The radiation of cynodonts and the ground plan of mammalian morphological diversity

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SUPPLEMENTARY MATERIAL AND METHODS

(a) Taxon-character dataset

Two cladistic matrices [1,2] provided the foundations for a new, revised, and expanded taxon-character data set that includes all major cynodont clades from Late Permian to Early Jurassic. After checking these matrices for instances of character duplications and conflicting codings, we merged them and consulted additional works [2–15] for further character inclusion and/or coding refinements (Datasets S2, S3, S9, S10). If different authors gave conflicting codings of a character, then the most recent codings were scrutinized and either endorsed or changed as appropriate in light of available data from specimens and/or illustrations. J. B. B. checked the majority of characters against original specimens, where possible. After all relevant data had been scrutinised, taxon descriptions were surveyed to glean additional data: Van Heerden [16] for Nanictosaurus; Crompton [17] for Aleodon; Crompton [18], Savage and Waldman [19], Sues [20] and Luo and Sun [21] for Oligokyphus; Brink [22] for Cynosaurus; Crompton [23] for both Scalenodon angustifrons and ‘Scalenodon’ hirschoni; Abdala and Ribeiro [24] for Santacruzodon; Bonaparte and Barberena [25] for Therioherpeton; Bonaparte [26] and Martinelli and Rougier [9] for Chaliminia; Barberena [27] for Traversodon; Hopson [28] for Gomphodontosuchus; Flynn et al. [29] and Kammerer et al. [10] for Menadon; Bonaparte et al. [3] and Soares et al. [30] for Riograndonia; Abdala and Teixeira [31] and Abdala and Smith [32] for Luangwa and Aleodon; Sidor and Hancox [7] for Elliotherium; Liu and Powell [33] for Andescynodon; Reichel et al. [11] for Protuberum; Gow [34] for Diarthrognathus; Sues and Jenkins [35] for Kayentatherium; Gao et al. [12] for Beishanodon; Oliveira et al. [14] for Trucidocynodon.

Some taxa require comments. Relative to the data matrices in [1,2], Charassognathus adds to Late Permian and basal cynodonts. Nanictosaurus augments Late Permian taxa and also adds to the sample of epicynodonts in general. Beishanodon, Sinognathus, Cricodon and
*Langbergia* add to the diversity of Trirachodontidae. *Traversodon, Andescynodon, Dadadon, Santacruzodon, Scalenodontoides, Scalodon attridgei, Arctotraversodon, Boreogomphodon* and *Nanogomphodon* add to Traversodontidae. These were diverse and successful tetrapods in the Triassic, but were poorly represented in the cladistic matrices in [1,2]. *Traversodon* is a Ladinian-Carnian traversodontid. *Andescynodon* is possibly transitional between Olenekian–Anisian and Ladinian–Carnian traversodontids. *Scalenodontoides* is Rhaetian, and represents the only known record of a South African traversodontid. *Menadon* and *Protuberum* are both known from fairly complete specimens; *Protuberum* displays an unusual morphology relative to other traversodontids. *Trucidocynodon* was included in our matrix as it is a close relative of *Ecteninion*. Despite the incompleteness of *Therioherpeton*, this genus has diagnostic cranial, dental and postcranial (a humerus) features, and belongs to a group not represented in either of the data matrices in [1,2]. *Tritylodon* and *Bienotherium* add to the Tritylodontidae. Finally, *Riograndia, Chaliminia, Diarthrognathus* and *Elliotherium* are fairly complete members of Tritheledontidae, and cover the geographical range of this clade: *Riograndia* and *Chaliminia* are from South America, whilst *Diarthrognathus* and *Elliotherium* are from South Africa.

**(b) Stratigraphic assignments**

The time scale of the Triassic is poorly resolved with very few radiometric dates to calibrate against [3,36–38]. We endeavoured to bin the species as precisely as possible within a time bin (whether that was the lower, middle or upper part of a stage or the stage in total) and date the age of the taxa as being the midpoint of that time bin. The duration and age boundaries of stages were based on the timescale from [40], though modified in agreement with recent work [37] suggesting a longer Norian and shorter Carnian durations [38] than formerly thought. All stratigraphic data can be found in Datasets S1, S11.
(c) **Phylogenetic analyses**

We used identical settings for all maximum parsimony analyses with PAUP* [39] and TNT [40], as follows: heuristic searches with 5000 random stepwise addition sequences, holding a single tree in memory during each step, using a tree bisection-reconnection branch swapping algorithm, and collapsing all tree branches that have minimum length of zero. After this initial run, we applied a new search to all the trees in memory, but with the option of saving multiple trees. These settings were employed in three analyses: 1) analysis with unordered and equally weighted characters; 2) analysis with all characters reweighted using the maximum values of their respective rescaled consistency indices (from the first analysis); 3) analysis with implied weights [41]. We ran implied weights analyses several times, each time increasing the integer value for Goloboff’s K constant of concavity [41], until tree shape became stable (for K = 3). Branch support for the implied weights tree was assessed via 1000 bootstrapping replicates in TNT, with a 50% threshold value for bootstrap support.

(d) **Time-calibrated cynodont phylogeny**

The branch durations for the tree (i.e. branch lengths in millions of years; Myr) were obtained with methods developed in [42,43]. Below, we supply the tree in a format (i.e. object of class ‘phylo’) that is readable by the ‘R’ ape package [44]. The time-calibrated tree is reproduced in figure S3a.

```nexus
#NEXUS
BEGIN TAXA;
DIMENSIONS NTAX = 54;
TAXLABELS
Charassognathus
Dvinia
Procynosuchus
Cynosaurus
Progalesaurus
```
Galesaurus
Nanictosaurus
Thrinaxodon
Platycranialus
Lumkuia
Ecteninion
Aleodon
Chiniquodon
Probainognathus
Trucidoynodon
Therioherpeton
Riograniad
Diarthrognytus
Pachygenelus
Elliotherium
Chaliminia
Brasilitherium
Brasilodon
Morganucodon
Sinoconodon
Oligokyphus
Kayentatherium
Bienotherium
Tritylodon
Cynognathus
Diademodon
Beishanodon
Sinognathus
Trirachodon
Cricodon
Langbergia
Andescynodon
Pascualgnathus
Scalenodonangustifrons
Luangwa
Traversodon
Scalenodonattridgei
Scalenodonhirschoni
Nanogomphodon
Arctotraversodon
Boreogomphodon
Massetognathus
Dadadon
Santa cruzodon
Menadon
Gomphodontosuchus
Protuberum
Scalenodontoides
Exaeretodon
BEGIN TREES;

TRANSLATE

1 Charassognathus,
2 Dvinia,
3 Procynosuchus,
4 Cynosaurus,
5 Progalesaurus,
6 Galesaurus,
7 Nanictosaurus,
8 Thrinaxodon,
9 Platycraniellus,
10 Lumkuia,
11 Ecteninion,
12 Aleodon,
13 Chiniquodon,
14 Probainognathus,
15 Trucidocynodon,
16 Therioherpeton,
17 Riograndia,
18 Diarthrognathus,
19 Pachygenelus,
20 Elliotherium,
21 Chaliminia,
22 Brasilitherium,
23 Brasilodon,
24 Morganucodon,
25 Sinoconodon,
26 Oligokyphus,
27 Kayentatherium,
28 Bienotherium,
29 Tritylodon,
30 Cynognathus,
31 Diademodon,
32 Beishanodon,
33 Sinognathus,
34 Trirachodon,
35 Cricodon,
36 Langbergia,
37 Andescynodon,
38 Pascualgnathus,
39 Scalenodonangustifrons,
40 Luangwa,
41 Traversodon,
42 Scalenodonattridgei,
43 Scalenodonhirschoni,
44 Nanogomphodon,
45 Arctotraversodon,
46 Boreogomphodon,
47 Massetognathus,
(e) Cynodont phylogeny with branches expressed as number of changes under ACCTRAN and DELTRAN and with correction for missing entries

Character-state changes (uncorrected for missing entries) under the accelerated transformation (ACCTRAN) are provided below for the tree branches. To create an object of class phylo, the final block in the previous file (parenthetical notations) should be replaced with the following:

```
TREE * UNTITLED = [&R]
```
In order to obtain a phylo object with branch changes corrected through patristic dissimilarity [45] (i.e. taking into account missing data), the following ACCTRAN block should be used:

\[
\text{TREE} \ast \text{UNTITLED} = \{&R\}
\]

The tree block with the branches expressed as uncorrected number of character-state changes under a delayed transformation (DELTRAN) is as follows:
When patristic dissimilarity is introduced, the modified branch lengths yield the following DELTRAN tree block:

\[
\text{TREE * UNTITLED = \{&R\}}
\]

(1:0.02380952381,((2:0.0283464566968346,3:0.04081632653):0.03333333333,(4:0.009009009009,(5:0.02727272727272727,6:0.01379310345):0.02666666667,((7:0.024390243902439,8:0.0275862069):0.02666666667,((9:0.02727272727,10:0.01379310345):0.02666666667,((11:0.0044068394145161,12:0.0008557980317073):0.004379562044):0.0030467163167601,13:0.004379562044):0.0030467163167601):0.004379562044):0.0030467163167601,14:0.00873505014,((15:0.0069464234791064,16:0.0034013605452381):0.00873505014)\)

(f) Cynodont phylogeny with branches expressed as rates

With information on branch durations and on character-state changes under ACCTRAN and DELTRAN optimizations (both corrected through the patristic dissimilarity), we obtain the following tree blocks in which the tree branches are expressed as rates (figure S3b, c):

For ACCTRAN:

\[
\text{TREE * UNTITLED = \{&R\}}
\]

(1:0.02380952381,((2:0.0283464566968346,3:0.04081632653):0.03333333333,(4:0.009009009009,(5:0.01704545454375,6:0.01379310345):0.0082410526315789,((7:0.05355555555,8:0.028053766972855):0.04363636363636363,((9:0.0028053766972855,10:0.0028053766972855):0.04363636363636363,((11:0.0044068394145161,12:0.0008557980317073):0.004379562044):0.0030467163167601,13:0.004379562044):0.0030467163167601,14:0.00873505014)\)
For DELTRAN:

TREE * UNTITLED = [&R]

(1:0.023809522381,(2:0.030708661413079,3:0.1224489796022449):0.1,4:0.004914004914
8935,(5:0.0170454545473,6:0.013793103435):0.0112280701768421,((7:0.05321507760387
02,8:0.011221507893047,(0.0271186400728296,(10:0.01966305939
714286,(11:0.0039661554733118,((12:0.2564102564130,13:0.0119047610427619):0.1333333333
35,(14:0.0157563025214286,(15:0.008577724955035:0.0115236875817974):017:0.008
631270573051,((18:0.0256739490512,19:0.01218978102):0.00243733053956:0.20:0.0
48925451204343,21:0.0206117359701511,0.0022443890278235):0.089775561116973:0
006769172933603,(22:0.0247570144858712,23:0.00516243940236:0.0101503759319
818,((24:0.0160689934576043,25:0.00596711456767,0.012955699356825,26:0.0111401
9150326738,(27:0.0021087709254214,(28:0.29:0.0147951501875606:0.0018247353010278:
0.0164226177084295:0.0403185664522751:0.008063713290455:0.01184210526232247:
0.021428571434613,0.0112676056338921:0.088507042259472:0.00639420635:0.1333
3333333333:0.00883080162465,(30:0.0189523558578377,31:0.0057568267:0.0578627
6578138,((24:0.14463640016532263,0.0792646006371271,0.09160306354231572,(34:0.0
768696951823857,((22:0.0247570144858712,23:0.00516243940236:0.0101503759319
5:0.0549618320593905:0.0732824227550143,37:0.03137254902,38:0.0166666666:0.01
0.043942246237279,39:0.0017010901153239,40:0.1124722196014971,41:0.012571204085
413,((42:0.04462314359488,(43:0.03487785973777047,44:40,45:0.0174239906359773,46:0.
323588461291119,33:0.003201589703893:0.0057238514504256:0.0202291584331668:0.
0050757286078243,((47:0.014509528216051,48:0.0337594684683111,49:0.02152166115
28527,0.0045912877126086,0.0120546225085363,50:0.010185136067064,51:0.001444
9576493175,52:0.098271379156779,53:0.007302992834455:0.0086935944582844:0.0}
For each of the 11 time intervals discussed in the main text, we selected the mid point of the interval duration (Dataset S1). For diversity, we used both taxa that appear in the phylogeny and the total number of known taxa from Permian to Lower Jurassic. For disparity, we used un-rarefied mean values of each of the four indices. We performed correlations (Spearman’s correlation coefficient) with and without generalized differencing of the time series [46]. The generalised differencing method removes trends in time series, eliminates autocorrelation by calculating differences between the values in any two adjacent intervals, but accounting for the strength of autocorrelation in adjacent intervals [47]. We show plots of un-rarefied mean disparity values and total cynodont diversity from Permian to Early Jurassic in figure S4.

(h) **An explanatory note on Ripley’s K function**

Let us consider $n$ data points in a sample. Let $A$ be the area (e.g. optimal observation window) where the $n$ points are. Let $\lambda$ be the average density of the points, that is, $\lambda = n/A$. Let $d_{ij}$ be the Euclidean distance between the $i^{th}$ and $j^{th}$ points. Let $s$ be the radius of a circle such that, for a completely random distribution of the $n$ points, $K(s) = \pi s^2$. The left term of the equation is the Ripley’s $K$ function for spatial randomness, increasing in proportion to the square of $s$, where $s$ can take increasing values depending on the distance scale (small to large distances between taxa). For the $n$ data points, the pattern of distribution is expressed by the following formula:

$$ K(s) = \frac{1}{\lambda n} \sum_i \sum_{j \neq i} I(d_{ij} \leq s), \text{ with } 1 \leq i \leq n \text{ and for } j \neq i $$
The function \( I(d_{ij} \leq s) \) is 1 if the argument \((d_{ij} \leq s)\) holds true, and 0 otherwise. Technicalities aside, the distances along which the \( K \) function is calculated are dimension-less. In figure 2d, the distance values on the horizontal axis of the \( K \) plot are the \( d_{ij} \) values. The above summary of the \( K \) function relates to a two-dimensional pattern, but the function can also be calculated for several dimensions.

(i) **An explanatory note on Mantel test and phylogenetic signal**

As explained in the main text, we employed the Mantel tests to correlate pair-wise generalised Euclidean distances with phylogenetic distances. We recall that the former are the inter-taxon distances generated from the cladistic data matrix, whereas the phylogenetic distances are the inter-taxon distances calculated in millions of years using branch durations (the phylogenetic distances were further transformed by taking their square-root values [48]). We further recall that the Mantel test was introduced solely as a test of the association between the two distance matrices, and not as a test of phylogenetic signal. A seminal paper on the performance of this test [49] has questioned its power when used in analyses of phylogenetic signal. In that same paper, explicit recommendations are offered for the use of the Mantel test exclusively in those cases in which species data can only be expressed as pair-wise distances. This is certainly the case for the morphological distances built from the data matrix. Also, we should bear in mind that signal refers solely to the statistical dependence among traits in taxa that results from the phylogenetic proximity of those taxa [49,50].

Here, we adapted two widely employed methods for testing phylogenetic signal in our data, but we urge caution in their application and interpretation. The first method relies on the K-statistic of Blomberg et al. [51]. The K-statistic is the variance of independent contrasts for a trait divided by the expected variance under a Brownian model of trait evolution [51,52]. A comparison is then made between the K value for the trait and a null distribution of K values.
built from re-shuffling the trait at random across the tips of a tree. The K-statistic and p value
were obtained for each of the 20 PCo axes used in disparity analyses. Each axis represents a
‘trait’, and the PCo scores are the trait values across our 54-taxon sample. Calculations were
performed in the ‘R’ phytools package [53]. The second method, devised by Klingenberg and
Gidaszewski [54], is implemented in the morphometric package MorphoJ [55]. In the original
formulation, a test of phylogenetic signal is devised through permutation of shape data across
the tips of the tree (the statistic is the sum over all tree branches of the total amount of squared
change), e.g. [56]. Here, we apply the test to the PCo scores. MorphoJ requires the phylogeny
with branch lengths and the set of PCo scores imported as a tabulation of co-variates, after the
specification of a taxon grouping (a classifier) identical to the 54-taxon set.

The reason for urging caution in the application of these methods is that in our case, the
tree topology and the PCo scores hinge upon the same data matrix. However, although some
elements of circularity might be involved, we note that both approaches are not conceptually
different from analyses of characters relative to a tree built from those very characters.

SUPPLEMENTARY RESULTS

(a) Cynodont phylogeny

A maximum parsimony search with all characters unordered and of equal unit weight yielded
486 trees, 526 steps long, with ensemble consistency index (C.I.) of 0.3525 (excluding all the
uninformative characters), ensemble retention index (R.I.) of 0.7188, and ensemble rescaled
consistency index (R.C.) of 0.2569. The base of the cynodont radiation is fully resolved in the
strict consensus (figure S1a), except for a trichotomy formed by Platycraniellus, a clade with
Nanictosaurus and Thrinaxodon as sister taxa, and the eucynodonts. Loss of resolution affects
the base of the probainognathians and, more apically, the tritheledonts. Mammals are placed
in a clade with Brasilitherium and Brasilodon (as successive outgroups). This wider clade, in
turn, forms the sister-group to a clade of tritheledonts plus tritylodonts. In the cynognathians, loss of resolution affects for the most part trirachodontids. The agreement subtree includes 45 of the 54 taxa, with the following taxa deleted: *Platycraniellus, Ecteninion, Trucidocynodon, Riograndidia, Pachygenelus, Diarthrognathus, Andescynodon, Nanogomphodon* and *Menadon* (figure S1b). Character reweighting by the maximum value of the rescaled consistency index results in nine trees, the strict consensus of which is reported in figure S1c. The nine trees are 141.99613 steps long (C.I. = 0.5469; R.I. = 0.8328; R.C. = 0.4661. Two trichotomies within cynognathians affect *Arctotraversodon, Boreogomphodon* and *Nanogomphodon*, as well as *Gomphodontosuchus, Menadon* and a clade of immediately more apical taxa. The single tree from the implied weights (figures 1, S3a) is 532-step long, with a C.I. of 0.3485 (excluding uninformative characters), a R.I. of 0.7138 and a R.C. of 0.2522. The most salient difference in taxon arrangement relative to the trees from previous analyses is the position of mammals as sister-group to tritylodonts. Bootstrap support above the 50% threshold value occurs in very few clades, as follows: tritylodonts (95%), mammals (81%), a clade including *Nanictosaurus* and *Thrinaxodon* (63%), a clade including *Dvinia* and *Procynosuchus* (60%) and eucynodonts (53%).

(b) Phylogenetic signal

The K-statistic values for the first 20 PCo axes, and associated significance, are as follows:

| PCo1: K = 1.036851, p = 0.001;  |
| PCo2: K = 2.128994, p = 0.001;  |
| PCo3: K = 0.5637574, p = 0.009; |
| PCo4: K = 0.430949, p = 0.016;  |
| PCo5: K = 0.3757458, p = 0.022; |
| PCo6: K = 0.269345, p = 0.077;  |
| PCo7: K = 0.837169, p = 0.001;  |
| PCo8: K = 0.2731058, p = 0.095; |
| PCo9: K = 0.2061463, p = 0.19;  |
| PCo10: K = 0.175391, p = 0.35;  |
| PCo11: K = 0.1311685, p = 0.665; |
| PCo12: K = 0.4668876, p = 0.013; |
PCo13: $K = 0.2739074, p = 0.097$;
PCo14: $K = 0.1336754, p = 0.644$;
PCo15: $K = 0.1151144, p = 0.78$;
PCo16: $K = 0.139438, p = 0.573$;
PCo17: $K = 0.1506301, p = 0.496$;
PCo18: $K = 0.1105352, p = 0.823$;
PCo19: $K = 0.08680619, p = 0.941$;
PCo20: $K = 0.08075433, p = 0.958$.

Thus, signal is detected in axes PCo1–5 and PCo7. For the first three axes, the K values show that the PCo scores are more similar than we would expect under the Brownian model of trait evolution (particularly on PCo2), and less similar on PCo3. However, it is difficult to provide a satisfactory interpretation for this result. The higher-than-expected similarity in PCo2 scores might be related to the separation of derived cynognathians and probainognathians from most basal members of each of these clades and from epicynodonts. A similar reasoning might be applied to PCo1, where tritylodonts and tritheledonts are distinctly set aside from other taxa.

With the application of the test proposed by Klingenberg and Gidaszewski, permutation tests for the distribution of PCo scores allow us to reject a null hypothesis of no phylogenetic signal for axes PCo1–13 ($p \ll 0.05$).
SUPPLEMENTARY DATASETS

**Dataset S1.** Temporal data on cynodonts and mammaliamorphs from Permian through to Early Jurassic, with information on first and last appearance data (FAD, LAD) in Myr and taxonomic assignments.

**Dataset S2.** Data matrix. Symbols are as follows: & = polymorphic condition; - = inapplicable state; ? = unknown state.

**Dataset S3.** List of characters used in phylogenetic, disparity and rate analyses. For each character, we provide ‘keys’ indicating the original literature sources were the character was used and its position in the relevant data sets. For example, character 1 in our list is identified by two keys, A21 and R22, to signify that it corresponds to character 21 in Abdala et al. 2006 and to character 22 in Reichel et al. 2009. Abbreviations: A, Abdala et al. 2006; AB, Abdala 2007; B, Bonaparte et al. 2001; BO, Botha et al. 2007; G, Gao et al. 2010; HK, Hopson & Kitching 2001; K, Kammerer et al. 2008; KA, Kammerer et al. 2012; L, Liu & Olsen 2010; M, Martinelli et al. 2005; MR, Martinelli & Rougier 2007; O, Oliveira 2006; OS, Oliveira et al. 2010; R, Reichel et al. 2009; SH, Sidor & Hancox 2006.

**Dataset S4.** Pair-wise inter-taxon distances.

**Dataset S5.** PCo scores (coordinates) of taxa on the 54 PCo axes.

**Dataset S6.** Complete rarefaction profiles of four disparity indices for the three major cynodont groups.

**Dataset S7.** Complete rarefaction profiles of four disparity indices for the 11 time intervals.

**Dataset S8.** Distribution of ACCTRAN and DELTRAN rates by groups and through time.

**Dataset S9.** Distribution of missing data (both unknown and inapplicable states) in the data matrix.

**Dataset S10.** Nature and preservation of excluded taxa.
**Supplementary References**


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Van Heerden, J. 1976 The cranial anatomy of Nanictosaurus rubidgei and the


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SUPPLEMENTARY FIGURES

Figure S1. Results of phylogenetic analyses. (a) Strict consensus of 486 trees resulting from analysis with all characters unordered and of equal unit weight. (b) Agreement subtree from the same analysis. (c) Strict consensus of nine trees obtained from reweighting characters by the maximum value of their rescaled consistency indices.

Figure S2. Plots of rarefied mean disparity values and 95% confidence intervals for four metrics. (a–d) Group disparity (B = basal taxa plus epicynodonts; C = cynognathians; P = probainognathians); (e–h) temporal disparity (for intervals t1–t9, see text).

Figure S3. Cynodont phylogeny. (a) Tree with time-calibrated branch lengths (see also figure 1 in the main text). (b) Tree with branches drawn in proportion to ACCTRAN rates. (c) Tree with branches drawn in proportion to DELTRAN rates. Green and red circles mark branches with significantly high and significantly low rates, respectively.

Figure S4. Plots of cynodont disparity and diversity through time. Mean un-rarefied disparity values for four disparity indices are represented by white circles; the total cynodont diversity (along right vertical axis) is represented by grey squares (for intervals t1–t11, see main text). (a) Sum of ranges vs. diversity. (b) Root-product of ranges vs. diversity. (c) Sum of variances vs. diversity. (d) Root-product of variances vs. diversity.
figure S1
figure S2
figure S3
figure S4