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## The quality of the fossil record of anomodonts (Synapsida, Therapsida)



### *La qualité du registre fossile des Anomodontes (Synapsida, Therapsida)*

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## ABSTRACT

The quality of the fossil record of anomodont synapsids, one of the major clades of Permian–Triassic terrestrial tetrapods, is assessed. A Character Completeness Metric (CCM2) is calculated for each taxon and consecutive time intervals at a global scale and in the South African Karoo Basin. The mean completeness score is 66.80% (globally) and 77.37% (regionally) with completeness ranging between 60.12% and 91.33% per time interval. Up-to-date taxic, phylogenetic and residual diversity estimates confirm the general biodiversity trends recovered by recent analyses. The consistently high CCM2 scores throughout their evolutionary history together with a lack of correlation with biodiversity patterns and sampling proxies document a high quality of the known anomodont fossil record. In fact, when compared to other vertebrate groups, the completeness values for anomodonts are exceptionally high. Yet, whether this pattern results from the unrivalled record of the Karoo Basin or whether it is clade-specific and unique to anomodonts remains to be tested.

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## R É S U M É

La qualité du registre fossile des synapsidés fossiles, l'un des clades majeurs des tétrapodes terrestres du Permo–Trias, est étudiée. Un score métrique CCM2 est calculé pour chaque taxon et pour chaque intervalle de temps consécutif, à une échelle globale et dans le Karoo d'Afrique du Sud. Le score moyen de complétude (ou d'aboutissement ou de parachèvement) pour les Anomodontes est compris entre 66,80% (au niveau global) et 77,37% (au niveau régional), avec une complétude comprise entre 60,12 et 91,33% selon l'intervalle de temps. Les estimations récentes de diversité taxique, phylogénétique et résiduelle confirment les tendances de la biodiversité générale, mises en évidence par les analyses récentes. Les scores de CCM2, toujours élevés au cours de leur histoire, ainsi qu'un manque de corrélation avec les diagrammes de biodiversité et les proxies échantillonnés, attestent la grande qualité du registre fossile des Anomodontes. En effet, comparées avec les autres groupes de vertébrés, les valeurs de complétude pour les Anomodontes sont exceptionnellement hautes. Cependant, il reste à vérifier si cette complétude résulte d'un registre inégalé dans le bassin du Karoo, ou s'il est spécifique du clade des Anomodontes.

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## 1. Introduction

It is well accepted that the fossil record of terrestrial organisms is much more fragmentary than that of marine organisms. Nonetheless, the quality of the fossil record of terrestrial vertebrates is generally considered to be adequate, providing a good representation of their evolutionary history (Benton, 1998). However, recent paleobiodiversity studies investigating patterns of vertebrate diversity on land have focused especially on the impact of potential biases in the vertebrate fossil record at various geographic, temporal, and taxonomic scales and most of these studies demonstrated a close relationship between taxic diversity patterns and different proxies for rock availability (e.g., Barrett et al., 2009; Benson and Mannion, 2012; Benson et al., 2013; Benton et al., 2011; Bernard et al., 2010; Butler et al., 2009; Butler et al., 2011; Fröbisch, 2008, 2013a, b; Irmis and Whiteside, 2012; Kalmar and Currie, 2010; Lloyd, 2012; Lloyd et al., 2008; Mannion et al., 2011; Rook et al., 2013; Ruta and Benton, 2008; Ruta et al., 2011; Upchurch et al., 2011; Wall et al., 2011). In contrast, paleobiodiversity studies across the Permian–Triassic boundary suggest that the high diversity of tetrapods in the Late Permian and the subsequent diversity drop in the Early Triassic are not controlled by rock availability or collecting efforts. Instead they persist despite a divergent signal in rock sampling, underlining the impact of the end-Permian mass extinction event in the terrestrial realm (Benton et al., 2004; Fröbisch, 2013a, b; Irmis and Whiteside, 2012). Overall, the quality of the fossil record of terrestrial tetrapods is still poorly understood, requiring the application of more rigorous methods to the tetrapod fossil record. Additional scrutiny of the record of individual clades has the potential to provide significant new insights by detecting taxonomic differences in the quality of the fossil record.

In this context, the Permian–Triassic tetrapod clade of anomodont therapsids is an ideal case study. Anomodonts are the most speciose and morphologically diverse clade of Permian–Triassic terrestrial tetrapods, representing the dominant herbivores of their time and dominating terrestrial vertebrate ecosystems in numbers of individuals and occupation of ecological guilds (Fröbisch, 2009; Hotton, 1986; Pearson et al., 2013). They ranged in body size from very small (10–15 cm body length) to large (2–3 m body length), and included fully terrestrial, semi-aquatic, fossorial and arboreal ecomorphs with a wide range of feeding adaptations (Cluver, 1978; Cox, 1972; Fröbisch, 2006; Fröbisch and Reisz, 2009, 2011; Germain and Laurin, 2005; Krilloff et al., 2008; Ray et al., 2005; Surkov and Benton, 2008). Anomodonts had a global distribution with fossils known from every continent, but only very few taxa, e.g. *Lystrosaurus* and *Diictodon*, actually had a cosmopolitan biogeographic range (Angielczyk and Sullivan, 2008; Fröbisch, 2009). Among synapsids, Anomodontia was one of only three major clades that survived the end-Permian mass extinction and the only tetrapod clade that experienced a true bottleneck with major radiations before and after the end-Permian event (Fröbisch, 2008, 2013a, b; Fröbisch et al., 2010). The fossil record of anomodonts is best known from the Beaufort Group of the South African Karoo Basin, which documents

a continuous Middle Permian to Middle Triassic record of sedimentation and consequently of terrestrial ecosystems in southern Pangaea (Nicolas and Rubidge, 2009, 2010; Rubidge, 1995, 2005; Smith et al., 2012).

For the purpose of this study, we analyzed the quality of the fossil record of Anomodontia using a taxic and phylogenetic approach and applying a variety of methods, ranging from simple diversity measures up to the character completeness metrics introduced by Mannion and Upchurch (Mannion and Upchurch, 2010). With respect to the completeness metrics, it is important to note that this approach represents a relative rather than an absolute measure of completeness, investigating the fossil record of a group as reflected in a phylogenetic dataset. Even when the completeness metric is 100%, this does not mean that all taxa that were present at a given time are also recorded in the fossil record. Nonetheless, the methodology provides valuable insights regarding the quality of the known fossil record of a clade through time and with respect to its individual members.

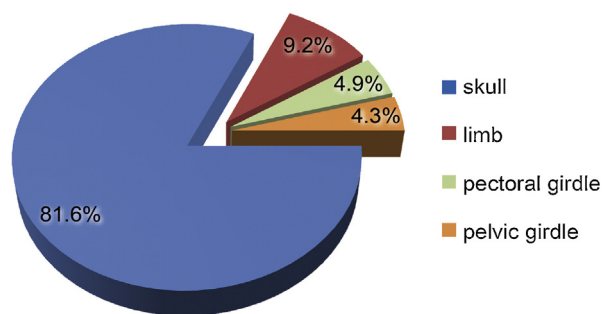
## 2. Material and methods

The main purpose of this study is to assess the quality of the known fossil record of anomodonts. For this, we calculated a completeness metric for the different anomodont taxa based on a recently published, comprehensive phylogenetic dataset of anomodonts and further calculated mean completeness per time bin. This analysis was performed at the global scale by considering all anomodont taxa that were included in the phylogeny. In addition we compared taxic and phylogenetic diversity estimates of anomodonts through time. All analyses were performed at the species level. To evaluate potential biases and influences on anomodont completeness, we compared regional completeness values to a number of proxies for rock volume and sampling effort at the scale of the South African Karoo Basin, e.g. outcrop area, number of specimens, number of localities, and number of individuals per taxon. For details of the analyses see below. Data sources used in this study include the recently published monograph on anomodont relationships by Kammerer et al. (2011) for the completeness and phylogenetic diversity estimate, the studies by Fröbisch (2008, 2009, 2013a, b) for the taxic diversity estimate, the study by King (1991) for outcrop area, the Karoo Database (Nicolas and Rubidge, 2009, 2010; Smith et al., 2012) for the number of specimens and localities.

### 2.1. Character Completeness Metrics

Mannion and Upchurch (2010) introduced two metrics as a means of quantifying the completeness of the fossil record of a clade, applying it to sauropodomorph dinosaurs as their case study. These metrics are as follows:

- the Skeletal Completeness Metric (SCM) represents a value that approximates the completeness of a given specimen (SCM1) or taxon (SCM2) based on the number of elements preserved and their physical bulk, achieved by assigning percentages to different divisions of the skeleton, whereas;



**Fig. 1.** Percentage of phylogenetic characters relating to each skeletal region in Anomodontia. Color available online.

**Fig. 1.** Pourcentage de caractères phylogénétiques reflétant chaque zone du squelette chez les Anomodontes. En couleur sur Internet.

- the Character Completeness Metric (CCM) attempts to describe the completeness of a given specimen (CCM1) or taxon (CCM2) by quantifying the amount of phylogenetically relevant information preserved in different parts of a skeleton.

Brocklehurst et al. (2012) applied this approach to Mesozoic birds but only used the CCM, arguing that it is a more appropriate metric than the SCM to evaluate the relationship between the quality of the fossil record and taxic diversity. In the present study we follow this approach for the same reasons. Following Brocklehurst et al. (2012), we also exclusively consider the CCM2 variant of the CCM, for which the combined information from all individuals is considered for taxon completeness rather than only the single most complete individual (Mannion and Upchurch, 2010). This provides the most complete measure of anatomical information about a given taxon.

For the purpose of this study, the CCM2 for the different anomodont species was determined based on the recently published phylogenetic dataset of Kammerer et al. (2011), which represents the most comprehensive (87 taxa, 71% of all anomodont species), balanced and up-to-date phylogenetic analysis of Permian and Triassic anomodonts. This dataset is a compilation of phylogenetic characters selected from 26 different references and the majority of character codings are based on personal examination of holotypes and additional specimens as well as information from original descriptions. A total of 163 characters were divided into four anatomical parts of the skeleton (skull, pectoral girdle, pelvic girdle, and limb). The only vertebral character in the dataset was included with characters of the pelvic girdle, as it is often identified based on the articular facets of the sacral ribs on the medial side of the ilium. The majority of anomodont characters relate to the anatomy of the skull (81.60%), followed by the limbs (9.20%), pectoral girdle (4.91%), and pelvic girdle (4.29%) (Fig. 1). In addition, we further subdivided these anatomical groupings of the characters based on the individual or multiple skeletal elements to which they refer (see Supplementary data). Using this approach, a completeness score was determined for each taxon included in the phylogenetic data matrix. In addition, an average CCM2 for each time bin was calculated in order to detect fluctuations through time.

## 2.2. Completeness and sampling bias

The fossil record is generally considered to be strongly influenced by a number of different biases (Alroy et al., 2001; Peters and Foote, 2001; Smith, 2001). An example for this particular study is that a lower completeness (CCM2 score) could be the result of a smaller number of preserved specimens in a given time bin. Hence, sampling effort may cause biases that could be reflected in a lower or higher mean CCM2, merely because a lack of sampling effort may mean not as many “good” or complete specimens are found, and vice versa. For this reason, we tested our CCM2 for correlation with three different proxies:

- number of localities;
- outcrop area and;
- number of individuals.

For this part of the study, we restricted our analyses to the well-studied Karoo Basin, South Africa. Smith et al. (2012) published an up-to-date compilation of the number of individuals per taxon for each Assemblage Zone (AZ). In addition, we extracted the number of localities (farms) from the Karoo Database and ordered them by time bin. Outcrop area values for the individual assemblage zones were taken from King (1991). We also tested for correlation between completeness (CCM2 score) with taxic, phylogenetic and residual diversity estimates (see below), for example to test for potential Lagerstätten effects.

We calculated the correlations using:

- the non-parametric tests: Spearman’s rank correlation and Kendall’s tau, and;
- Pearson’s product-moment correlation.

With the Shapiro–Wilk normality test, we examined our data for normal distribution. We executed generalized differencing of time series (<http://www.graemetlloyd.com/pubdata/functions.2.r>). Statistics were performed using computer language “R” (R Development Core Team, 2012).

## 2.3. Anomodont diversity

To determine the diversity pattern of anomodonts through time we compared taxic and phylogenetic diversity estimates to gain a comprehensive picture. Our taxic diversity estimate is based on the recent studies by Fröbisch (2008, 2009, 2013a, b). For the phylogenetic diversity estimate we used the phylogeny of Kammerer et al. (2011) as framework and plotted it on three different time scales following Fröbisch (2008, 2009). The stratigraphic correlations of the South African assemblage zones with the international marine stages are based on Rubidge (2005; see also Fröbisch, 2009). Therein, the assemblage zone boundary dates match perfectly with the recently published radiometric dates in Rubidge et al. (Rubidge et al., 2013). A phylogenetic approach to determine diversity estimates by incorporating ghost lineages has long been suggested as means to avoid obvious biases resulting from a literal reading of the fossil record (Norell, 1992; Norell and Novacek, 1992). We followed the criteria of

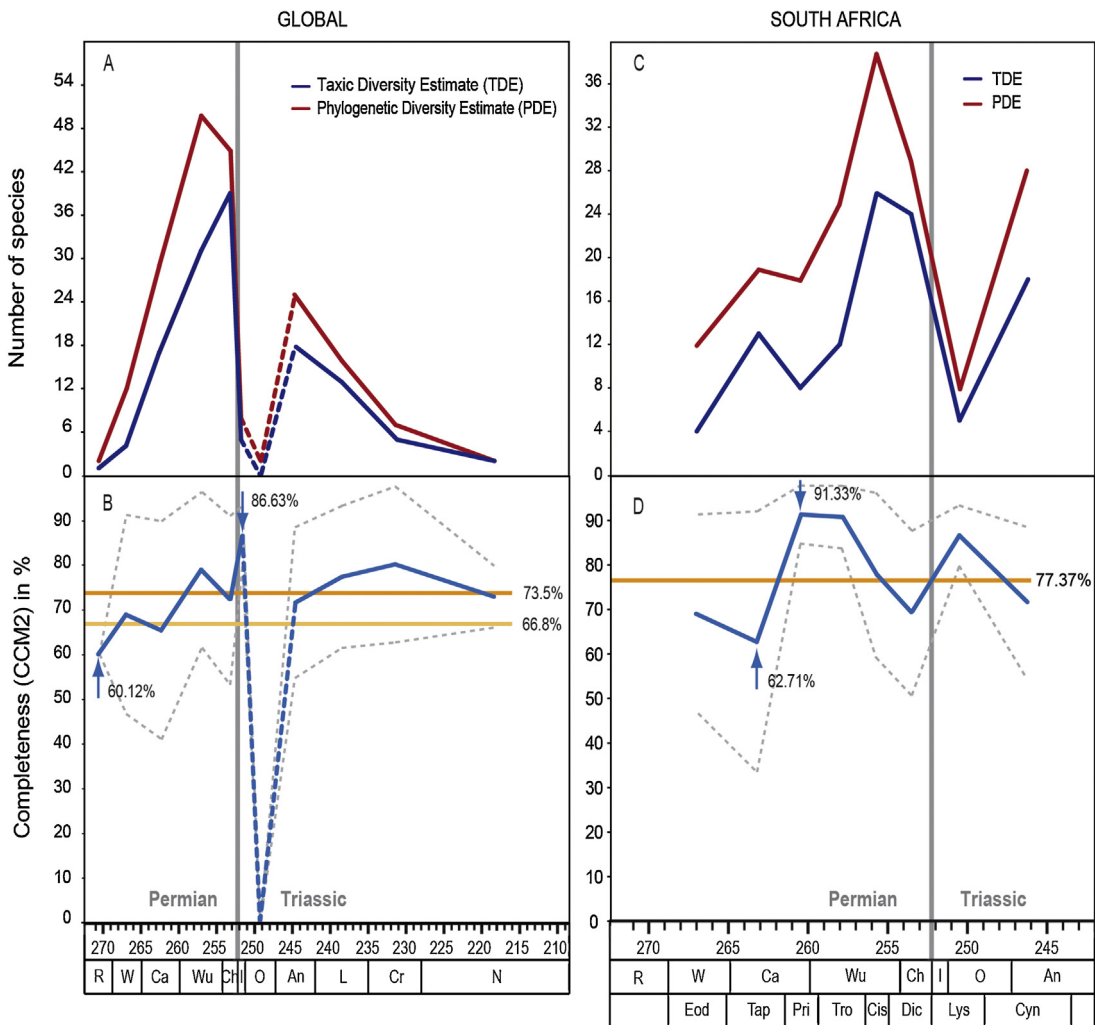
Cavin and Forey (2007) for the marking ghost lineages. Finally, we calculated residual diversity estimates following the methods introduced by Smith and McGowan (Smith and McGowan, 2007) and refined by Lloyd (Lloyd, 2012) implemented in “R” (R Development Core Team, 2012)

### 3. Results

#### 3.1. Completeness of the anomodont fossil record

For the global scale, Fig. 2B shows the mean completeness (CCM2) score plotted against substages of the

Standard Global Chronostratigraphic Scale SGSC, which indicates an average completeness of 66.80% for the known anomodont fossil record. Anomodont completeness starts off relatively low with a CCM2 score of only 60.12% in the Middle Permian (Roadian) and thereafter more or less continuously increases throughout the Permian. The highest mean completeness level is recorded in the Earliest Triassic (Induan) with 86.63% followed by a drop down to the lowest CCM2 score of 0% in the anomodont-devoid Olenekian. Excluding the Olenekian, the mean CCM2 increases to 73.47%. The mean values for the Anisian, Ladinian and Carnian form a plateau increasing only slightly from 71.68% to 80.25% of completeness.



**Fig. 2.** A) Taxic (blue) and phylogenetic (red) diversity estimates and B) Character Completeness Metric (CCM2) of anomodonts at the global scale. Dark-orange line represents the mean CCM2 score excluding the Olenekian stage, whereas the light-orange line represents the mean CCM2 score including the Olenekian stage. Dotted lines indicate the artificial decline in anomodont richness and completeness caused by a gap in their fossil record in the late Early Triassic (Olenekian). C) Taxic (blue) and phylogenetic (red) diversity estimates and D) Character Completeness Metric (CCM2) of anomodonts at the regional scale of the South African Karoo Basin. The dark-orange line indicates the mean CCM2 score for all assemblage zones. Color available online.  
**Fig. 2.** A) Estimations de la diversité dans les taxons (bleu) et la phylogénie (rouge). B) *Character Completeness Metric* (CCM2) chez les Anomodontes à l'échelle globale. La ligne orange foncé représente le score moyen CCM2 excluant l'étage Olenékien, tandis que la ligne orange clair le représente en incluant l'étage Olenékien. Les lignes pointillées indiquent le déclin dans la richesse et la complétude des Anomodontes, causées par une lacune dans leur registre au Trias inférieur tardif (Olenékien). C) Estimations de la diversité pour les taxons (bleu) et la phylogénie (rouge) et D) *Character Completeness Metric* (CCM2) des Anomodontes à l'échelle régionale du bassin du Karoo d'Afrique du Sud. La ligne orange foncé indique le score moyen CCM2 pour toutes les zones d'assemblage. En couleur sur Internet.

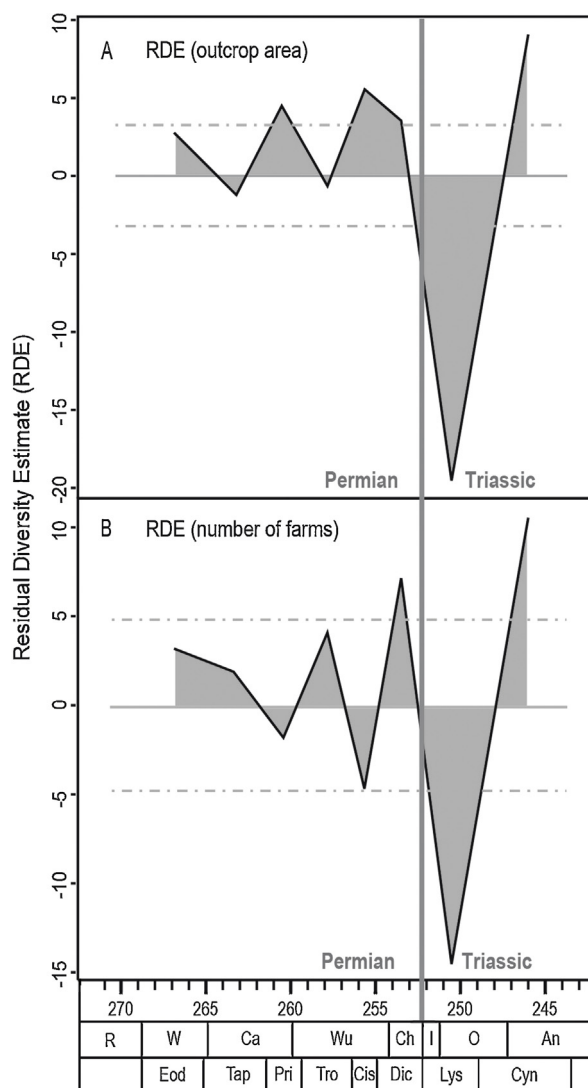


At the regional scale of the South African Karoo Basin, the mean completeness (CCM2) score for the anomodont fossil record is 77.37%, which is higher than for the global scale, with the highest completeness values in the early Late Permian *Pristerognathus* (91.33%) and *Tropidostoma* (90.75%) assemblage zones (Fig. 2D). The lowest completeness scores are recorded in the late Middle Permian *Tapinocephalus* AZ with 62.71%. After the early Late Permian high, anomodont completeness drops down to 69.17% in the Latest Permian *Dicynodon* AZ. However, most interestingly, the quality of the fossil record of anomodonts increases from the Late Permian to the Early Triassic despite the impact of the end-Permian extinction event, confirming the same signal at the global scale.

### 3.2. Anomodont diversity

Figs. 2A and 2C show the taxic diversity estimate (TDE) and phylogenetic diversity estimate (PDE) over time at the global scale and the regional scale of the South African Karoo Basin. Anomodont TDE at the global scale (Fig. 2A) shows a consistent increase from one genus (Roadian) up to the maximum of thirty-nine genera in the Changhsingian. In the Induan, TDE collapses down to five genera and the Olenekian is completely devoid of anomodonts, which certainly represents an artificial gap and hence a bias of their fossil record. After the Permian–Triassic Boundary (PTB), the generic richness reaches a second peak of eighteen genera in the Anisian, followed by a subsequent decrease until the end of the Triassic. The pattern of anomodont PDE is very similar. It increases continuously throughout the Permian from one genus in the Roadian up to nineteen genera, but this overall peak is already reached in the Wuchiapingian rather than in the Latest Permian Changhsingian as in the TDE. The lowest level of PDE is recorded in the Olenekian, where just two genera are predicted. Thereafter, anomodont PDE rises to seven genera in the Anisian, followed by a final decline until the end of the Triassic.

The diversity pattern at the regional AZ-scale of the South African Karoo Basin demonstrates a similar pattern to that at the global scale but with some minor differences (Fig. 2C). For example, the first peak of TDE is already in the late Middle Permian *Tapinocephalus* AZ (Capitanian), followed by a distinct decline in the *Pristerognathus* AZ, where anomodont richness decreases from thirteen to eight genera. After this first decline, the observed occurrence increases continuously to a second and overall peak of 26 genera in the *Cistecephalus* AZ (boundary Wuchiapingian and Changhsingian). Hence, like in the PDE but in contrast to the TDE at the global scale, the TDE in South Africa does not collapse right after the overall peak. In the Latest Permian *Dicynodon* AZ (Changhsingian) the number of genera (24) is still high. However, a rapid decline occurs in the Earliest Triassic *Lystrosaurus* AZ with only five known genera. Following this, anomodont diversity increases one last time to 18 genera in the *Cynognathus* AZ followed by their final extinction at the end of Triassic. The phylogenetic diversity estimate counted for the AZ-scale shows two peaks over time: after a trough in the *Tapinocephalus* AZ, the PDE reaches a peak of thirteen genera in the *Tropidostoma*



**Fig. 3.** Residual diversity estimates (RDEs) for South African anomodonts based on A) outcrop area and B) number of farms (localities), with one dashed-dotted line indicating 1.96 standard deviations (95% confidence intervals) of the model.

**Fig. 3.** Estimations de la diversité résiduelle (RDEs) pour les Anomodontes sud-africains, basées A) sur la surface de l'affleurement et B) sur le nombre de fermes (localités), avec lignes pointillées-tirées indiquant les déviations standard de 1,96 (intervalles de confiance de 95%) du modèle.

and *Cistecephalus* assemblage zones. Then the PDE shows a similar decline to the PDE at the SGCS-scale. The overall minimum is represented by just three genera in the *Lystrosaurus* AZ. A second and final peak is recorded for the *Cynognathus* AZ with ten genera. The residual diversity estimates at the AZ-scale are based on the outcrop and the number of farms per assemblage zone as proxies for rock volume (Fig. 3). The former is in good correspondence with recently published estimates (Fröbisch, 2013b), which used the same proxy but slightly older taxonomic treatments, for example regarding *Dicynodon* (Kammerer et al., 2011). Interestingly, there is a minor divergent signal between the RDEs using the different proxies, sometimes

displaying peaks or troughs, respectively, in the same time zones. However, none of these divergent signals are significant as they are within the confidence intervals. More importantly, the general pattern of all curves is identical:

- there is no significant trough at the end of the Middle Permian;
- there is a significant diversity peak in the Late Permian;
- there is a significant diversity trough in the Earliest Triassic, and;
- there is a significant diversity peak in the Middle Triassic.

### 3.3. Anomodont completeness and diversity in the light of sampling biases

The Shapiro–Wilk test confirms that all data series used in this study have a normal distribution (see [Supplementary data](#)). Subsequent correlation tests between biodiversity data, completeness scores and sampling proxies suggest a strong independence of these variables. Only at the global scale, the taxic and phylogenetic diversity show a borderline significant correlation with the completeness (CCM2) scores ([Table 1](#); see also [Supplementary data](#)). However, this result changes into a weak and statistically nonsignificant correlation, when the anomodont-devoid Olenekian time bin is excluded from the analysis (see Discussion and Conclusion). This is further supported by our regional investigations of anomodont completeness, demonstrating a lack of statistically significant correlation between either taxic or phylogenetic diversity and completeness (CCM2) in South Africa ([Table 1](#)).

As a result of the well-studied assemblage zones in the South African Karoo Basin, we have been able to investigate different controls such as outcrop area in square kilometres, number of specimens and number of localities, to examine to what extent anomodont diversity and completeness are potentially biased by sampling effects. To test for potential biases caused by human sampling effort it is necessary to look at:

- the potential influence of the number of specimens (abundance) on the number of species (richness);
- to what extent the number of localities biases the number of species as well as the number of specimens, and;
- how far anomodont completeness (CCM2 score) is prejudiced by the number of localities.

None of our tests display a significant correlation, rejecting these aspects of human sampling effort.

In general, the magnitude of each assemblage zone could have an impact on the fossil record, which is the reason why we have tested the outcrop area (km<sup>2</sup>) versus number of species as well. There is no evidence for a bias caused by geological factors, when considering the complete data. However, previous studies have demonstrated that Early Triassic time intervals represent distinct outliers with unusually low taxon counts despite increased sampling as a result of the end-Permian mass extinction ([Benton et al., 2004](#); [Fröbisch, 2008, 2013a, b](#); [Irmis and Whiteside, 2012](#)). Hence, the Early Triassic *Lystrorhynchus*

**Table 1**

Pearson's product moment correlation coefficients and probability values (*P*) of the statistical comparisons of time series, comparing completeness (CCM2), biodiversity estimates, and sampling proxies after generalized differencing. Bold font indicates statistically significant correlations. Abbreviations: PDE, phylogenetic diversity estimate; RDE, residual diversity estimate; TDE, taxic diversity estimate.

**Tableau 1**

Coefficients de corrélation de Pearson et probabilité (*P*) des comparaisons statistiques de séries temporelles comparant complétude (CCM2), estimations de biodiversité et proxys d'échantillonnage, après différenciation généralisée. En gras sont indiquées les corrélations statistiquement significatives. Abréviations : PDE, estimation de diversité phylogénétique ; RDE, estimation de diversité résiduelle ; TDE, estimation de diversité dans le taxon.

A) Global stages	<i>P</i>	
<i>Including Olenekian time bin</i>		
TDE vs mean CCM2	0.643	<b>0.045</b>
PDE vs mean CCM2	0.675	<b>0.032</b>
<i>Without Olenekian time bin</i>		
TDE vs mean CCM2	0.256	0.505
PDE vs mean CCM2	0.292	0.445
B) Local Stages	<i>P</i>	
<i>Including Olenekian time bin</i>		
TDE vs mean CCM2	-0.429	0.336
PDE vs mean CCM2	-0.209	0.653
Outcrop area (km <sup>2</sup> ) vs mean CCM2	-0.297	0.517
Number of specimens ( <i>n</i> ) vs mean CCM2	0.519	0.232
Number of farms ( <i>n</i> ) (localities) vs mean CCM2	-0.093	0.842
Outcrop area (km <sup>2</sup> ) vs TDE	0.303	0.508
Number of specimens ( <i>n</i> ) vs TDE	0.199	0.669
Number of farms ( <i>n</i> ) (localities) vs TDE	0.702	0.079
Outcrop area (km <sup>2</sup> ) vs number of specimens ( <i>n</i> )	0.325	0.476
<i>Without Lystrorhynchus AZ</i>		
Outcrop area (km <sup>2</sup> ) vs TDE	0.978	<b>0.001</b>
Number of specimens ( <i>n</i> ) vs TDE	0.757	0.081
Number of farms ( <i>n</i> ) (localities) vs TDE	0.884	<b>0.019</b>
TDE vs PDE	0.920	<b>0.009</b>
RDE (outcrop area) vs mean CCM2	-0.484	0.330
RDE (number of farms) vs mean CCM2	-0.459	0.359
RDE (outcrop area) vs PDE	0.354	0.491
RDE (number of farms) vs PDE	-0.671	0.145

AZ was here subsequently excluded from the respective datasets in an additional set of analyses to test the impact of the end-Permian extinction event on the relationship between anomodont diversity, completeness, and sampling proxies. After exclusion of the *Lystrorhynchus* AZ from all data series, anomodont TDE shows a statistically significant and strong positive correlation with outcrop area as well as the number of farms ([Table 1](#); see also [Supplementary data](#)).

As the completeness metric (CCM2) comprises information from multiple specimens for each anomodont species based on their phylogenetic character codings, a high completeness score could simply reflect a high abundance of the species. Hence, we tested whether there is a correlation between the CCM2 scores and the number of specimens. However, there is no statistically significant correlation between these variables, rejecting the hypothesis that abundance drives completeness in the anomodont fossil record ([Table 1](#)).

Finally, we calculated residual diversity estimates (RDE) for anomodonts based on the proxies for outcrop area and number of farms (localities) and subsequently tested for

potential correlation between RDE and CCM2 as well as the phylogenetic diversity estimate (PDE). It is notable that in contrast to some previous studies (Mesozoic birds), there is no significant correlation between RDE and completeness. Moreover, residual diversity estimates for anomodonts are also not correlated with phylogenetic diversity estimates.

#### 4. Discussion and conclusion

This study presents an up-to-date assessment of the quality of the known fossil record of anomodont synapsids, one of the major clades of Permian–Triassic terrestrial tetrapods. In addition, potential sampling biases are considered. The analyses were performed by calculating a Character Completeness Metric (CCM2) for each anomodont taxon and for consecutive time intervals at a global SGSC scale as well as the regional scale of the South African Karoo Basin (Figs. 2B and 2D). At the global scale, anomodont mean completeness per time bin increases more or less continuously from a low in the Middle Permian (Roadian) throughout the Permian to peak in the Earliest Triassic (Induan), followed by consistently high mean values in the Middle and Late Triassic. In South Africa, the mean completeness per time bin first drops to a low in the late Middle Permian *Tapinocephalus* AZ, before reaching the highest values in the early Late Permian *Pristerognathus* and *Tropidostoma* assemblage zones. Thereafter, anomodont completeness drops down again in the Latest Permian *Dicynodon* AZ, followed by another peak in the Early Triassic *Lystrosaurus* AZ. Although these patterns may seem random or counterintuitive at first sight, they reveal some interesting signals and support qualitative observations in South Africa. First, there is a clear inverse relationship between raw taxic diversity and completeness of Anomodontia through time with low species richness indicating high completeness (Figs. 2C and 2D). Second, the low completeness values in the *Tapinocephalus* AZ are supported by the qualitative observation that several taxa therein are known from fragmentary material (e.g., *Colobodectes*, *Lanthanostegus*, *Proscitodon*). Likewise, in the *Cistecephalus* and *Dicynodon* assemblage zones, high diversity and taxonomic issues have made it difficult to reliably associate postcrania with members of *Dicynodon* sensu lato (Kammerer et al., 2011) and there is seemingly rare taxa that also don't have known postcrania (e.g., *Pelanomodon*, *Compsodon*, *Cistecephaloides*). In contrast, many of the *Pristerognathus* and *Tropidostoma* assemblage zone taxa are represented by fairly complete material (e.g., *Dicynodontoides*, *Diictodon*, *Endothiodon*, *Tropidostoma*). In the Triassic, it is not surprising that the completeness values for the *Lystrosaurus* AZ are so high, as the dominating genus *Lystrosaurus* is represented by extremely high numbers of specimens. Finally, on the average postcrania of Middle and Late Triassic taxa seem to be more commonly preserved, collected and described, explaining the comparably high values in completeness.

At the global scale, the mean completeness score for Anomodontia is greater than 66.80% and, if the anomodont-devoid Olenekian time bin is excluded, the mean score increases to 73.50%. Anomodont completeness per stage ranges from a minimum of 60.12% to a maximum of 86.63%.

At the regional scale of the South African Karoo Basin, the mean completeness of anomodonts calculated over the entire time interval is, with 77.37%, even higher than at the global stage and completeness per assemblage zone ranges between 62.71% and 91.33%.

When these values are compared to the two other vertebrate groups, for which this method has been applied, it is obvious that the average completeness of the known anomodont fossil record is extremely high. Mesozoic birds and sauropodomorph dinosaurs have a much greater variation of mean completeness scores per time interval, ranging between 2 and 80% (Mesozoic birds) as well as 20 and 70% (Sauropodomorpha), and the average completeness scores for the entire times series are much lower as well with 34.48% (Mesozoic birds) and 38.36% (Sauropodomorpha) (Brocklehurst et al., 2012; Mannion and Upchurch, 2010). Hence, the values for Anomodontia are more balanced and consistently higher, indicating an overall higher quality of the known fossil record for this group of fossil vertebrates.

However, one has to keep in mind that the methodology employed represents a relative measure of completeness rather than an absolute, investigating the known fossil record instead of its entirety. Even when the CCM2 indicates a completeness of 100%, this does not mean that all taxa that were present at a given time are also recorded in the fossil record. Hence, we are able to state that the described anomodont taxa are known from comparably and consistently complete material, indicating that their fossil record provides a good picture of their anatomical diversity. However, this study does not address the question how this relates to the true original diversity of Anomodontia.

Moreover, at this point it is important to stress the predominance of the skull in the anomodont fossil record and specifically its use in the taxonomy and phylogeny of this clade (Fig. 1). It is a well-known phenomenon that during the early stages of therapsid research, particularly in South Africa, a strong collecting preference for skulls resulted in a distinct collection effort bias. This applies specifically to anomodonts but also to other therapsid and possibly tetrapod groups. The main reason for this is likely that the sheer abundance of therapsid fossils in the South African Karoo Basin, and particularly anomodonts as the most abundant tetrapod clade, prompted researchers to selectively collect only the best preserved and most diagnostic parts of a skeleton, which usually is the skull. In fact, the skulls of anomodonts and therapsids in general are much more compact, robust, and fused than in other tetrapod clades, for example, birds and sauropodomorphs where phylogenetic characters are much more evenly distributed across the skeleton, skulls are fragile, and thus some taxa are based on extremely incomplete material that are nevertheless distinct.

In addition to analyzing the quality of the fossil record of anomodonts, we further performed an up-to-date investigation of anomodont biodiversity patterns (species richness), calculating taxic and residual and for the first time phylogenetic diversity estimates for anomodonts by incorporating ghost lineages throughout the entire Permian–Triassic evolutionary history of the group. The patterns of biodiversity recovered on this

study generally support the results of recent analyses of anomodont richness at global and regional scales (Fröbisch, 2008, 2013a, b). Therein, anomodont diversity increases throughout the Permian with varying support for a minor mid-Permian (end-Guadalupian) extinction (only in the raw TDE at the regional scale of the Karoo Basin), collapses in the Earliest Triassic and reaches a second peak in the Middle Triassic before their final decline in the Late Triassic. These patterns are consistent when considering ghost lineages. Residual diversity estimates show significant peaks in the Late Permian and Middle Triassic and the only significant trough in the Early Triassic (Fig. 3).

The investigation of phylogenetic relationships using cladistics is a basic tool in evolutionary biology and frequently forms the basis for various additional quantitative analyses (Brooks et al., 2007), including among others research in biogeography, biodiversity, disparity, ecomorphology, and investigations of the quality of the fossil record. For the present study, we used phylogenetic approaches as the backbone for analyzing biodiversity patterns (comparing taxic, residual, and phylogenetic diversity estimates) and the quality of the fossil record of anomodont synapsids. In general, it can be noted that the Character Completeness Metric (CCM2) introduced by Mannion and Upchurch (2010) is a suitable and valuable approach to investigate the fossil record of a clade within a phylogenetic framework as all relevant (phylogenetically informative) morphological characters are considered. This methodology further increases our understanding of the quality of the fossil record and biodiversity patterns of extinct animals and the influence of the fossil record on the phylogeny in general (Brocklehurst et al., 2012).

However, as the fossil record has been shown to be at least in parts biased by sampling, the question arises whether the completeness score for anomodonts can be seen as independent variable or whether it is biased by sampling. For this purpose we tested potential correlations of anomodont biodiversity trends (TDE, PDE, and RDEs), completeness scores and various sampling proxies (geologic and anthropogenic) at the regional scale of the South African Karoo Basin (see material and methods for details). Our analysis suggests that all these variables seem to be independent of one another, as they generally lack a significant correlation with one another, the only exception being TDE and PDE when tested for correlation with the CCM2 at the global scale. However, the latter correlation changes into a weak and statistically nonsignificant correlation, when the Olenekian time bin is excluded from the analysis. This is of particular importance because the Olenekian time bin lacks any named anomodont material, resulting in an artificial diversity and completeness trough. This is further supported by our regional investigations of anomodont completeness, demonstrating a lack of statistically significant correlation between taxic, phylogenetic or residual diversity and completeness (CCM2) in South Africa (Table 1). Hence, we here accept that the CCM2 scores of anomodonts are not correlated with any diversity estimates of the group. This is in contrast to a recent study of the completeness of the fossil record of Mesozoic birds, which suggested that such a correlation in birds is the result of a Lagerstätten effect that strongly controls

the fossil record of this specific group and potentially all small-bodied or less robust vertebrates in general (Brocklehurst et al., 2012). In addition, the CCM2 scores of Anomodontia are neither significantly correlated with the number of specimens (abundance), nor with the number of localities per AZ, indicating that anthropogenic sampling effort has no impact on the completeness of the anomodont fossil record. Anomodont completeness (CCM2) further shows no correlation with outcrop area per assemblage zone, suggesting that rock record bias is also not a factor.

Finally, there is no correlation between sampling proxies and taxic diversity estimates, when the complete data series is considered. However, when the Early Triassic (*Lystrosaurus* AZ) outliers with unusually low taxon counts despite increased sampling as a result of the end-Permian mass extinction are excluded (see material and methods for details), anomodont TDE shows a statistically significant and strong positive correlation with outcrop area as well as the number of farms (Table 1; see also Supplementary data). Residual diversity estimates (RDE) for anomodonts based on the proxies for outcrop area and number of farms (localities) were subsequently tested for potential correlation with the CCM2 as well as the phylogenetic diversity estimate (PDE). In contrast to some previous studies (Mesozoic birds) there is no significant correlation between RDE and completeness. In addition, residual diversity estimates for anomodonts are also not correlated with phylogenetic diversity estimates, suggesting that at least for South African anomodonts both corrected diversity curves do not reflect an identical signal. This seems to result from inconsistent patterns in the Permian, specifically with varying support for a mid-Permian (end-Guadalupian) extinction.

In conclusion, the consistently high CCM2 scores throughout the evolutionary history of Anomodontia together with their lack of correlation with biodiversity patterns and sampling proxies document a high quality of the known anomodont fossil record. In fact, the comparison of CCM2 scores of anomodonts with other vertebrate groups (Mesozoic birds and sauropodomorph dinosaurs) emphasizes that the fossil record of anomodonts is exceptionally good. However, whether this pattern is a result of the unrivalled fossil record of specifically Permian–Triassic terrestrial tetrapods in the South African Karoo Basin or whether it is clade-specific and unique to anomodonts remains to be tested.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2013.07.007>.

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