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DO CLADISTIC AND MORPHOMETRIC DATA CAPTURE COMMON PATTERNS OF MORPHOLOGICAL DISPARITY?

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Abstract: The distinctly non-random diversity of organismal form manifests itself in discrete clusters of taxa that share a common body plan. As a result, analyses of disparity require a scalable comparative framework. The difficulties of applying geometric morphometrics to disparity analyses of groups with vastly divergent body plans are overcome partly by the use of cladistic characters. Character-based disparity analyses have become increasingly popular, but it is not clear how they are affected by character coding strategies or revisions of primary homology statements. Indeed, whether cladistic and morphometric data capture similar patterns of morphological variation remains a moot point. To address this issue, we employ both cladistic and geometric morphometric data in an exploratory study of disparity focussing on caecilian amphibians. Our results show no impact on relative intertaxon distances when different coding strategies for cladistic characters were used or when revised concepts of homology were considered. In all instances, we found no statistically significant difference between pairwise Euclidean and Procrustes distances, although the strength of the correlation among distance matrices varied. This suggests that cladistic and geometric morphometric data appear to summarize morphological variation in comparable ways. Our results support the use of cladistic data for characterizing organismal disparity.

Key words: disparity, evolution, morphospace, constraints, Gymnophiona.

THE diversity of organismal form (disparity) was a topic of enquiry long before evolutionary theory became established. However, within the context of descent with modification, the decidedly discontinuous and non-random range of organismal form achieves greater significance. Do heterogeneities of morphospace occupation reflect optimality, constraint, contingency and selection or merely that insufficient time has elapsed for the exploration and saturation of theoretical morphospace? In attempting to explain such heterogeneities, it is necessary to investigate organismal disparity within a comparative framework. This has been done using data sets of continuous measurements (traditional morphometrics) or landmarks (geometric morphometrics; Foote 1997; Klingenberg 2010). However, the collection of morphometric data can become problematic when extended to a broad and diverse taxonomic sample, because of practical and/or theoretical limits to the selection of morphometric variables in highly divergent taxa (e.g. restrictions on choice of biologically homologous landmarks; difficulties in establishing homologies across diverse taxa). In these cases, other data sources (such as cladistic characters; Wills *et al.* 1994) offer an alternative basis for quantitative treatments of disparity.

A practical, if not theoretical, distinction can be drawn between analyses of disparity based on geometric mor-

phometric data and those that exploit character matrices that have been targeted primarily at phylogeny reconstruction. The latter has become an increasingly popular approach to distilling organismal disparity in studies with ever-increasing taxonomic scope and breadth (Briggs *et al.* 1992; Wills *et al.* 1994; Wills 1998*a*; Brusatte *et al.* 2008, 2014; Prentice *et al.* 2011; Thorne *et al.* 2011; Butler *et al.* 2012; Foth *et al.* 2012). However, it remains unclear whether results from different kinds of data and analyses are congruent: do analyses of disparity based on morphometric and cladistic data sets support correlated patterns of taxon distribution in morphospace and/or similar profiles of relative disparity changes? Different disparity indices capture different aspects of morphology and, therefore, are not expected to produce similar patterns. However, previous studies have suggested that similar patterns might be retrieved (Villier and Eble 2004). Indeed, if different sources of morphological data could be shown, at least in some cases, to deliver comparable results, then it may be possible to gain greater insights into morphological complexity, its origin and its evolution. Furthermore, cladistic characters are invariably designed and defined so as to represent individual hypotheses of biological homology, and there are different approaches to defining characters, such that these alternative hypotheses are correctly implemented in phylogenetic analysis (Maddison 1993; Wilkinson 1995; Hawkins *et al.* 1997; Hawkins 2000). However, the impact of alternative character coding strategies upon inferred patterns of disparity remains unexplored, as is the impact of revisions of cladistic data sets in the light of new concepts of biological homology.

Here, we use caecilian amphibians as an empirical case study of the extent to which geometric morphometric and discrete character data sets may be seen as 'equivalent' in terms of providing congruent inferences of patterns of disparity, as well as exploring the impact of character design and revision on analyses of organismal disparity.

MATERIALS AND METHODS

Our analyses were based on caecilian amphibians because they were the subject of a classic study of the impact of character coding strategies for phylogenetic analysis (Forey and Kitching 2000) that is readily extended to investigating the impact of those coding strategies for disparity studies. The original morphological data set on which the recoding experiments were based (Wake 1993) is comprised of cranial neurological characters related to, among others, the hypoglossal nerve and the olfactory, optic, otic and vomeronasal organs and includes a preponderance of multistate characters (15 of 34) resulting from composite coding *sensu* Wilkinson (1995). Forey

and Kitching (2000) converted the multistate characters into binary presence/absence characters (total: 77 characters) using binary reductive coding, demonstrating that differences in coding strategy are sufficient to produce different branching patterns in phylogenies inferred with parsimony analysis. To explore the effects of cladistic coding strategies on disparity analyses, we contrast Euclidean distance matrices derived from the original multistate and recoded binary character matrices. Some of the hypotheses of homology represented in the original data set (Wake 1993) were subsequently critiqued, and we use the revised cladistic data matrix (Wilkinson 1997, table 1: 26 characters) to explore the impact of revisions in concepts of biological homology on disparity analyses. The taxon sample in Wilkinson (1997) was subsampled to match that of Wake (1993) and Forey and Kitching (2000).

We applied geometric morphometric methods (Bookstein 1991; Adams *et al.* 2013) to explore the equivalence of landmark-based morphometric and discrete character data sets in disparity analyses. Morphometric data were taken from Sherratt *et al.* (2014), comprising 60 3D landmarks conforming to either type I or II (Bookstein 1991), and chosen according to strict definitions of biological homology. The landmarks were digitized on 3D caecilian skull models built from high-resolution X-ray computed tomography (HRXCT). Rendered skull models were assembled with VGStudio MAX v2.0 (Volume Graphics GmbH; http://www.volumegraphics.com). The landmarks were digitized using Landmark Editor v3.6 (Wiley *et al.* 2005). The landmark data were subjected to a full Procrustes alignment in MorphoJ v1.04b (Klingenberg 2011) to remove the effects of translation, rotation and scaling. Resulting Procrustes distances were subjected to principal component analysis (PCA). HRXCT scans were made of most taxa present in the cladistic data sets, with the exceptions of *Caecilia thompsoni* and *Epicrionops bicolor*. These two taxa were used in place of *C. occidentalis* and *E. petersi*, respectively, in the geometric morphometric data set because neither *C. occidentalis* nor *E. petersi* were available for HRXCT analyses. In both cases, the original taxa and their replacements are from the same geographical region (Colombia and Ecuador) and are congeneric (Taylor 1968; Wilkinson *et al.* 2011). Shape analysis of cranial variation in caecilians indicates conserved morphologies among sampled species in these two genera (Sherratt *et al.* 2014). Thus, it is likely that the replacement taxa are sufficiently closely related and morphologically similar to the original taxa to serve as suitable substitutes in our analyses.

We used pairwise distances between species to measure disparity. Cladistic matrices were formatted for MATRIX (Wills 1998*b*), from which generalized Euclidean distances were derived and subjected to principal coordinates analysis (PCoA) in GINKGO (De Cáceres *et al.* 2007).

For the geometric morphometric data set, full Procrustes distances were extracted using Morphologika2 v2.5 (O'Higgins and Jones 1998). Mantel tests were carried out in R 3.1.2 (R Development Core Team 2014) using the package vegan (Oksanen *et al.* 2013) to establish the strength and significance of linear correlations among Euclidean distance matrices derived from the different character data sets and between those and the tangent space distances from the morphometric data set. In the context of this study, simple correlation tests are appropriate to evaluate major differences in patterns of morphospace occupation based on various data sets. In addition to Mantel tests, we also examined the correlation among distance matrices through Procrustes superimposition (Peres-Neto and Jackson 2001) to establish the degree of concordance of data point distributions in multivariate spaces generated from our different analyses. Procrustes superimposition was performed in vegan.

We also determined whether the different metrics produce similar relative disparities between clades. Given our small sample size and the fact that recognized monophyletic groups among caecilians are represented by very few taxa in our study, we opted for data set resampling to establish whether cladistic and geometric morphometric (landmark) data produce: (1) similar relative disparities within subsamples; and (2) similar relative differences in disparity between two subsamples. Disparity was calculated as the average-squared distance between taxa within morphospace. Obviously, morphospaces built from different morphological data will not be equally scaled and the resulting disparity values are not directly comparable. Resampling enables a comparison of the metrics that is independent of the relative scaling, meaning the relative trends are important, not the specific disparity values. For instance, a sample that is considered morphologically disparate compared to other samples based on landmarks should also be morphologically disparate based on cladistic characters. Resampling was conducted by: (1) randomly selecting 5 of the 11 species of caecilians without substitution, creating morphospaces based on the two metrics and comparing the disparity based on those two different metrics; or (2) randomly selecting two 5-species non-overlapping samples without replacement, creating morphospaces based on the two metrics independently for each of the two samples, calculating the disparity based on the two different metrics in each sample, then comparing the difference in measured disparity between the two groups with the two different metrics. Each test was based on 1000 replicate samples.

We anticipate that strong correlations indicate similar signal in different morphometric data (landmarks; characters) as well as different types of cladistic characters (skeletal cranial; neurological).

RESULTS

Plots of taxa in the multivariate space generated from the character-based analyses are shown using only the first three PCo axes, or PC axes in the case of the morphometric data (Fig. 1); the percentage of total variance summarized by those axes is reported in Table 1. When different coding strategies for the same data set are employed (Fig. 1A–B), the pattern and relative distribution of taxa in morphospace are visually indistinguishable (the obvious mirroring of taxa on axis 2 of Fig. 1A–B is an artefact of the arbitrary direction of ordination). In comparison, taxa are more dispersed in the plot based on Wilkinson's revised cladistic data set (Wilkinson 1997; Fig. 1C), while analysis of the geometric morphometric data set (Fig. 1D) produces a clustering more similar to those obtained from the two alternative codings of the original data set. Representatives of the caecilian families Rhinatrematidae and Scolecomorphidae occur at the extremes of the envelope of morphospace delimited by all taxa in the PCoA/PCA of all data sets.

The results of the Mantel and Procrustes superimposition tests for each pair of data sets are presented in Table 2. With the Mantel test, all comparisons were statistically significant at the 0.05 threshold level, and the pairwise distances from the cladistic data sets show evidence of correlation at the 0.001 significance level. The highest correlation is between data derived from multistate vs binary codings, suggesting that, although different phylogenetic hypotheses are derived from recoding practice, this has little effect on relative distributions of taxa in morphospace. This is probably because the binary coding has the effect of redistributing states among taxa such that, on average, pairwise distances are preserved. The correlation decreases when the Wilkinson recoding is compared with the multistate or binary recoding. This is partly expected, as Wilkinson's (1997) matrix presented significant amendments to several codings in previous analyses. The lowest correlations involve geometric morphometric data and each of the other categories (binary, multistate, Wilkinson). Geometric vs binary correlation is moderate, but the other two comparisons are lower. However, the comparisons between morphometric and cladistic data sets still show that about half of the distance matrix structure is preserved, suggesting that landmarks and cladistic characters can still retrieve a similar signal. With the Procrustes superimposition test, five of the six pairwise comparisons between distance matrices were significant. The only non-significant comparison is between geometric morphometric vs multistate coding. These results are in broad agreement with those from the Mantel test, and it was noted that with the Mantel test, the comparison between geometric morphometric vs multistate coding was weak and only marginally significant.
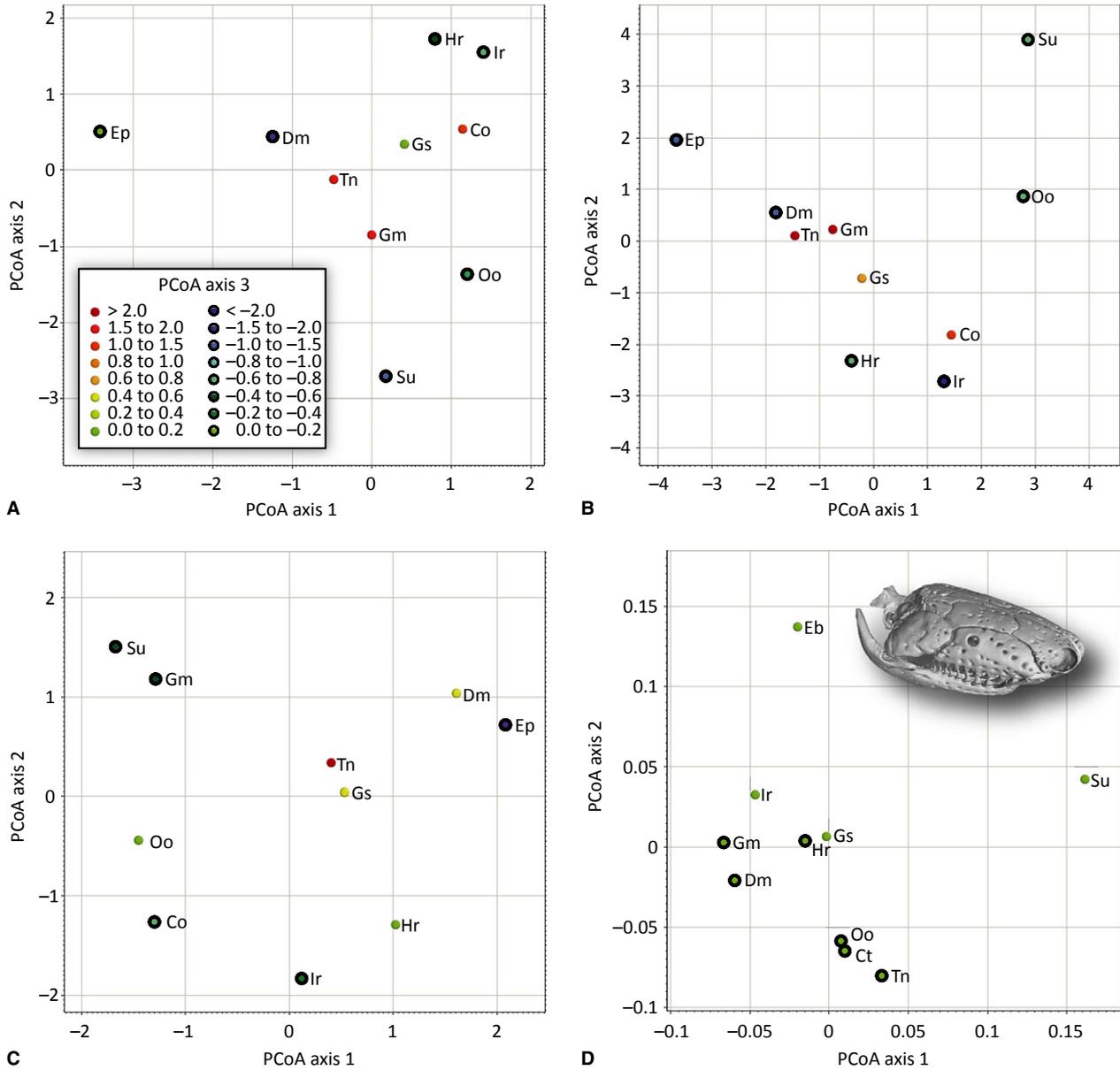
FIG. 1. Morphospace occupation by the 10 caecilian species in the cladistic data sets represented by: A, multistate character coding; B, binary character coding; C, with revised concepts of the character homology; and D, a geometric morphometric data set; the representative skull is from *Caecilia tentaculata*. Plots of the first three principal coordinate axes for each data set. *Abbreviations*: Co, *Caecilia occidentalis*; Ct, *Caecilia thompsoni*; Dm, *Dermophis mexicanus*; Eb, *Epicrionops bicolor*; Ep, *Epicrionops petersi*; Gm, *Gymnopis multiplicata*; Gs, *Geotrypetes seraphini*; Hr, *Hypogeophis rostratus*; Ir, *Idiocranium russeli*; Oo, *Oscaecilia ochrocephala*; Su, *Scolecomorphus ulugurensis*; Tn, *Typhlonectes natans*.

The partial disparity based on subsamples (5 of the 10 taxa) of the multistate and geometric morphometric data (Fig. 2A) showed a strong correlation (Spearman's $\rho = 0.6196$, $p = 0.001$). In addition, splitting the taxa into two random groups and comparing the relative disparity based on the multistate and geometric morphometric data (Fig. 2B) again showed a strong correlation (Spearman's $\rho = 0.6612$; $p = 0.001$). This indicates a strong consistency in the estimation of morphological diversity as well as the distribution of taxa within morphospace between metrics.

DISCUSSION

Homology concepts in morphometric analysis can be readily defined such that they are reproducible (Klingen-

TABLE 1. Percentage variance summarized on the first three PCoA axes (PC axes for morphometric data) for the pairwise distances for each of the four data sets.

| Data set | Percentage variance summarized | | | |
	Axis 1	Axis 2	Axis 3	Sum
Multistate character matrix	17.9818	15.3967	12.6129	45.9914
Binary character matrix	14.1910	13.2169	11.4439	38.8518
Revised character matrix	23.3341	16.9740	12.6014	52.9094
Geometric morphometric matrix	26.6064	25.3768	14.1383	66.1214

TABLE 2. Mantel and Procrustes superimposition tests, used to analyse correlation between the Euclidean distance matrices of each cladistic data set and Procrustes distances of the geometric morphometric data set.

Data sets	Spearman	p	Kendall	p	Pearson	p	Procrustes	p
Multistate coding vs Binary coding	0.6654	0.001	0.5073	0.001	0.6717	0.001	0.9138	0.007
Multistate coding vs Wilkinson (*sensu* Olson and Miller 1999) recoding	0.5784	0.001	0.4173	0.001	0.5874	0.001	0.8943	0.002
Binary coding vs Wilkinson (1997) recoding	0.7359	0.001	0.5811	0.001	0.7849	0.001	0.935	0.001
Geometric morphometric vs Multistate coding	0.3554	0.035	0.2532	0.03	0.3813	0.025	0.843	0.141
Geometric morphometric vs Binary coding	0.6642	0.001	0.4967	0.001	0.6429	0.002	0.9138	0.008
Geometric morphometric vs Wilkinson (1997) recoding	0.6587	0.001	0.485	0.001	0.6454	0.001	0.8943	0.002

The distances calculated were compared using Spearman's rank rho values, where p is the permutational probability derived from data set reshuffling.

berg 2008), but biological homology for phylogenetic analysis is sometimes more subjective because 'different workers will perceive and define characters in different ways' (Smith 1994). Hence, there is a long-running debate and extensive literature on the appropriateness of different character coding strategies in representing concepts of anatomical homology for phylogenetic analysis, particularly for parsimony analysis (de Pinna 1991; Forey and Kitching 2000). Intuitively, cladistic data sets compiled for phylogenetic analysis, but exploited for disparity analysis, will perpetuate these contingencies of character coding strategies (and interpretations of biological homology) as artefacts in plots of morphospace occupation and its evolution. However, the results of our analyses do not support this intuition.

Thus, Euclidean distance matrices derived from the cladistic data sets that use different character coding strategies (Fig. 1A–B) are invariably highly correlated (Table 2), suggesting that alternative codings of the same underlying variation all capture something of the disparity implicit in the underlying variation. Considering the relatively small taxon sample used here, our results are promising. Revision of concepts of biological homology appears to have had no substantial impact upon perceived disparity given that the Euclidean distance matrix derived from Wilkinson's revised data set (Wilkinson 1997) is comparable with the two representations of Wake's (1993) data set, which was the subject of his critique (Table 2). This may occur

because revisions to cladistic data sets are approximately randomly distributed and usually encompass only a small percentage of the total set of characters.

Perhaps the most surprising result, given that morphometric and cladistic data are based on different (albeit related) anatomical characters, is that the Euclidean distance matrices from all of the cladistic data sets are all moderately correlated with morphometric distances. Ultimately, this suggests that the cladistic and geometric morphometric data sets capture morphological disparity in a sufficiently similar way that they appear to describe the same phenomenon. This conclusion is important if we seek to obtain a more general understanding of the evolution of organismal disparity.

From a biological perspective, it is important to note that none of the neuroanatomical characters were replicated in the cranial shape data set except for presence/absence of the stapes (Ch1 of ear data/landmarks 47–50), and perhaps also the autapomorphic angle of nasal cavity (Ch2 of olfactory–vomeronasal system data/landmarks 1 and 2 relative to others). Thus, finding congruence between the morphometric and cladistic data sets suggests concerted evolution of soft tissue and hard tissue of the caecilian head, potentially due to morphological integration (*sensu* Olson and Miller 1999). It has been suggested that some of the variation in cranial shape is due to ecological differences among species, particularly in how much the head is used during head-first burrowing in
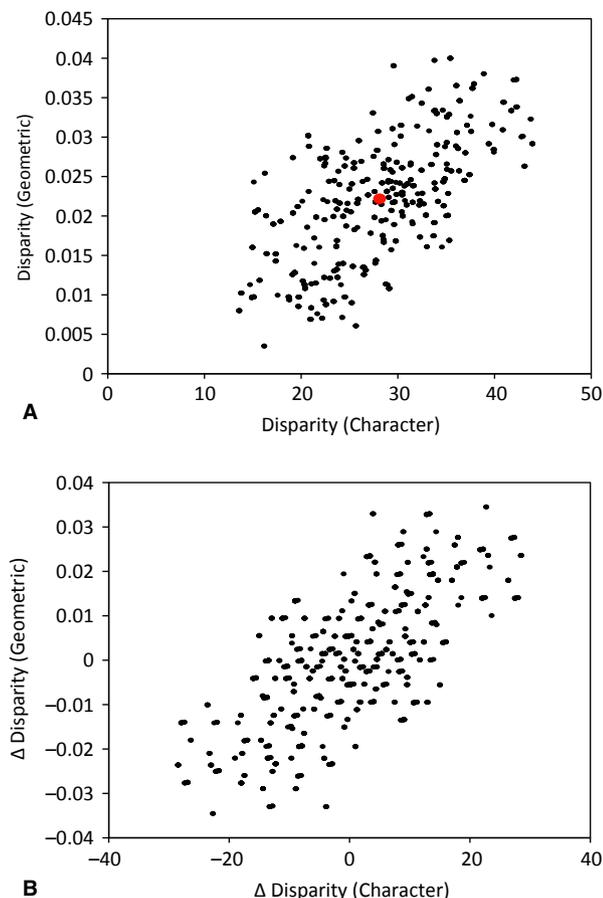
FIG. 2. Partial disparity of subsamples and the difference in disparity between subsamples based on multistate character coding and the geometric morphometric data set. Disparity is calculated as the average-squared distance between taxa within morphospace. A, partial disparity of 1000 subsamples of five random caecilian species; disparity of the entire data set is shown in red. B, the difference in disparity between two random and non-overlapping groups of five caecilian species based on the two metrics.

caecilians (Sherratt *et al.* 2014 and references therein). The similar patterns of diversification shown by neuro-anatomical characters, which pertain to sensory structures that may be more or less important in these habitats, highlight that to understand ecomorphological variation, we should be looking at a range of phenotypic data. Furthermore, cranial shape is clearly phylogenetically structured at the family level (Sherratt *et al.* 2014) and, thus, from this we can infer that the neuroanatomical characters also retain a degree of phylogenetic signal.

Can these conclusions be generalized? This is not, unfortunately, a topic that can be addressed readily through simulation study, and so to answer this question, comparable empirical analyses of other groups are needed. Nevertheless, our results are encouraging in that they support the use of cladistic discrete character data sets as a more scalable proxy for morphometric characterization of organismal disparity. Indeed, discrete character data sets are perhaps preferable in the sense that, in addition to encompassing the gain and loss of structures, they readily allow all aspects of organismal biology to be captured, as opposed to morphometrics which, for entirely practical reasons, is invariably only ever applied to proxy components of anatomy, such as the skull of vertebrates (as in the present study), where readily comparable structures permit clear identification of homologous landmarks. As such, discrete character data sets may offer the greatest potential in facilitating tests of general hypotheses, such as maximal initial disparity, using data sets at the grandest taxonomic scale. Although there is a vast resource of published data sets from phylogenetic analyses, this objective warrants the construction of bespoke supermatrices that capture not only the similarities but also the differences between taxa.

DATA ARCHVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.mm5m1

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