

**Ecomorphological change  
in lobe-finned fishes (Sarcopterygii):  
disparity and rates**

**by**

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## ABSTRACT

Patterns of vertebrate cranial/post-cranial trait diversification are not well-understood. Two ecological hypotheses, the ‘head-first’ model and the ‘stages’ model, predict the ordered decoupling of cranial/post-cranial ecomorphological diversification. Rate (tempo) analyses and macroevolutionary model-fitting (mode) analyses are often used to test whether cranial traits or post-cranial traits diversify earlier in vertebrates. Here we reconstructed the tempo and mode of cranial/post-cranial trait evolution in lobe-finned fishes (Sarcopterygii), a group containing coelacanths, lungfishes, and tetrapodomorph fishes, to test for differences in the timing of vertebrate cranial/post-cranial trait diversification. We collected full-skeletal geometric morphometric coordinate and PC-reduced data for 57 species of aquatic and semi-aquatic lobe-fins since the Paleozoic. We performed rate, raw disparity through time, phylogenetic signal and model-fitting (multivariate BM, EB and OU) analyses using both coordinate data and PC-reduced data but did not model-fit the coordinate data due to computational constraints. The BM (best fit model) rate parameter is highest for post-cranial traits but cranial trait disparity is highest throughout the majority of lobe-fin evolution, supporting the ‘head-first’ model, with peaks in the Middle to Upper Devonian and Jurassic. We also find that PCA reduction increases trait variance, creating bias in favor of early post-cranial trait diversification. We conclude that cranial ‘head-first’ ecomorphological diversification drove the early Paleozoic radiation of aquatic and semi-aquatic lobe-fins, but more research may be needed to understand conflicting patterns in the Mesozoic when taxonomic diversity was substantially lower among “living fossils”.

Ecomorphological change in lobe-finned fishes (Sarcopterygii): disparity and rates

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## Introduction

Our knowledge of the role of ecology in determining the relative timing and rate of cranial to post-cranial trait evolution is limited. High rates of evolution (tempo) and support for different models (mode) of evolution are often used as indicators of the relative timing of trait diversification (Sallan and Friedman, 2012; Anderson et al. 2013; Muschick et al. 2014). Various hypotheses that have been proposed explain how and why the rates and timing of cranial and post-cranial evolution might differ. Streelman and Danley (2003) proposed the ‘stages’ model which says that habitat diversification precedes trophic morphological diversification in vertebrates. More broadly, Streelman and Danley’s (2003) hypothesis may be viewed as the  $\beta$  niche of a group evolving before its  $\alpha$  niche *sensu* Ackerly et al. (2006) where macrohabitat affinity ( $\beta$  niche) diversification precedes within-community niche ( $\alpha$  niche) diversification. A second hypothesis, the ‘head-first’ model, uses the converse argument and ascribes more importance to the cranial ( $\alpha$  niche) skeleton rather than the post-cranial ( $\beta$  niche) skeleton as the primary driver of early ecomorphological diversification (Sallan and Friedman, 2012).



Few empirical studies have attempted to answer whether cranial functional morphology, associated with the use of new resources ( $\alpha$  niche), or post-cranial functional morphology, associated with locomotion through different habitats ( $\beta$  niche), contributes most to the ecomorphological diversification of vertebrates. Even fewer studies analyze both the tempo and mode of evolution of a group when testing the ‘stages/head-first’ models. Streebman and Danley (2003) support the ‘body-first’ (post-cranial) argument for extant vertebrates but do not provide any empirical data. Anderson et al. (2011) showed an early increase in gnathostome (including lobe-fin) jaw disparity in the early Devonian (Emsian) followed by relative stasis, indicative of a ‘head-first’ pattern, but did not examine post-cranial disparity. Similarly, Anderson et al. (2013) studied the tempo of early tetrapods and found a ‘body-first’ pattern but again did so using only cranial jaw traits, with qualitative terrestriality standing in for post-cranial change. Little can be concluded about differential cranial/post-cranial ecomorphological diversification without studying both sets of traits. Sallan and Friedman (2012) on the other hand, found cranial and post-cranial evidence that the mode of separate radiations of ray-finned (Actinopterygii) fishes showed a ‘head-first’ (cranial) pattern. This was the first study to use full skeletal geometric morphometric data to test the ‘stages/head-first’ models. Furthermore, Muschick et al. (2014) studied the mode of evolution of six ecologically-relevant traditional morphometric measurements in cichlid fishes and also found a head-first pattern although their model-fitting results did not corroborate their other analyses.

The tempo and mode of early lobe-finned fishes (Sarcopterygii), including our closest “fish” relatives, is vastly understudied in the context of modern comparative methods. Previous studies are taxonomically or methodologically limiting and study only select groups (coelacanths, lungfish or digitated tetrapods), use taxonomic origination as a proxy for disparity

(Schaeffer, 1952) or use only discrete character traits including traditional morphometrics measurements (Schaeffer, 1952; Cloutier, 1991; Lloyd et al. 2011; Anderson et al. 2011; Anderson et al. 2013). Among these, Cloutier (1991) identified a shift in the rates of coelacanth cranial and post-cranial traits in the Permian. Lloyd et al. (2011) found rate differences between groups of lungfish with significant decreases toward the crown; however, this was tested using (primarily cranial) cladistic characters. Other aquatic vertebrate groups have also been shown to undergo similar patterns of ecomorphological diversification. Ray-finned fishes often exhibit a ‘head-first’ pattern early in their history (Dornburg et al. 2011; Sallan and Friedman, 2012; Muschick et al. 2014; Price et al. 2014) as well as cranial (Alfaro et al. 2009) and post-cranial (Dornburg et al. 2011) rate shifts.

We are interested in which pattern of skeletal diversification is characteristic of the majority of vertebrate geological history. We chose lobe-fins to study the ‘stages/head-first’ model due to their long phylogenetic history and availability of museum specimens/fossil reconstructions. Lobe-fins have diversified over a long 419 Ma history (Zhu et al. 2009) and have persisted through several mass extinction and mass depletion events. The diversification of aquatic lobe-fins preceded that of semi-aquatic digitated tetrapods (Sallan and Coates, 2010). Early tetrapods did not evolve and diversify until the late Devonian <382.7 Mya (Clack, 2006) and Carboniferous (Sallan and Coates, 2010), respectively. Of coincident stochastic, catastrophic events, the Devonian Hangenberg mass extinction (359 Mya), unlike the Devonian Kellwasser mass depletion (374 Mya), restructured ecosystems and resulted in a bottleneck of the major fish groups such that terrestrial lobe-fins became dominant at the expense of aquatic and semi-aquatic lobe-fins (Sallan and Coates, 2010). Previous studies have noted that early lobe-fin diversity is much higher than previously realized (Clack, 2006). Lobe-finned fishes, whose fossil record

contains >600 species (this study), remain a largely understudied group in terms of their diverse functional morphology. Here we study the tempo and mode of aquatic and semi-aquatic lobe-fin cranial and post-cranial functional traits to test the ‘stages/head-first’ models of ecomorphological diversification over 419 Ma and describe the associated changes in skeletal disparity at four different geological time scales.

## Methods

We found >600 species with partial remains (Appendix A) using a literature search; our analyses use 57 species of fully-preserved (cranial and post-cranial) lobe-fins (Appendix B). Stratigraphic upper and lower dates of origination were collected from the literature for all taxa (Appendix B). We collected phylogenetic data using *Mesquite* version 2.75 (Maddison and Maddison, 2011) for groups primarily from Bockmann et al. (2013) with some modifications (Kemp, 1994; Cloutier and Ahlberg, 1996; Clement, 2005; Friedman, 2007; Clement, 2009; Snitting, 2009; Wen et al. 2013). These data constitute every major group of lobe-fins (Bockmann et al. 2013) with the exception of canowindrids. Of the sampled groups, every group had several species as representatives in our data with the exception of earlier lobe-fins, onychodontiforms, rhizodonts and elpistostegalians+relatives which were represented in our data set by *Guiyu*, *Strunius*, *Gooloogongia*, and *Tinirau*, respectively. All geometric morphometric data were taken from literature reconstructions or from museum specimens from the London Natural History Museum. In cases where reconstructions from the literature featured varying jaw positions, pectoral fin positions, or pectoral and pelvic fins placed along the midline of the organism rather than on its lateral side indicating bilateral symmetry, we used *Photoshop* to adjust jaw and fin positions to standard closed and lateral positions, respectively.

Ecologically relevant landmarks and semilandmarks were collected and processed using *tpsDig* version 1.4 (Rohlf, 2004), *tpsDig2* version 2.17 (Rohlf, 2013a), and *tpsUtil* version 1.58 (Rohlf, 2013b). We collected 27 and 20 cranial and 26 and 150 post-cranial landmarks and semilandmarks, respectively (Appendix C). As noted above, previous studies that have used geometric morphometrics to study lobe-fins have only studied a single lobe-fin group (Friedman and Coates, 2006) or only the cranial (jaw) morphology of single group (Anderson et al. 2011; Anderson et al. 2013). This necessitated the use of a new set of landmarks to encompass high lobe-fin cranial and postcranial disparity. We designed a landmark scheme based on known morphological indicators of prey capture and locomotion (Boily and Magnan, 2002; Webb, 1982; Webb 2002; Webb and Weihs, 2011) such as jaw/opercular structure and fin position/shape to serve as proxies for a species'  $\alpha$ - and  $\beta$ -niche. The tree, species images, and code used in this study are all available from the authors upon request.

We superimposed each configuration (the cranial and post-cranial landmarks) to remove the effects of translation, rotation and scaling using *geomorph* version 2.1.1 (Adams and Otárola-Castillo, 2013) in R version 3.13 (R Development Core Team, 2008). Semi-landmarks were slid using the bending-energy criterion. The resulting coordinates were averaged for each genus; all analyses used genus-level averaged data. For all analyses that could be done using the full set of shape variables (all coordinates), we used all the data. For analyses that could not be done using such high-dimensional data given the small number of taxa in this study, we reduced the dimensionality using a principal components analysis (PCA, Table 1-2). The PCs in our cranial and post-cranial datasets were analyzed as a single multivariate dataset using the model-fitting methods described below. Our analyses of lobe-fin tempo includes analyses of rate and estimates

of pairwise raw disparity relative to time whereas our analyses of mode encompass model-fitting approaches and PCA analyses. All analyses in this study were performed in *R* version 3.13.

Table 1. Cranial PC-reduced data. St. Dev.; standard deviation, Propor. Var.; proportion of variance, Cumul. Propor.; cumulative proportion of variance.

	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>PC4</b>	<b>PC5</b>	<b>PC6</b>	<b>PC7</b>	<b>PC8</b>	<b>PC9</b>	<b>PC10</b>
<b>St. Dev.</b>	0.192	0.097	0.091	0.079	0.071	0.059	0.058	0.051	0.045	0.041
<b>Propor. Var.</b>	0.412	0.105	0.093	0.070	0.057	0.039	0.037	0.030	0.023	0.019
<b>Cumul. Propor.</b>	0.412	0.517	0.610	0.680	0.736	0.775	0.812	0.842	0.865	0.884

Table 2. Post-cranial PC-reduced data. St. Dev.; standard deviation, Propor. Var.; proportion of variance, Cumul. Propor.; cumulative proportion of variance.

	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>PC4</b>	<b>PC5</b>	<b>PC6</b>	<b>PC7</b>	<b>PC8</b>	<b>PC9</b>	<b>PC10</b>
<b>Std. Dev.</b>	0.210	0.089	0.074	0.071	0.057	0.050	0.038	0.036	0.033	0.030
<b>Propor. Var.</b>	0.555	0.099	0.069	0.063	0.041	0.031	0.018	0.017	0.014	0.011
<b>Cumul. Propor.</b>	0.555	0.654	0.723	0.787	0.828	0.859	0.877	0.894	0.908	0.919

### Tree-scaling and PCA analyses

As previously mentioned, many studies have fit macroevolutionary models to determine patterns of diversification, but few have examined the order of skeletal trait diversification and even fewer; used fossil data. Paleontological data, unlike neontological data, must be fitted to macroevolutionary models using trees that are time scaled using stratigraphic information, which produce non-ultrametric trees with branch lengths based on time. The use of non-ultrametric trees in this study (and every other study which uses non-ultrametric trees) restricts us from performing any tree transformations. We time-scaled our trees using the ‘equal method’ (Bell and Lloyd, 2014), which increases the time of root divergence and apportions time equally to later zero-length branches, in favor of the ‘mbl’ method (Laurin, 2004), which subtracts time apportioned to later branches to maintain the temporal structure of events. We chose minimum branch lengths of 1 Ma and resolved polytomies by order of appearance using the ‘timeres’ option in the *paleotree* package version 2.3 (Bapst, 2012). We preferred the ‘equal’ over the ‘mbl’ method because preliminary analyses showed that Early Burst (EB, see below) model

optimization failed more frequently when analyzing our post-cranial data (>99% of trees). However, EB model optimization still failed often when fitting post-cranial data (>97%), and subsequently cranial data (<40%). We assume that unsampled trees do not have a large effect on our results; most species have a small ‘lower’ and ‘upper’ age of origination range (standard deviation = 9.46 Ma). In this study we used the first 1000 optimized trees for each analysis and average across each tree to calculate relevant statistics and p-values.

We used *geomorph* and the first tree from our model-fitting analyses to plot cranial and post-cranial PCs 1-4 according to a color scheme corresponding to different lobe-fin groups. Each color-coded point corresponds to one of nine monophyletic groups of early lobe-fins concordant with Bockmann et al. (2013). Additionally, we plotted cranial and post-cranial PCs 1 and 2 at the Era, Period, Epoch, and Age geologic time scales to qualitatively analyze changes in morphospaces through time. Some PC plot bins contain >1 Period, Epoch, or Age to accommodate low diversity/limited sampling, (e.g. Silurian and Mesozoic).

#### Disparity and Rate Analyses

One benefit that fossil data has when determining the order of skeletal diversification is that fossils allow us to directly quantify raw disparity relative to time. We calculated raw disparity for each sampled bin for the Era, Period, Epoch, and Age time-scales using *geomorph* to test whether cranial/post-cranial diversification patterns are emergent at different time scales. We also conducted two forms of pairwise disparity tests for all consecutive geological intervals. The first pairwise disparity test we used was, *morphol.disparity* in *geomorph*, which we ran for 1000 iterations using both our coordinate and PC-reduced data. *morphol.disparity* uses group disparity as a test statistic and evaluates it through permutation where the residuals are randomized between groups. We recoded *morphol.disparity* to also output 95% confidence

intervals using a bootstrapping technique. The second test we used was a new kind of “log-likelihood ratio test”, different from the more frequently used log-likelihood ratio test, this new “log-likelihood ratio test” tests for differences in the variance between pairs of time bins (Finarelli and Flynn, 2007). We then conducted analyses of rate using the *compare.evol.rates* function in *geomorph* for which we used the coordinate and PC-reduced data and ran for 1000 iterations. *compare.evol.rates* assumes a Brownian Motion (BM) process and uses a BM rate formula as well as data simulated using BM to test for different evolution rates between clades, using pairs of evolution rates as a test statistic. This was done, assuming that the BM model describes our data well, to study potential differential group contributions to the analyses performed in this study.

#### Model-fitting analyses

To fit the models to our data, we used an unpublished multivariate version of the *fitContinuous* function in *geiger* (Harmon et al. 2008), *fitContinuousMV*, (provided to us courtesy of Graham Slater) and *ouchModel* in *mvSLOUCH* (Bartoszek et al. 2012). *fitContinuousMV* was used to fit the BM and EB models to our data while *ouchModel* was used to fit the OU (Ornstein-Uhlenbeck) model since *fitContinuousMV* requires a tree transformation before fitting the OU model but *ouchModel* does not. We use BM as the null model with EB showing high rates of evolution concentrated at the root. We included OU in this analysis because OU-like processes have been shown to fit paleontological bony fish (ray-finned fish) data (Sallan and Friedman, 2012). Support for an OU process may be interpreted as early or late divergence depending on the evolutionary rate and rebound parameters. We collected log-likelihoods, AIC scores (Akaike, 1974), AICc scores, and akaike weights for the first set of 1000 trees and data that was successfully optimized. Lastly, we used *geomorph* to calculate the

phylogenetic signal of our shape and PC-reduced data. *geomorph* calculates phylogenetic signal using a generalized multivariate ‘K-statistic’ where values  $>1$  represent high phylogenetic signal relative to the signal expected for a BM process (Blomberg et al. 2003), and uses BM simulations to test for statistical significance under the null that  $K = 0$ ; simulations were ran for 1000 iterations.

## Results

### PC Plots

All species were plotted on PC1 PC2 cranial and post-cranial morphospaces (Fig. 1-2). PC3 and PC4 cranial/post-cranial morphospaces were also plotted (Appendix D.1). The all-species PC1 morphospace (Fig. 1) shows us two distinct clusters of morphotypes, one consisting of coelacanths/lungfish and a second consisting of all other lobe-fins. This discrete difference contributes 41.2% (PC1) of the cranial trait variance. PC1 depicts variation from an elongated anterior skull/jaw with a small coronoid process (such as *Guiyu*) to a much shorter anterior skull/jaw with a large coronoid process typical of coelacanths and lungfishes, reflecting a stronger, faster bite and developed jaw musculature. Coelacanths and lungfish span the entirety of cranial PC2 morphospace while other groups clump around the center value with the exception of *Strunius*, a late-diverging (Middle Devonian) onychodontiform. Cranial PC2 is aligned with the disparity between the deepness of the skull and length of primarily the rostrum, reflecting mostly differences in coelacanth/lungfish feeding strategy in addition to the cranial morphology on the positive extreme of PC1.

The all-species PC2 morphospace (Fig. 2) shows a relatively more continuous distribution between groups, generally ranging from coelacanths to lungfish to other lobe-fins. This continuous shift contributes 55.5% (PC2) cumulative post-cranial trait variance. Post-



cranial PC2 is a dimension of variation from short bodies with short distances between each fin (typical of coelacanths) to elongated bodies with posteriorly-placed (including fused) fins with the exception of an anteriorly-placed pectoral fin, a body shape typical of lungfishes and semi-aquatic lobe-fins. Post-cranial PC2 reflects approximately a 45° change in the angle between the first dorsal fin and the pelvic fin as well as the expansion of the fin bases and the space between them. Cranial PC1 and PC2 plots at the Era scale (Appendix E.1-2), Period scale (Appendix E.3-7), Epoch scale (Appendix E. 8-13) and Age scale (Appendix E. 14-18) and post-cranial PC1 and PC2 plots at the Era scale (Appendix F.1-2), Period scale (Appendix F.3-7), Epoch scale (Appendix F. 8-13) and Age scale (Appendix F. 14-18) show a general bimodal pattern between coelacanth/lungfish and other semi-aquatic lobe-fins early in geologic history. Later in geologic history (post-Devonian) coelacanths and lungfish are the sole members of time bins, but expand through morphospace rather than clumping.

#### Analyses of Disparity and Rate

We plotted disparity at 4 different geologic time scales for our coordinate data (Figs. 3-5) and PC-reduced data (Appendix G. 1-3) to observe potential differences in disparity through time between cranial and post-cranial data as well as the relative cranial to post-cranial disparity. Cranial (Fig. 2) and post-cranial (Fig. 3) disparity both generally decrease through geologic time. We observe that significant changes in both cranial and post-cranial disparity happen over different geological scales. Our analyses suggest that cranial disparity significantly increases into the Middle/Upper Devonian (Givetian-Frasnian), as well as into the Mesozoic (Lower Triassic and Cretaceous) and significantly decreases into the Middle/Upper Triassic and Jurassic. Post-cranial disparity on the other hand, significantly increases into the Upper Devonian (Frasnian) and Mesozoic (Lower Triassic), and significantly decreases in the Upper Devonian (Famennian),

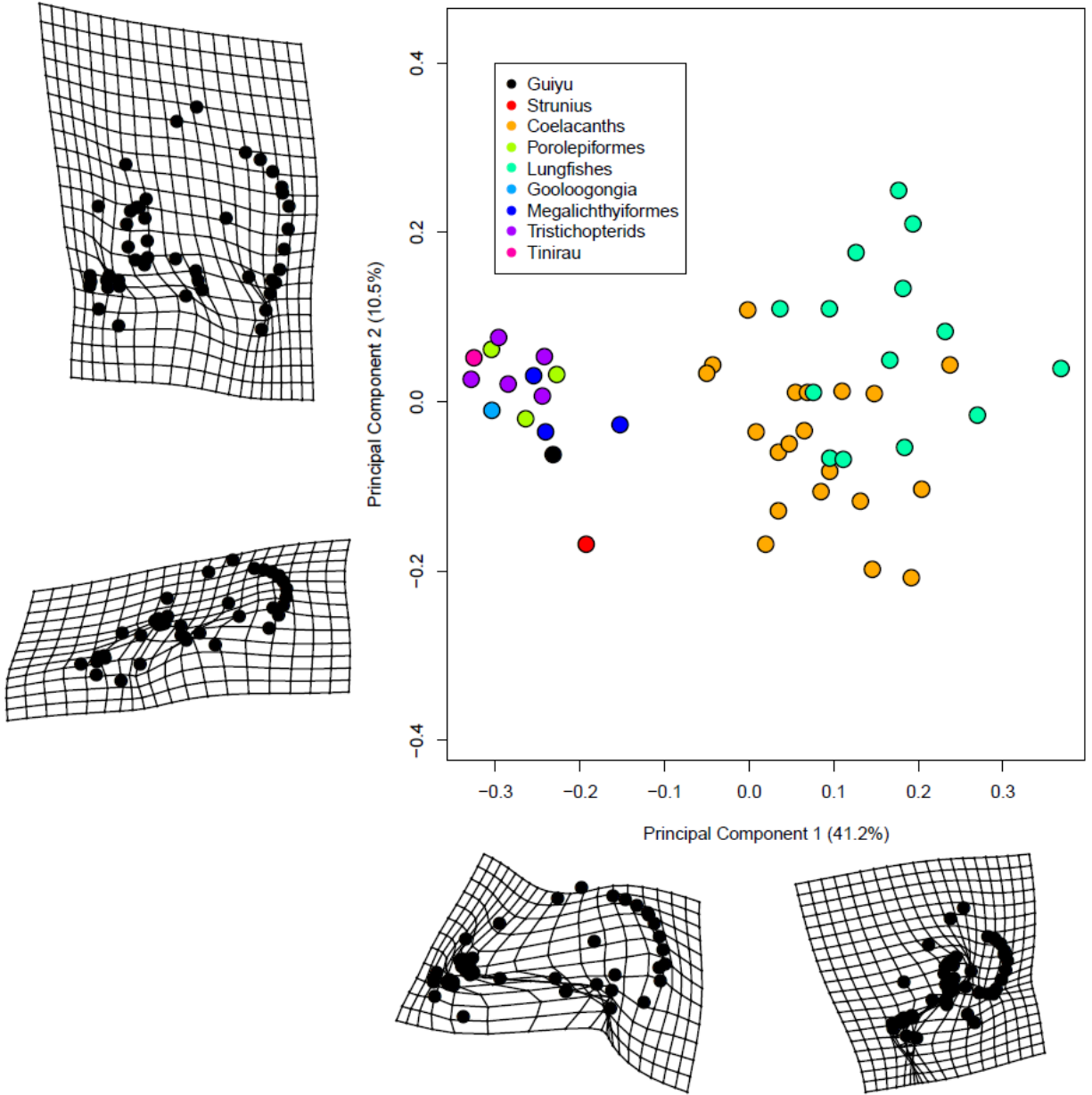


Fig. 1. PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

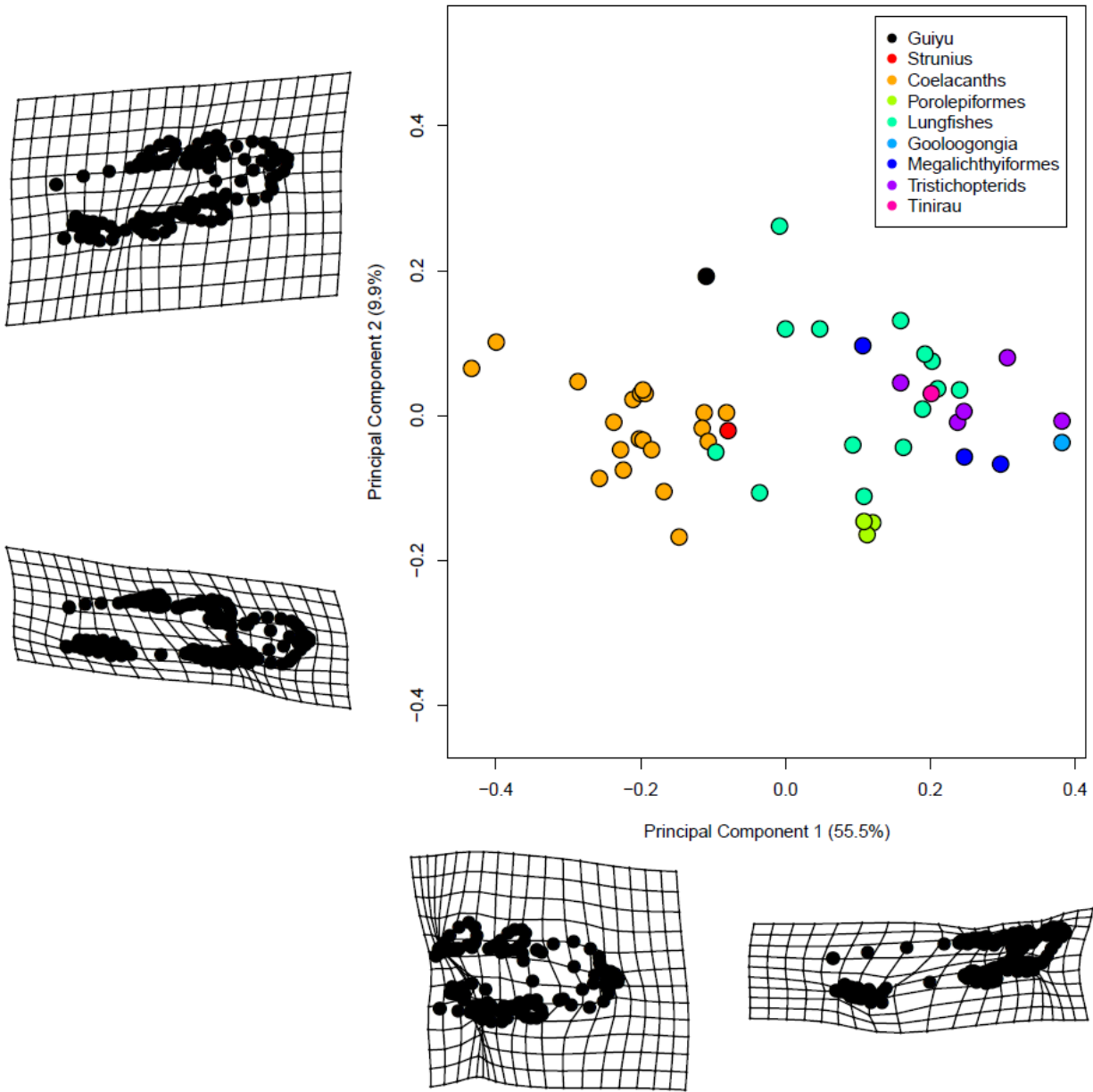


Fig. 2. PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

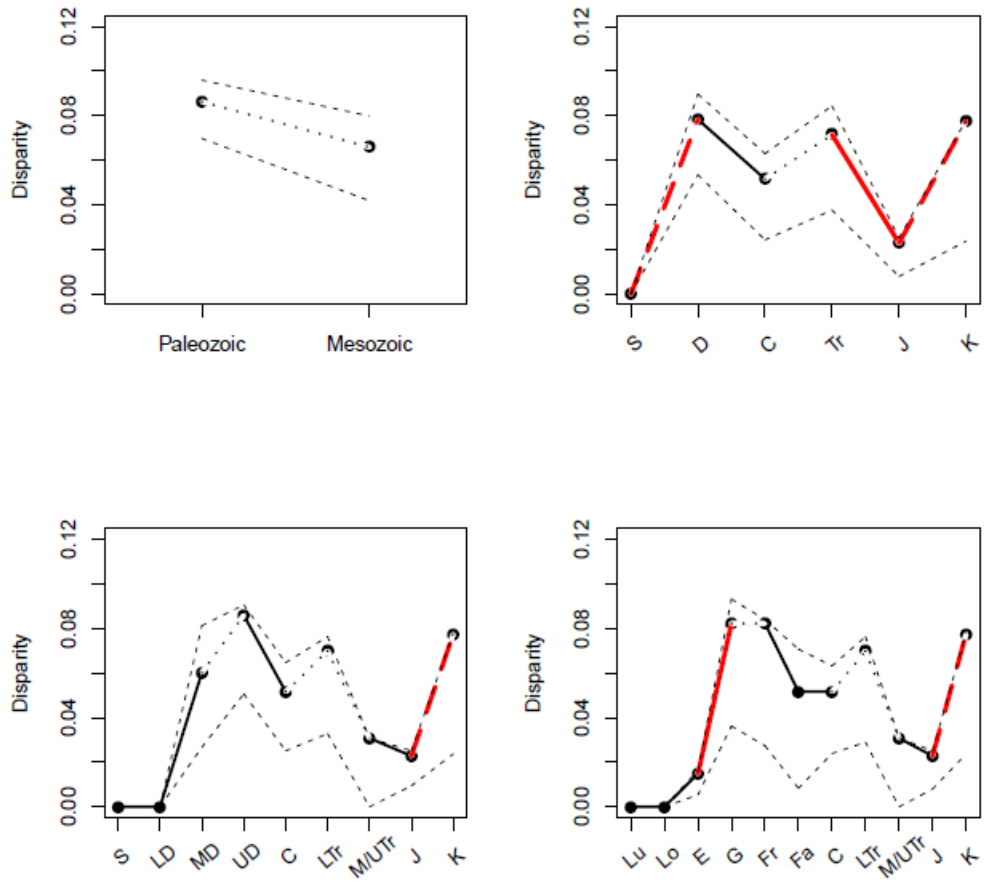


Fig. 3. Cranial disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. Dashed black lines represent 95% confidence intervals. Dotted lines represent significant likelihood-ratios. Dashed red lines represent significant permutation tests. Solid red lines represent significant likelihood ratios and permutation tests. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.

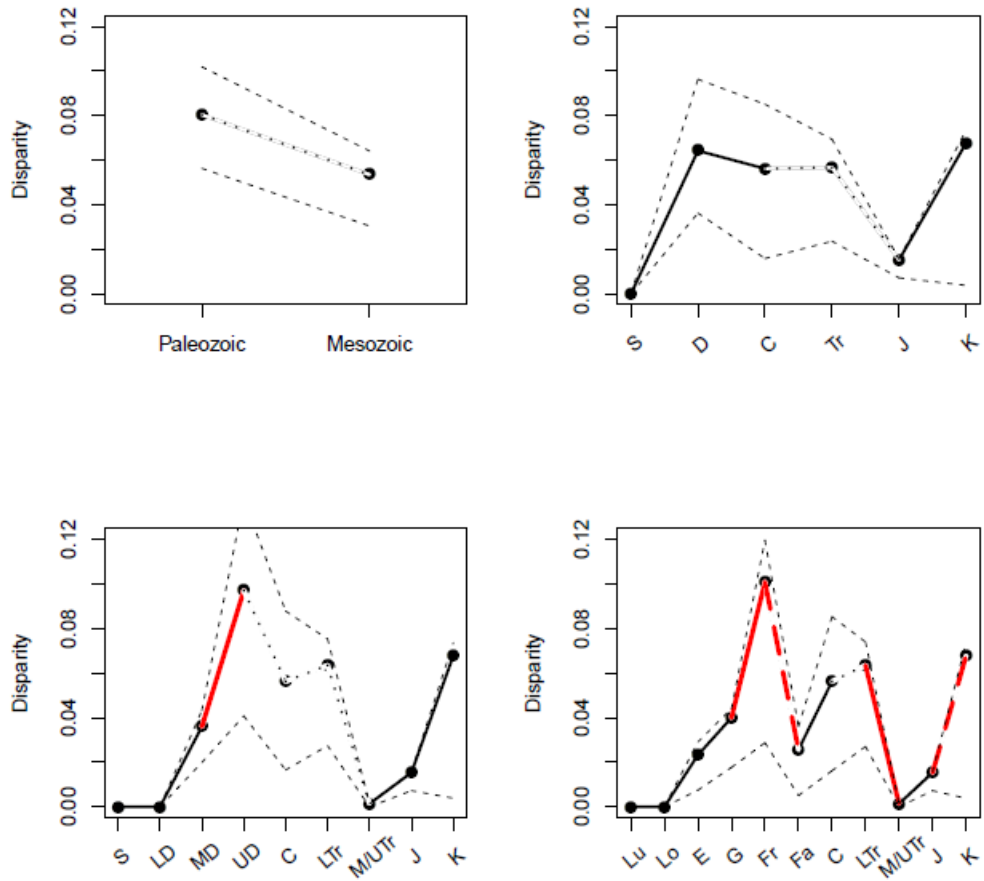


Fig. 4. Post-cranial disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. Dashed black lines represent 95% confidence intervals. Dotted lines represent significant likelihood-ratios. Dashed red lines represent significant permutation tests. Solid red lines represent significant likelihood ratios and permutation tests. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.

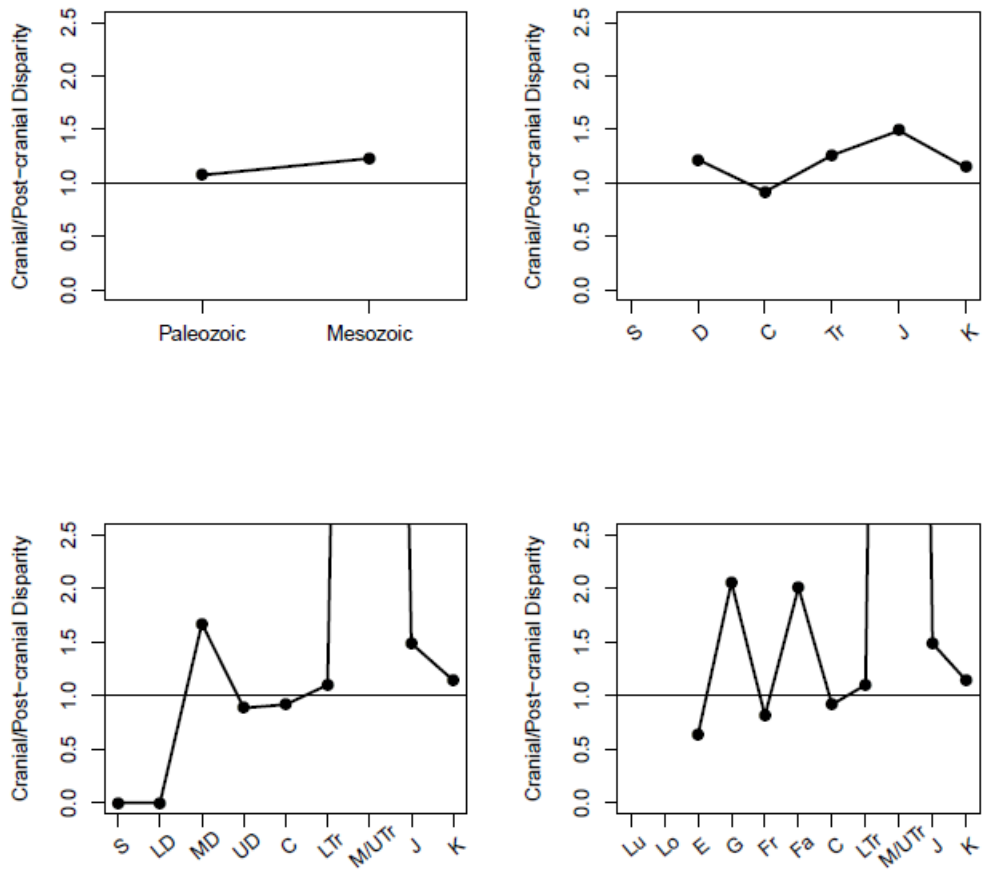


Fig. 5. Cranial:Post-cranial disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.

Carboniferous, and Middle/Upper Triassic. Cranial to post-cranial disparity peaks into the Middle and Upper Devonian (Givetian and Famennian) and into the earlier Mesozoic while decreasing into the Carboniferous and later Mesozoic. PC-reduced data show a similar pattern including a significant decrease in cranial disparity into the Carboniferous, an increase in post-cranial disparity into the Givetian, and Lower Triassic/Cretaceous cranial:post-cranial disparity about equal to one. We found that 20/45 cranial and 24/45 post-cranial coordinate data pairwise rate tests (Appendix H.1-2) for each of the 9 monophyletic groups used in this study were significant. However, only 8/45 cranial and 7/45 post-cranial PC-reduced data pairwise rate tests (Appendix H. 3-4) were significant. These results, however, are dependent on post-hoc error rate correction.

#### Analyses of evolutionary mode

Akaike weights revealed overwhelming support for BM for both cranial and post-cranial data (73.63% and 66.15% support, respectively). The rate parameter of the BM model was highest for the post-cranial data ( $.013 < .015$ ), both variances = 0. Cranial and post-cranial data had about equal EB support whereas OU support was disproportionate, post-cranial data had higher OU support (EB: 24.76% and 22.24%; OU: 1.61% and 11.61%). However, EB had a rate change parameter of zero and its rate parameter equaled the BM rate parameter, effectively making cranial and post-cranial BM model support 98.39% and 88.39%, respectively. Phylogenetic signal was insignificant for both coordinate and PC-reduced data ( $p > .05$ ).

#### Discussion

Our coordinate and PC-reduced data disparity plots (Fig. 5 and Appendix G.3) revealed largely the same pattern, however, the PC-reduced data had a much lower absolute cranial and post-cranial disparity showing that the differences between both analyses were due to the overall

decrease in raw disparity (sum of the diagonal elements of the group covariance matrix) resulting from PC reduction. Both datasets show a Givetian, Famennian, Middle/Upper Triassic and Jurassic increase in cranial/post-cranial trait diversification rates. Both datasets also show an Eifelian, Frasnian, and Carboniferous decrease or near equal rate of cranial/post-cranial trait diversification. Only the coordinate data plots suggest that the Lower Triassic and Cretaceous are both periods of high cranial/post-cranial diversification; however, our PC-reduced data suggests the opposite. All of the above disparity changes are significant with the exception of the Eifelian, Carboniferous, and the Cretaceous. However, the corresponding Middle and Upper Triassic cranial and post-cranial PC plots (Appendices E.13 and F.13) indicate that the high cranial/post-cranial trait diversification pattern seen in this time may only be an apparent increase; our dataset during the Middle and Upper Triassic included only coelacanths. We can confidently say that the Givetian, Famennian, Middle and Upper Triassic, and Jurassic were all periods of high cranial/post-cranial trait diversification while the Frasnian was a period of low cranial/post-cranial trait diversification. Cranial/post-cranial disparity rates are typically decoupled except during the Frasnian and Lower Triassic where cranial and post-cranial disparity both increase. The pairwise rate analyses between the coordinate data and the PC-reduced data show contradicting results. More pairwise tests were significant for the coordinate data, indicating differences in evolutionary rate between most lobe-fin groups. However, the PC-reduced data indicate that most lobe-fin groups have significantly similar rates of morphological evolution. Judging by the disparity and rate analyses, we argue that PC reduction systematically biases our interpretations of the tempo of lobe-fin evolution.

Our model-fitting analyses showed overwhelming support for BM (>88%) when model-fitting the first 5 and 4 cranial and post-cranial PCs, respectively. BM support may indicate



similar timing of evolution, may only reflect the relationship between little morphological change over a relatively long time scale (419 Ma, Appendices E-F), or may reflect the nature of many PCs with low variance (Tables 1-2) distributed throughout our tree, rather than few PCs with high variance distributed towards the root of our tree (PCs 1-2, Tables 1-2). A lack of EB support may be taken as evidence for an equal rate of cranial to post-cranial trait diversification. We observed more instances of significant high periods of cranial trait diversification throughout lobe-fin evolutionary history than the converse.

We have shown how PC reduction leads to apparent increases in post-cranial trait change as well as differences in between-group rates. Our interpretation of the model-fitting results is rendered dubious given our findings of how PCA biases our other results and despite >88% model support, BM might not be the true mode of lobe-fin evolution. The combined arbitrary use of X number of PCs and our current knowledge of PCs necessitates the development of new multivariate/multirate comparative methods. Problems with the current treatment of multivariate data using univariate model-fitting have recently been discussed in the literature (Uyeda et al. 2015). Uyeda et al. (2015) describes in detail how analyzing highly-multivariate data univariately essentially turns constant-rate multivariate BM data (analyzed univariately, unlike in this study) into data appearing to have evolved by an EB process.

We argue that lobe-fin cranial functional ecomorphological diversification precedes post-cranial ecomorphological diversification, in support of the ‘head-first’ model. In all of our analyses we used 5 cranial PCs and 4 post-cranial PCs, the 4 post-cranial PCs had a higher cumulative variance than the 5 cranial PCs, however, we still observed more instances of high cranial to post-cranial trait diversification. Our coordinate data supports high cranial/post-cranial diversification during the Givetian, Famennian, Lower Triassic and Jurassic. Our coordinate data

also suggests, as others have before (Cloutier, 1991; Lloyd et al. 2011) that each group of lobe-fin evolves at different rates while our PC-reduced data showed the opposite, implying that multi-rate macroevolutionary models would best fit our data. These results as well as the results of Uyeda et al. (2015) “highlight the need for truly multivariate [and multirate] phylogenetic comparative methods”. More data are needed to more accurately infer the phylogenetic signal of our data, the low ( $<1$ ) phylogenetic signal of our PC-reduced data approached  $p < .05$  significance. It is possible that limited sampling of randomly-resolved trees biased our results but this is unlikely given low species origination date ranges (standard deviation = 9.46 Ma). The limited sampling of species relative to the abundant diversity of early lobe-fins (Appendix A) may have also biased our results. However, we stress that our analysis includes most major groups of early lobe-fin (Bockmann et al. 2013) and that low taxonomic sampling is only apparent; most early lobe-fin species are lungfish or other coelacanths known exclusively from limited remains such as tooth plates or scales. In fact, given the general pattern of taxonomic diversity of lobe-fins in the fossil record (Sallan and Coates, 2010), we argue that our results are realistic due to the relatively low and then high diversity of coelacanth/lungfish to other lobe-fins during the Paleozoic and then into the Mesozoic. It is also possible that our phylogenetic signal, and to a lesser extent, disparity and rate analyses were subject to bias from statistical noise introduced from our landmark scheme, resulting in many PCs of low (1%) to moderate (5%) variation. However, here we rely exclusively on significant results to determine the order of skeletal diversification.

It has been suggested that high rates of cranial (jaw) evolution drove lobe-fin diversification, especially in the Emsian-Eifelian (Anderson et al. 2011; Anderson et al. 2013). Anderson et al (2011) performed an analysis which contained many groups of early jawed-fish to

infer an Emsian-Eifelian peak of cranial diversification followed by stasis. Friedman and Coates (2006) also suggests post-Devonian stasis in lobe-fin ecomorphology. However, here we show evidence for a later early lobe-fin peak of cranial diversification Eifelian-Givetian, followed by a second (Famennian), third (Lower Triassic) and fourth (Jurassic) peak rather than an Emsian-Eifelian peak followed by stasis. We presented evidence that the Frasnian was a period of low cranial/post-cranial diversification; however, both cranial and post-cranial traits were increasing at this time. Sallan and Coates (2010) found that only the end-Famennian/Devonian Hangenberg mass extinction (and not the end-Frasnian Kellwasser mass depletion) significantly changed early vertebrate compositions. Our evidence indicates that while the Kellwasser mass depletion was not associated with decreased rates of morphological evolution, the Hangenberg mass extinction was associated with significantly decreased rates of post-cranial evolution, implying extinction selectivity. It is clear that early aquatic and semi-aquatic lobe-fins have a long evolutionary history of ecomorphological diversification which may be explained by extinction selectivity and differences in between-group rates of evolution.

### **Conclusion**

In conclusion, current data show evidence for a ‘head-first’ pattern where cranial ecomorphological diversification precedes that of the post-cranial early and throughout the majority of aquatic and semi-aquatic lobe-fin evolution. The inclusion of more Mesozoic taxa has potential to change the observed pattern, however, we show evidence that the relative group diversities in this study are similar to previous estimates. These observations are similar to previous observations on the cranial diversification of lobe-fins and the effect of mass extinctions vs. mass depletions on trait diversification. We also discuss the systematic bias that PCA introduces into our evolutionary tempo and mode analyses and stress the need for new

multivariate, multirate phylogenetic comparative methods. It is possible that among these methods, a method of weighing PCs during comparative analyses will alleviate some PCA bias. Lastly, we emphasize the high amount of taxonomic and morphological disparity exhibited by these groups of early lobe-fins, particularly that of post-Devonian coelacanths and lungfish which are often overlooked due to the false assumption of them having very low diversity.

### **Future Directions**

Given the distinct patterns of ecomorphological change and methodological problems identified in this study, future goals of this project are to identify in detail how these patterns might differ over shorter time scales with much higher sampling (Devonian and Mesozoic) while using updated methodologies. A first step might be to identify why so few trees were able to be model-fitted, it is possible that failure to model-fit certain pairs of trees and data reflect a problem with the optimization code we used or a problem with our stratigraphic data. The Devonian has a wealth of other well-preserved lobe-fin taxa which were not sampled in this study that when studied in isolation, might reveal new, taxon-specific changes in morphospace. Likewise, more sampling is needed in the Mesozoic to qualify the patterns observed here as real changes in disparity, not just artifacts of limited sampling or methodology. The lobe-fin fossil record is filled with partial remains which might also help identify potential (preservational) bias in the results presented here. No papers have studied the relationship between taxonomic diversity and morphological disparity using modern comparative methods; doing so may further elucidate patterns of lobe-fin evolution and change preconceptions of lobe-fins as “low-disparity lineages” or “living fossils”. Methodologically, current studies are limited in their ability to fit macroevolutionary models to highly multivariate (coordinate) data. This may be achieved by transforming the PC variance of all PCs for all taxa, such that the structure of the sum of

pairwise Euclidean distances between species is maintained, relative to the coordinate data.

Although this may render individual PCs uninformative as traits, it will allow us to perform a PC reduction (possibly by using consecutive permutation tests to eliminate low variance PCs) while controlling for univariate PC bias described by Uyeda et al. (2015).

## **APPENDICES**

## APPENDIX A

### Appendix A. Aquatic and semi-aquatic lobe-fins identified in this study.

#	Genus	species	Citation
1	<i>Acanthostega</i>	<i>gumari</i>	Clack, 2002
2	<i>Acherontiscus</i>	<i>caledoniae</i>	Carroll, 1969; Carroll, 1998; Panchen, 1977
3	<i>Achoania</i>	<i>jarviki</i>	Zhu et al. 2001
4	<i>Adelargo</i>	<i>schultzei</i>	Johanson and Ritchie, 2000
5	<i>Adelogyrinus</i>	<i>simnorhynchus</i>	Brough and Brough, 1967
6	<i>Adelospondylus</i>	<i>watsoni</i>	
7	<i>Adololopas</i>	<i>moyasmithae</i>	Campbell and Barwick, 1998
8	<i>Allenkyperus</i>	<i>montanus</i>	Lund and Lund, 1984
9	<i>Alcoveria</i>	<i>brevis</i>	
10	<i>Amadeodipterus</i>	<i>kencampbelli</i>	Young and Schultze, 2005
11	<i>Ameghinoceratodus</i>	<i>iheringi</i>	Apestequia et al. 2007
12	<i>Andreyevichthys</i>	<i>epitomus</i>	
13	<i>Antlerpeton</i>	<i>clarkii</i>	Thomson, 1998
14	<i>Apateon</i>	<i>caducus</i>	Sanchez et al. 2010
15	<i>Apateon</i>	<i>gracilis</i>	
16	<i>Apateon</i>	<i>pedestris</i>	Sanchez et al. 2010
17	<i>Apatorhynchus</i>	<i>opistheretmus</i>	Friedman and Daeschler, 2006
18	<i>Aphelodus</i>	<i>anapes</i>	Kemp, 1993
19	<i>Archaeoceratodus</i>	<i>avus</i>	Kemp, 1997
20	<i>Archaeoceratodus</i>	<i>djelleh</i>	Kemp, 1997
21	<i>Archaeoceratodus</i>	<i>rowleyi</i>	Kemp, 1997
22	<i>Archaeoceratodus</i>	<i>theganus</i>	Kemp, 1997
23	<i>Archaeonectes</i>	<i>pertusus</i>	Marshall, 1986
24	<i>Archaeotylus</i>	<i>ignotus</i>	Marshall, 1986
25	<i>Archichthys</i>	<i>portlocki</i>	Jeffery, 2006
26	<i>Arganodus</i>	<i>arganensis</i>	Martin, 1979
27	<i>Arganodus</i>	<i>atlantis</i>	Marshall, 1986
28	<i>Arganodus</i>	<i>dorotheae</i>	Case, 1921
29	<i>Arganodus</i>	<i>multicristatus</i>	Vorobjeva and Minikh, 1968
30	<i>Arganodus</i>	<i>tiguidiensis</i>	Soto and Perea, 2010
31	<i>Ariguna</i>	<i>formosa</i>	Kemp, 1994
32	<i>Asiatoceratodus</i>	<i>atlantis</i>	Kemp, 1998
33	<i>Asiatoceratodus</i>	<i>sharovi</i>	Vorobyeva, 1967
34	<i>Asiatoceratodus</i>	<i>tiguidensis</i>	
35	<i>Atlantoceratodus</i>	<i>iheringi</i>	Cione et al. 2007
36	<i>Atlantoceratodus</i>	<i>patagonicus</i>	Agnoilin, 2010
37	<i>Axelia</i>	<i>elegans</i>	
38	<i>Axelia</i>	<i>robusta</i>	
39	<i>Axelrodichtys</i>	<i>araripensis</i>	Forey, 1998
40	<i>Axelrodichtys</i>	<i>maiseyi</i>	de Carvalho, 2013
41	<i>Aztecia</i>	<i>mahalae</i>	Johanson and Ahlberg, 2001
42	<i>Balanerpeton</i>	<i>woodi</i>	
43	<i>Baphedidae</i>		
44	<i>Baphetes</i>		
45	<i>Barameda</i>	<i>decipiens</i>	Long, 1989
46	<i>Barameda</i>	<i>mitchelli</i>	Holland et al. 2007
47	<i>Barwickia</i>	<i>downunda</i>	Long and Clement, 2009
48	<i>Beelarongia</i>		
49	<i>Belemnocerca</i>	<i>prolata</i>	Wendruff and Wilson, 2013
50	<i>Beltanodus</i>	<i>ambilobensis</i>	Marshall, 1986
51	<i>Bogdanovia</i>	<i>orientalis</i>	
52	<i>Branchiosaurus</i>		
53	<i>Bruenohopteron</i>	<i>murphyi</i>	Schultze and Reed, 2012
54	<i>Bunoderma</i>	<i>baini</i>	
55	<i>Bukkanodus</i>	<i>jesseni</i>	Johanson et al. 2007
56	<i>Cabonnichthys</i>	<i>burnsi</i>	Ahlberg and Johanson, 1997
57	<i>Caerorhachis</i>	<i>bairdi</i>	Ruta et al. 2007
58	<i>Callistiopterus</i>	<i>clappi</i>	
59	<i>Canningius</i>		

60	<i>Canowindra</i>	<i>grossi</i>		92	<i>Ceratodus</i>	<i>kaupi</i>	Marshall, 1986
61	<i>Caridosuctor</i>	<i>populosum</i>	Lund and Lund, 1984	93	<i>Ceratodus</i>	<i>latissimus</i>	
62	<i>Casineria</i>	<i>kiddi</i>		94	<i>Ceratodus</i>	<i>madagascariensis</i>	Marshall, 1986
63	<i>Cathlorhynchus</i>	<i>trismodipterus</i>		95	<i>Ceratodus</i>	<i>minor</i>	Marshall, 1986
64	<i>Cathlorhynchus</i>	<i>zengi</i>		96	<i>Ceratodus</i>	<i>multicristatus</i>	Marshall, 1986
65	<i>Ceratodus</i>	<i>africanus</i>	Soto and Perea, 2010	97	<i>Ceratodus</i>	<i>nageshwarai</i>	
66	<i>Ceratodus</i>	<i>altus</i>		98	<i>Ceratodus</i>	<i>nargun</i>	Marshall, 1986
67	<i>Ceratodus</i>	<i>arenaceus</i>		99	<i>Ceratodus</i>	<i>obtusum</i>	
68	<i>Ceratodus</i>	<i>arganensis</i>	Marshall, 1986	100	<i>Ceratodus</i>	<i>parvus</i>	
69	<i>Ceratodus</i>	<i>argentinus</i>	Apesteguia et al. 2007	101	<i>Ceratodus</i>	<i>pectinatus</i>	Marshall, 1986
70	<i>Ceratodus</i>	<i>avus</i>	Marshall, 1986	102	<i>Ceratodus</i>	<i>planasper</i>	
71	<i>Ceratodus</i>	<i>bovisrivi</i>		103	<i>Ceratodus</i>	<i>planus</i>	
72	<i>Ceratodus</i>	<i>concinus</i>	Marshall, 1986	104	<i>Ceratodus</i>	<i>priscus</i>	
73	<i>Ceratodus</i>	<i>cruciferus</i>		105	<i>Ceratodus</i>	<i>rectangularis</i>	
74	<i>Ceratodus</i>	<i>curvus</i>		106	<i>Ceratodus</i>	<i>robustus</i>	
75	<i>Ceratodus</i>	<i>daedaleus</i>		107	<i>Ceratodus</i>	<i>rucinatus</i>	
76	<i>Ceratodus</i>	<i>disauris</i>		108	<i>Ceratodus</i>	<i>sturii</i>	Kemp, 1998
77	<i>Ceratodus</i>	<i>dorotheae</i>	Marshall, 1986	109	<i>Ceratodus</i>	<i>tiguidensis</i>	Soto and Perea, 2010
78	<i>Ceratodus</i>	<i>donensis</i>		110	<i>Ceratodus</i>	<i>vinslovii</i>	
79	<i>Ceratodus</i>	<i>emarginatus</i>		111	<i>Ceratodus</i>	<i>wollastoni</i>	Marshall, 1986
80	<i>Ceratodus</i>	<i>felchi</i>		112	<i>Chagrinia</i>	<i>enodis</i>	Forey, 1998
81	<i>Ceratodus</i>	<i>formosus</i>		113	<i>Changxinia</i>	<i>aspratilis</i>	
82	<i>Ceratodus</i>	<i>frazieri</i>		114	<i>Chaoceratodus</i>	<i>portezuelensis</i>	Apesteguia et al. 2007
83	<i>Ceratodus</i>	<i>gibbus</i>		115	<i>Chinlea</i>	<i>sorenseni</i>	
84	<i>Ceratodus</i>	<i>guentheri</i>		116	<i>Chirodipterus</i>	<i>australis</i>	Miles, 1977
85	<i>Ceratodus</i>	<i>gustasoni</i>		117	<i>Chirodipterus</i>	<i>liangchengi</i>	Zhu, 2000
86	<i>Ceratodus</i>	<i>heshanggouensis</i>		118	<i>Chirodipterus</i>	<i>onaweyensis</i>	Marshall, 1986
87	<i>Ceratodus</i>	<i>heteromorphus</i>		119	<i>Chirodipterus</i>	<i>potteri</i>	
88	<i>Ceratodus</i>	<i>hieroglyphus</i>		120	<i>Chirodipterus</i>	<i>wildungensis</i>	Marshall, 1986
89	<i>Ceratodus</i>	<i>humei</i>	Marshall, 1986	121	<i>Chrysolepis</i>	<i>orlensis</i>	
90	<i>Ceratodus</i>	<i>hunterianus</i>		122	<i>Cladarosymblema</i>	<i>narrienense</i>	
91	<i>Ceratodus</i>	<i>kannemeyeri</i>		123	<i>Coccoderma</i>	<i>bavaricum</i>	



124	<i>Coccoderma</i>	<i>gigas</i>		156	<i>Ctenodus</i>	<i>ornattis</i>	
125	<i>Coccoderma</i>	<i>nudum</i>		157	<i>Ctenodus</i>	<i>quadratus</i>	
126	<i>Coccoderma</i>	<i>suevicum</i>	Forey, 1998	158	<i>Ctenodus</i>	<i>robertsoni</i>	Sharp and Clack, 2013
127	<i>Coelacanthopsis</i>	<i>curta</i>		159	<i>Ctenodus</i>	<i>romeri</i>	Sharp and Clack, 2013
128	<i>Coelacanthus</i>	<i>banffensis</i>		160	<i>Ctenodus</i>	<i>serratus</i>	
129	<i>Coelacanthus</i>	<i>elegans</i>	Moy-Thomas, 1935	161	<i>Ctenodus</i>	<i>wagneri</i>	
130	<i>Coelacanthus</i>	<i>granulatus</i>	Forey, 1991; Moy-Thomas and Westoll, 1935	162	<i>Delatitia</i>	<i>breviceps</i>	
131	<i>Coelacanthus</i>	<i>harlemensis</i>		163	<i>Deltaherpeton</i>	<i>hiemstrae</i>	Bolt and Lombard, 2010
132	<i>Coelacanthus</i>	<i>lunzensis</i>		164	<i>Dendrerpeton</i>		
133	<i>Coelacanthus</i>	<i>madagascariensis</i>	Moy-Thomas, 1935	165	<i>Densignathus</i>	<i>rowei</i>	Daeschler, 2000
134	<i>Coelacanthus</i>	<i>welleri</i>		166	<i>Devonosteus</i>	<i>proteus</i>	Marshall, 1986
135	<i>Colosteus</i>			167	<i>Diabolepis</i>	<i>speratus</i>	Campbell and Barwick, 2001
136	<i>Conchodus</i>	<i>elkneri</i>	Marshall, 1986	168	<i>Dictyonosteus</i>	<i>arcticus</i>	
137	<i>Conchodus</i>	<i>jeroffewi</i>	Marshall, 1986	169	<i>Diplocercides</i>	<i>davisi</i>	
138	<i>Conchodus</i>	<i>ostreaeformis</i>	Marshall, 1986	170	<i>Diplocercides</i>	<i>heiligenstockiensis</i>	
139	<i>Conchodus</i>	<i>parvulus</i>	Marshall, 1986	171	<i>Diplocercides</i>	<i>jaekeli</i>	
140	<i>Conchopoma</i>	<i>arctatum</i>	Marshall, 1986	172	<i>Diplocercides</i>	<i>kayseri</i>	
141	<i>Conchopoma</i>	<i>edesi</i>	Marshall, 1986	173	<i>Diplopterus</i>	<i>agassizi</i>	
142	<i>Conchopoma</i>	<i>exanthematicum</i>	Marshall, 1986	174	<i>Diplurus</i>	<i>longicaudatus</i>	
143	<i>Conchopoma</i>	<i>gadiforme</i>	Kuhn, 1967; Thomson, 1969	175	<i>Diplurus</i>	<i>newarki</i>	Shultze, 2004
144	<i>Crassigyrinus</i>	<i>scoticus</i>		176	<i>Dipnorhynchus</i>	<i>cathlesae</i>	
145	<i>Cryptolepis</i>	<i>grossi</i>		177	<i>Dipnorhynchus</i>	<i>kiandrensis</i>	Marshall, 1986
146	<i>Ctenodus</i>	<i>allodens</i>	Sharp and Clack, 2013	178	<i>Dipnorhynchus</i>	<i>lehmani</i>	Marshall, 1986
147	<i>Ctenodus</i>	<i>cristatus</i>	Sharp and Clack, 2013	179	<i>Dipnorhynchus</i>	<i>susmilchi</i>	Marshall, 1986
148	<i>Ctenodus</i>	<i>flabelliformis</i>		180	<i>Dipnotuberculus</i>	<i>gnathodus</i>	
149	<i>Ctenodus</i>	<i>interruptus</i>	Sharp and Clack, 2013	181	<i>Dipterus</i>	<i>calvini</i>	
150	<i>Ctenodus</i>	<i>levis</i>		182	<i>Dipterus</i>	<i>contraversus</i>	
151	<i>Ctenodus</i>	<i>minutus</i>		183	<i>Dipterus</i>	<i>crassus</i>	
152	<i>Ctenodus</i>	<i>murchisoni</i>	Sharp and Clack, 2013	184	<i>Dipterus</i>	<i>fourmarieri</i>	
153	<i>Ctenodus</i>	<i>nelsoni</i>		185	<i>Dipterus</i>	<i>johnsoni</i>	
154	<i>Ctenodus</i>	<i>obioenais</i>		186	<i>Dipterus</i>	<i>macropterus</i>	
155	<i>Ctenodus</i>	<i>onbliquus</i>		187	<i>Dipterus</i>	<i>marginalis</i>	

188	<i>Dipterus</i>	<i>microsoma</i>	Marshall, 1986	220	<i>Eusthenodon</i>	<i>wangsjoii</i>	Clement, 2002
189	<i>Dipterus</i>	<i>mordax</i>		221	<i>Eusthenopteron</i>	<i>farloviensis</i>	
190	<i>Dipterus</i>	<i>murchisoni</i>		222	<i>Eusthenopteron</i>	<i>foordi</i>	Thomson, 1969
191	<i>Dipterus</i>	<i>nelsoni</i>	Marshall, 1986	223	<i>Eusthenopteron</i>	<i>kurshi</i>	Zupins, 2008
192	<i>Dipterus</i>	<i>oervigi</i>	Marshall, 1986	224	<i>Eusthenopteron</i>	<i>obruchevi</i>	
193	<i>Dipterus</i>	<i>radiatus</i>		225	<i>Eusthenopteron</i>	<i>savesoderberghi</i>	
194	<i>Dipterus</i>	<i>sherwoodi</i>		226	<i>Eusthenopteron</i>	<i>traquairi</i>	
195	<i>Dipterus</i>	<i>uddeni</i>		227	<i>Ferganoceratodus</i>	<i>jurassicus</i>	
196	<i>Dipterus</i>	<i>valenciennesi</i>	Ahlberg and Trewin, 1995; Moy-Thomas, 1939	228	<i>Ferganoceratodus</i>	<i>martini</i>	Cavin et al. 2007
197	<i>Dobrogeria</i>	<i>aegyssensis</i>		229	<i>Fleurantia</i>	<i>denticulata</i>	Ahlberg and Trewin, 1995
198	<i>Doleserpeton</i>			230	<i>Ganorhynchus</i>	<i>caucasius</i>	Marshall, 1986
199	<i>Dolichopareias</i>	<i>disjectus</i>	Brough and Brough, 1967	231	<i>Ganorhynchus</i>	<i>rigauxi</i>	
200	<i>Dongshanodus</i>	<i>qujingensis</i>	Marshall, 1986	232	<i>Ganorhynchus</i>	<i>splendens</i>	Marshall, 1986
201	<i>Doragnathus</i>	<i>woodi</i>		233	<i>Garnbergia</i>	<i>ommata</i>	
202	<i>Duffichthys</i>	<i>mirabilis</i>		234	<i>Gavinia</i>		
203	<i>Ectosteorhachis</i>	<i>nitidus</i>		235	<i>Gephyrostegus</i>		
204	<i>Edenopteron</i>	<i>keithcrooki</i>	Young et al. 2013	236	<i>Geptolepis</i>	<i>donensis</i>	
205	<i>Eldeceon</i>	<i>rolfei</i>		237	<i>Glyptolepis</i>	<i>baltica</i>	
206	<i>Elginerpeton</i>	<i>pancheni</i>	Ahlberg, 1995; Ahlberg et al. 2005	238	<i>Glyptolepis</i>	<i>dellei</i>	
207	<i>Elpistostege</i>	<i>watsoni</i>		239	<i>Glyptolepis</i>	<i>groenlandica</i>	
208	<i>Eoactinistia</i>	<i>foreyi</i>	Johanson et al. 2006	240	<i>Glyptolepis</i>	<i>leptopterus</i>	
209	<i>Eoetenodus</i>	<i>microsoma</i>		241	<i>Glyptolepis</i>	<i>paucidens</i>	Forey, 1998
210	<i>Eoherpeton</i>	<i>watsoni</i>		242	<i>Glyptopomus</i>	<i>bystrowi</i>	
211	<i>Epiceratodus</i>	<i>forsteri</i>		243	<i>Glyptopomus</i>	<i>elginensis</i>	
212	<i>Equinoxiodus</i>	<i>alcantarensis</i>	Toledo et al. 2011	244	<i>Glyptopomus</i>	<i>kinnairdi</i>	Thomson, 1969
213	<i>Erikiia</i>	<i>janvieri</i>		245	<i>Glyptopomus</i>	<i>minor</i>	
214	<i>Erikiia</i>	<i>jarviki</i>	Zhu, 2000	246	<i>Glyptopomus</i>	<i>sayerei</i>	
215	<i>Esconichthys</i>	<i>apopyris</i>		247	<i>Gnathorhiza</i>	<i>bothrotreta</i>	Marshall, 1986
216	<i>Eucritta</i>	<i>melanolimnetes</i>	Clack, 2001	248	<i>Gnathorhiza</i>	<i>dikeloda</i>	Marshall, 1986
217	<i>Euporosteus</i>	<i>eifelianus</i>		249	<i>Gnathorhiza</i>	<i>noblensis</i>	Marshall, 1986
218	<i>Euporosteus</i>	<i>yunnanensis</i>	Zhu et al. 2012	250	<i>Gnathorhiza</i>	<i>pusillus</i>	Marshall, 1986
219	<i>Eusthenodon</i>	<i>gavini</i>	Johanson and Ritchie, 2000	251	<i>Gnathorhiza</i>	<i>serrata</i>	Marshall, 1986

252	<i>Gogodipterus</i>	<i>paddyensis</i>	Marshall, 1986	284	<i>Holodipterus</i>	<i>meemannae</i>	Clement, 2009; Pridmore et al. 1991
253	<i>Gogonasmus</i>	<i>andrewsae</i>	Holland and Long, 2009	285	<i>Holodipterus</i>	<i>elderae</i>	
254	<i>Gooloogongia</i>	<i>loomesi</i>	Johanson and Ahlberg, 2001	286	<i>Holodipterus</i>	<i>gogoensis</i>	Marshall, 1986
255	<i>Gosfordia</i>	<i>truncata</i>	Kemp, 1994	287	<i>Holodipterus</i>	<i>longi</i>	
256	<i>Graphiurichthys</i>	<i>callopterus</i>		288	<i>Holophagus</i>	<i>striolaris</i>	
257	<i>Greererpeton</i>	<i>burkemorani</i>		289	<i>Holopterygius</i>	<i>nudus</i>	Friedman and Coates, 2006
258	<i>Greiserolepis</i>	<i>minusensis</i>		290	<i>Holoptychius</i>	<i>americanus</i>	
259	<i>Greiserolepis</i>	<i>tulensis</i>		291	<i>Holoptychius</i>	<i>bergmanni</i>	Downs et al. 2013
260	<i>Grenfellia</i>	<i>meemannae</i>	Johanson and Ritchie, 2000	292	<i>Holoptychius</i>	<i>decoratus</i>	
261	<i>Griphognathus</i>	<i>minutidens</i>	Marshall, 1986	293	<i>Holoptychius</i>	<i>flemingi</i>	Berg, 1947; Moy-Thomas, 1939
262	<i>Griphognathus</i>	<i>sculpta</i>	Marshall, 1986	294	<i>Holoptychius</i>	<i>giganteus</i>	Schultze and Chorn, 1998
263	<i>Griphognathus</i>	<i>whitei</i>	Ahlberg et al. 2001	295	<i>Holoptychius</i>	<i>granulatus</i>	
264	<i>Grossipterus</i>	<i>crassus</i>	Marshall, 1986	296	<i>Holoptychius</i>	<i>hallii</i>	
265	<i>Grossius</i>			297	<i>Holoptychius</i>	<i>jarviki</i>	Cloutier, 1996
266	<i>Guiyu</i>	<i>oneiros</i>	Zhu et al. 2012	298	<i>Holoptychius</i>	<i>murchisoni</i>	
267	<i>Guizhoucoelacanthus</i>			299	<i>Holoptychius</i>	<i>nobilissimus</i>	
268	<i>Gyroptychius</i>	<i>agassizi</i>	Moy-Thomas, 1939	300	<i>Holoptychius</i>	<i>pustulosus</i>	
269	<i>Gyroptychius</i>	<i>antarcticus</i>		301	<i>Holoptychius</i>	<i>quebecensis</i>	
270	<i>Gyroptychius</i>	<i>dolichotatus</i>		302	<i>Holoptychius</i>	<i>radiatus</i>	
271	<i>Gyroptychius</i>	<i>elgae</i>		303	<i>Holoptychius</i>	<i>scheii</i>	
272	<i>Gyroptychius</i>	<i>greenlandicus</i>		304	<i>Holoptychius</i>	<i>tuberculatus</i>	Newman, 1890
273	<i>Gyroptychius</i>	<i>pauli</i>		305	<i>Hongkongichthys</i>	<i>youngi</i>	Zhu, 2000
274	<i>Hadronector</i>	<i>donbairdi</i>	Lund and Lund, 1984	306	<i>Howidipterus</i>	<i>donnae</i>	Clement, 2009; Long and Clement, 2009
275	<i>Hainbergia</i>	<i>granulata</i>		307	<i>Howittichthys</i>	<i>warrenae</i>	Long and Holland, 2008
276	<i>Hamodus</i>	<i>lutkevitchi</i>		308	<i>Hyneria</i>	<i>lindae</i>	
277	<i>Harajicadipterus</i>	<i>youngi</i>	Clement, 2009	309	<i>Hynerpeton</i>	<i>basseti</i>	Daeschler, 2000
278	<i>Heddeleichthys</i>	<i>dalgliesiensis</i>	Snitting, 2009; Schultze and Reed, 2012	310	<i>Ichnomylax</i>	<i>karatajae</i>	Reisz et al. 2004
279	<i>Heimenia</i>	<i>ensis</i>	Mondejar-Fernandez and Clement, 2012	311	<i>Ichnomylax</i>	<i>kurnai</i>	Long et al. 1994
280	<i>Heliodus</i>	<i>lesleyi</i>	Marshall, 1986	312	<i>Ichnorhynchus</i>	<i>kurnai</i>	
281	<i>Heptanema</i>	<i>paradoxum</i>		313	<i>Ichthyostega</i>	<i>eigili</i>	Ahlberg and Clack, 1998
282	<i>Holodipterus</i>	<i>kiprijanowe</i>	Marshall, 1986	314	<i>Ichthyostega</i>	<i>kochi</i>	Ahlberg and Clack, 1998
283	<i>Holodipterus</i>	<i>sanctacrucensis</i>	Marshall, 1986	315	<i>Ichthyostega</i>	<i>stensioei</i>	Clack and Neinger, 2000

316	<i>Ichthyostega</i>	<i>watsoni</i>	Ahlberg and Clack, 1998	348	<i>Letognathus</i>	<i>hardingi</i>	Brazeau, 2005
317	<i>Indocoelacanthus</i>	<i>robustus</i>	Jain, 1974	349	<i>Libys</i>	<i>polypterus</i>	
318	<i>Iowadipterus</i>	<i>halli</i>	Campbell and Barwick, 1998	350	<i>Libys</i>	<i>superbus</i>	
319	<i>Iranorhynchus</i>	<i>seyedemamii</i>	Marshall, 1986	351	<i>Ligulalepis</i>		
320	<i>Jakubsonia</i>	<i>livnensis</i>		352	<i>Litoptychius</i>	<i>bryanti</i>	Coates and Friedman, 2010
321	<i>Jarvikia</i>	<i>arctica</i>	Marshall, 1986	353	<i>Livoniana</i>	<i>multidentata</i>	Ahlberg et al. 2000
322	<i>Jarvikia</i>	<i>lebedevi</i>		354	<i>Lochmocercus</i>	<i>aciculodontus</i>	Lund and Lund, 1984
323	<i>Jarvikina</i>	<i>wenjukowi</i>	Schultze and Reed, 2012; Vorobjeva, 1977	355	<i>Lohsania</i>	<i>utahensis</i>	
324	<i>Jessenia</i>			356	<i>Loxomma</i>		
325	<i>Kenichthys</i>	<i>campbelli</i>	Zhu and Ahlberg, 2004	357	<i>Lualabaea</i>	<i>henryi</i>	
326	<i>Koharalepis</i>	<i>jarviki</i>		358	<i>Lualabaea</i>	<i>lerichei</i>	
327	<i>Kyrinion</i>			359	<i>Luckeus</i>	<i>abudda</i>	Young and Schultze, 2005
328	<i>Laccognathus</i>	<i>embryi</i>	Downs et al. 2011	360	<i>Luopingcoelacanthus</i>	<i>eurylacrimalis</i>	Wen et al. 2013
329	<i>Laccognathus</i>	<i>grossi</i>		361	<i>Macropoma</i>	<i>lewesiensis</i>	Forey, 1998
330	<i>Laccognathus</i>	<i>panderi</i>		362	<i>Macropoma</i>	<i>mantelli</i>	Thomson, 1969
331	<i>Lamprotolepis</i>	<i>fradkini</i>		363	<i>Macropoma</i>	<i>praecursor</i>	
332	<i>Lamprotolepis</i>	<i>verrucosa</i>		364	<i>Macropoma</i>	<i>willemoesii</i>	Lambers, 1996
333	<i>Langdenia</i>	<i>campylognatha</i>	Wang et al. 2010	365	<i>Macropoma</i>	<i>speciosum</i>	
334	<i>Langlieria</i>	<i>socqueti</i>	Clement et al. 2009	366	<i>Macropomoides</i>	<i>orientalis</i>	Forey, 1991
335	<i>Latimeria</i>	<i>chalumnae</i>	Thomson, 1969	367	<i>Mahalalepis</i>	<i>resima</i>	
336	<i>Latimeria</i>	<i>menadoensis</i>		368	<i>Mandageria</i>	<i>fairfaxi</i>	Johanson and Ahlberg, 1997
337	<i>Latvius</i>	<i>grewingki</i>		369	<i>Marsdenichthys</i>	<i>longioccipitus</i>	Holland et al. 2010
338	<i>Latvius</i>	<i>niger</i>		370	<i>Mawsonia</i>	<i>gigas</i>	
339	<i>Latvius</i>	<i>obrutus</i>		371	<i>Mawsonia</i>	<i>lavocati</i>	
340	<i>Latvius</i>	<i>porosus</i>		372	<i>Mawsonia</i>	<i>libyca</i>	
341	<i>Laugia</i>	<i>groenlandica</i>	Forey, 1998; Thomson, 1969	373	<i>Mawsonia</i>	<i>tegamensis</i>	
342	<i>Lavocatodus</i>	<i>casieri</i>		374	<i>Mawsonia</i>	<i>ubangiensis</i>	
343	<i>Lavocatodus</i>	<i>giganteus</i>		375	<i>Medoevia</i>	<i>lata</i>	
344	<i>Lavocatodus</i>	<i>humei</i>		376	<i>Meemania</i>	<i>eos</i>	Zhu et al. 2010
345	<i>Lavocatodus</i>	<i>protopteroides</i>		377	<i>Megadonichthys</i>	<i>kurikae</i>	
346	<i>Lepidosiren</i>	<i>paradoxa</i>	Thomson, 1969	378	<i>Megalichthys</i>	<i>hibberti</i>	
347	<i>Lethiscus</i>	<i>stocki</i>		379	<i>Megalichthys</i>	<i>laticeps</i>	

380	<i>Megalocephalus</i>			412	<i>Nesides</i>	<i>schmidti</i>	Berg, 1947
381	<i>Megalocoelacanthus</i>	<i>dobiei</i>	Dutel et al. 2012	413	<i>Nigerpeton</i>		
382	<i>Megapleuron</i>	<i>rochei</i>	Marshall, 1986	414	<i>Nilsenia</i>	<i>nordica</i>	Marshall, 1986
383	<i>Megapleuron</i>	<i>zangerli</i>	Marshall, 1986	415	<i>Notorhizodon</i>	<i>mackelveyi</i>	
384	<i>Megapomus</i>			416	<i>Obruchevichthys</i>	<i>gracilis</i>	
385	<i>Megistolepis</i>	<i>klementzi</i>		417	<i>Occidens</i>	<i>portlocki</i>	
386	<i>Melanognathus</i>	<i>canadensis</i>	Marshall, 1986	418	<i>Oervigia</i>	<i>nordica</i>	Marshall, 1986
387	<i>Metaceratodus</i>	<i>kaopen</i>	Cione and Gouiric-Cavalli, 2012	419	<i>Onychodus</i>	<i>firouzi</i>	
388	<i>Metaceratodus</i>	<i>wichmanni</i>	Cione and Gouiric-Cavalli, 2012	420	<i>Onychodus</i>	<i>hopkinsi</i>	
389	<i>Metaceratodus</i>	<i>wollastoni</i>	Apestequia et al. 2007	421	<i>Onychodus</i>	<i>jaekeli</i>	
390	<i>Metaxygnathus</i>	<i>denticulus</i>		422	<i>Onychodus</i>	<i>jandemarrai</i>	Andrews et al. 2005
391	<i>Microceratodus</i>	<i>angolensis</i>	Antunes et al. 1990	423	<i>Onychodus</i>	<i>sigmoides</i>	
392	<i>Microsaur</i>	<i>sp.</i>		424	<i>Onychodus</i>	<i>yassensis</i>	
393	<i>Miguashaia</i>	<i>bureaui</i>	Cloutier, 1996	425	<i>Ophiderpeton</i>	<i>nanum</i>	
394	<i>Miguashaia</i>	<i>grossi</i>	Forey et al. 2000	426	<i>Orlovichthys</i>	<i>limnatus</i>	
395	<i>Mioceratodus</i>	<i>anemosyrus</i>	Kemp, 1998; Kemp, 1997	427	<i>Ossinodus</i>	<i>pueri</i>	Warren, 2007
396	<i>Mioceratodus</i>	<i>diaphorus</i>	Kemp, 1997	428	<i>Osteolepis</i>	<i>macrolepidotus</i>	Berg, 1947; Thomson, 1969
397	<i>Mioceratodus</i>	<i>gregoryi</i>	Kemp, 1998; Kemp, 1997	429	<i>Osteolepis</i>	<i>microlepidotus</i>	Moy-Thomas, 1939
398	<i>Mioceratodus</i>	<i>poastrus</i>	Kemp, 1997	430	<i>Osteolepis</i>	<i>panderi</i>	Thomson, 1969
399	<i>Moenkopia</i>	<i>wellesi</i>	Schaeffer and Gregory, 1965	431	<i>Osteoplax</i>	<i>erosa</i>	
400	<i>Monongahela</i>	<i>dunkardensis</i>	Marshall, 1986	432	<i>Osteopleurus</i>	<i>milleri</i>	
401	<i>Monongahela</i>	<i>stenodonta</i>	Marshall, 1986	433	<i>Osteopleurus</i>	<i>newarki</i>	
402	<i>Muranjilepis</i>	<i>winterensis</i>	Young and Schultze, 2005	434	<i>Owensia</i>	<i>chooi</i>	Holland, 2009
403	<i>Mylacanthus</i>	<i>lobatus</i>		435	<i>Palaedaphus</i>	<i>abeli</i>	
404	<i>Mylacanthus</i>	<i>spinosus</i>		436	<i>Palaedaphus</i>	<i>devoniensis</i>	
405	<i>Namatozodia</i>	<i>pitikanta</i>	Kemp, 1993	437	<i>Palaedaphus</i>	<i>ferquensis</i>	
406	<i>Nasogalukus</i>	<i>chorni</i>	Schultze, 2000	438	<i>Palaedaphus</i>	<i>insignis</i>	Marshall, 1986
407	<i>Neoceratodus</i>	<i>eyrensis</i>	Kemp, 1997	439	<i>Palaedaphus</i>	<i>livenensis</i>	Marshall, 1986
408	<i>Neoceratodus</i>	<i>forsteri</i>	Thomson, 1969	440	<i>Palaeomolgophis</i>	<i>scoticus</i>	Brough and Brough, 1967
409	<i>Neoceratodus</i>	<i>nargun</i>	Kemp, 1997	441	<i>Palatinichthys</i>	<i>laticeps</i>	Witzmann and Schoch, 2012
410	<i>Neoceratodus</i>	<i>palmeri</i>		442	<i>Paleolophus</i>	<i>yunnanensis</i>	
411	<i>Nesides</i>	<i>heiligenstockiensis</i>		443	<i>Panderichthys</i>	<i>rhombolepis</i>	

444	<i>Papposaurus</i>	<i>traquari</i>		476	<i>Protopterus</i>	<i>amphibius</i>	
445	<i>Paraceratodus</i>	<i>germaini</i>	Schultze, 2004	477	<i>Protopterus</i>	<i>annectens</i>	Thomson, 1969
446	<i>Paraglyptolepis</i>	<i>karkiensis</i>		478	<i>Protopterus</i>	<i>crassidens</i>	
447	<i>Parapanderichthys</i>	<i>stolbovi</i>		479	<i>Protopterus</i>	<i>dolloi</i>	
448	<i>Parasagenodus</i>	<i>sibiricus</i>	Marshall, 1986	480	<i>Protopterus</i>	<i>elongus</i>	
449	<i>Parnaibaia</i>	<i>maranhaoensis</i>	Yabumoto, 2008	481	<i>Protopterus</i>	<i>lybicus</i>	
450	<i>Pederpes</i>	<i>finneyae</i>	Clack and Finney, 2005	482	<i>Protopterus</i>	<i>nigeriensis</i>	
451	<i>Pentlandia</i>	<i>macroptera</i>	Moy-Thomas, 1939	483	<i>Protopterus</i>	<i>polli</i>	
452	<i>Pentlandia</i>	<i>macropterus</i>		484	<i>Protopterus</i>	<i>protopteroideus</i>	Marshall, 1986
453	<i>Phaneropleuron</i>	<i>andersoni</i>	Moy-Thomas, 1939; Ahlberg and Trewin, 1995	485	<i>Protopterus</i>	<i>regulatus</i>	
454	<i>Phaneropleuron</i>	<i>elegans</i>		486	<i>Psarolepis</i>	<i>romeri</i>	Yu et al. 1998
455	<i>Pholidogaster</i>			487	<i>Pseudosauripterus</i>	<i>anglicus</i>	
456	<i>Pilliarhynchus</i>	<i>longi</i>		488	<i>Ptychoceratodus</i>	<i>acutus</i>	
457	<i>Pinnalongus</i>	<i>saxoni</i>		489	<i>Ptychoceratodus</i>	<i>concinus</i>	
458	<i>Piveteauia</i>	<i>madagascariensis</i>	Thomson, 1969	490	<i>Ptychoceratodus</i>	<i>donensis</i>	Marshall, 1986
459	<i>Platycephalichthys</i>	<i>bischofi</i>		491	<i>Ptychoceratodus</i>	<i>guentheri</i>	
460	<i>Platycephalichthys</i>	<i>rohoni</i>		492	<i>Ptychoceratodus</i>	<i>hislopianus</i>	Marshall, 1986
461	<i>Platycephalichthys</i>	<i>skuensis</i>		493	<i>Ptychoceratodus</i>	<i>iheringi</i>	
462	<i>Platyethmoidia</i>	<i>antarctica</i>		494	<i>Ptychoceratodus</i>	<i>ornatus</i>	
463	<i>Polyosteorhynchus</i>	<i>beargulchensis</i>		495	<i>Ptychoceratodus</i>	<i>pattinsonae</i>	
464	<i>Polyosteorhynchus</i>	<i>simplex</i>	Lund and Lund, 1984	496	<i>Ptychoceratodus</i>	<i>phillipsi</i>	Kemp, 1996
465	<i>Polyplocodus</i>	<i>leptognathus</i>		497	<i>Ptychoceratodus</i>	<i>rectangulatus</i>	Marshall, 1986
466	<i>Porolepis</i>	<i>brevis</i>		498	<i>Ptychoceratodus</i>	<i>serratus</i>	Kemp, 1998; Marshall, 1986
467	<i>Porolepis</i>	<i>foxi</i>	Johanson et al. 2013	499	<i>Ptychoceratodus</i>	<i>szechuanensis</i>	Marshall, 1986
468	<i>Porolepis</i>	<i>posnaniensis</i>		500	<i>Ptychoceratodus</i>	<i>virapa</i>	
469	<i>Porolepis</i>	<i>uralensis</i>		501	<i>Pycnacanthus</i>	<i>fischeri</i>	
470	<i>Potamoceratodus</i>	<i>guentheri</i>	Pardo et al. 2010	502	<i>Pycnoctenion</i>	<i>jacuticus</i>	
471	<i>Powichthys</i>	<i>spitsbergensis</i>		503	<i>Pycnoctenion</i>	<i>siberiacus</i>	
472	<i>Proceratodus</i>	<i>carlinvillensis</i>	Marshall, 1986	504	<i>Qingmenodus</i>	<i>yui</i>	Lu and Zhu, 2010
473	<i>Proceratodus</i>	<i>wagneri</i>		505	<i>Quebecius</i>	<i>quebecensis</i>	Cloutier, 1996
474	<i>Proterogyrinus</i>			506	<i>Rebellatrix</i>	<i>divaricerca</i>	Wendruff and Wilson, 2012
475	<i>Protopterus</i>	<i>aethiopicus</i>		507	<i>Reidus</i>	<i>hilli</i>	Graf, 2012

508	<i>Remigolepis</i>			540	<i>Sagenodus</i>	<i>inaequalis</i>	Marshall, 1986
509	<i>Retodus</i>	<i>tuberculatus</i>		541	<i>Sagenodus</i>	<i>periprion</i>	
510	<i>Rhabdoderma</i>	<i>aegyptiaca</i>		542	<i>Sagenodus</i>	<i>quadratus</i>	
511	<i>Rhabdoderma</i>	<i>aldengeri</i>		543	<i>Sagenodus</i>	<i>quinquecostatus</i>	
512	<i>Rhabdoderma</i>	<i>ardrossense</i>		544	<i>Sagenodus</i>	<i>serratus</i>	
513	<i>Rhabdoderma</i>	<i>cometi</i>		545	<i>Sagenodus</i>	<i>vinslovii</i>	
514	<i>Rhabdoderma</i>	<i>davisi</i>		546	<i>Sassenia</i>	<i>groenlandica</i>	Forey, 1998
515	<i>Rhabdoderma</i>	<i>elegans</i>	Thomson, 1969	547	<i>Sassenia</i>	<i>tuberculata</i>	
516	<i>Rhabdoderma</i>	<i>exiguum</i>		548	<i>Sauripterus</i>	<i>anglicus</i>	
517	<i>Rhabdoderma</i>	<i>huxleyi (dumfregia)</i>		549	<i>Sauripterus</i>	<i>taylori</i>	Davis et al. 2004
518	<i>Rhabdoderma</i>	<i>madagascariensis</i>		550	<i>Scaumenacia</i>	<i>curta</i>	Ahlberg and Trewin, 1995
519	<i>Rhabdoderma</i>	<i>phillipsi</i>		551	<i>Scleracanthus</i>	<i>asper</i>	
520	<i>Rhabdoderma</i>	<i>stensioei</i>		552	<i>Screbinodus</i>	<i>ornatus</i>	Jeffery, 2012
521	<i>Rhabdoderma</i>	<i>tingleyense</i>		553	<i>Sengoerichthys</i>	<i>ottomani</i>	Janvier et al. 2007
522	<i>Rhabdoderma?</i>	<i>abdenense</i>	Forey and Young, 1985	554	<i>Shoshonia</i>	<i>arctopteryx</i>	Friedman et al. 2007
523	<i>Rhabdoderma?</i>	<i>corrugatum</i>		555	<i>Sigournea</i>	<i>multidentata</i>	Bolt and Lombard, 2006
524	<i>Rhabdoderma?</i>	<i>granulostriatum</i>		556	<i>Silvanerpeton</i>	<i>miripedes</i>	Ruta and Clack, 2006
525	<i>Rhinodipterus</i>	<i>kimberleyensis</i>	Clement, 2012	557	<i>Sinocoelacanthus</i>	<i>fengshanensis</i>	
526	<i>Rhinodipterus</i>	<i>secans</i>	Marshall, 1986	558	<i>Sinodipterus</i>	<i>beibei</i>	Qiao and Zhu, 2009
527	<i>Rhinodipterus</i>	<i>ulrichi</i>	Marshall, 1986	559	<i>Sinostega</i>	<i>pani</i>	Zhu et al. 2002
528	<i>Rhipis</i>	<i>moorseli</i>		560	<i>Soederberghia</i>	<i>groenlandica</i>	Friedman, 2007
529	<i>Rhipis</i>	<i>tuberculata</i>		561	<i>Soederberghia</i>	<i>simpsoni</i>	Ahlberg et al. 2001
530	<i>Rhizodopsis</i>	<i>minor</i>		562	<i>Sorbitohynchus</i>	<i>deleaskitus</i>	Zhu, 2000
531	<i>Rhizodopsis</i>	<i>sauroides</i>		563	<i>Spathicephalus</i>	<i>mirus</i>	
532	<i>Rhizodopsis</i>	<i>savinkovi</i>		564	<i>Speonesydrium</i>	<i>iani</i>	Campbell and Barwick, 2007
533	<i>Rhizodus</i>	<i>anceps</i>		565	<i>Spermatodus</i>	<i>pustulosus</i>	
534	<i>Rhizodus</i>	<i>hibberti</i>		566	<i>Spodichthys</i>	<i>buetleri</i>	Snitting, 2008
535	<i>Rhynchodipterus</i>	<i>elginensis</i>	Berg, 1947; Ahlberg et al. 2001	567	<i>Sterropterygion</i>	<i>brandei</i>	
536	<i>Ribbo</i>	<i>sp.</i>		568	<i>Sterropterygion</i>	<i>markovskiyi</i>	
537	<i>Robinsondipterus</i>	<i>longi</i>	Long, 2010	569	<i>Stomiahykus</i>	<i>thlaodus</i>	Marshall, 1986
538	<i>Sagenodus</i>	<i>barrandei</i>		570	<i>Straitonia</i>	<i>waterstoni</i>	Marshall, 1986
539	<i>Sagenodus</i>	<i>copeanus</i>		571	<i>Strepsodus</i>	<i>arenosus</i>	Jeffery, 2006

572	<i>Strepsodus</i>	<i>brockbanki</i>	Jeffery, 2006	604	<i>Tungsenia</i>	<i>paradoxa</i>	Lu et al. 2012
573	<i>Strepsodus</i>	<i>dawsoni</i>	Jeffery, 2006	605	<i>Undina</i>	<i>barroviensis</i>	
574	<i>Strepsodus</i>	<i>hardingi</i>		606	<i>Undina</i>	<i>cirinensis</i>	
575	<i>Strepsodus</i>	<i>sauroides</i>	Jeffery, 2006	607	<i>Undina</i>	<i>gulo</i>	Forey, 1998
576	<i>Strunius</i>	<i>rolandi</i>	Ginter, 2001	608	<i>Undina</i>	<i>penicillata</i>	
577	<i>Strunius</i>	<i>walteri</i>	Andrews, 1973; Thomson, 1969	609	<i>Undina</i>	<i>purbeckensis</i>	
578	<i>Styloichthys</i>	<i>changae</i>	Zhu and Yu, 2002	610	<i>Uranolophus</i>	<i>wyomingensis</i>	Marshall, 1986
579	<i>Sunwapta</i>	<i>grandiceps</i>	Marshall, 1986	611	<i>Uronemus</i>	<i>lobatus</i>	Thomson, 1969
580	<i>Swenzia</i>	<i>latimerae</i>	Clement, 2005	612	<i>Uronemus</i>	<i>splendens</i>	Marshall, 1986
581	<i>Synaptoptylus</i>	<i>newelli</i>		613	<i>Utaherpeton</i>	<i>franklini</i>	
582	<i>Synthetodus</i>	<i>calvinus</i>		614	<i>Uzunbulaklepis</i>	<i>obruchevi</i>	
583	<i>Synthetodus</i>	<i>trisulcatus</i>	Marshall, 1986	615	<i>Ventalepis</i>	<i>ketleriensis</i>	
584	<i>Syphonodus</i>	<i>panderi</i>		616	<i>Ventastega</i>	<i>curonica</i>	Ahlberg et al. 2008
585	<i>Taeniolepis</i>	<i>trautschodi</i>		617	<i>Viluichthys</i>	<i>fradkini</i>	
586	<i>Tarachomyxax</i>	<i>oepiki</i>		618	<i>Viluichthys</i>	<i>verrucosa</i>	
587	<i>Tellerodus</i>	<i>sturii</i>	Marshall, 1986	619	<i>Vorobjevaia</i>	<i>dolodon</i>	
588	<i>Thaumatolepis</i>	<i>edelsteini</i>		620	<i>Westlothiana</i>	<i>lizae</i>	
589	<i>Thursius</i>	<i>estonicus</i>		621	<i>Westollrhynchus</i>	<i>lehmani</i>	
590	<i>Thursius</i>	<i>fischeri</i>		622	<i>Whatcheeria</i>	<i>deltae</i>	
591	<i>Thursius</i>	<i>macrolepidotus</i>	Thomson, 1969	623	<i>Whiteia</i>	<i>africanus</i>	
592	<i>Thursius</i>	<i>minor</i>		624	<i>Whiteia</i>	<i>groenlandica</i>	
593	<i>Thursius</i>	<i>moythomasi</i>	Thomson, 1969	625	<i>Whiteia</i>	<i>nielseni</i>	
594	<i>Thursius</i>	<i>pholidotus</i>	Moy-Thomas, 1939; Thomson, 1969	626	<i>Whiteia</i>	<i>tuberculata</i>	
595	<i>Thursius</i>	<i>talsiensis</i>		627	<i>Whiteia</i>	<i>woodwardi</i>	Forey, 1998
596	<i>Thursius</i>	<i>wudingensis</i>	Zhu, 2000	628	<i>Wimania</i>	<i>multistriata</i>	
597	<i>Thysanolepis</i>	<i>micans</i>		629	<i>Wimania</i>	<i>sinuosa</i>	
598	<i>Ticinepomis</i>	<i>peyeri</i>	Forey, 1998	630	<i>Xeradipterus</i>	<i>hatcheri</i>	Clement and Long, 2010
599	<i>Tiktaalik</i>	<i>roseae</i>	Shubin et al. 2014	631	<i>Yambira</i>	<i>thompsoni</i>	Johanson and Ritchie, 2000
600	<i>Tinirau</i>	<i>clackae</i>	Swartz, 2012	632	<i>Ymeria</i>	<i>denticulata</i>	Clack et al. 2012
601	<i>Tranodis</i>	<i>castrensis</i>	Marshall, 1986	633	<i>Youngichthys</i>	<i>xinhuanensis</i>	
602	<i>Tristichopterus</i>	<i>alatus</i>	Moy-Thomas, 1939	634	<i>Youngolepis</i>	<i>praecursor</i>	Thanh et al. 1995
603	<i>Tulerpeton</i>	<i>curtum</i>		635	<i>Yunnancoelacanthus</i>	<i>acrotuberculatus</i>	Wen et al. 2013



## APPENDIX B

Appendix B. List of species used in analyses. Data includes 57 species in 49 genera. Cranial and Post-cranial headers indicate whether species represent a genus in the respective subset. Lower and Upper are the boundaries of the earliest date of appearance of a genus in Mya.

<b>Genus</b>	<b>species</b>	<b>Cranial</b>	<b>Post-cranial</b>	<b>Lower</b>	<b>Upper</b>
<i>Allenkypterus</i>	<i>montanus</i>	1	1	323	323
<i>Ariguna</i>	<i>formosa</i>	1	1	252.17	247.2
<i>Asiatoceratodus</i>	<i>atlantis</i>	1	0	252.17	247.2
	<i>sharovi</i>	0	1		
<i>Axelrodichtys</i>	<i>araripensis</i>	1	1	113	100.5
<i>Cabonnichthys</i>	<i>burnsi</i>	1	1	372.2	358.9
<i>Caridosuctor</i>	<i>populosum</i>	1	1	330.9	323.2
<i>Coelacanthus</i>	<i>granulatus</i>	1	1	358.9	298.9
	<i>madagascariensis</i>	1	0		
<i>Conchopoma</i>	<i>gadiforme</i>	1	1	323.2	298.9
<i>Diplurus</i>	<i>newarki</i>	1	1	237	201.3
<i>Dipterus</i>	<i>valenciennesi</i>	1	1	419.2	410.8
<i>Eusthenopteron</i>	<i>foordi</i>	1	1	384	382.7
	<i>kurshi</i>	1	0		
<i>Fleurantia</i>	<i>denticulata</i>	1	1	382.7	372.2
<i>Gooloogongia</i>	<i>loomesi</i>	1	1	372.2	358.9
<i>Griphognathus</i>	<i>sculpta</i>	0	1	382.7	372.2
	<i>whitei</i>	1	0		
<i>Guiyu</i>	<i>oneiros</i>	1	1	425.6	423
<i>Gyroptychius</i>	<i>agassizi</i>	1	1	393.3	387.7
<i>Hadronector</i>	<i>donbairdi</i>	1	1	330.9	323.2
<i>Heddleichthys</i>	<i>dalgliesiensis</i>	1	1	372.2	358.9
<i>Heimania</i>	<i>ensis</i>	1	1	387.7	382.7
<i>Holophagus</i>	<i>striolaris</i>	1	1	157.3	152.1
<i>Holopterygius</i>	<i>nudus</i>	1	1	382.7	372.2
<i>Holoptychius</i>	<i>flemingi</i>	1	1	393.3	387.7
	<i>jarviki</i>	1	1		
<i>Latimeria</i>	<i>chalumnae</i>	1	1	163.5	157.3
<i>Laugia</i>	<i>groenlandica</i>	1	1	252.17	247.2
<i>Lochmocercus</i>	<i>aciculodontus</i>	1	1	331	323
<i>Luopingcoelacanthus</i>	<i>eurylacrimalis</i>	1	1	247.2	237
<i>Macropoma</i>	<i>lewesiensis</i>	1	1	157.3	152.1
	<i>mantelli</i>	1	1		
	<i>praecursor</i>	1	0		

	<i>speciosum</i>	1	1		
<i>Macropomoides</i>	<i>orientalis</i>	1	1	100.5	93.9
<i>Mandageria</i>	<i>fairfaxi</i>	1	1	372	359
<i>Microceratodus</i>	<i>angolensis</i>	1	1	252.17	247.2
<i>Miguashaia</i>	<i>bureaui</i>	1	1	387.8	382.7
<i>Neoceratodus</i>	<i>forsteri</i>	1	1	113	100.5
<i>Osteolepis</i>	<i>macrolepidotus</i>	1	1	393.3	387.7
	<i>microlepidotus</i>	1	1		
	<i>panderi</i>	0	1		
<i>Paraceratodus</i>	<i>germaini</i>	1	1	252.17	247.2
<i>Parnaibaia</i>	<i>maranhaoensis</i>	1	1	164	145
<i>Pentlandia</i>	<i>macroptera</i>	0	1	387.3	384.99
	<i>macropterus</i>	1	1		
<i>Polyosteorhynchus</i>	<i>simplex</i>	1	1	331	323
<i>Protopterus</i>	<i>annectens</i>	1	1	99.6	93.5
<i>Quebecius</i>	<i>quebecensis</i>	1	1	382.7	372.2
<i>Rhabdoderma</i>	<i>elegans</i>	1	1	358.9	346.7
	<i>madagascariensis</i>	1	1		
<i>Rhinodipterus</i>	<i>kimberleyensis</i>	1	1	387.7	382.7
<i>Rhynchodipterus</i>	<i>elginensis</i>	1	1	372	359
<i>Scaumenacia</i>	<i>curta</i>	1	1	382.7	372.2
<i>Strunius</i>	<i>walteri</i>	1	1	387.7	382.7
<i>Thursius</i>	<i>macrolepidotus</i>	0	1	393.3	387.7
	<i>moythomasi</i>	0	1		
	<i>pholidotus</i>	1	1		
<i>Tinirau</i>	<i>clackae</i>	1	1	393.3	387.7
<i>Tristichopterus</i>	<i>alatus</i>	1	1	387.7	382.7
<i>Undina</i>	<i>gulo</i>	1	1	157.3	152.1
	<i>penicillata</i>	0	1		
<i>Whiteia</i>	<i>woodwardi</i>	1	1	252.17	247.2

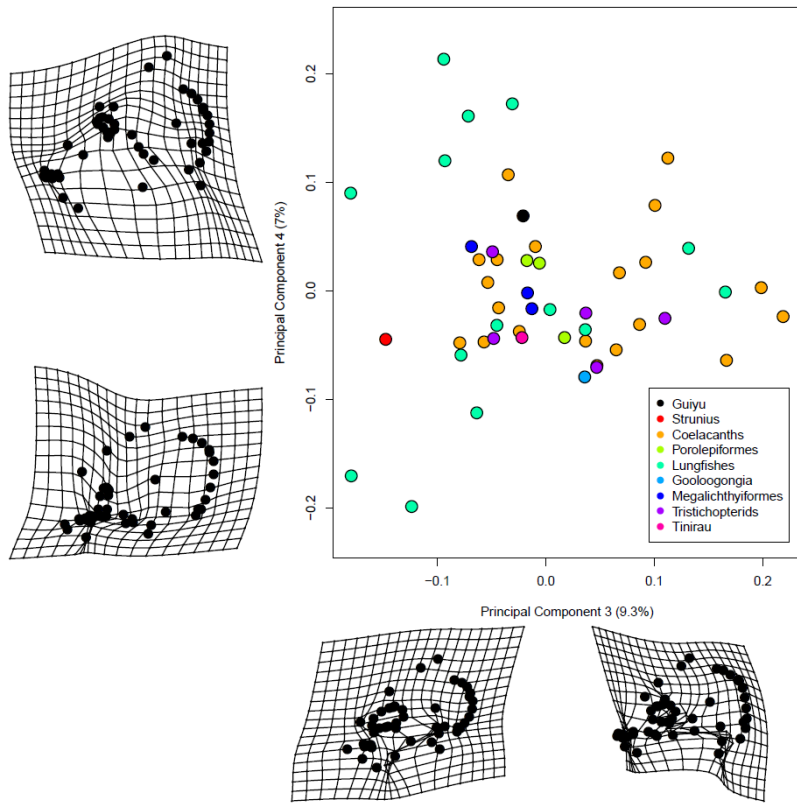
## APPENDIX C

Appendix C. List of cranial and post-cranial landmarks. Cranial landmarks 16-17 were positioned along the orbit. Cranial landmarks 18-21 were positioned midway along the dorsal-ventral axis of the (sub)operculum. All post-cranial “base” (semi)landmarks were positioned clockwise starting at the dorsal end of the cranial skeleton (left lateral view), the pectoral fin was also coded in this way as if it were rotated clockwise to fit along the body outline. Lungfish cranial landmarks: 3 of the dorsal-most and posterior-most skull bones in lungfish were used as functional parietal, postparietal, and extrascapular homologs sometimes including the “E”, “AB”, and the supratemporal bones. Lungfish post-cranial landmarks: the second dorsal fin functional homolog is known to start along the same dorso-ventral axis as the pectoral fin. We assumed the end of the second dorsal fin and the end of the anal fin (start and end of caudal fin, respectively) is positioned along the same dorsal-ventral axis halfway between the start of the ventral fin and end of the caudal fin lobe.

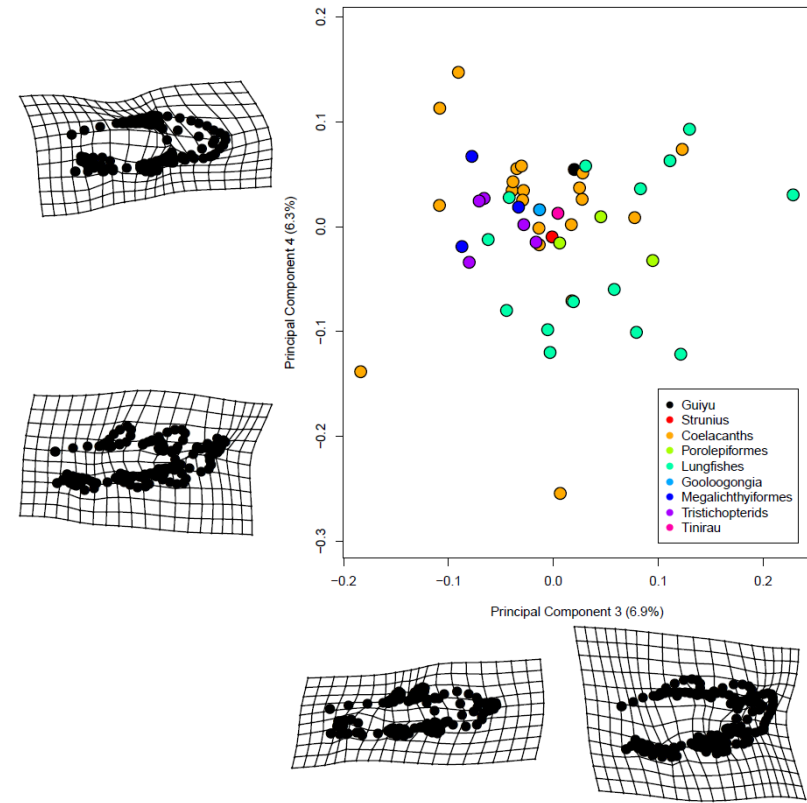
Landmark	Position
1	Antero-dorsal tip of premaxilla
2	Antero-ventral tip of premaxilla
3	Postero-dorsal tip of premaxilla
4	Postero-dorsal tip of premaxilla
5	Antero-dorsal tip of maxilla
6	Antero-ventral tip of maxilla
7	Postero-dorsal tip of maxilla
8	Postero-dorsal tip of maxilla
9	Antero-ventral tip of upper jaw
10	Anterior edge of parietal
11	Posterior edge of parietal
12	Anterior edge of extrascapular
13	Posterior edge of extrascapular
14	Antero-ventral tip of lacrimal
15	Postero-ventral tip of jugal
16	Dorsal lacrimal-jugal joint
17	Dorso-orbital tip of postorbital
18	Anterior operculum
19	Posterior operculum
20	Anterior suboperculum
21	Posterior suboperculum
22	Anterior tip of dentary
23	Dorsal-most tip of dentary-angular joint
24	Coronoid
25	Posterior-most tip of angular
26	Posterior-most tip of submandibular elements
27	Anterior-most tip of submandibular elements
28-37	Semilandmarks surrounding orbit
38-47	Semilandmarks along opercular opening
1	Postero-dorsal tip of cranial skeleton
2-3	Base of first dorsal fin lobe
4-5	Base of first dorsal fin

6-7	Base of second dorsal fin lobe
8-9	Base of second dorsal fin
10-11	Base of caudal fin lobe
12-13	Base of caudal fin
14-15	Base of anal fin lobe
16-17	Base of anal fin
18-19	Base of pelvic fin lobe
20-21	Base of pelvic fin
22-23	Base of pectoral fin lobe
24-25	Base of pectoral fin lobe
26	Postero-ventral tip of cranial skeleton
27-36	Semilandmarks along first dorsal fin lobe edge
37-46	Semilandmarks along first dorsal fin edge
47-56	Semilandmarks along second dorsal fin lobe edge
57-66	Semilandmarks along second dorsal fin edge
67-76	Semilandmarks along caudal fin lobe edge
77-96	Semilandmarks along caudal fin edge
97-106	Semilandmarks along anal fin lobe edge
107-116	Semilandmarks along anal fin edge
117-126	Semilandmarks along pelvic fin lobe edge
127-136	Semilandmarks along pelvic fin edge
137-146	Semilandmarks along pectoral fin lobe edge
147-156	Semilandmarks along pectoral fin edge
157-176	Semilandmarks along body passing through all lobe bases

## APPENDIX D

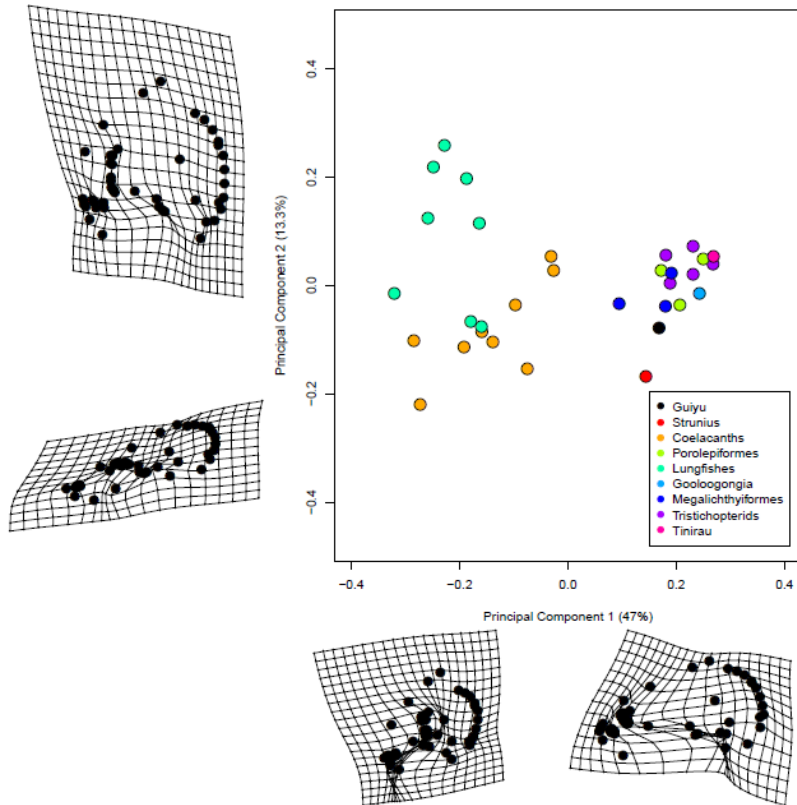


Appendix D.1. PC3 and PC4 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

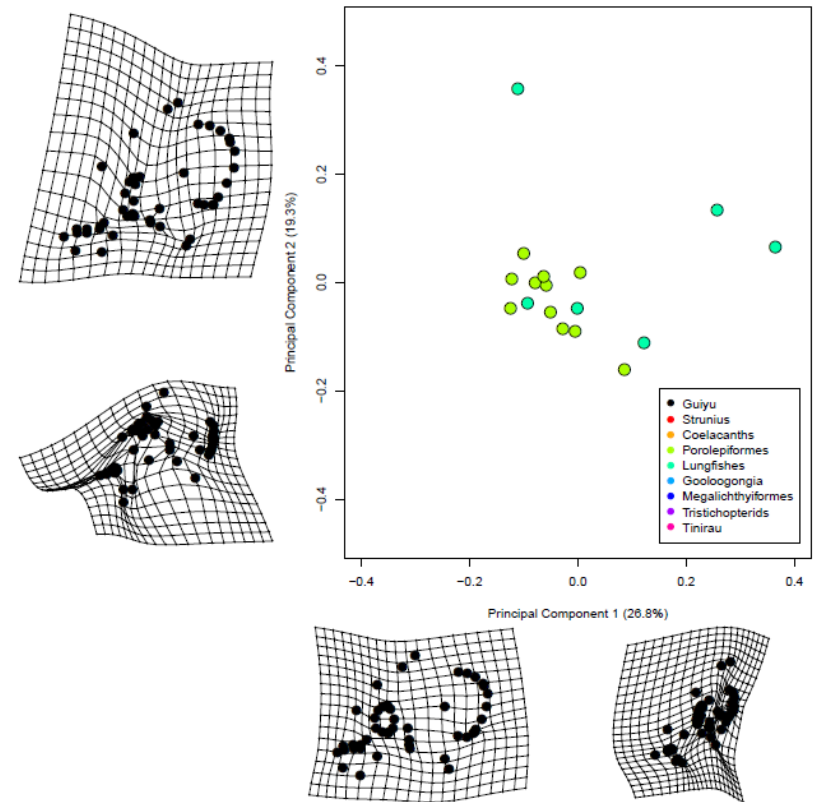


Appendix D.2. PC3 and PC4 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

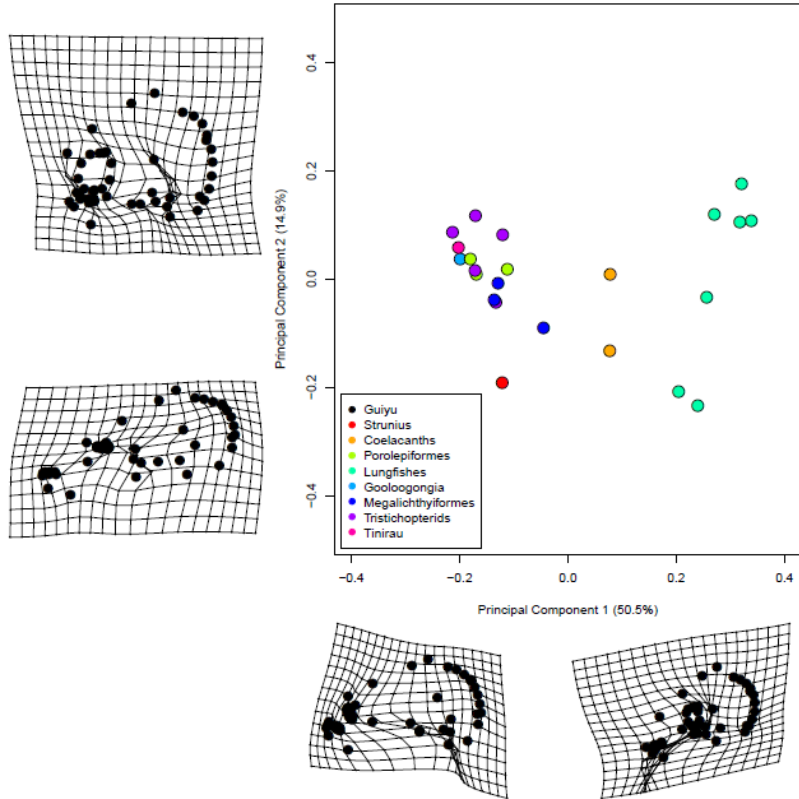
## APPENDIX E



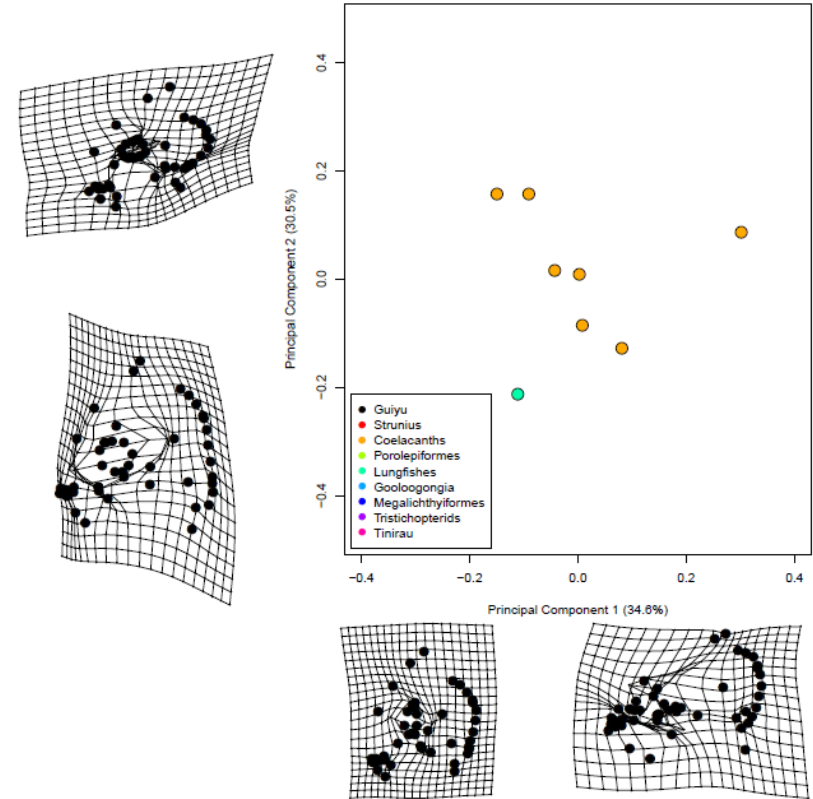
Appendix E.1. Paleozoic (Era-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



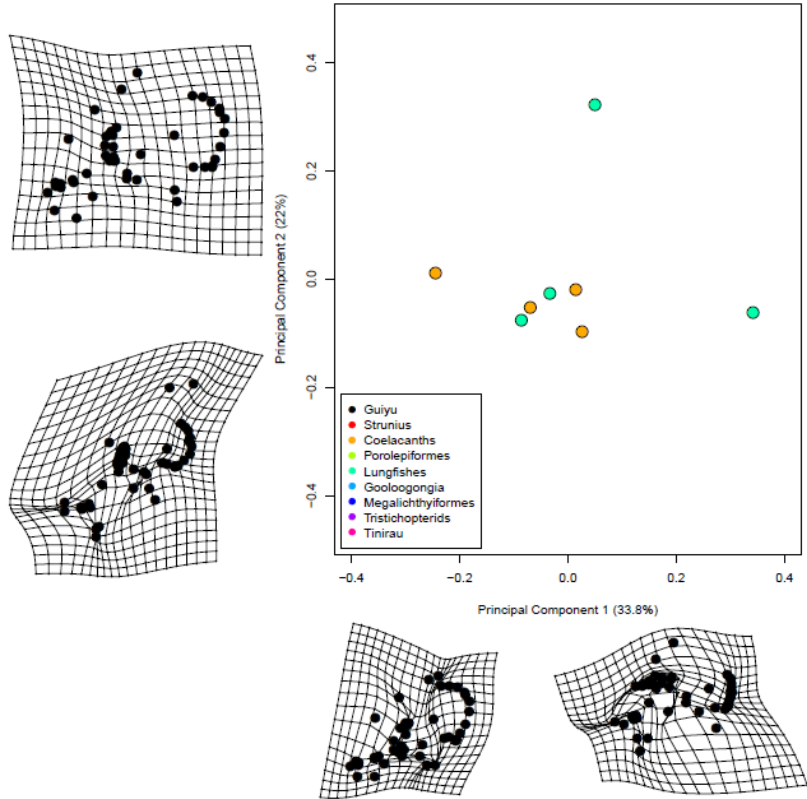
Appendix E.2. Mesozoic (Era-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



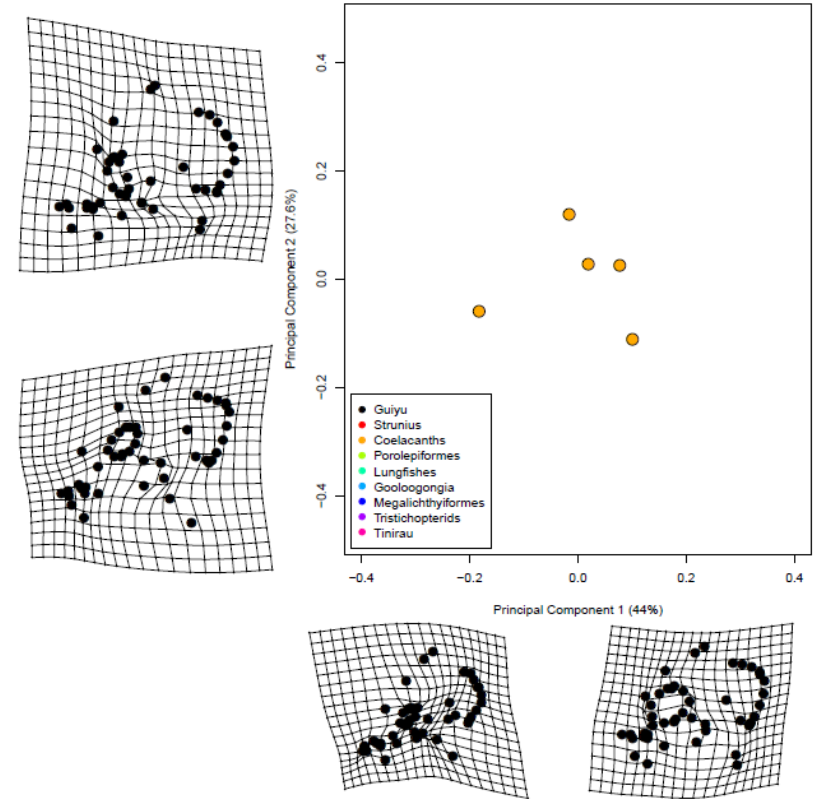
Appendix E.3. Devonian (Period-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



Appendix E.4. Carboniferous (Period-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

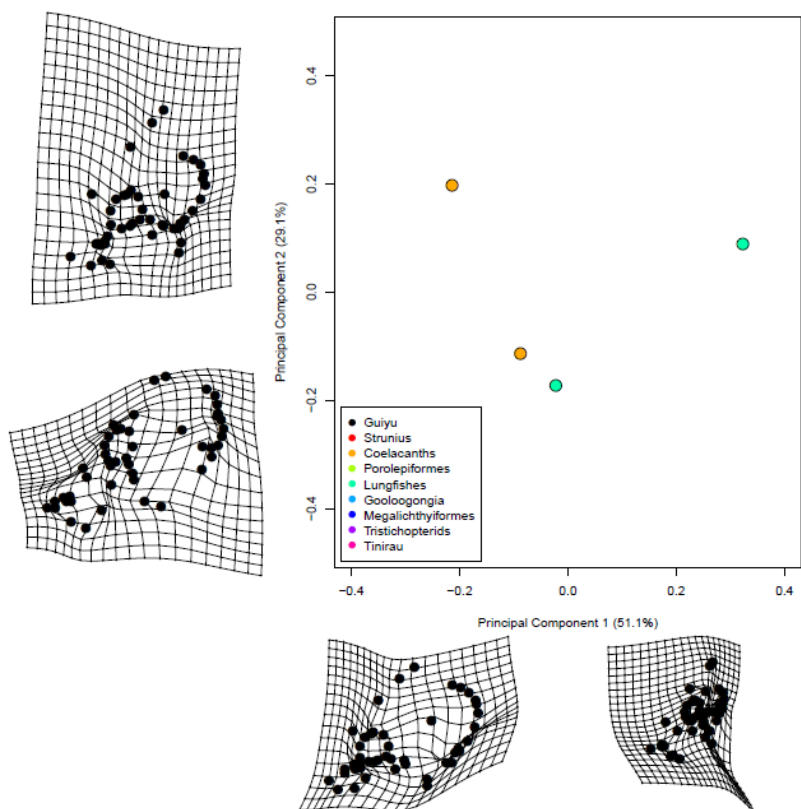


Appendix E.5. Triassic (Period-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

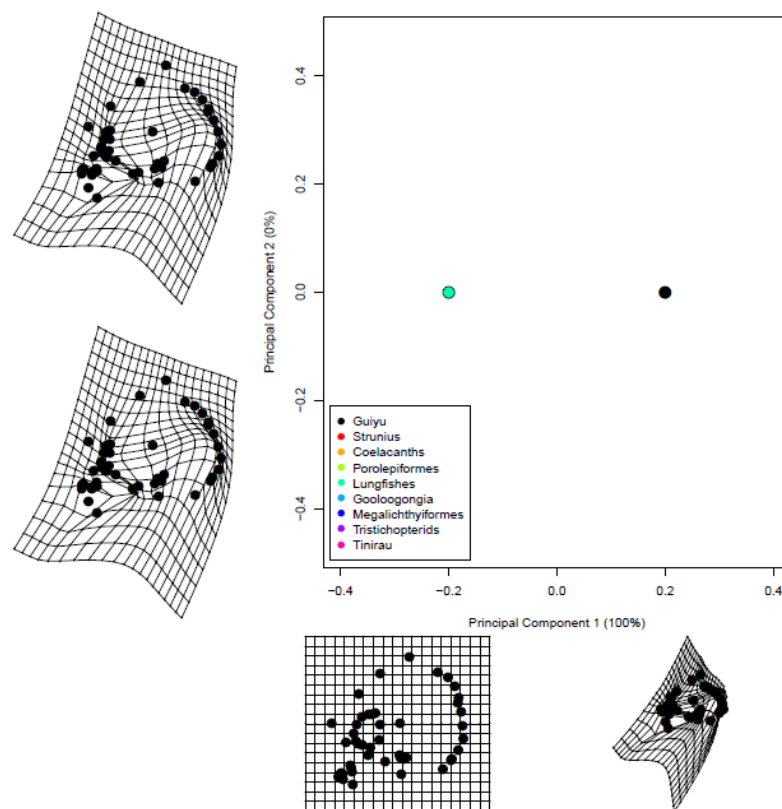


Appendix E.6. Jurassic (Period-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

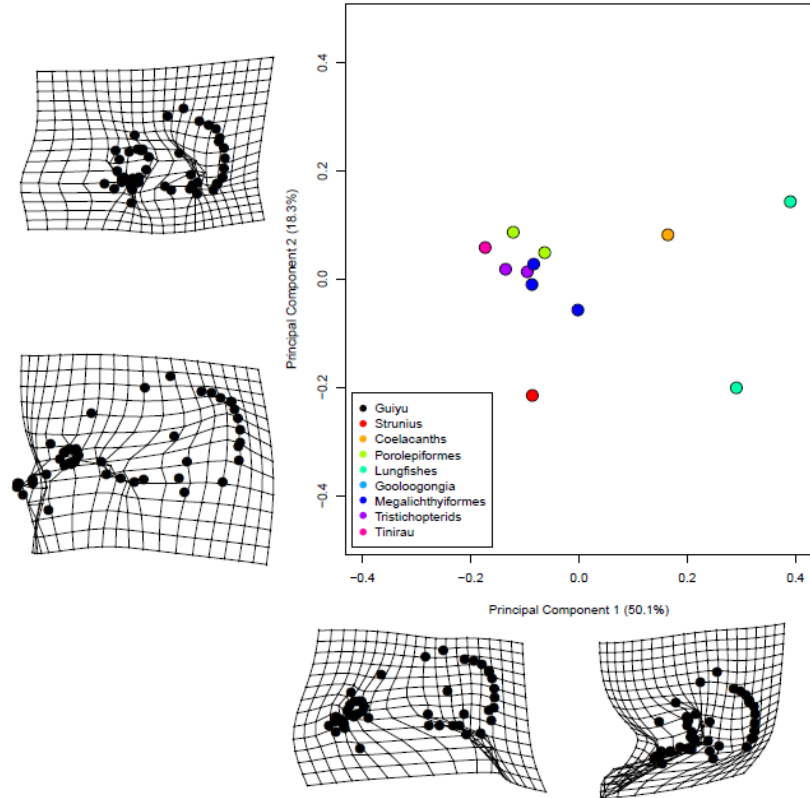




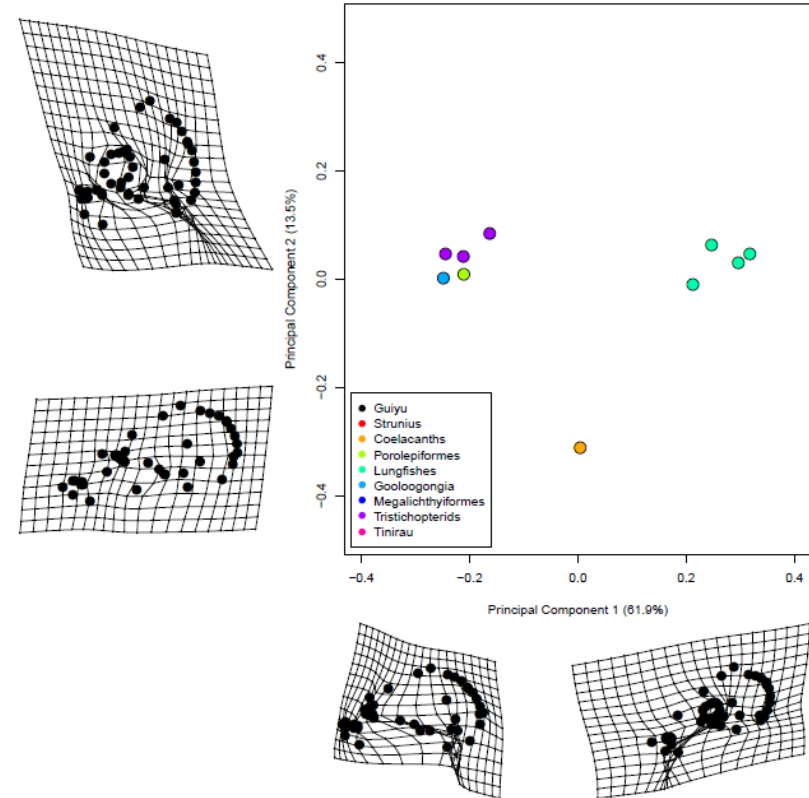
Appendix E.7. Cretaceous (Period-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



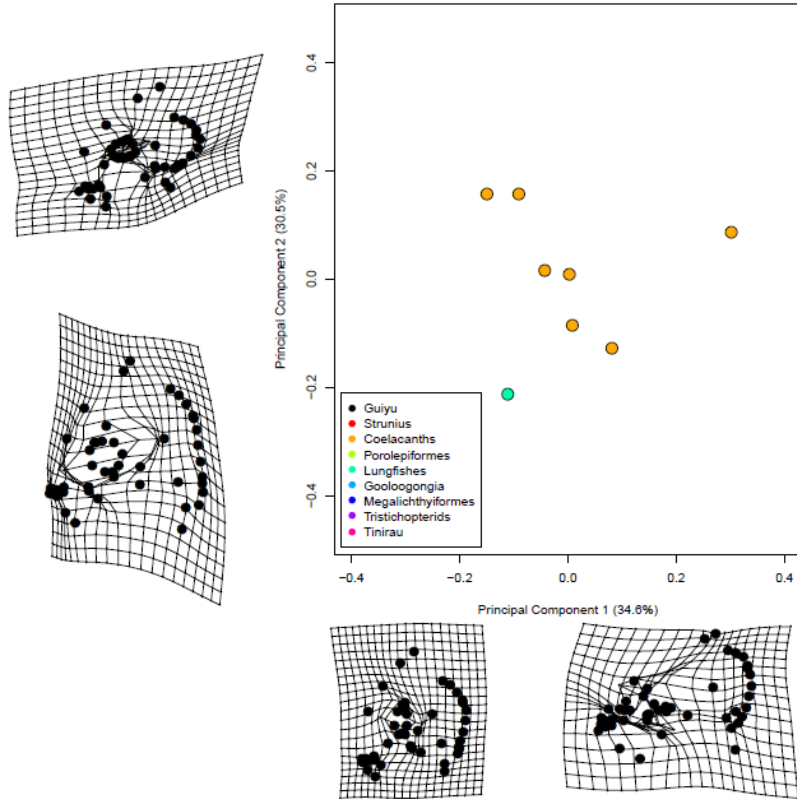
Appendix E.8. Lower Devonian (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC. Guiyu (Silurian) was added to this time scale to visualize an early lobe-fin morphospaces.



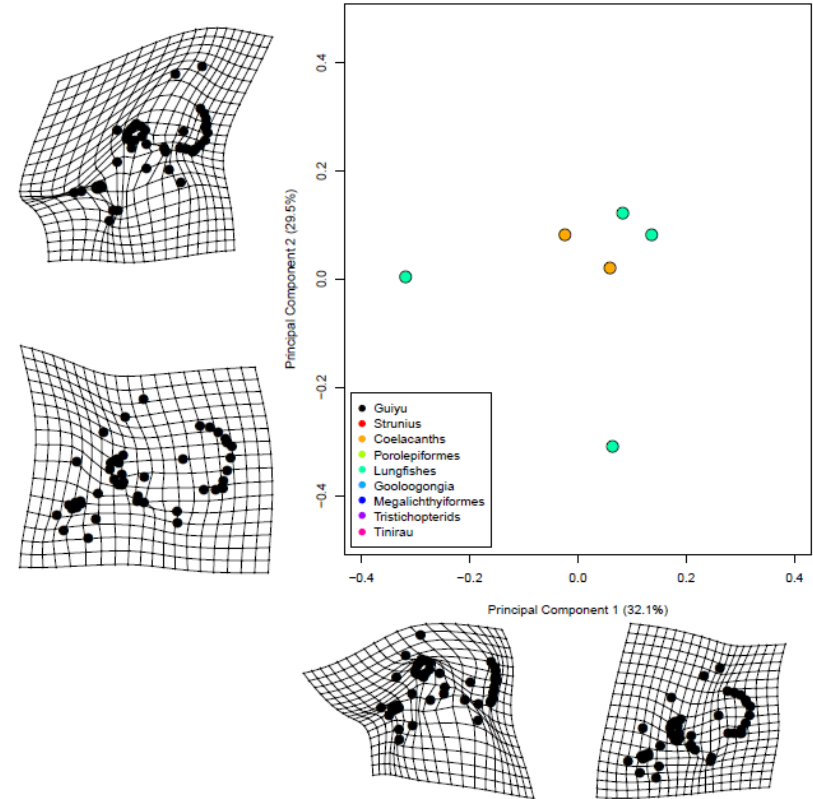
Appendix E.9. Middle Devonian (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



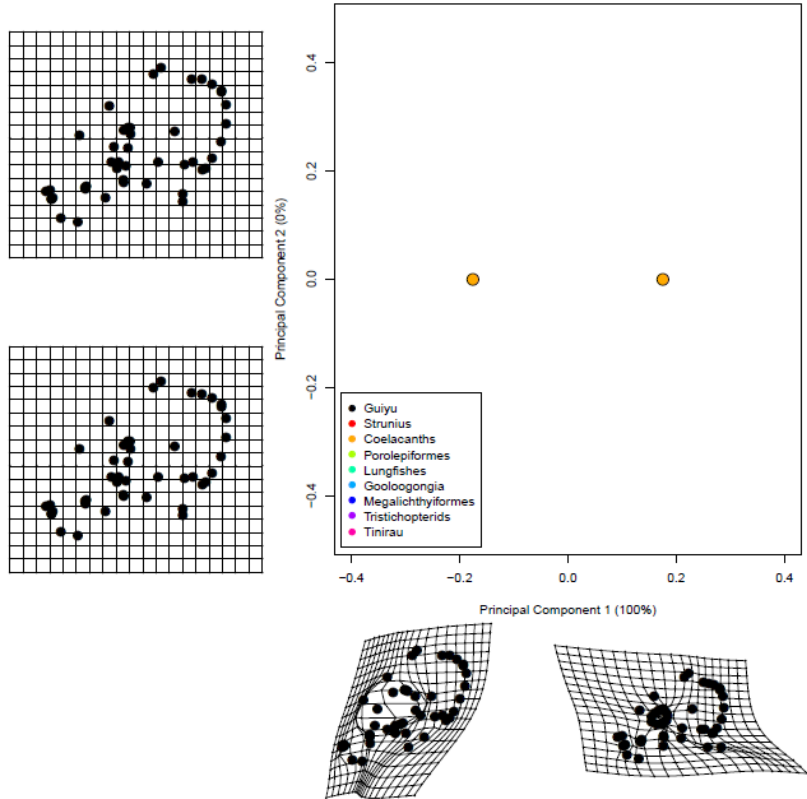
Appendix E.10. Upper Devonian (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



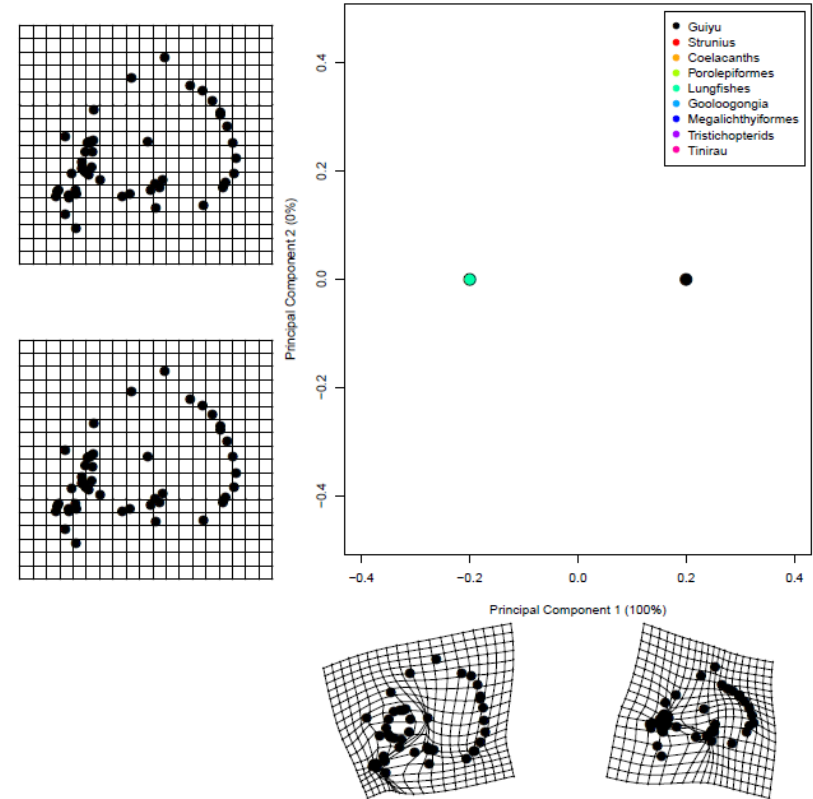
Appendix E.11. Carboniferous (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



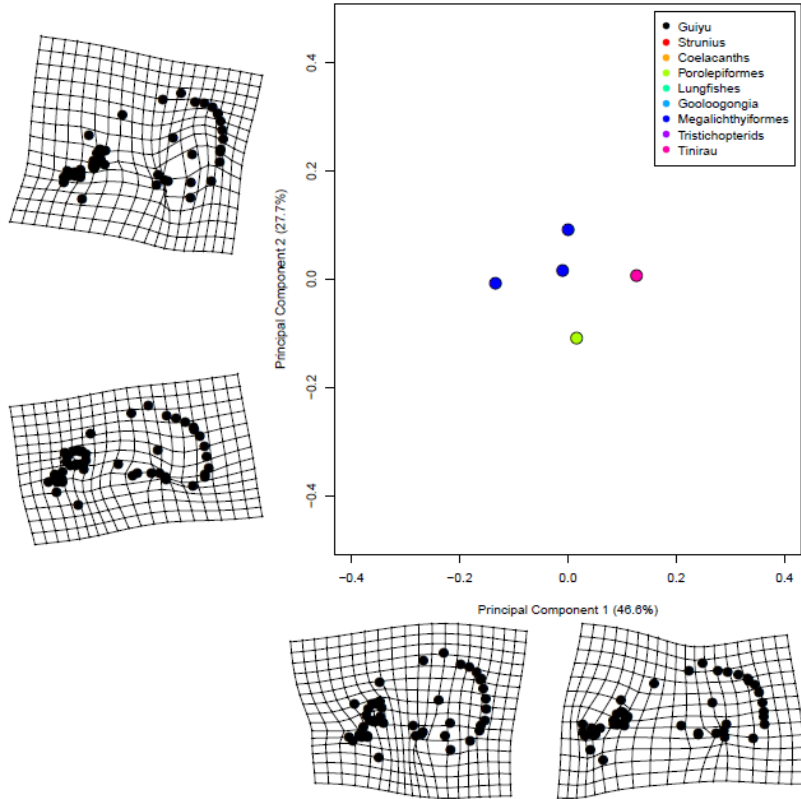
Appendix E.12. Lower Triassic (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



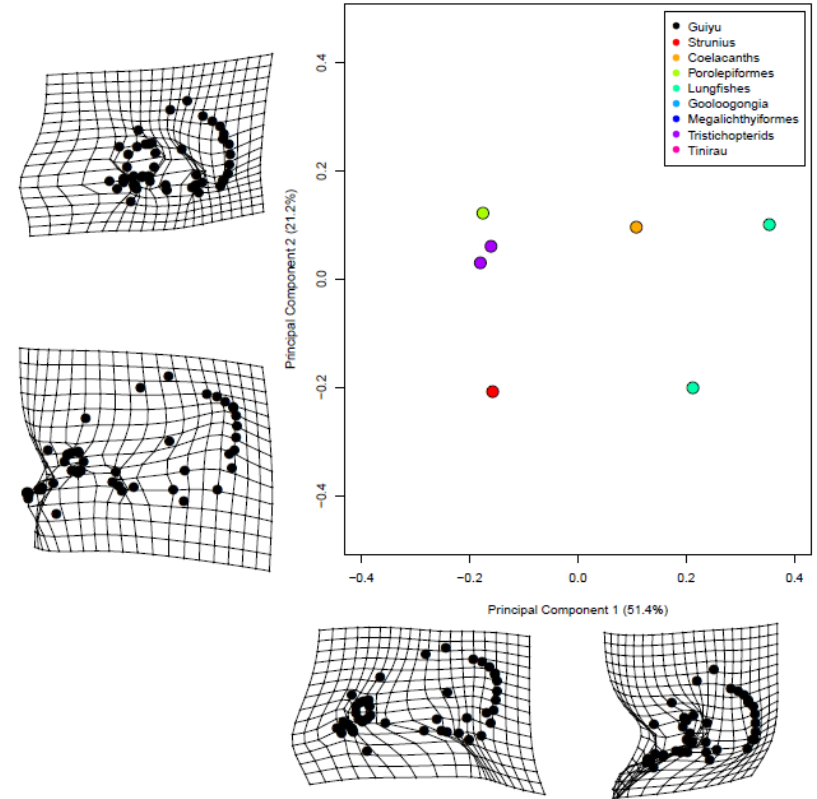
Appendix E.13. Middle/Upper Triassic (Epoch-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



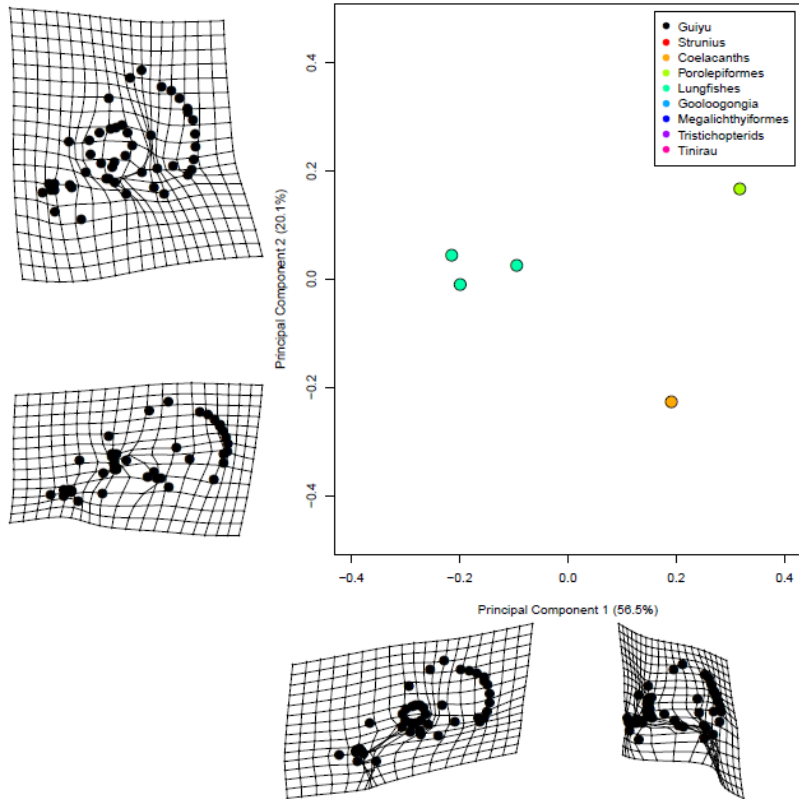
Appendix E.14. Lochkovian (Age-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC. Guiyu (Silurian) was added to this time scale to visualize an early lobe-fin morphospaces.



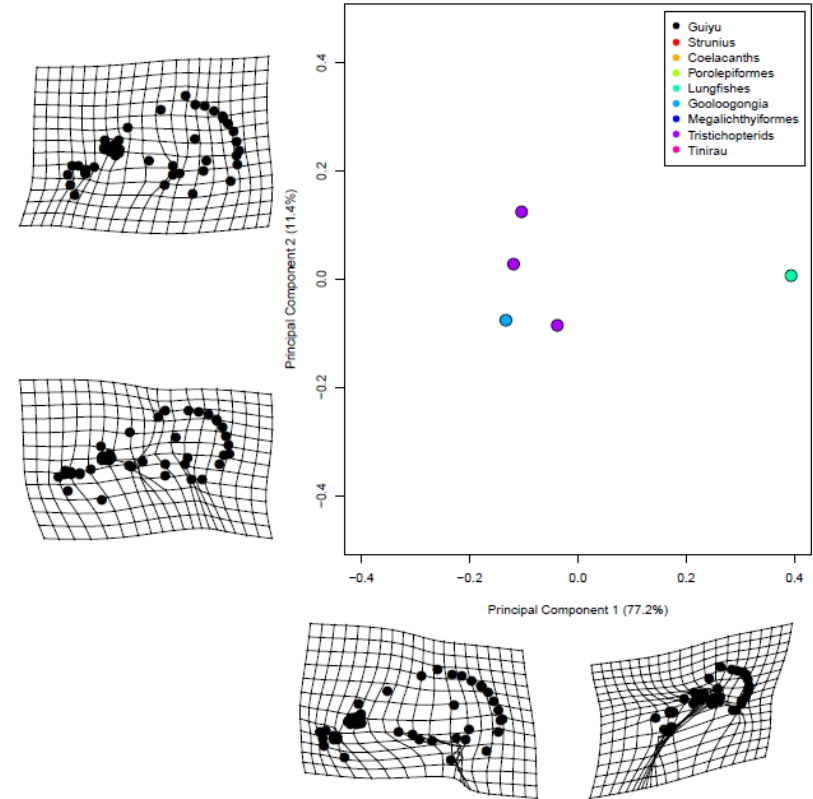
Appendix E.15. Eifelian (Age-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



Appendix E.16. Givetian (Age-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

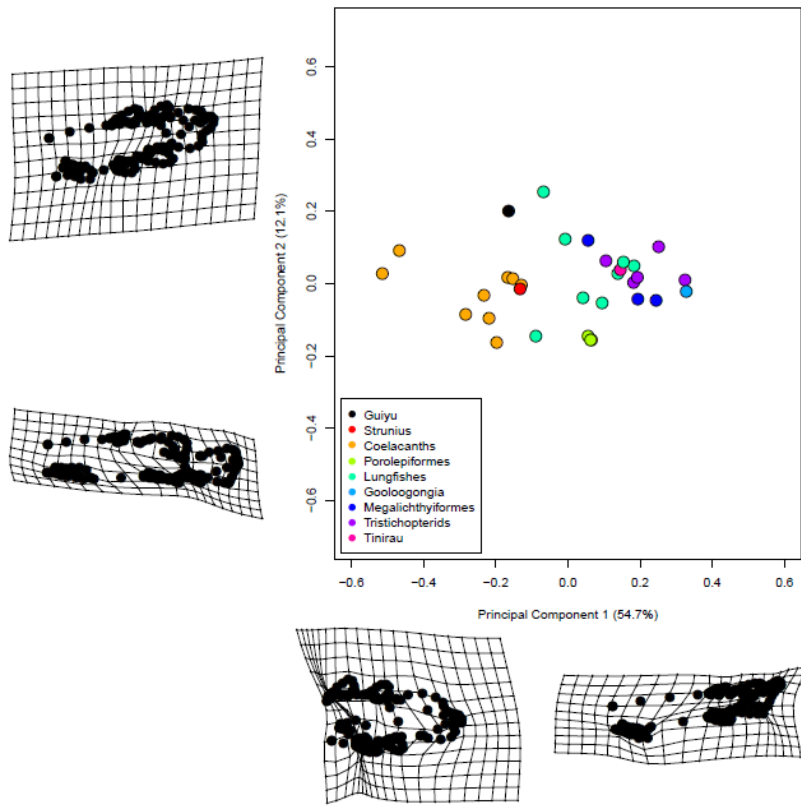


Appendix E.17. Frasnian (Age-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

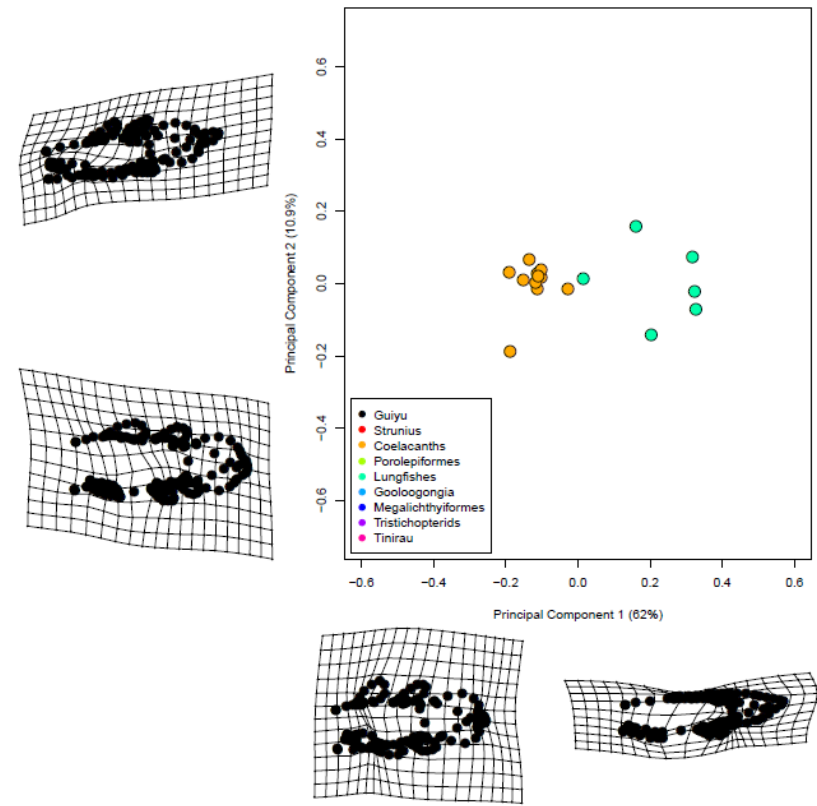


Appendix E.18. Famennian (Age-scale) PC1 and PC2 Cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

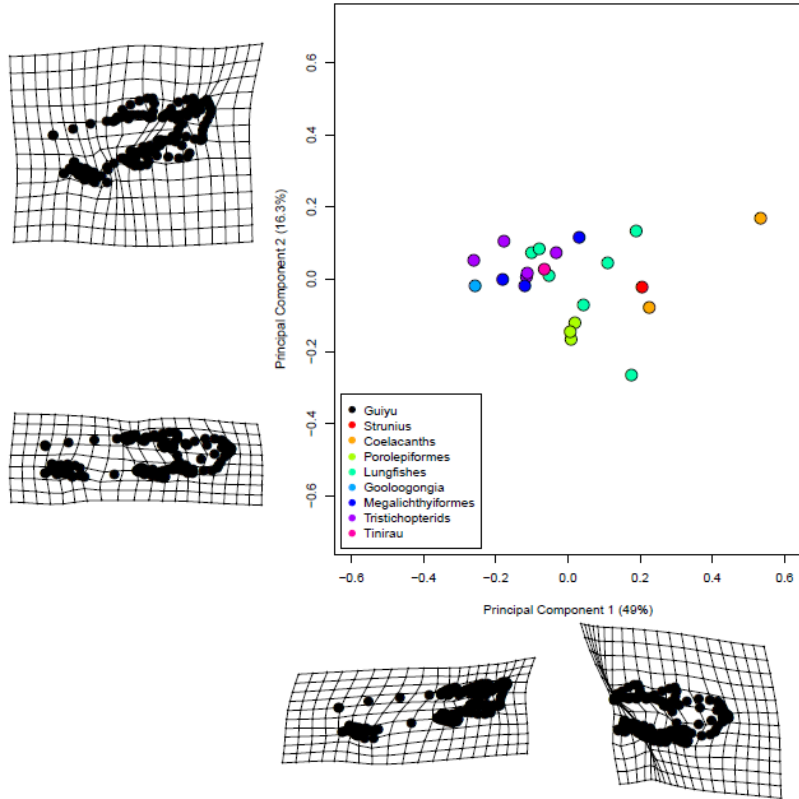
## APPENDIX F



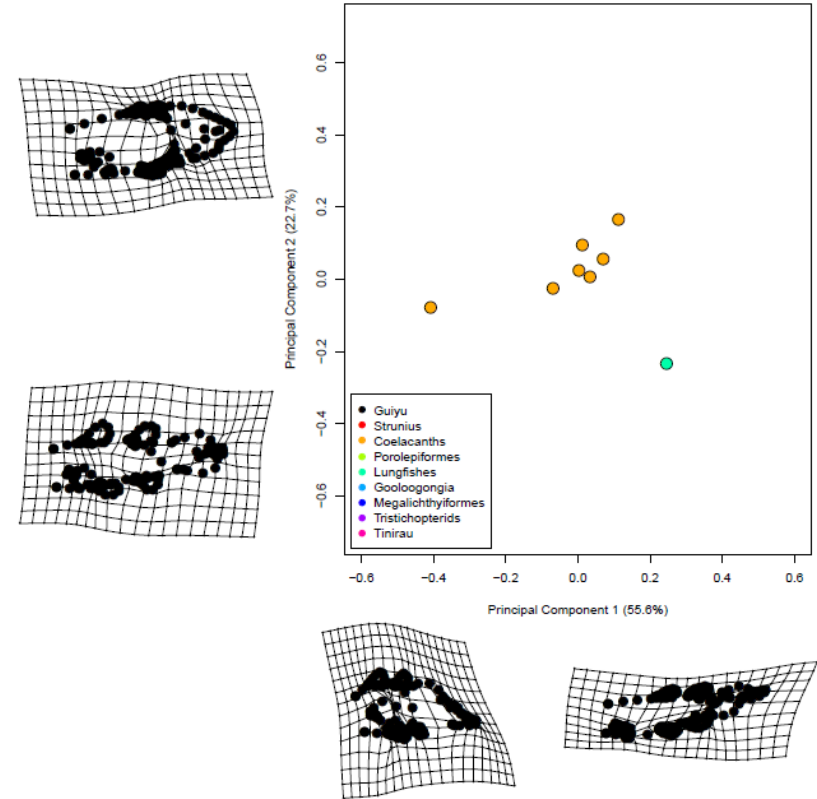
Appendix F.1. Paleozoic (Era-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



Appendix F.2. Mesozoic (Era-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

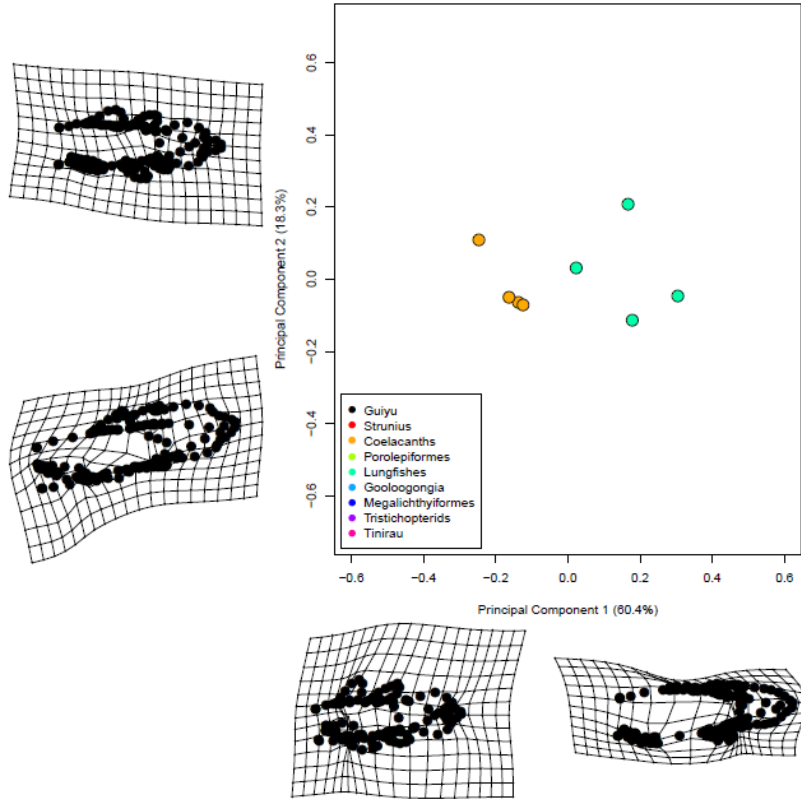


Appendix F.3. Devonian (Period-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

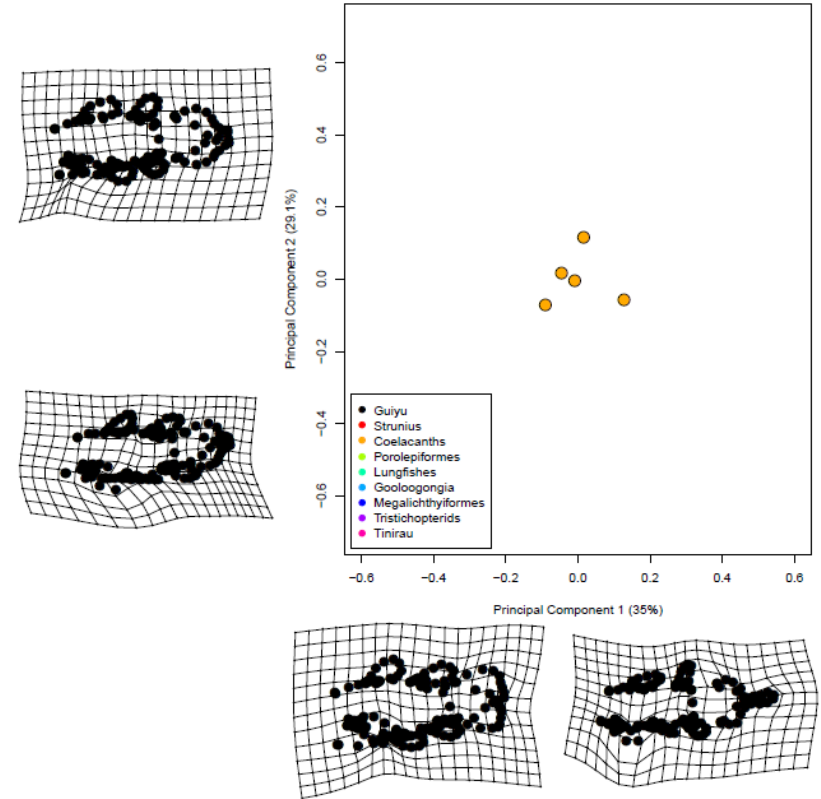


Appendix F.4. Carboniferous (Period-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

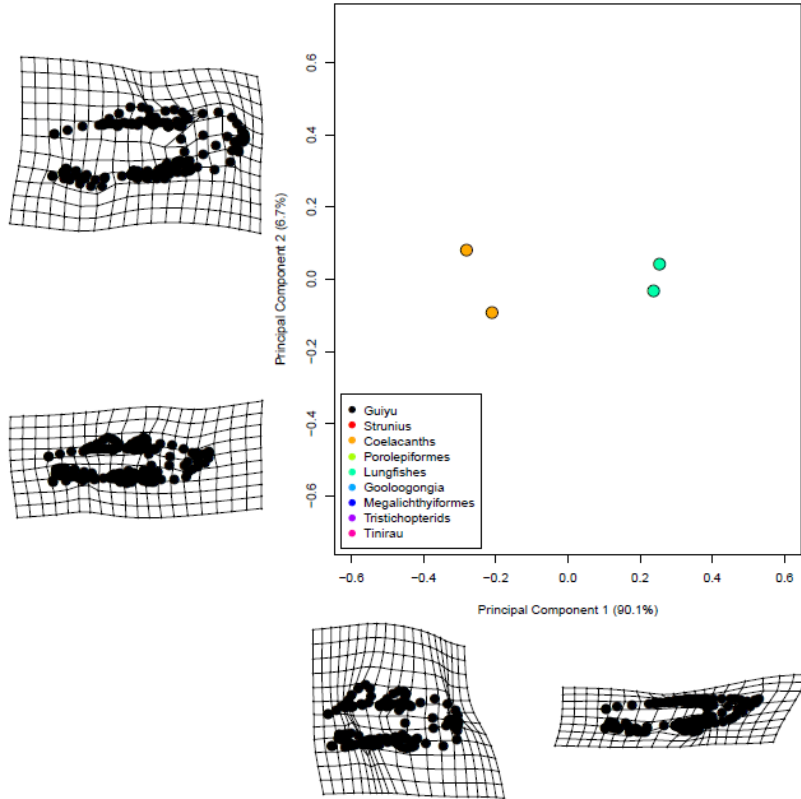




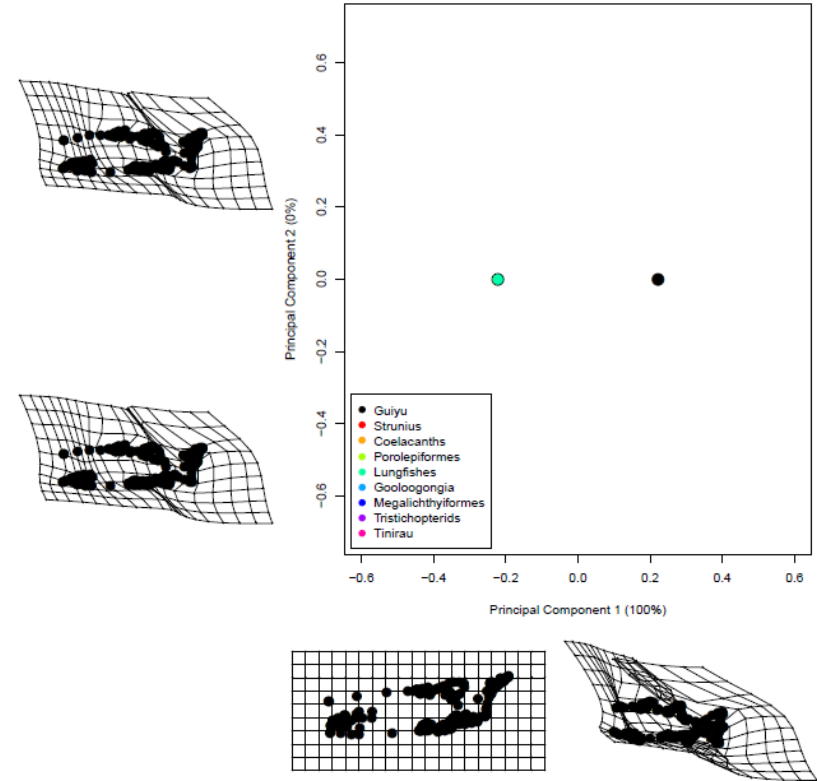
Appendix F.5. Triassic (Period-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



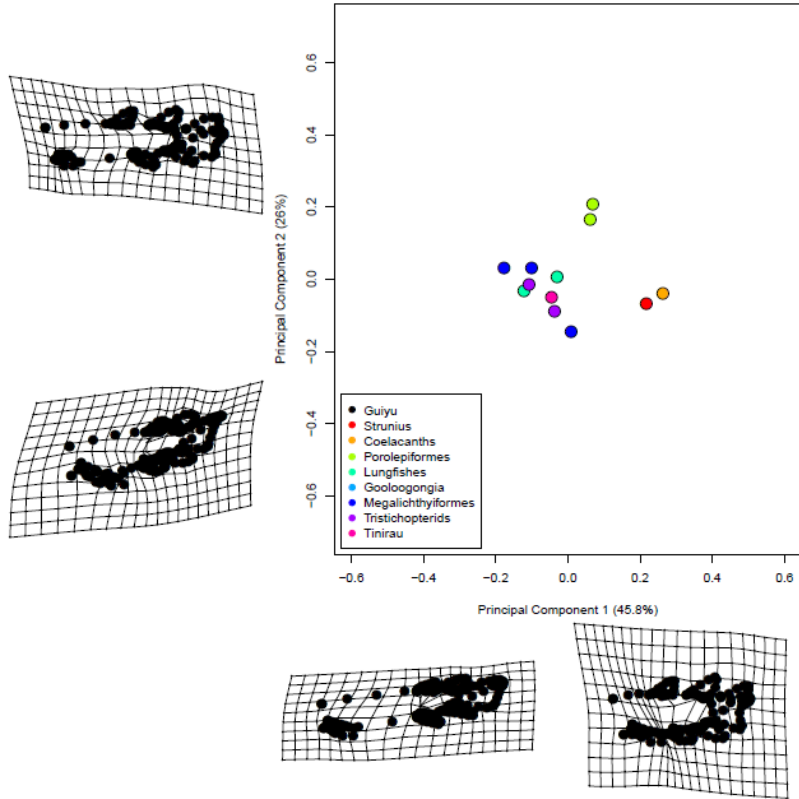
Appendix F.6. Jurassic (Period-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



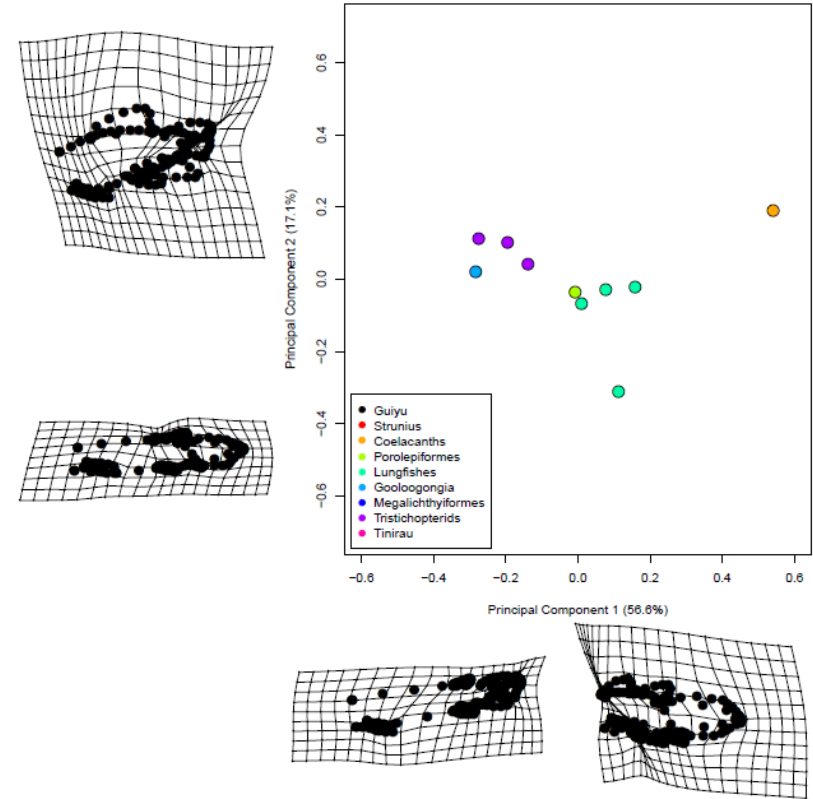
Appendix F.7. Cretaceous (Period-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



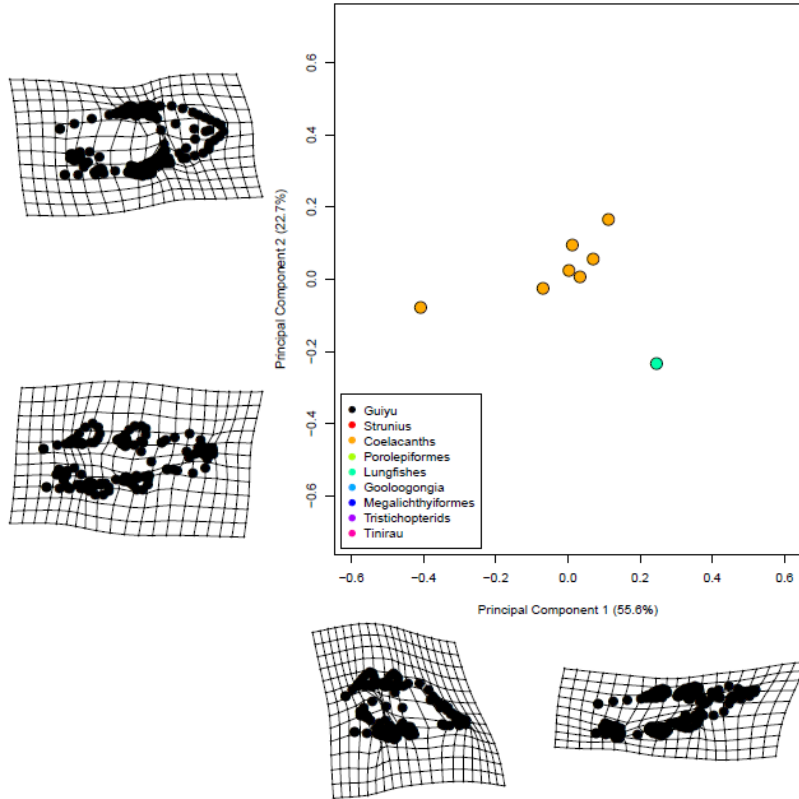
Appendix F.8. Lower Devonian (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC. Guiyu (Silurian) was added to this time scale to visualize an early lobe-fin morphospaces.



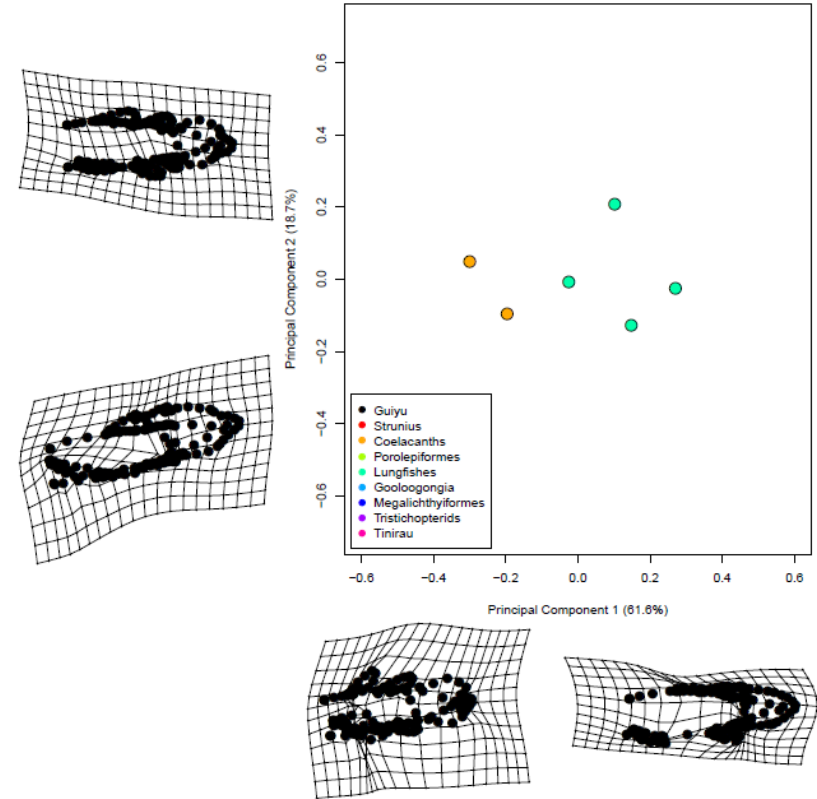
Appendix F.9. Middle Devonian (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



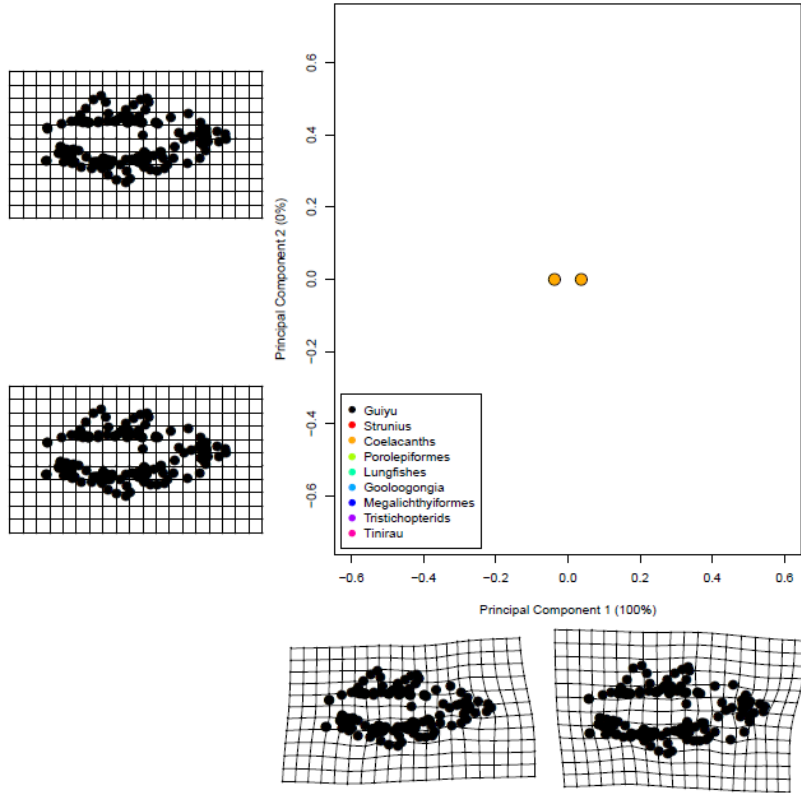
Appendix F.10. Upper Devonian (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



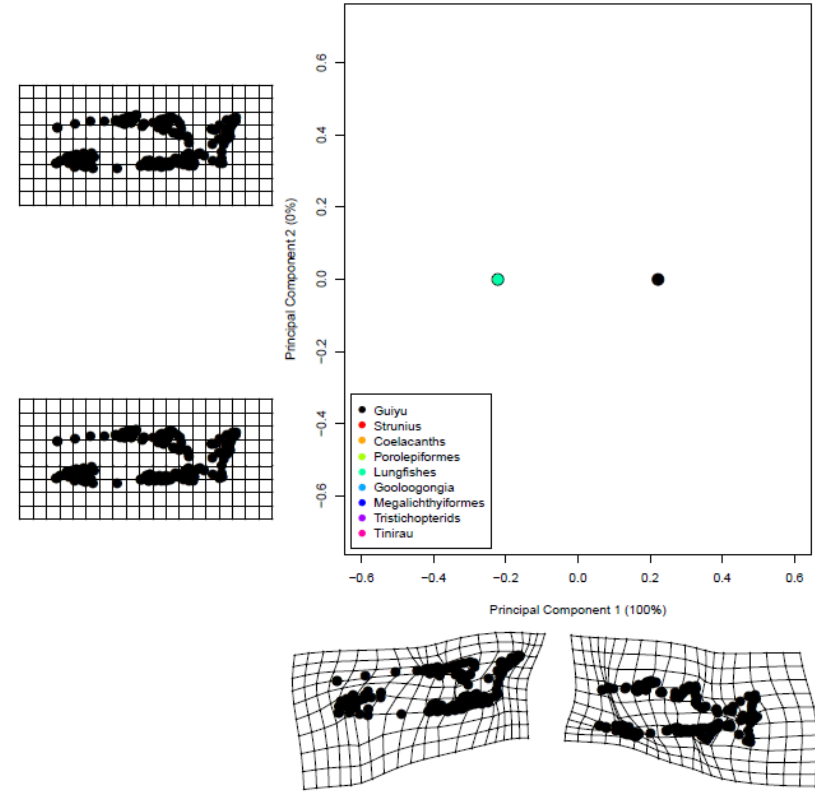
Appendix F.11. Carboniferous (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



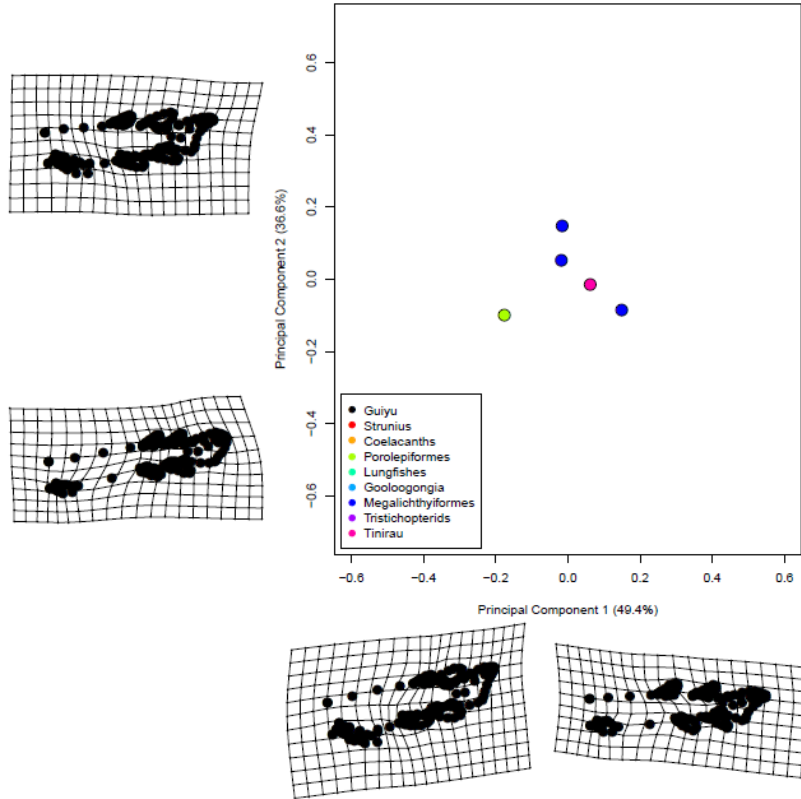
Appendix F.12. Lower Triassic (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



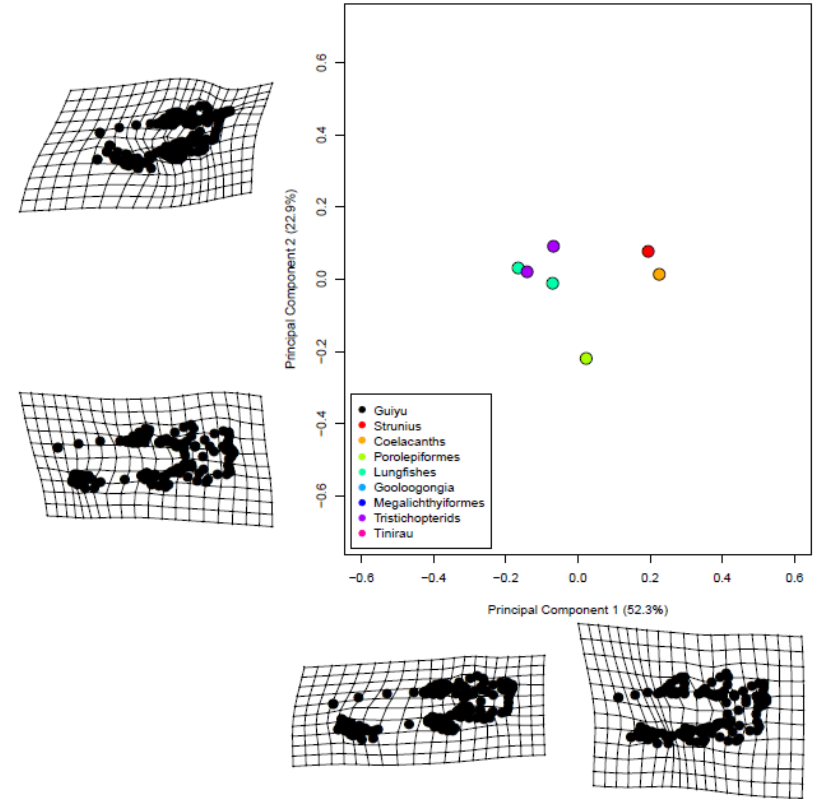
Appendix F.13. Middle and Upper Triassic (Epoch-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



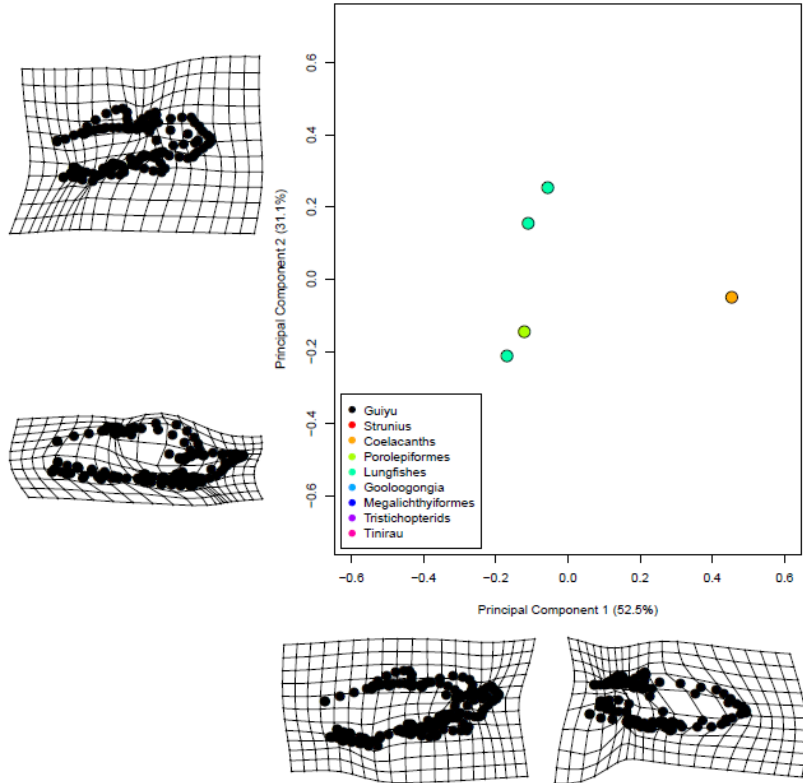
Appendix F.14. Lochkovian (Age-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC. Guiyu (Silurian) was added to this time scale to visualize an early lobe-fin morphospaces.



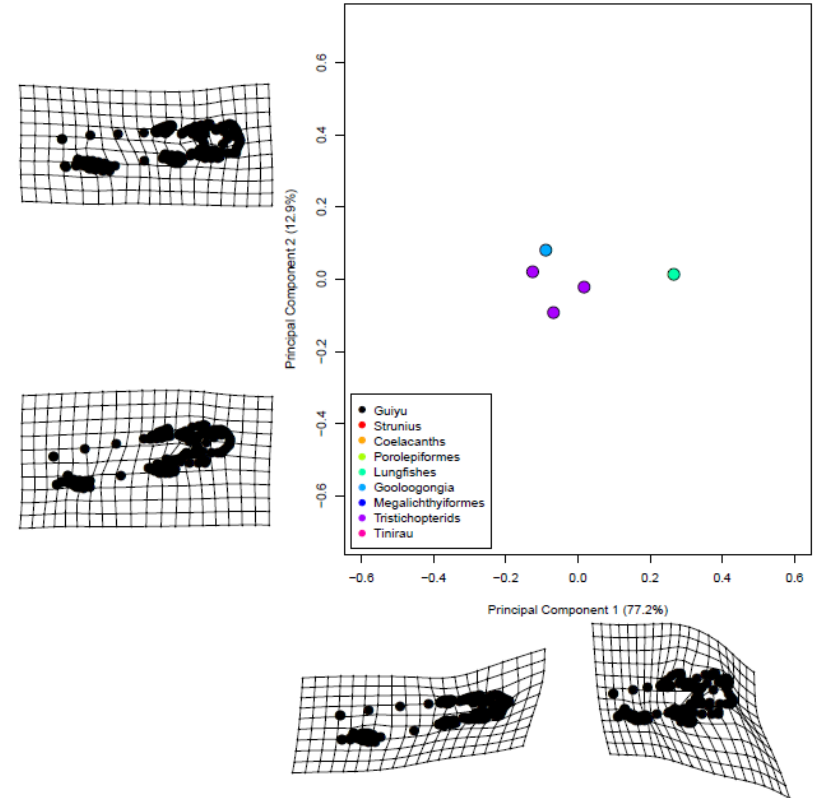
Appendix F.15. Eifelian (Age-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



Appendix F.16. Givetian (Age-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

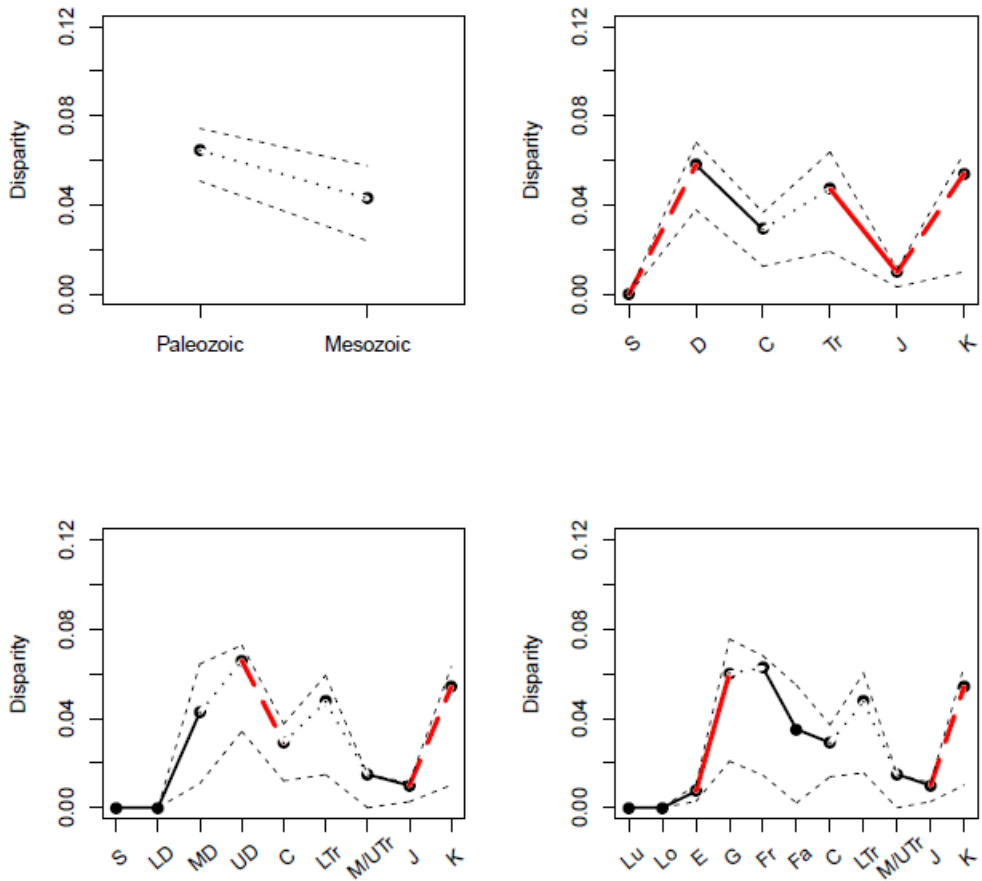


Appendix F.17. Frasnian (Age-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.



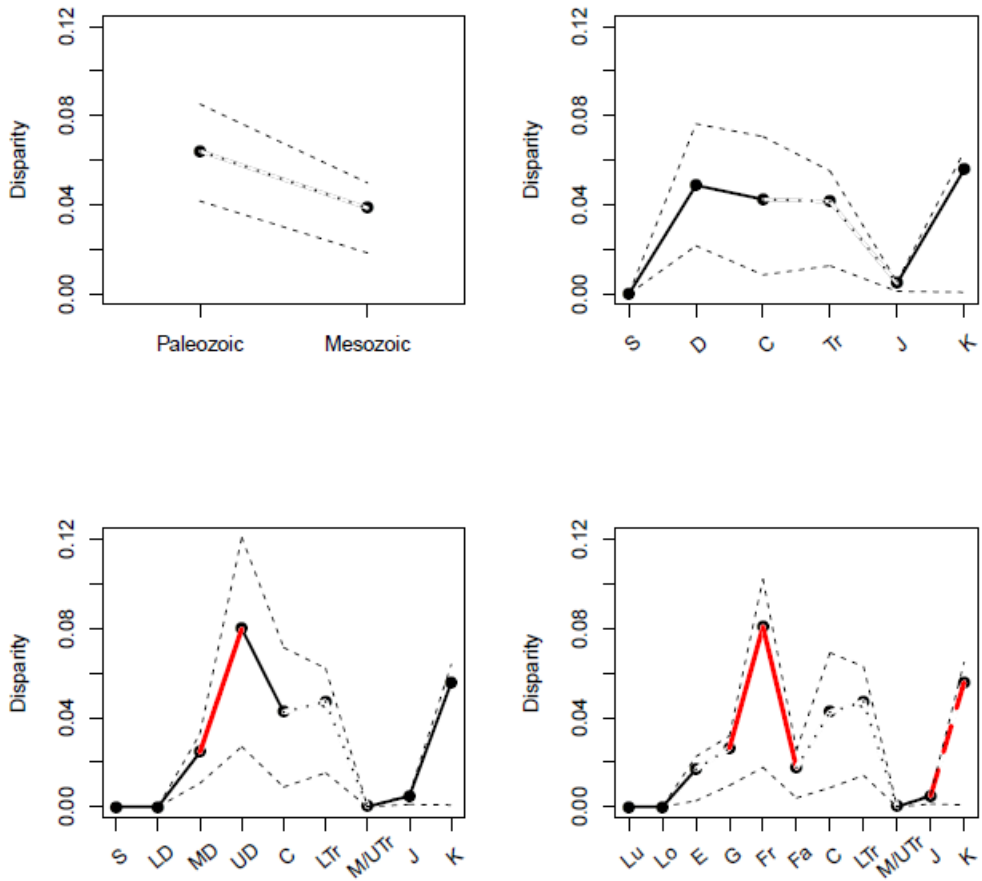
Appendix F.18. Famennian (Age-scale) PC1 and PC2 Post-cranial Morphospace. Points are color-coded according to monophyletic groups. Figures along PC axes represent the morphology of the individual at the respective extreme of each corresponding PC.

## APPENDIX G

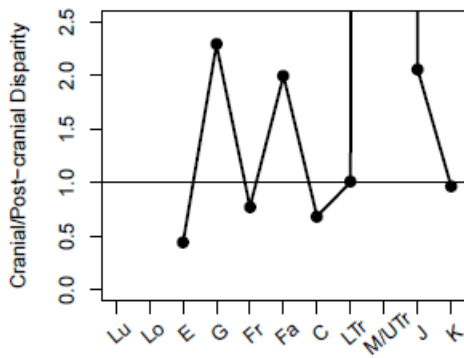
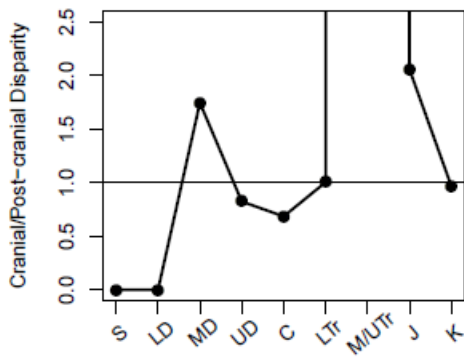
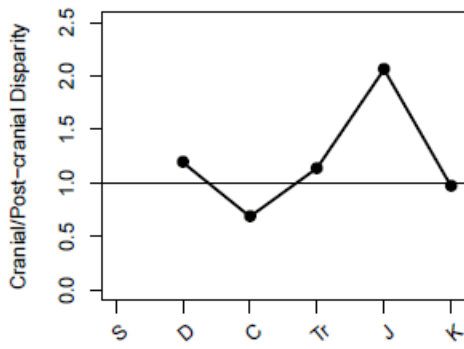
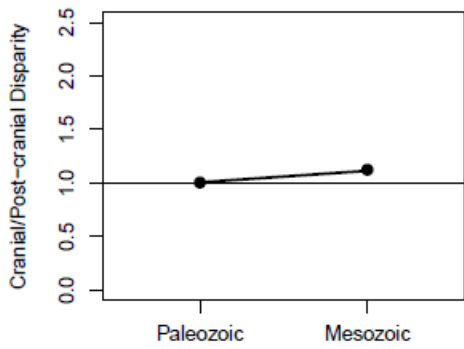


Appendix G.1. Cranial PC disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. Dashed black lines represent 95% confidence intervals. Dotted lines represent significant likelihood-ratios. Dashed red lines represent significant permutation tests. Solid red lines represent significant likelihood ratios and permutation tests. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.





Appendix G.2. Post-cranial PC disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. Dashed black lines represent 95% confidence intervals. Dotted lines represent significant likelihood-ratios. Dashed red lines represent significant permutation tests. Solid red lines represent significant likelihood ratios and permutation tests. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.



Appendix G.3. Cranial:Post-cranial PC disparity through time at the Era (top left), Period (top right), Epoch (bottom left), and Age (bottom right) geologic time scales. L: Lower; M: Middle; U: Upper; S: Silurian; D: Devonian; C: Carboniferous; Tr: Triassic; J: Jurassic; K: Cretaceous; Lu: Ludfordian; Lo: Lochkovian; E: Eifelian; G: Givetian; Fr: Frasnian; Fa: Famennian.

## APPENDIX H

Appendix H.1. Cranial coordinate pairwise rate tests. Significant ( $p < .05$ ) values in red. Coela.: coelacanths; Porolepi.: porolepiformes; Lung.: lungfishes; Megalichthyi.: megalichthyiformes; Tristichopt.: tristichopterids.

	<b>Guiyu</b>	<b>Strunius</b>	<b>Coela.</b>	<b>Porolepi.</b>	<b>Lung.</b>	<b>Gooloogongia</b>	<b>Megalichthyi.</b>	<b>Tristichopt.</b>	<b>Tinirau</b>
<b>Guiyu</b>	1.000	1.000	1.000	1.000	0.001	1.000	0.862	0.991	1.000
<b>Strunius</b>	NA	1.000	0.006	0.003	0.001	0.003	0.079	0.026	0.741
<b>Coelacanths</b>	NA	NA	1.000	0.346	0.001	0.135	0.141	0.001	0.007
<b>Porolepiformes</b>	NA	NA	NA	1.000	0.001	0.406	0.067	0.001	0.003
<b>Lungfishes</b>	NA	NA	NA	NA	1.000	0.001	0.001	0.001	0.001
<b>Gooloogongia</b>	NA	NA	NA	NA	NA	1.000	0.034	0.001	0.003
<b>Megalichthyiformes</b>	NA	NA	NA	NA	NA	NA	1.000	0.040	0.059
<b>Tristichopterids</b>	NA	NA	NA	NA	NA	NA	NA	1.000	0.050
<b>Tinirau</b>	NA	NA	NA	NA	NA	NA	NA	NA	1.000

Appendix H.2. Post-cranial coordinate pairwise rate tests. Significant ( $p < .05$ ) values in red. Coela.: coelacanths; Porolepi.: porolepiformes; Lung.: lungfishes; Megalichthyi.: megalichthyiformes; Tristichopt.: tristichopterids.

	<b>Guiyu</b>	<b>Strunius</b>	<b>Coela.</b>	<b>Porolepi.</b>	<b>Lung.</b>	<b>Gooloogongia</b>	<b>Megalichthyi.</b>	<b>Tristichopt.</b>	<b>Tinirau</b>
<b>Guiyu</b>	1.000	1.000	0.999	1.000	0.267	1.000	0.886	0.998	0.969
<b>Strunius</b>	NA	1.000	0.167	0.004	0.001	0.001	0.001	0.016	0.001
<b>Coelacanths</b>	NA	NA	1.000	0.001	0.001	0.001	0.001	0.002	0.001
<b>Porolepiformes</b>	NA	NA	NA	1.000	0.001	0.026	0.001	0.179	0.001
<b>Lungfishes</b>	NA	NA	NA	NA	1.000	0.001	0.010	0.001	0.001
<b>Gooloogongia</b>	NA	NA	NA	NA	NA	1.000	0.082	0.180	0.001
<b>Megalichthyiformes</b>	NA	NA	NA	NA	NA	NA	1.000	0.030	0.001
<b>Tristichopterids</b>	NA	NA	NA	NA	NA	NA	NA	1.000	0.001
<b>Tinirau</b>	NA	NA	NA	NA	NA	NA	NA	NA	1.000

Appendix H.3. Cranial PC-reduced pairwise rate tests. Significant ( $p < .05$ ) values in red. Coela.: coelacanths; Porolepi.: porolepiformes; Lung.: lungfishes; Megalichthyi.: megalichthyiformes; Tristichopt.: tristichopterids.

	<b>Guiyu</b>	<b>Strunius</b>	<b>Coela.</b>	<b>Porolepi.</b>	<b>Lung.</b>	<b>Gooloogongia</b>	<b>Megalichthyi.</b>	<b>Tristichopt.</b>	<b>Tinirau</b>
<b>Guiyu</b>	1.000	0.947	0.995	0.983	0.036	0.953	0.865	0.990	0.916
<b>Strunius</b>	NA	1.000	0.566	0.476	0.002	0.556	0.462	0.694	0.820
<b>Coelacanths</b>	NA	NA	1.000	0.695	0.001	0.798	0.466	0.624	0.381
<b>Porolepiformes</b>	NA	NA	NA	1.000	0.001	0.910	0.422	0.556	0.328
<b>Lungfishes</b>	NA	NA	NA	NA	1.000	0.001	0.004	0.001	0.002
<b>Gooloogongia</b>	NA	NA	NA	NA	NA	1.000	0.464	0.670	0.421
<b>Megalichthyiformes</b>	NA	NA	NA	NA	NA	NA	1.000	0.414	0.404
<b>Tristichopterids</b>	NA	NA	NA	NA	NA	NA	NA	1.000	0.527
<b>Tinirau</b>	NA	NA	NA	NA	NA	NA	NA	NA	1.000

Appendix H.4. Post-cranial PC-reduced pairwise rate tests. Significant ( $p < .05$ ) values in red. Coela.: coelacanths; Porolepi.: porolepiformes; Lung.: lungfishes; Megalichthyi.: megalichthyiformes; Tristichopt.: tristichopterids.

	<b>Guiyu</b>	<b>Strunius</b>	<b>Coela.</b>	<b>Porolepi.</b>	<b>Lung.</b>	<b>Gooloogongia</b>	<b>Megalichthyi.</b>	<b>Tristichopt.</b>	<b>Tinirau</b>
<b>Guiyu</b>	1.000	0.890	0.973	0.987	0.628	0.937	0.829	0.988	0.629
<b>Strunius</b>	NA	1.000	0.894	0.542	0.014	0.311	0.115	0.483	0.360
<b>Coelacanths</b>	NA	NA	1.000	0.329	0.001	0.198	0.015	0.215	0.188
<b>Porolepiformes</b>	NA	NA	NA	1.000	0.002	0.500	0.162	0.777	0.098
<b>Lungfishes</b>	NA	NA	NA	NA	1.000	0.104	0.183	0.004	0.003
<b>Gooloogongia</b>	NA	NA	NA	NA	NA	1.000	0.581	0.525	0.068
<b>Megalichthyiformes</b>	NA	NA	NA	NA	NA	NA	1.000	0.174	0.015
<b>Tristichopterids</b>	NA	NA	NA	NA	NA	NA	NA	1.000	0.083
<b>Tinirau</b>	NA	NA	NA	NA	NA	NA	NA	NA	1.000

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