9), and their completeness is relatively high (Figure 2). Species at this time are found in high abundance mostly at palaeolatitudes of 40–70˚S (Figures 9 and 11) within the Beaufort Group in South Africa and the Puesto Viejo and Rosario do Sul groups of South America. These stratigraphic units consist of banded shales, mudstones, and fine-grained sandstones, indicative of low energy fluvial and floodplain depositional environments (e.g. Smith et al. 1993; Zerfass et al. 2003; Ottone et al. 2014). Badgley (1986) also noted that low energy fluvial environments have the potential to preserve a high proportion of small-bodied taxa, even if remains are mostly scattered and disarticulated. The Early–Middle Triassic climate of these high palaeolatitude Gondwanan regions was also highly seasonal, with periods of sustained aridification and reduced precipitation, interspersed by intense sporadic flooding (Dubiel et al. 1991; Smith et al. 1993; Zerfass et al. 2003; Pires et al. 2005; Pace et al. 2007). Highly variable climatic conditions have the potential to preserve concentrated fossil deposits of relatively complete individuals due to the aggregation of species in drought conditions (Smith 1993; Viglietti et al. 2013), reduced chemical weathering (Behrensmeyer 1978), or through mummification via windblown dust (Smith and Botha-Brink 2014). Furthermore, extreme flash floods can also preserve highly complete specimens through rapid burial and flooding of dens/burrows, as has been observed in some cynodonts (e.g. Smith 1993; Fernandez et al. 2013). It has also been suggested that both the synapsids (e.g. cynodonts) and archosauromorphs that survived the P/T extinction were well adapted to these stressful climatic conditions, allowing them to thrive, which might explain the relatively high cynodont diversity in the Early Triassic (Smith and Botha-Brink 2014) (Figures 2, 4 and 5).

On a global scale, values for all three cynodont completeness metrics decline from the Ladinian onwards, reaching a minimum in the Rhaetian (Figures 2, 4A). By contrast, observed diversity increases until the Carnian, declining in the Norian and thereafter. This contrasting trend of diversity and completeness was also noted by Lukic-Walther et al. (2019). They suggested that the reduction in completeness (using CCM in their case) throughout the latter half of the Triassic could be due to either a change in taxonomic practice (i.e. naming species based on poorly preserved fragmentary material) and/or a shift in cynodont body size evolution, potentially altering the preservation potential of the group. Behrensmeyer (1978) proposed that the rate of degradative taphonomic processes should operate more rapidly on smaller-bodied taxa as they have a higher surface area to volume ratio, providing a potential explanation as to why small cynodont taxa tend to have lower completeness values than their larger-bodied counterparts (Figures 8 and 9). Furthermore, global climate became increasingly humid from the Ladinian onwards (Zerfass et al. 2003; Tanner 2018), which might have led to increased weathering rates and elevated soil acidity. Humid conditions would thus affect the rate at which organic material corrodes on the surface (Behrensmeyer 1978; Fernández-Jalvo et al. 2010), and this might have severely impacted the completeness of skeletons of small taxa. Furthermore, taphonomic processes might vary between different sized taxa (Badgley 1986), with species <60 kg more commonly found as isolated remains (likely the case for cynodonts, see Figure 9), and larger taxa more often found as articulated skeletons (Brown et al. 2013). This might explain why the skeletons of larger-bodied taxa (e.g. sauropodomorphs) from the same deposits as cynodonts retain relatively high completeness during the Late Triassic (Mannion and Upchurch 2010; Cashmore et al. 2020). Collection techniques might also affect completeness values for Late Triassic and Early Jurassic taxa. For example, Lukic-Walther et al. (2019) noted that the Late Triassic record is characterised by intensive sieving and screen-washing sampling techniques, which is especially characteristic of collections from Rhaetian deposits. This method typically yields disarticulated and incomplete material, and indeed several Late Triassic cynodonts have been discovered this way (e.g. Sues et al. 1994; Godefroit 1999; Datta et al. 2004*;* Sulej et al. 2020). Therefore, genuine declines in diversity, a trend towards smaller body size, and a change in collection techniques likely all contribute to the Late Triassic decline in cynodont completeness.

Despite the apparent reduced number of rich tetrapod-bearing formations in the Early Jurassic relative to other Paleozoic and Mesozoic epochs (Benton et al. 2013), notably high completeness values have been observed at this time for sauropodomorphs (Mannion and Upchurch 2010), pterosaurs (Dean et al. 2016), ichthyosaurs (Cleary et al. 2015), and plesiosaurs (Tutin and Butler 2017). A small number of Early Jurassic formations have yielded exceptionally preserved specimens of these taxa, such as the upper Elliot Formation in South Africa for sauropodomorphs (e.g. McPhee et al. 2017) and the Blue Lias Formation in the UK for pterosaurs, plesiosaurs, and ichthyosaurs (e.g. Owen 1870). By contrast, there is no equivalent peak in cynodont completeness at this time. The majority of Jurassic and Cretaceous cynodont species are Laurasian and exhibit a lower completeness than their earlier Gondwanan counterparts (Figure 6). This low Laurasian completeness might partly result from certain environmental conditions during the Jurassic; for example, European localities that have yielded several cynodont remains are characterised by high humidity (Ruffell et al. 2002; Sellwood and Valdes 2008; Bougeault et al. 2017). The global peak in completeness during the Pliensbachian results from almost complete skeletons of the tritylodontid *Kayentatherium wellesi* (SCM of 92%) in the USA (Sues 1986), and the extensive number of disarticulated remains attributed to *Oligokyphus major* (SCM of 75%) from fissure fill deposits in the UK (Kühne 1956). These two taxa make up 50% of known Pliensbachian non-mammaliaform cynodont diversity (Figure 2). By contrast, the majority of European taxa have completeness values below 2%, composed mostly of isolated dental fragments, e.g. from the Gres à Avicula Formation in France (Godefroit and Battail 1997; Sigogneau-Russell 1983). Low completeness values throughout the remainder of the Mesozoic likely reflect genuine declines in diversity and abundance of non-mammaliaform cynodonts (Ruta et al. 2013; Lukic-Walther et al. 2019), reducing the likelihood of their preservation. Their reduced diversity might have resulted from increased competition, as their decline coincides with the emergence and diversification of Mammaliaformes, including morganucodontids and multituberculates (Newham et al. 2014).

Stratigraphic congruence of early cynodont evolutionary relationships

Despite low completeness for early cynodonts relative to most other clades, SCI (77%) and GER (85%) are high (Table 6), suggesting the group's phylogeny is generally stratigraphically congruent. By way of comparison, the values of SCI and GER for pelycosaurs are 54% and 58%, respectively (Brocklehurst and Fröbisch 2014). The high SCI and GER values of cynodonts contrast with their low MSM* values (22%). It has been observed that tetrapods in general have a lower MSM* (<50%) than plants, fishes, or echinoderms, but higher than arthropods and molluscs (O'Connor and Wills 2016). MSM* has been found to be heavily biased by tree size and shape (Siddall 1998), more so than SCI and GER, and it does not correlate strongly with other metrics (O'Connor and Wills 2016). Furthermore, MSM* is negatively correlated with the number of taxa included within the tree (O'Connor and Wills 2016), which might explain why the value for cynodonts is low given the relatively high number of taxa used here. Whereas the SCI, GER, and MSM* are more strictly measures of congruence, the RCI is better characterised as a measure of the completeness of the fossil record, defined as the ratio of the sum of observed ranges of taxa to the sum of the ghost ranges of taxa (Benton and Storrs 1994). The RCI score for cynodonts (45%) is lower than those of the SCI and GER. Lower RCI values can result from inaccurate phylogenies and/or a poor fossil record (Wagner 2000). However, given that the SCI and GER scores are higher than for other clades, this suggests that the congruence between phylogeny and stratigraphy for cynodonts is no worse than for other clades, and likely better. As such, we interpret the lower RCI value to more likely reflect a poor fossil record, as is further supported by the low completeness values relative to other clades (Figure 10).

The impact of diagnosability on fossil record completeness

Several authors have commented that the completeness of the fossil record potentially influences diversity reconstructions of any given clade (e.g. Benton et al. 2004; Eiting and Gunnell 2009; Mannion and Upchurch 2010; Brocklehurst et al. 2012; Brocklehurst and Fröbisch 2014). A spatiotemporal bin containing multiple complete skeletons might be expected to have high diversity, because such specimens should be more confidently assigned to species level given the increased opportunity to preserve and therefore identify autapomorphies (Mannion and Upchurch 2010). This appears to be the case for Mesozoic birds and pterosaurs, which are both characterised by a positive correlation between diversity and completeness (CCM in both cases), with a substantial proportion of their fossil records known from Lagerstätten (Brocklehurst et al. 2012; Dean et al. 2016). The fossil record of bats is also highly dependent on Lagerstätten (Brown et al. 2019), with a higher average CCM than cynodonts, but a significantly lower mean average SCM (Table 5). Whereas the low SCM of bats might be explained by rapid taphonomic degradation and disarticulation as a result of their small and fragile skeletons (e.g. Behrensmeyer 1978; Badgley 1986), their higher CCM could be because even disarticulated postcranial remains of bats are more phylogenetically informative relative to those of cynodonts. For example, postcranial characters account for approximately 50% of the total character completeness score in bats (Brown et al. 2019), compared to just over 10% in cynodonts (Lukic-Walther et al. 2019).

A positive correlation between cynodont diversity and CCM in some of our analyses (Table 3), but no correlation with SCM, could be explained by differences in diagnosability of fossil remains between this group and other tetrapod clades. Several cynodont species are known only from teeth and dental fragments, but cynodont dentition is often highly diagnostic (e.g. the gomphodont dentition exhibited in Cynognathia), making it easier to confidently assign incomplete material to lower taxonomic levels. Consequently, cynodont phylogenetic matrices are biased towards cranial and dental characteristics, resulting in a fossil record which might have low skeletal completeness relative to character completeness and diversity. The phylogenetic matrices of parareptilian tetrapods and anomodonts are also dominated by cranial characteristics (Walther and Fröbisch 2013), but members of these groups are generally more difficult to identify to lower taxonomic levels (i.e. genus or species) based on very limited material (e.g. isolated teeth), so that fewer nominal taxa used in phylogenetic analyses for those groups are known from fragments alone. Temporal pairwise comparisons show no significant correlation between the CCM of cynodonts and parareptilian tetrapods or anomodonts. This lack of correlation might be because both anomodonts and parareptilian tetrapods were genuinely much more abundant than cynodonts during the late Permian (Nicolas and Rubidge 2010; Fröbisch 2014; MacDougall et al. 2019), thereby increasing their preservation potential.

Similarly, a spatiotemporal bin dominated by highly incomplete specimens might be expected to have low observed diversity, due to a lack of preserved autapomorphies, meaning specimens can only be confidently assigned to higher taxonomic levels (Mannion and Upchurch 2010). However, Brocklehurst and Fröbisch (2014) recovered a significant negative correlation between completeness and diversity for pelycosaurs. This is most readily explained whereby multiple fragmentary specimens of the same species have been misdiagnosed as separate taxa, thus resulting in an overly-inflated diversity estimate

(Mannion and Upchurch 2010; Brocklehurst et al. 2012; Brocklehurst and Fröbisch 2014). It is possible that this issue is much more pervasive in groups with relatively low diagnosability.

Uncertainty in the timing of mammalian character acquisition

The origin of mammals from Triassic cynodonts is often cited as one of the best-documented macroevolutionary transitions in the fossil record (e.g. Hopson 1987), and we do not dispute this characterization. With that said, however, there is clear variation in the completeness of the cynodont record, and accordingly some sections of this transition are better understood than others. The spatiotemporal gaps in the cynodont record have particular influence on our understanding of the timing and sequence of acquisition of mammalian characters, and thus interpretations of selective forces shaping cynodont evolution.

Despite the low diversity of late Permian cynodonts, their completeness is relatively high (Figure 2), owing mostly to cranial material. Even these earliest known cynodonts already display a number of mammal-like cranial features related to increased efficiency of masticatory processing (Figure 12). One such feature is a shallow fossa on the coronoid process of the dentary paired with a flared zygomatic arch, placing the coronoid process near the middle of the temporal fenestra (Rubidge and Sidor 2001). This placement is widely observed across late Permian cynodonts, including *Dvinia*, *Procynosuchus, Charassognathus*, and *Abdalodon* (Hopson 1987; Kammerer 2016), and has been taken as evidence for the differentiation of the plesiomorphically unipartite adductor mandibulae into the more mammalian condition of the temporalis and masseter muscles (Barghusen 1968). Several late Permian cynodonts also show development of a secondary palate (Figure 12a), although it is incomplete in most taxa (e.g. *Procynosuchus*; Kemp 1979). A complete secondary palate is first observed at the node containing the Early Triassic *Thrinaxodon* and latest Permian *Nanictosaurus* (Pusch et al. 2019), indicating an origin of this morphology shortly before the P/T boundary.

The time of origin of the complete bony secondary palate and extension of the masseter onto the base of the dentary can be determined with a high degree of confidence, given that these characters appear during the peak of cynodont completeness in the late Permian–Early Triassic (Figures 2, 12). Similarly, there is robust support for the initial appearance of derived features characterizing the major cynodont subclade Eucynodontia in the Early or early Middle Triassic. In general (and perhaps unsurprisingly), many of the canonical exemplars used to illustrate the transitional series in cynodont evolution (e.g. Hopson 1987; Hopson and Kitching 2001; Rubidge and Sidor 2001) hail from the best-sampled, most complete, and most species-rich segment of non-mammaliaform cynodont history, such that we can have reasonable confidence that the suite of increasingly derived 'mammalian' features characterizing taxa such as *Procynosuchus*, *Thrinaxodon*, *Lumkuia*, and *Probainognathus* evolved close to the first appearances of these taxa in the fossil record.

By contrast, it is much more difficult to establish the time of origin for the mammal-like features (including those cited above) seen in the very earliest cynodonts. Cynodonts are unique among the major therapsid subclades in lacking a middle Permian (Guadalupian) record, although recent phylogenetic analyses indicate they must have originated by that time (Huttenlocker 2009). The ghost lineage between presumed cynodont origins (at some point in the middle Permian) and their first appearance in the late Permian record hinders our understanding of the assembly of mammalian characters. Did these characters appear rapidly, as part of coordinated changes in the masticatory system, or by gradual, stepwise addition? Our results indicate that additional sampling, at either localities or size classes beyond those currently sampled, will be necessary to address this question. Known Permian cynodont species are almost entirely restricted to high southern palaeotitudes in southern Africa (Figure 5), with substantially rarer records from lower northern palaeolatitudes (Figure 7), and the possibility that early cynodont diversification was occurring outside this handful of sampled basins must be considered.

Although the latest Permian and Early Triassic record accords reasonable confidence regarding the assembly of mammal-like cranial features in cynodonts, the postcranial signal is less clear. The earliest Triassic cynodont fossils are among the most complete known from any time bin, e.g. *Galesaurus planiceps* and *Thrinaxodon liorhinus* from South Africa. The nearly-complete postcrania of these species illustrate a number of derived features (Figure 12), demonstrating a differentiated vertebral column, reduced lumbar ribs, and a more mammalian structure of the manus (Jenkins 1971; Butler et al. 2019: Figure 12b). However, because of the low completeness of postcranial remains from the late Permian (Figure 2), it is difficult to confirm these features as novel to the Early Triassic (and thus possibly related to selective forces associated with ecological change across the P/T boundary). In particular, the lack of known postcrania in the earliest cynodonts (charassognathids) and later Permian relatives of *Galesaurus* and *Thrinaxodon* (e.g. *Cynosaurus* and *Nanictosaurus*) makes it difficult to reconstruct the origins of these morphologies; they probably evolved in the Permian (based on phylogenetic bracketing), but the sequence and timing of origin is unknown. Until more complete postcranial remains of cynodonts are discovered from the late Permian, this will remain unresolved.

Eucynodontia is made up of two subclades, Cynognathia and Probainognathia (Hopson and Kitching, 2001), both of which are found globally in the Triassic. Even the earliest-known eucynodonts (from the latest Early or earliest Middle Triassic) are clearly identifiable as belonging to one of these subclades, and, in the case of the most 'basal' cynognathian (*Cynognathus* itself), show a circum-Gondwanan distribution. Although eucynodonts may well have been part of a rapid burst of post-extinction Triassic diversification also observed in coeval diapsid reptiles, the extensive geographic range of an already highly-specialized taxon like *Cynognathus* suggests that there is a missing record for the earliest phase of eucynodont evolution. Whether this is best attributed to temporal (i.e. greater separation between the *Lystrosaurus* and *Cynognathus* Assemblage Zones than usually thought; see Ottone et al. 2014) or geographic (i.e. eucynodonts originating outside of the well-sampled Gondwana basins; see Gao et al. 2010 for possible evidence of this) gaps is currently uncertain.

A final problem, comparable to the origins of Cynodontia and to a lesser extent Eucynodontia, concerns the early evolution of Mammaliamorpha, the clade containing mammaliaforms and their near-outgroups such as brasilodontids and tritylodontids (Kemp 1983; Liu and Olsen 2010; Martinelli 2016). In terms of cranial and postcranial morphology, these groups share many similarities with early Mammaliaformes (Figure 12), particularly regarding the loss of a postorbital bar, an expanded dentary, and highly modified dentition (Lucas and Luo 1993; Kemp 2005; Sullivan et al. 2013; Martinelli 2016; Martinelli et al. 2017; Guignard et al. 2019) (Figure 12c-f). The majority of 'basal' (i.e. non-mammaliaform) mammaliamorph diversity and their greatest skeletal completeness is found in the Jurassic; yet, based on phylogenetic relationships, its various subclades must have diverged by the Carnian, leaving extensive ghost lineages in the Late Triassic. The timing and assembly of the highly derived morphologies characteristic of groups such as the rodent-like tritylodontids is essentially unknown; the record seems biased against this group, as the relevant time intervals (late Middle and early Late Triassic) otherwise involve peaks in cynodont richness. Definite tritylodontids do not appear in the record until the latest Triassic (terminal Rhaetian), their record is almost exclusively Laurasian (with *Tritylodon* itself being a notable outlier), and it exhibits extremely low completeness (Figures 4–7).

The poor Triassic record of tritylodontids and other early mammaliamorphs impedes our understanding of the adaptive origins and initial function of several notable mammalian postcranial characters, such as epipubic bones (Fourie 1963; Parrington 1978). Epipubic bones in extant mammals are best known in marsupials, where they support the pouch; in the absence of a broader sample, it would be tempting to infer that they evolved for that purpose. However, the presence of epipubic bones in the pouchless, oviparous monotremes and numerous other fossil mammals (e.g. 'basal' eutherians, Novacek et al. 1997; multituberculates, Kielan-Jaworowska 1969), indicates that this is not the case, and their function in extant marsupials has likely been co-opted (Reilly and White, 2003; Reilly et al. 2009; White, 1989). Critical to interpretation of the initial acquisition of epipubic bones is their function in tritylodontids, the first cynodont group in which they appear. Unfortunately, the low completeness of the Late Triassic–Early Jurassic cynodont fossil record makes it hard to determine how and why such synapomorphic traits evolved.

CONCLUSIONS

Completeness of the non-mammaliaform cynodont fossil record is highest between the late Permian and the early Late Triassic. This early record is dominated by species from southern Africa and South America. During this time, these continents experienced highly variable climates, alternating between arid and monsoonal conditions, both of which can favour the preservation of skeletons. Completeness decreases from the Norian (middle Late Triassic) onwards, which might be a result of a genuine decline in non-mammaliaform cynodont diversity and abundance, combined with a shift in body size evolution. However, this also likely reflects the negative effect of increasingly humid conditions on fossil preservation, especially with the shift from a Gondwanan to a predominantly Laurasian fossil record from the Jurassic onwards.

The incompleteness of the early cynodont fossil record has implications for our understanding of the timing of the acquisition of mammal-like characteristics. For example, characters like complex, multicusped dentition, a masseteric fossa on the dentary, and development of a secondary palate are present in even the earliest cynodonts; we cannot tell when these characters first appeared, in what sequence they evolved, or infer the selective pressures that may have favoured their evolution, due to the poor Permian fossil record for the group. Similar issues cloud our understanding of the origins of several major cynodont subclades as well. Early members of Tritylodontidae, one of the cynodont subclades thought to be most closely related to mammaliaforms, first appear in the Late Triassic fossil record, but are already highly apomorphic and exhibit derived mammal-like features, such as an expanded dentary and the presence of epipubic bones. It is probable that these characters originated earlier in the Triassic, but poor sampling of postcranial elements, particularly at small body size, has obscured this record. Increased scope and geographic breadth of P/T microvertebrate sampling may ameliorate such issues, but the historical dominance of dental elements in such samples means that substantial uncertainty concerning the evolution in mammalian postcrania is likely to remain.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:
https://datadryad.org/stash/share/el5_BWNNdRxPSz8GLC3rP03AUgIGKZuIINAU1om3HzY

REFERENCES

ABDALA, F. and RIBEIRO, A. M. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida: Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **286**, 202-217.

ABDALA, F., GAETANO, L. C., SMITH, R. M. H., and RUBIDGE, B. S. 2019. A new large cynodont from the Late Permian (Lopingian) of the South African Karoo Basin and its phylogenetic significance. *Zoological Journal of the Linnean Society*, **186**, 983-1005.

ABDALA, F., GAETANO, L. C., MARTINELLI, A. G., SOARES, M. B., HANCOX, P. J. and RUBIDGE, B. S. 2020. Non-mammaliaform cynodonts from western Gondwana and the significance of Argentinean forms in enhancing understanding of the group. *Journal of South American Earth Sciences,* **104**, 102884.

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

ALLISON, P. A. and BRIGGS, D. E. G. 1993. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology,* **21**, 65-68.

ALROY, J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology,* **53**, 1211-1235.

ANGIELCZYK, K. D. and KAMMERER, C. F. 2018. Non-mammalian synapsids: the deep roots of the mammalian family tree. In Asher, R. and Zachos, F. (eds). *Handbook of Zoology: Mammalia*. DeGruyter, Berlin, 117-198.

BADGLEY, C. 1986. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology,* **12**, 119-142.

BARGHUSEN, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor musculature. *Postilla,* **166**, 1-49.

BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T. and FURRER, H. 2012. Float or sink: modelling the taphonomic pathway of marine crocodiles (Mesoeucrocodylia, Thalattosuchia) during the death-burial interval. *Palaeobiodiversity and Palaeoenvironments,* **92**, 83-98.

BEHRENSMEYER, A. K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology,* **4**, 150-162.

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

BELL, M. A. and LLOYD, G. T. 2015. strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology,* **58**, 379-389.

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

BENTON, M. J., RUTA, M., DUNHILL, A. M. and SAKAMOTO, M. 2013. The first half of tetrapod evolution, sampling proxies, and the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **372**, 18-41.

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

BONAPARTE, J. F., MARTINELLI, A. G. and SCHULTZ, C. L. 2005. New information on Brasilodon and Brasilitherium (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia*, **8**, 25–46.

BOTHA, J. and SMITH, R. M. H. 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* **45**, 502-514.

BOTHA, J., ABDALA, F. and SMITH, R. 2007. The oldest cynodont: new clues on the origin and early diversification of the cynodontian. *Zoological Journal of the Linnean Society,* **149**, 477-492.

BOUGEAULT, C., PELLENARD, P., DECONINCK, J. –F., HESSELBO, S. P., DOMMERGUES, J. –L., BRUNEAU, L., COCQUEREZ, T., LAFFONT, R., HURET, E. and THIBAULT, N. 2017. Climatic and palaeoceanographic changes during the Pliensbachian (Early Jurassic) inferred from clay mineralogy and stable isotope (C-O) geochemistry (NW Europe). *Global and Planetary Change,* **149**, 139-152.

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

BROCKLEHURST, N., UPCHURCH, P., MANNION, P. D. and O'CONNOR, J. 2012. The Completeness of the Fossil Record of Mesozoic Birds: Implications for Early Avian Evolution. *PLoS ONE,* **7**, e39056.

BROWN, C. M., EVANS, D. C., CAMPIONE, N. E., O'BRIEN, L. J. and EBERTH, D. A. 2013. Evidence for size bias in the Dinosaur Park Formation (Campanian, Alberta), a model for

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 bat fossil record. *Palaeontology,* **62**, 757-776.

BUTLER, E., ABDALA, F. and BOTHA-BRINK, J. 2019. Postcranial morphology of the Early Triassic epicynodont *Galesaurus planiceps* (Owen) from the Karoo Basin, South Africa. *Papers in Palaeontology,* **5**, 1-32.

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

COHEN, K. M., FINNEY, S. and GIBBARD, P. L. 2012. International Chronostratigraphic Chat: International Commission on Stratigraphy. www.stratigraphy.org.

COLBERT, E. H. and KITCHING, J. W.. 1977. Triassic Cynodont Reptiles From Antarctica. *American Museum Novitates,* **2611**, 1-30

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. J., ALROY, J., CARRANO, M. T., CLEARY, T. J., DUNNE, E. M., MANNION, P. D., UHEN, M. D., and BUTLER, R. J. 2020. The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling biases. *Proceedings of the Royal Society B* 287: 20200372.

CREIGHTON, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. *Journal of Zoology,* **191**, 435-443.

CROMPTON, A. W., OWERKOWICZ, T., BHULLAR, B. –A. S. and MUSINSKY, C. 2017. Structure of the nasal region of non-mammalian cynodonts and mammaliaforms: Speculations on the evolution of mammalian endothermy. *Journal of Vertebrate Palaeontology,* **37**, e1269116.

DAMIANI, R. J. 2004. Temnospondyls of the Beaufort Group (Karoo Basin) of South Africa and their Biostratigraphy. *Gondwana Research,* **7**, 165-173.

DATTA, P. M., DAS, D. P. and LUO, Z. –X. 2004. A Late Triassic dromatheriid (Synapsida: Cynodontia) from India. *Annals of the Carnegie Museum,* **73**, 72-84.

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

EITING, T. P. and GUNNELL, G. F. 2009. Global Completeness of the Bat Fossil Record. *Journal of Mammalian Evolution,* **16**, 151-173.

FERNANDEZ, V., ABDALA, F., CARLSON, K. J., COOK, D. C., RUBIDGE, B. S., YATES, A. and TAFFOREAU, P. 2013. Synchrotron reveals Early Triassic odd couple: Injured amphibian and aestivating therapsid share burrow. *PLoS ONE,* **8**, e64978.

FERNÁNDEZ-JALVO, Y., ANDREWS, P., PESQUERO, D., SMITH, C., MARÍN-MONFORT, D., SÁNCHEZ, B., GEIGL, Q. –M. and ALONSO, A. 2010. Early bone diagenesis in temperate environments: Part 1: Surface features and histology. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **288**, 62-81.

FOUNTAINE, T. M. R., 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.

FOURIE, S. 1963. A new Tritylodontid from the Cave Sandstone of South Africa. *Nature*, **198**, 201.

FRÖBISCH, J. 2014. Chapter 18: Synapsid Diversity and the Rock Record in the Permian-Triassic Beaufort Group (Karoo Supergroup), South Africa. *In* KAMMERER, C. F., ANGIELCZYK, K. D. and FRÖBISCH, J. (eds). Early Evolutionary History of the Synapsida. *Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht, pp. 305-319.

GAO, K.-Q., FOX, R. C., ZHOU, C.-F. and LI, D.-Q. 2010. A new nonmammalian eucynodont (Synapsida: Therapsida) from the Triassic of northern Gansu Province, China, and its biostratigraphic and biogeographic implications. *American Museum Novitates*, **3685**, 1-25.

GODEFROIT, P. and BATTAIL, B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas* **19**, 567-631.

GODEFROIT, P. 1999. New traversodontid (Therapsida: Cynodontia) teeth from the Upper Triassic of Habay-la-Vielle (southern Belgium). *Paläontologische Zeitschrift,* **73**, 385-394.

GUIGNARD, M. L., MARTINELLI, A. G. and SOARES, M. B. 2019. The postcranial anatomy of *Brasilodon quadrangularis* and the acquisition of mammaliaform traits among non-mammaliaform cynodonts. *Plos One*, **14**, e0216672.

HENDRICKX, C., ABDALA, F. and CHOINIERE, J. N. 2019. A proposed terminology for the dentition of gomphodont cynodonts and dental morphology in Diademodontidae and Trirachodontidae. *PeerJ*, **7**: e6752.

HOPSON, J. A. 1987. The mammal-like reptiles: a study of transitional fossils. *The American Biology Teacher*, **49**, 16-26.

HOPSON, J. A. and KITCHING, J. W. 1972. A revised classification of cynodonts (Reptilia: Therapsida). *Palaeontologia africana* **14**, 71-85.

HOPSON, J. A. and KITCHING, J. W. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology*, **156**, 5-35.

HUELSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology*, **20**, 470-483.

HUTTENLOCKER, A. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society*, **157**, 865-891.

IVAKHNENKO, M. F. 2012. Permian Cynodontia (Theromorpha) of Eastern Europe. *Paleontological Journal,* **46**, 199-207.

IVAKHNENKO, M. F. 2013. Cranial morphology of *Dvinia prima* Amalitzky (Cynodontia, Theromorpha). *Paleontological Journal*, **47**, 210-222.

JENKINS, F. A. 1971. The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History,* **36**, 1-28.

JONES, K. E., ANGIELCYZK, K. D., POLLY, P. D., HEAD, J. J., FERNANDEZ, V., LUNGMUS, J. K., TULGA, S. and PIERCE, S. E. 2018. Fossils reveal the complex evolutionary history of the mammalian regionalised spine. *Science,* **361**, 1249-1252.

KAMMERER, C. F. 2016. A new taxon of cynodont from the *Tropidostoma* Assemblage Zone (upper Permian) of South Africa, and the early evolution of Cynodontia. *Papers in Palaeontology,* **2**, 387-397.

KEMP, T. S. 1979. The primitive cynodont *Procynosuchus*: Functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **285**, 72-122.

KEMP, T. S. 1983. The relationships of mammals. *Zoological Journal of the Linnean Society,* **77**, 353-384.

KEMP, T. S. 2005. The Origin and Evolution of Mammals. Oxford University Press, Oxford.

KERMACK, D. M. Kermack. 1982. A new tritylodontid from the Kayenta formation of Arizona. *Zoological Journal of the Linnean Society* **76**, 1-17

KIELEN-JAWOROWSKA, Z. 1969. Discovery of a Multituberculate Marsupial Bone. *Nature,* **222**, 1091-1092.

KIELAN-JAWOROWSKA, Z., CIFELLI, R. L. and LUO, Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. Columbia University Press, New York.

KÜHNE, D. G. 1956. The Liassic therapsid *Oligokyphus*. *British Museum (Natural History),* London.

LANGER, M. C. 2005. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences* **19**, 205-218.

LANGER, M. C., RIBEIRO, A. M., SCHULTZ, C. L. and FERIGOLO, J. 2007. The continental tetrapod-bearing Triassic of south Brazil. *In* LUCAS, S. G. and SPIELMAN, J. A. (eds). The global Triassic. *New Mexico Museum of Natural History and Science Bulletin* **41,** 201-218.

LIU, J. and OLSEN, P. 2010. The phylogenetic relationships of Eucynodontia (Amniota: Synapsida). *Journal of Mammalian Evolution,* **17**, 151-176.

LLOYD, G. T. 2008. Generalized differencing of time series. http://www.graemetlloyd.com/methgd.html

LOPATIN, A. V. and AGADJANIAN, A. K. 2008. A Tritylodont (Tritylodontidae, Synapsida) from the Mesozoic of Yakutia. *Doklady Biological Sciences,* **419**, 107-110.

LUCAS, S. G. and LUO, Z. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. *Journal of Vertebrate Paleontology,* **13**, 309-334.

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

MACDOUGALL, M. J., BROCKLEHURST, N. and FRÖBISCH, J. 2019. Species richness and disparity of parareptiles across the end-Permian mass extinction. *Proceedings of the Royal Society B,* **286**: 20182572.

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

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

MARCHETTI, L., VOIGT, S. and KLEIN, H. 2017. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). *Historical Biology*, **31**, 748-783.

MARTINELLI, A. G., SOARES, M. B. and SCHWANKE, C. 2016. Two new cynodonts (Therapsida) from the Middle-Early Late Triassic of Brazil and comments on the South American probainognathians. *PLoS ONE,* **11**, 0162945.

MARTINELLI, A. G., ELTINK, E., DA-ROSA, A. A. S. and LANGER, M. C. 2017. A new cynodont from the Santa Maria formation, south Brazil, improves Late Triassic probainognathian diversity. *Papers in Palaeontology,* **3**, 401-423.

MATSUOKA, H., KUSUHASHI, N., and CORFE, I. J. 2016. A new Early Cretaceous tritylodontid (Synapsida, Cynodontia, Mammaliamorpha) from the Kuwajima Formation (Tetori Group) of central Japan. *Journal of Vertebrate Paleontology*, **36**, e1112289.

MCPHEE B. W., BORDY, E. M., SCISCIO, L. and CHONIERE, 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.

MOCKE, H. B., GAETANO, L. C. and ABDALA, F. 2020. A new species of the carnivorous cynodont *Chiniquodon* (Cynodontia, Chiniquodontidae) from the Namibian Triassic*. Journal of Vertebrate Paleontology,* **39:** e1754231.

NEWHAM, E., BENSON, R., UPCHURCH, P. and GOSWAMI, A. 2014. Mesozoic mammaliaform diversity: The effect of sampling corrections on reconstructions of evolutionary dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **412**, 32-44.

NICOLAS, M. and RUBIDGE, B. S. 2010. Changes in Permo-Triassic terrestrial tetrapod ecological representation in the Beaufort Group (Karoo Supergroup) of South Africa. *Lethaia,* **43**, 45-59.

NOVACEK, M. J., ROUGIER, G. W., WIBLE, J. R., MCKENNA, M. C., DASHZEVEG, D. and HOROVITZ, I. 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature,* **389**, 483-486.

O'CONNOR, A. and WILLS, M. A. 2016. Measuring stratigraphic congruence across trees, higher taxa, and time. *Systematic Biology,* **65**, 792-811.

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.

OTTONE, E. G., MONTI, M., MARSICANO, C. A., DE LA FEUNTE, M. S., NAIPAUER, M., ARMSTRONG, R. and MANCUSO, A. 2014. A new Late Triassic age for the Puesto Viejo Group (San Rafael depocenter, Argentina): SHRIMP U—Pb zircon dating and biostratigraphic correlations across southern Gondwana. *Journal of South American Earth Sciences,* **56**, 186-189.

OWEN, R. 1870. Monograph of the Fossil Reptilia of the Liassic Formations. *Palaeontographical Society Monographs,* **27**, 41-81.

PACE, D. W., GASTALDO, R. A. and NEVELING, J. 2009. Early Triassic aggradational and degradational landscapes of the Karoo Basin and evidence for climate oscillation following the P-Tr event. *Journal of Sedimentary Research,* **79**, 316-331.

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

PARRINGTON, F. R. 1978. A further account of Triassic mammals. *Philosophical Transactions of the Royal Society,* **282**, 177-204.

PAVANATTO, A. E. B., PRETTO, F. A., KERBER, L., MÜLLER, R. T., DA-ROSA, A. A. S., DIAS-DA-SILVA, S. D. 2018. A new Upper Triassic cynodont-bearing fossiliferous site from southern Brazil, with taphonomic remarks and description of a new traversodontid taxon. *Journal of South American Earth Sciences*, **88**, 179-196.

POL, D. and NORELL, M. A. 2001. Comments on the Manhattan stratigraphic measure. *Cladistics,* **17**, 285-289.

PUSCH, L. C., KAMMERER, C. F. and FRÖBISCH, J. 2019. Cranial anatomy of the early cynodont *Galesaurus planiceps* and the origin of mammalian endocranial characters. *Journal of Anatomy*, **234**, 592-621.

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

REILLY, S. M. and WHITE, T. D. 2003. Hypaxial Motor Patterns and the Function of Epipubic Bones in Primitive Mammals. *Science,* **299**, 400-402.

REILLY, S. M., MCELROY, E. J. and WHITE, T. D. 2009. Abdominal muscle function in ventilation and locomotion in new world opossums and basal eutherians: Breathing and running with and without epipubic bones. *Journal of Morphology,* **270**, 1014-1028.

RODRIGUES, P. G., RUF, I. and SCHULTZ, C. L. 2013. Digital Reconstruction of the Otic Region and Inner Ear of the Non-Mammalian Cynodont *Brasilitherium riograndensis* (Late Triassic, Brazil) and Its Relevance to the Evolution of the Mammalian Ear. *Journal of Mammalian Evolution,* **20**, 291-307.

ROWE, T. 1988. Definition, Diagnosis, and Origin of Mammalia. *Journal of Vertebrate Paleontology,* **8**, 241-264.

R CORE TEAM. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

RUBIDGE, B. S. and SIDOR, C. A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics,* **32**, 449-480.

RUFFELL, A., MCKINLEY, J. M. and WORDEN, R. H. 2002. Comparison of clay mineral stratigraphy to other proxy palaeoclimate indicators in the Mesozoic of NW Europe. *Philosophical Transactions of the Royal Society A,* **360**, 675-693.

RUTA, M., BOTHA-BRINK, J., MITCHELL, S. A. and BENTON, M. J. 2013. The radiation of cynodonts and the ground plan of mammalian morphological diversity. *Proceedings of the Royal Society B,* **280**, 20131865.

SCHULTZ, C. L., MARTINELLI, A. G., SOARES, M. B., PINHEIRO, F. L., KERBER, L., HORN, B. L. D., PRETTO, F. A., MÜLLER, R. T. and MELO, T. P. 2020. Triassic faunal successions of the Paraná Basin, southern Brazil. *Journal of South American Earth Sciences,* **104**, 102846.

SELLWOOD, B. W. and VALDES, P. J. 2008. Jurassic Climates. *Proceedings of the Geologists' Association,* **119**, 5-17.

SIDDALL, M. E. 1998. Stratigraphic fit to phylogenies: A proposed solution. *Cladistics,* **14**, 201-208.

SIDOR, C. A. and SMITH, R. M. H. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* **47**, 535-556.

SIDOR, C. A. and HOPSON, J. A. 2018. *Cricodon metabolus* (Cynodontia: Gomphodontia) from the Triassic Ntawere Formation of northeastern Zambia: patterns of tooth replacement and a systematic review of the Trirachodontidae. *Journal of Vertebrate Paleontology*. **37** (supplement), 39-64.

SIGOGNEAU-RUSSELL, D. 1983. Nouveaux taxons de mammifères rhétiens. *Acta Palaeontologica Polonica* **28**, 233-249.

SMITH, R. AND BOTHA, J. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. *Comptus Rendes Palevol,* **4**, 636-636.

SMITH, R. M. H. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the Southwestern Karoo Basin of South Africa. *PALAIOS,* **8**, 45-67*.*

SMITH, R. M. H. and BOTHA-BRINK, J. 2014. Anatomy of a mass extinction: Sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **396**, 99-118.

SMITH, R. M. H., ERIKSSON, P. G. and BOTHA, W. J. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of Southern Africa. *Journal of African Earth Sciences (and the Middle East),* **16**, 143-169.

SMITH, R. M. H., RUBIDGE, B. S., DAY, M. O. and BOTHA, J. 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. *South African Journal of Geology* **123**, 131-140.

SUES, H.-D. 1985. First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. *Journal of Vertebrate Paleontology* **5**, 328-335.

SUES, H.-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology* **151**, 217-268.

SUES, H. –D. 2001. On *Microconodon,* a Late Triassic cynodont from the Newark Supergroup of Eastern North America. *Bulletin of the Museum of Comparative Zoology,* **156**, 37-48.

SUES, H. –D. and MUNK, W. 1996. A remarkable assemblage of terrestrial tetrapods from the Zechstein (Upper Permian: Tatarian) near Korbach (northwestern Hesse). *Palaeontologische Zeitschrift,* **70**, 213-223.

SUES, H. –D., OLSEN, P. E. and KROEHLER, P. A. 1994. Small tetrapods from the Upper Triassic of the Richmond basin (Newark Supergroup), Virginia. In Fraser, N. C. and Sues, H. –D. (eds). *In the Shadow of the Dinoaurs*. Cambridge University Press, 161-170.

SULEJ, T., NIEDŹWIEDZKI, G., TAŁANDA, M., DRÓŻDŻ, D. and HARA, E. 2020. A new early Late Triassic non-mammaliaform eucynodont from Poland. *Historical Biology,* **32**, 80-92.

SULLIVAN, C., LIU, J., ROBERTS, E. M., HUANG, T. D., YANG, C. and ZHONG, S. 2013. Pelvic morphology of a tritylodontid (Synapsida: Eucynodontia) from the Lower Jurassic of China, and some functional and phylogenetic implications. *Comptes Rendus Palevol,* **12**, 505-518.

TANNER, L. H. 2018. Climates of the Late Triassic: Perspectives, Proxies and Problems. In: TANNER, L. (ed). The Late Triassic World. *Topics in Geobiology*, **46**. Springer, Cham, 59-90.

TATARINOV, L. P. and MATCHENKO, E. N. 1999. A find of an aberrant tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo Region. *Paleontological Journal*, **33**, 422-428.

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**, 563-573.

VARNHAM, G. L., MANNION, P. D. and KAMMERER, C. F. 2020. Data from: Completeness of the early cynodont fossil record and its influence on interpretations of the timing of acquisition of mammalian characteristics. *Dryad Digital Repository*. https://datadryad.org/stash/share/el5_BWNNdRxPSz8GLC3rP03AUgIGKZuIINAU1om3HzY

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.

VIGLIETTI, P. A., SMITH, R. M. H. and COMPTON, J. S. 2013. Origin and palaeoenvironmental significance of *Lystrosaurus* bonebeds in the earliest Triassic Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **392**, 9-21.

VIGLIETTI, P. A., SMITH, R. M. H., ANGIELCZYK, K. D., KAMMERER, C. F., FRÖBISCH, J. and RUBIDGE, B. S. 2016. The *Daptocephalus* Assemblage Zone (Lopingian), South Africa: A proposed biostratigraphy based on a new compilation of stratigraphic ranges. *Journal of African Earth Sciences* **113**, 153-164.

WAGNER, P. J. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology,* **49**, 463-479.

WALLACE, R. V. S., MARTÍNEZ, R. and ROWE, T. 2019. First record of a basal mammaliamorph from the early Late Triassic Ischigualasto Formation of Argentina. *PLoS ONE* **14**: e0218791.

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

WANG, G. and SONG, M. 2011. Ckmeans.1d.dp: optimal *k*-means clustering in one dimension by dynamic programming. *The R Journal,* **3**, 29-33.

WHITE, T. D. 1989. An analysis of epipubic bone function in mammals using scaling theory. *Journal of Theoretical Biology,* **139**, 343-357.

WILLS, M. A. 1999. Congruence between phylogeny and stratigraphy: Randomization tests and the gap excess ratio. *Systematic Biology,* **48**, 559-580.

WYND, B. M., PEECOCK, B. R., WHITNEY, M. R., SIDOR, C. A. 2017. The first occurrence of *Cynognathus crateronotus* (Cynodontia: Cynognathia) in Tanzania and Zambia, with implications for the age and biostratigraphic correlation of Triassic strata in southern Pangea. *Journal of Vertebrate Paleontology,* **37**, 228-239.

ZERFASS, H., LAVINA, E. L., SCHULTZ, C. L., GARCIA, A. J. V., FACCINI. U. F. and CHEMALE, F. 2003. Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: contribution to Southwestern Gondwana palaeogeorgaphy and palaeoclimate. *Sedimentary Geology,* **161**, 85-105.

FIGURES

FIGURE 1. Skeletal outline of a representative early cynodont, *Thrinaxodon liorhinus* (modified from Kemp 2005: fig. 3.50b), highlighting the body regions used to partition the skeleton. These regions of the skeleton were further subdivided into individual elements (see Table 1) to calculate the Skeletal Completeness Metric (SCM).

FIGURE 2. Global patterns of number of species, mean SCM, mean CCM, and mean BSCM of early cynodonts through time: A, using stage-level time bins; and B, using ‘equal’-length time intervals. In each case, the grey bars illustrate the time intervals used. The grey points represent all SCM values for each species known for each stage. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 3. Box-and-whisker plots showing the distribution of early cynodont SCM values for each time period. The median average completeness value is shown by the horizontal black bar in each plot.

FIGURE 4. Number of early cynodont species and mean SCM through time in: A, Laurasia; and B, Gondwana. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 5. Number of early cynodont species and mean SCM through time in each palaeocontinent. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 6. Box-and-whisker plot showing the distribution of early cynodont SCM values for each palaeocontinent.

FIGURE 7. Number of early cynodont species and mean SCM through time at different palaeolatitudes. Light grey shading represents time period. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 8. Box-and-whisker plot showing the distribution of early cynodont SCM values for each body size cluster based on anteroposterior lengths of postcanine teeth.

FIGURE 9. Number of early cynodont species for each body size cluster through time. Light grey shading represents stages. Abbreviations: Gu, Guadalupian; Lop, Lopingian; E, early; M, middle; L, late.

FIGURE 10. Box-and-whisker plots showing the distribution of completeness data for several vertebrae groups: A, comparison of SCM data for cynodonts, pelycosaurs, parareptiles, bats, sauropodomorphs, non-avian theropods, plesiosaurs, and ichthyosaurs; B, comparison of CCM data for cynodonts, anomodonts, pelycosaurs, parareptiles, eutherians, Mesozoic birds, pterosaurs, and plesiosaurs. Silhouette images of representatives from each group were obtained from Phylopic (http.//phylopic.org) under: Public Domain license (https://creativecommons.org/publicdomain/zero/1.0/) with credit to Christine Axon (http://phylopic.org/image/94fda119-5435-4246-ad23-20b15f3bcb8d/), Steven Traver (http://phylopic.org/image/b02c8c23-4263-436a-9a3a-068fc851dbb7/ and http://phylopic.org/image/31e41454-b7b3-4c17-8e71-bd3ab4bca376/), Tasman Dixon (http://phylopic.org/image/b348100c-7ba8-410d-90df-963064987089/), Yan Wong (http://phylopic.org/image/18bfd2fc-f184-4c3a-b511-796aafcc70f6/), Scott Hartman (http://phylopic.org/image/ba6426aa-337e-4a90-8cdb-c6daac83d819/) and Dann Pigdon

(http://phylopic.org/image/74fce2bf-3fc0-497b-9083-b6f600a697fe/); Attribution-ShareAlike 3.0 Unported license (https://creativecommons.org/licenses/by-sa/3.0/) with no changes made with credit to Dmitry Bogdanov (http://phylopic.org/image/1f3e74df-30e6-422b-9ce2-db7df199f11d/); and Attribution 3.0 Unported license with no changes made (https://creativecommons.org/licenses/by/3.0/) with credit to Mathew Wedel (http://phylopic.org/image/7a99b167-b719-4233-946c-addf3ef1c06c/) and Gareth Monger (http://phylopic.org/image/f0c8064a-eefa-45ab-b3f2-6ea6fb7d17b3/ and http://phylopic.org/image/02651c35-768e-4570-9bad-90cac6911b52/).

FIGURE 11. Global palaeogeographic reconstructions illustrating the distribution of cynodont species included within this study (black dots) for the: A, Lopingian, (reconstructed at 256 Ma); B, Early Triassic (249 Ma); C, Middle Triassic (242 Ma); D, Late Triassic (219 Ma); E, Early Jurassic (187 Ma); F, Middle Jurassic (168 Ma); G, Late Jurassic (154 Ma); and H, Early Cretaceous (122 Ma). Reconstructions from the Paleobiology Database (https://paleobiodb.org/navigator/).

FIGURE 12. A time-scaled phylogenetic tree of early Cynodontia. The observed stratigraphic ranges of each species are colour-coded by palaeocontinent. The underlying stacked area graph represents the relative contribution of each paleocontinent to the completeness of the cynodont record in each stratigraphic stage. The appearances of notable mammalian-like features in the fossil record are also depicted: a, reduced lumbar ribs and differentiation of the vertebral column as exhibited by *Thrinaxodon*; b, an expanded secondary palate as exhibited by *Thrinaxodon*; c, enlargement of the dentary and expansion of the coronoid process displayed by *Lumkuia*; d, gomphodont dentition and advanced dental occlusion exhibited by *Massetognathus*; e, tritylodont dentition seen in *Oligokyphus*; f, a reduced number of skull bones and loss of postorbital bar illustrated by *Kayentatherium*. All anatomical illustrations are modified from Kemp (2005). Light grey shading represents stages.

TABLES

Table 1. Percentage contributions of each region of the cynodont skeleton to calculation of the Skeletal Completeness Metric.

Region	Percentage %
Skull	**25**
Skull	24
Teeth/Complete dentition	1
Vertebrae + Ribs	**43**
Cervical	5
Dorsal	15
Sacral	5
Ribs	10
Caudal	8
Pectoral Girdle	**6**
Forelimbs	**10**
Humerus	3
Radius	2
Ulna	2
Carpals	1
Metacarpals	1
Phalanges	1
Pelvic Girdle	**6**
Ilium	2
Ischium	2
Pubis	2

Hindlimb	**10**
Femur	3
Tibia	2
Fibula	2
Tarsals	1
Metatarsals	1
Phalanges	1

The percentages attributed to each region and the subdivisions within each region used to calculate the SCM.

Table 2. 'Equal'-length time bins.

Start Date of Time Bin (Ma)	Stages Included
259	Wuchiapingian, Changhsingian
252.3	Induan, Olenekian, Anisian
242	Ladinian
235	Carnian
221.5	Norian
205.6	Rhaetian
201.6	Hettangian, Sinemurian
189.6	Pliensbachian
183	Toarcian, Aalenian
171.6	Bajocian, Bathonian

164.7	Callovian, Oxfordian
155.7	Kimmeridgian, Tithonian
145.5	Berriasian, Valanginian
136.4	Hauterivian, Barremian
125.45	Aptian

Start dates for time bins with approximately “equal-length” intervals, and the stages included within that interval.

Table 3. Correlation test results for early cynodont diversity and completeness comparisons across time and space

Test	**S**	**p-value**	**rho**	**T**	**p-value**	**Tau**	**t**	**p-value**	**Cor**
Div/SCM	668	0.079	0.414	111	0.080	0.298	1.286	0.216	0.298
Div/BSCM	656	0.071	0.425	117	0.029*	0.368	1.899	0.075	0.418
Div/CCM	580	0.034	0.491	113	0.058	0.322	1.512	0.149	0.344
SCM/BSCM	120	2.20 x 10^{-16}*	0.895	149	9.03 x 10^{-07}*	0.743	9.515	3.19 x 10^{-08}*	0.918
SCM/CCM	344	0.001*	0.698	129	0.002*	0.509	3.248	0.005*	0.619
CCM/BSCM	426	0.005*	0.626	121	0.013*	0.415	2.794	0.012*	0.561
Div/SCM new time bins	222	0.064	0.512	63	0.062	0.385	2.488	0.029*	0.583

Div/BSCM new time bins	226	0.069	0.503	62	0.079	0.363	2.431	0.032*	0.574
Div/CCM new time bins	150	0.011*	0.670	68	0.014*	0.495	3.044	0.010*	0.660
SCM/BSCM new time bins	22	2.20×10^{-16}*	0.952	84	1.51×10^{-06}*	0.846	12.274	3.76×10^{-08}*	0.962
SCM/CCM new time bins	134	0.006*	0.705	70	0.007*	0.538	3.427	0.005*	0.703
CCM/BSCM new time bins	156	0.013*	0.657	67	0.019*	0.473	2.807	0.016*	0.630
Lat:Div/SCM	236	0.588	0.175	36	0.737	0.091	0.166	0.872	0.052
Lat:Div/BSCM	340	0.558	-0.189	28	0.545	-0.152	-1.089	0.302	-0.326
Lat:Div/CCM	166	0.177	0.420	42	0.250	0.273	1.933	0.082	0.521
Lat:BSCM/SCM	44	0.001*	0.846	56	0.001*	0.697	6.126	1.12×10^{-04}*	0.889
Lat:BSCM/CCM	112	0.040*	0.608	50	0.021*	0.515	1.875	0.090	0.510
Lat:CCM/SCM	26	2.20×10^{-16}*	0.909	58	2.40×10^{-04}*	0.758	3.528	0.005*	0.745

Statistical comparisons between completeness (SCM, CCM and BSCM) and diversity through time (using stages and the intervals described in Table 2) and across space (at 10˚ palaeolatitudinal bins) using Spearman's rank correlation coefficient, Kendall's Tau coefficient, and Pearson's correlation coefficient. Asterisks indicate statistically significant results, using a *p*-value=0.05 as the cut-off.

Table 4. Correlation test results from temporal pairwise comparisons of completeness of tetrapod clades

Test	**S**	**p-value**	**rho**
Cynodont/Ichthyosaur SCM	408	0.7270	0.1032967
Cynodont/Ichthyosaur BSCM	314	0.2806	0.3098901
Cynodont/Plesiosaur SCM	118	0.9816	0.01666667
Cynodont/Plesiosaur CCM	52	0.3556	-0.4857143
Cynodont/Sauropodomorph SCM	230	0.2166	0.3681319
Cynodont/Parareptile SCM	58	0.9635	-0.03571429
Cynodont/Parareptile CCM	80	0.3536	-0.4285714
Cynodont/Pterosaur CCM	34	0.03687*	0.7166667
Cynodont/Amonodont CCM	52	0.3599	0.3809524
Cynodont/Theropod SCM	250	0.2973	0.3131868

Cynodont completeness metrics (SCM, CCM and BSCM) were compared to those of other contemporaneous clades including ichthyosaurs, plesiosaurs, sauropodomorphs, parareptilian tetrapods, pterosaurs, anomodonts, and non-avian theropods using Spearman's correlation coefficient. Data was log-transformed and subject to generalised differencing prior to analysis. Asterisks indicate statistically significant results at p-value=0.5.

Table 5. Correlation test results of non-temporal comparisons of completeness of tetrapod clades

Test	W	p-value
Cynodont CCM/Anomodont CCM	9342	2.20 x 10^{-16}*
Cynodont SCM/ Ichthyosaur SCM	2078.5	2.20 x 10^{-16}*
Cynodont BSCM/Ichthyosaur BSCM	122.5	2.20 x 10^{-16}*
Cynodont CCM/ Parareptilian tetrapods CCM	2294	1.09 x 10^{-06}*
Cynodont SCM/ Parareptilian tetrapods SCM	2564.5	3.26 x 10^{-08}*
Cynodont CCM/Pelycosaur CCM	13581	0.565
Cynodont SCM/Pelycosaur SCM	11598	4.24 x 10^{-07}*
Cynodont CCM/Plesiosaur CCM	4026	2.90 x 10^{05}*
Cynodont SCM/Plesiosaur SCM	2963	3.92 x 10^{-15}*
Cynodont CCM/Pterosaur CCM	8654	0.069
Cynodont SCM/ Sauropodomorph SCM	13600	1.21 x 10-^{06}*
Cynodont CCM/ Eutherian CCM	46725	2.20 x 10^{-16}*
Cynodont SCM/ Bat SCM	19396	1.40 x 10^{-10}*
Cynodont BSCM/ Bat BSCM	46863	2.20 x 10^{-16}*
Cynodont CCM/ Bat CCM	21711	0.0131*
Cynodont SCM/ Theropod SCM	19385	5.30 x 10^{-05}*
Cynodont CCM/ Mesozoic bird CCM	6321	0.3812

Cynodont completeness metrics (SCM, CCM and BSCM) were compared to other clades, including values that do not overlap with cynodonts temporally using the Mann-Whitney U test. Clades included ichthyosaurs, plesiosaurs, sauropodomorphs, parareptilian tetrapods, pterosaurs, anomodonts, pelycosaurian-grade synapsids, eutherians, bats and non-avian theropods. Asterisks indicate statistically significant results at p-value=0.5.

Table 6. Stratigraphic and phylogenetic congruence test results

Metric	**Value**	**Estimated p-value**
SCI	0.765432	<0.000001
RCI	44.93839	<0.000001
GER	0.845810	<0.000001
MSM*	0.222069	<0.000001

Values of SCI, RCI, GER, and MSM* and their estimated p-values from the stratigraphic congruence analyses using the phylogenetic supertree.