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The evolution of cranial form and function in theropod dinosaurs: insights from geometric morphometrics

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RH: Geometric morphometrics of theropod dinosaurs

Abstract: Theropod dinosaurs, an iconic clade of fossil species including *Tyrannosaurus* and *Velociraptor*, developed a great diversity of body size, skull form, and feeding habits over their 160+ million year evolutionary history. Here we utilise geometric morphometrics to study broad patterns in theropod skull shape variation, and compare the distribution of taxa in cranial morphospace (form) to both phylogeny and quantitative metrics of biting behaviour (function). We find that theropod skulls primarily differ in relative anteroposterior length and snout depth, and to a lesser extent in orbit size and depth of the cheek region, and oviraptorosaurs deviate most strongly from the “typical” and ancestral theropod morphologies. Non-carnivorous taxa generally fall out in distinct regions of morphospace and exhibit greater overall disparity than carnivorous taxa, whereas large-bodied carnivores independently converge on the same region of morphospace. The distribution of taxa in morphospace is strongly correlated with phylogeny, but only weakly correlated with functional biting behavior. These results imply that phylogeny, not biting function, was the major determinant of theropod skull shape.

Keywords: biomechanics; Dinosauria; geometric morphometrics; macroevolution; Mesozoic; phylogenetic comparative methods; phylogenetic eigenvector regression; Theropoda

Introduction

Theropod dinosaurs have captured the public imagination because they include some of the largest terrestrial predators in earth history, most notably the iconic *Tyrannosaurus rex* (Paul, 1988; Brusatte *et al.*, 2010a). Not all theropods were colossal megapredators, however. Over their 160+ million year evolutionary history, non-avian theropods developed a great diversity of body size, skull morphologies, and feeding habits (Weishampel *et al.*, 2004). Species ranged from a few kilograms to over six tons in mass (Christiansen & Farina, 2004; Carrano, 2006; Therrien & Henderson, 2007), possessed an array of skull morphologies (including long-snouted, deep-skulled, crested, and toothless forms: Weishampel *et al.*, 2004), and experimented with a wide variety of diets (including pure carnivory, omnivory, and obligate herbivory) (Barrett, 2005; Zanno *et al.*, 2009; Zanno & Makovicky, 2011). New fossil discoveries are consistently revealing novel body plans and presumed ecological behaviors for Mesozoic theropods (Brusatte *et al.*, 2009; Longrich & Currie, 2009; Novas *et al.*, 2009; Xu *et al.*, 2009, 2011; Csiki *et al.*, 2010), leading to an ever-greater understanding of this remarkable group of fossil organisms.

Although theropods are archetypal dinosaurs in the public eye, and perhaps the most intensely studied dinosaur group, there has been little work on large-scale macroevolutionary patterns across theropod phylogeny and evolutionary history. In particular, there has been no quantitative documentation of broad patterns of skull shape variation in theropods, and little examination of how differences in cranial morphology relate to feeding behaviour (but see Rayfield, 2005; Sakamoto, 2010). As a result, several major questions remain unanswered. What are the principal ways in which theropod skulls vary, and which subgroups have the most atypical morphologies? Is cranial morphology tightly correlated to phylogeny and functional behaviour, and which of the two was more important in shaping theropod skull evolution? Did the evolution of non-carnivorous diets allow theropods to explore new, and

perhaps larger, regions of morphospace, as has been suggested but not yet tested (Zanno *et al.*, 2009)? Conversely, are colossal large-bodied theropods (a body type that independently evolved several times: Carrano, 2006) morphologically constrained relative to other species, as has been noted in some living mammals that solely eat meat (Holliday & Stepan, 2004)? Do distantly-related taxa with similar feeding styles converge on the same regions of morphospace?

We attempt to answer these questions with an integrated toolkit of morphological, functional, and phylogenetic data. As the basis for this study, we utilise geometric morphometrics to study variability in the shape of the theropod skull. These techniques, which model a series of specimens using homologous landmarks and utilise multivariate statistics to elucidate major patterns of shape variation, are commonly used in studies of fossil and living organisms (e.g., O'Higgins, 2000; Zelditch *et al.*, 2004; Stayton & Ruta, 2006; Pierce *et al.*, 2008, 2009; Young *et al.*, 2010, in press). However, geometric morphometrics have infrequently been used to study dinosaurs, and most studies have employed these methods to examine ontogenetic variation (Chapman, 1990; Egi & Weishampel, 2002), inform taxonomic decisions (Chapman, 1990), and study locomotory behaviour (Bonnar, 2004, 2007; Chinnery, 2004), rather than quantify large-scale macroevolutionary patterns over long time scales and within a phylogenetic context (but see Young & Larvan, 2010). Here, we present a novel landmark-based morphometric analysis that reveals major patterns of theropod skull variation and allows species to be plotted into a morphospace. The positions of taxa in morphospace are compared to phylogeny and quantitative measures of theropod biting performance (Sakamoto, 2010), giving insight into large-scale patterns and processes of theropod cranial evolution during the Mesozoic.

Materials and methods

Geometric morphometrics

We analyzed morphological variation in the cranium of non-avian Mesozoic theropod dinosaurs using two-dimensional geometric morphometrics, a quantitative technique utilised to summarize and study shape variation across a collection of specimens (Bookstein, 1991; O'Higgins, 2000; Zelditch et al., 2004). These methods are held to be superior to traditional morphometric techniques, often based on multivariate analysis of length and angle measurements, because they preserve geometry, are better able to separate shape from size-related variation, and better capture subtle sources of variation that are not easily summarized by simple measurements (O'Higgins, 2000; Rohlf, 2000).

We encapsulated the cranial geometry of 51 species of theropod using 24 type 1 and 2 homologous landmarks (Bookstein, 1991; O'Higgins, 2000), which were plotted on photographs and published reconstructions using the program tpsDig2 (Rohlf, 2010) (Fig. 1a). After plotting landmarks on all 51 specimens (one specimen per species) it became apparent that many specimens had a large number of landmarks that could not be plotted because of poor preservation or missing bones. Missing data are not ideal, because they reduce the statistical power of the analysis. Therefore, we proceeded with two datasets: a 26-taxon dataset that could be scored for all landmarks and a 36-taxon dataset that could be scored for a reduced set of 13 landmarks. The decision to use a 36 taxon/13 landmark dataset aimed to maximize both the number of taxa and landmarks that could be included, as well as permit inclusion of representatives of all major theropod subclades.

For both the 26- and 36-taxon datasets, landmark coordinates were superimposed using Generalized Procrustes Analysis (GPA) in MorphoJ (Klingenberg, 2011), which serves to minimize non-shape variation between specimens, such as that caused by size, position,

and rotation. This procedure produced a set of GPA “corrected” landmark coordinates, which were then converted into a covariance matrix and subjected to Principal Components Analysis (PCA), also using MorphoJ. This multivariate analysis assimilates data from all landmarks and reduces them into a distilled set of PC scores that summarize the skull shape of each taxon. Because our PCA of both the 26- and 36-taxon datasets revealed that one particular group of theropods, the short-and-deep-skulled oviraptorosaurs (*Osmolska et al.*, 2004), were outliers relative to all other taxa on PC1, we also performed supplementary analyses of each dataset with oviraptorosaurs excluded from the PCAs. These additional datasets included 24 and 31 taxa, respectively. Therefore, in the remainder of this paper, we will discuss four separate datasets: the 26- and 36-taxon datasets that include oviraptorosaurs and the 24- and 31-taxon datasets that do not.

Theropod skull function

As part of this study, we wish to compare theropod skull form (based on the morphometric analysis) with a measure of cranial function. We quantify theropod functional performance with a straightforward and well-established metric: the mechanical advantage (MA), defined as the ratio of the muscle moment arm (effort) to the biting moment, of three major cranial muscle groups (Westneat, 1994). MA measurements for several theropods were recently presented by Sakamoto (2010), and we built upon this study by adding measurements for 25 additional taxa (total of 60 taxa), thereby compiling a dataset of functional metrics for 35 of the 36 taxa included in the morphometric analysis. The MA measures for each muscle group were subjected to PCA (see Sakamoto [2010] for details), resulting in a set of PC scores for each taxon, which are useful proxies for function. We reiterate that the MA quantifies a very specific aspect of skull function, namely the strength and speed of the bite, and that other functional metrics may relate to skull shape in different ways. We chose MA because it is

straightforward to measure, it can be measured in a wide range of theropod specimens (unlike, for instance, estimates of skull strength generated from finite element analysis, which has only been conducted on a handful of taxa: Rayfield [2005]), has well understood mechanical properties (Westneat, 1994), and can be measured using two-dimensional skull images (and thus is roughly an equivalent type of proxy to the form proxies generated from the morphometric analysis).

Morphological disparity

Morphological disparity measures the anatomical variety exhibited by a group of organisms (Foote, 1993; Wills *et al.*, 1994; Ciampaglio *et al.*, 2001). Disparity calculations require some measure of morphological form for each organism being assessed, and we used PC scores from the PCA of the GPA corrected coordinates as a proxy for theropod skull shape.

Comparative disparity is assessed by binning taxa into various pre-defined groups (e.g., taxonomic, temporal, ecological) and calculating disparity metrics for each, which can then be compared to determine whether certain groups have a greater variety of morphological form than others.

We divided our taxa into dietary and taxonomic categories. Dietary categories included carnivores and non-carnivores, as well as large-bodied carnivores, carnivorous theropods that are not large-bodied, and all theropods that are not-large bodied (regardless of diet). Large-bodied is here defined as all taxa with skulls greater than 65 cm in length, a category that includes several independent radiations of colossal theropods such as abelisaurids, tyrannosauroids, and allosauroids (Carrano, 2006). Non-carnivorous theropods are identified based on published studies of theropod diet (see Zanno & Makovicky [2010] for an overview), and are here held to include the aberrant toothless ceratosaur *Limusaurus* (Xu *et al.*, 2009), as well as four clades: the ornithomimosaur (Kobayashi *et al.*, 1999;

Norell *et al.*, 2001; Barrett 2005; Zanno & Makovicky, 2011), therizinosauroids (Zanno *et al.*, 2009; Zanno & Makovicky, 2011), alvarezsaurids (Senter, 2005; Longrich & Currie, 2009; Zanno & Makovicky, 2011), and oviraptorosaurs (Zanno & Makovicky, 2011). Finally, taxonomic categories included: Basal Theropoda (paraphyletic), Ceratosauria, Basal Tetanurae (paraphyletic), Tyrannosauroidae, Oviraptorosauria, and Dromaeosauridae; categories at this taxonomic level were selected so that sample sizes were approximately equivalent, and so that groups were not nested within each other.

Four disparity metrics were calculated for each category: the sum and product of the ranges and variances on the first 5 PC axes generated from the 36-taxon morphometric dataset, using the program RARE (Wills, 1998). These same measures were then calculated for identical categories using the 31-taxon morphometric dataset in which oviraptorosaurs were excluded (disparity was not calculated using the 24- and 26-taxon datasets, because all taxa in these analyses are also included in the more inclusive 31- and 36-taxon datasets, respectively). The first five PC axes were chosen in both cases because these axes were deemed significant by reference to the “broken-stick” method, in which a scree plot (percentage of total variance against number of principal components) is examined for a significant break in its slope (following Wills *et al.*, 1994). Range measures summarize the entire spread of morphospace occupied by the taxa in question, whereas variance denotes mean dissimilarity among the taxa (their spread in morphospace) (Wills *et al.*, 1994). Statistical significance of disparity comparisons was assessed by the overlap or non-overlap of 95% confidence intervals, generated by bootstrapping, and rarefaction was used to assess whether disparity differences are robust to sample size differences between categories (variance metrics are usually more robust to sample size bias: Wills *et al.*, 1994; Butler *et al.*, in press).

Phylogenetic comparative methods

One major question is: is theropod skull shape significantly correlated with phylogeny? A strong phylogenetic signal means that closely related species tend to fall out closer in morphospace than more distantly related species (Klingenberg & Gidaszewski, 2010).

We used three methods to assess phylogenetic signal in the morphometric dataset, in each case using a composite theropod phylogeny for reference (see online supporting information). First, we performed a permutation test in MorphoJ in which the phylogeny is held constant and the PC scores for each taxon are randomly swapped across the tree 10,000 times (Klingenberg & Gidaszewski, 2010). The null hypothesis of no phylogenetic signal is discarded if less than 5% of permutations result in a tree length (calculated using squared change parsimony) that is shorter or equal to the value obtained from the original data. Second, we performed a multivariate phylogenetic eigenvector regression (MPVR) (Diniz-Filho *et al.*, 1998), in which phylogeny, represented by principal coordinate axes derived from a phylogenetic distance matrix, is regressed against form metrics (significant axes of PC scores from the morphometric analyses). The multivariate R^2 value and p -value represent the strength and significance of the correlation, respectively, between the form and phylogeny proxies. Third, we used the techniques of Blomberg *et al.* (2003), which compare the variance in phylogenetically independent contrasts (PICs) (Felsenstein, 1985) in PC1 scores with those computed from permutations of those scores across the same tree topology. If the variances for the original data are lower than those derived from the permutations, then there is a significant phylogenetic signal in the morphometric data (see online supporting information for full explanation).

Form vs. function

Another major question is: is theropod skull shape significantly correlated with function? We performed three correlation analyses on form and function metrics to assess this question. First we performed a two-block partial least squares (2B-PLS) analysis in MorphoJ, using Procrustes coordinates from the geometric morphometric analysis as the form metric block and the biomechanical coefficients standardized by their respective standard deviations as the function metric block. The RV coefficient was determined and the p -value was computed through 10000 permutations; these represent the strength and significance of the correlation, respectively, between the form and function proxies. Second, we performed a multivariate multiple regression (MMR) analysis in R, on the significant axes of PC scores for form (PC1 to PC5 or PC1 to PC7) and function (PC1 and PC2). The multivariate R^2 value and p -value represent the strength and significance of the correlation, respectively, between the two matrices. Third, we performed PIC correlation analyses on PC1 and PC2 of both form and function. Both sets of metrics were transformed into PICs and an ordinary least squares regression model was fitted through the origin for all pairwise comparisons of form and function metrics (i.e., PICs of PC1 and PC2 of form and function). Once again, R^2 value and p -value represent the strength and significance of the correlation, respectively. We also used the disparity methods described above to calculate measures of functional disparity for several dietary and taxonomic categories (based on PC1 and PC2 function scores), to assess whether clades with high morphological disparity also exhibit high functional variety.

Primary determinants of theropod skull shape

Finally, following from the above assessment of phylogenetic and functional signals in the morphometric data, another major question of interest is: does phylogeny or function better explain the range of variation in theropod skull shape? We addressed this question by

performing a series of MPVR that partition variance in morphometric form metrics (a matrix of PC scores) into components related solely to function, a combination of function and phylogeny, solely to phylogeny, and to other sources not explained by either function or phylogeny, following published protocols (Desedivses *et al.*, 2003) (see online supporting information for full explanation of this procedure).

Results

Morphospace occupation and major shape changes

The PCAs show that the majority of shape variation in both the 26- and 36-taxon datasets is summarized by the first two PC axes (46.2% and 18.6% of total variance, respectively, for the 26-taxon dataset; 56.9% and 16.5% for the 36-taxon dataset). A two-dimensional morphospace (PC1 vs. PC2) for the 36-taxon dataset is depicted in Figure 2 and the major changes in skull shape along the two primary PC axes, based on all 24 landmarks for the 26-taxon dataset, are shown in Figure 1b-c. The online supporting information includes plots of PC3 vs. PC4 for the 36-taxon study, as well as PC1-4 plots for the 26-taxon study and a diagram of major shape changes on the 13 landmarks in the 36-taxon study (Fig. S2, S3, S7). PC1 largely describes variation in the anteroposterior length of the skull, as well as the dorsoventral depth of the snout and the depth and size of the external naris. PC2 largely describes the size of the orbit (length and depth), the depth of the cheek region (the area underneath and slightly anterior to the orbit), and to a lesser extent, the depth of the temporal region (the area surrounding the lateral temporal fenestra). The caption for Figure 2 itemizes the specific changes (from negative to positive) along the two primary PC axes. In both the 26- and 36-taxon morphospaces, the most salient observation is that oviraptorosaurs are placed in a unique position on PC1, far separate from all other theropods. This is not true of PC2-4, however.

The PCAs for the two supplementary datasets excluding oviraptorosaurs (the 24- and 31-taxon datasets) also show that the majority of shape variation is summarized by the first two PC axes (38.6% and 19.5% of total variance, respectively, for the 24-taxon dataset; 37.9% and 23.13% for the 31-taxon dataset). A two-dimensional morphospace (PC1 vs. PC2) for the 31-taxon dataset is depicted in Figure 3; four-dimensional morphospaces (PC1 vs. PC2, PC3 vs. PC4) for both datasets are depicted in the online supporting information, along with diagrams depicting major shape changes on each landmark (Fig. S4, S5, S8, S9). With oviraptorosaurs excluded, PC1 in the 24-taxon dataset describes the depth of the snout and the size of the external naris (Figure S4), as it does in the full 26-taxon dataset with oviraptorosaurs included (Figure S2). However, this axis now also describes a large amount of variation in the depth of the orbit, cheek, and temporal region, which were summarized by PC2 when oviraptorosaurs were included. Furthermore, when oviraptorosaurs are excluded, PC2 largely describes the anteroposterior length of the snout, which was mainly a component of PC1 when oviraptorosaurs were included.

Both the outlying position of oviraptorosaurs on PC1 in the original 26- and 36-taxon analyses and the changes in PC loadings between the datasets that include and exclude oviraptorosaurs suggest that these short-skulled theropods contribute disproportionately to the PC analysis. PC1 of the original 26- and 36-taxon datasets largely, but not entirely, summarizes major shape differences between oviraptorosaurs and other theropods (but this is not true of successive PC axes). In other words, oviraptorosaurs are clearly the most aberrant theropods in terms of their skull shape (see further discussion of this point below).

Relationship between specimen size and PC scores

Although Procrustes Analysis largely factors out non-shape differences between specimens, such as those caused by size, there is still the possibility that some relationship between size

and PC scores remains (i.e., that some PC axes may be allometry, not shape, axes). Therefore, we tested whether the first three PC axes of all four datasets are significantly correlated with the centroid size of each specimen (Table S3). There is no significant relationship between size and PC3 for all datasets and between size and PC1 for the two datasets that include oviraptorosaurs (26- and 36-taxon datasets), but there is for the two datasets excluding oviraptorosaurs (24- and 31-taxon datasets). Similarly, there is a significant relationship between size and PC2 for all datasets. However, all of these significant relationships (except PC2 for the 31-taxon dataset) disappear when large-bodied taxa are removed. Therefore, although some relationship between size and PC scores remains, none of the axes (except perhaps for PC2 in the 31-taxon dataset) can be interpreted simply as allometry axes. PC1 and PC2 retain some information on body size in some datasets, but this is primarily because many of the largest theropods in the analysis have a similar skull shape. We interpret this as evidence of morphological convergence of the several independent radiations of large-bodied theropods.

Morphological disparity

When oviraptorosaurs are included, the most salient result of the disparity calculations is that non-carnivores have higher disparity than carnivores based on all four disparity metrics, but these results are statistically significant only for sum of variances and marginally insignificant for product of variances (there is only a very slight overlap of error bars; see online supporting information) (Table 1; Fig. S10). Although there is a clear sample size difference between the two categories ($n=26$ for carnivores, $n=10$ for non-carnivores), rarefaction analysis shows that when samples are equalized and disparity is subsampled, non-carnivores still have a greater disparity than carnivores at all sample sizes (Fig. S11). Similarly, large-bodied carnivores have significantly lower disparity than all other theropods,

but this pattern is almost entirely driven by the presence of non-carnivorous taxa (especially oviraptorosaurs) in the “other theropods” dataset (Fig. S13, S14). Indeed, when large-bodied carnivores are compared to all other (non-large-bodied) carnivores, the two groups are found to have statistically indistinguishable disparity (Fig. S13).

With that being said, the comparatively high disparity of non-carnivorous taxa compared to carnivorous taxa and the low disparity of large-bodied carnivores compared to other theropods seem to be driven largely by the presence of the highly aberrant oviraptorosaurs in the “non-carnivore” and “non-large-bodied carnivore” categories. When disparity metrics are calculated using the 31-taxon dataset that excludes oviraptorosaurs from the PCA, carnivores are now found to have higher disparity based on the range metrics and non-carnivores higher disparity based on the variance metrics, but none of these differences are statistically significant (Fig. S12). Furthermore, although large-bodied carnivores still have lower disparity than all other theropods, these results are no longer significant (Fig. S15).

In sum, therefore, these results indicate that non-carnivorous theropods as a whole do have higher disparity than carnivores (based on the significant and marginally insignificant results generated from the variance calculations), but this is mostly the result of the peculiar skull shapes of one particular non-carnivorous subclade, the oviraptorosaurs. When all other non-carnivores are binned together (ornithomimosaurids, alvarezsaurids, therizinosaurids, *Limusaurus*), they collectively have indistinguishable disparity from all carnivores. Oviraptorosaurs also largely cause the relatively high disparity of non-large-bodied theropods relative to large-bodied taxa. Therefore, large-bodied carnivores do have significantly lower disparity than all other theropods, but only if oviraptorosaurs are included and only if the “other theropod” category includes both carnivores and non-carnivores. The disparity of

large-bodied taxa is indistinguishable from that of smaller carnivores, or smaller carnivores plus all non-oviraptorosaur non-carnivores.

Disparity comparisons between taxonomic categories are mostly non-significant due to small sample sizes, but oviraptorosaurs and ceratosaurs (two groups including non-carnivorous taxa) have higher disparity than the entirely-carnivorous basal theropods, basal tetanurans, tyrannosauroids, and dromaeosaurids (Fig. S16). Some of the comparisons involving oviraptorosaurs are significant, which is strong evidence that this aberrant non-carnivorous clade exploited a greater swath of morphospace than other theropod subclades (see online supporting information). Tyrannosauroids, despite their great range of body size and noticeable differences in skull form between gracile and crested basal taxa and robust and deep-skull derived species, have similar measures of disparity as other carnivorous groups (basal theropods, basal tetanurans, dromaeosaurids). When these calculations are repeated using the 31-taxon dataset excluding oviraptorosaurs no significant differences between clades are found, although ceratosaurs still have relatively (but insignificantly) high disparity compared to other groups (Fig. S17).

Phylogenetic comparative methods

All three analyses indicate that theropod cranial form is significantly correlated with phylogeny. When subjected to the permutation test in MorphoJ, all four datasets are found to have significant phylogenetic signal (24-taxon dataset: tree length=0.16899822, $p < 0.001$; 26-taxon dataset: tree length=0.24750721, $p < 0.0001$; 31-taxon dataset: tree length=0.17546221, $p < 0.001$; 36-taxon dataset: tree length=0.26278840, $p < 0.0001$). Multivariate phylogenetic eigenvector regression reveals that form metrics (PC scores) exhibit significant correlations with phylogeny in all four datasets (all sample sizes, both with and without oviraptorosaurs) (Table S7). Finally, Blomberg's methods show that PC1 of form has a significant

phylogenetic signal (Table S8) in all datasets, whereas PC2 of form usually is significantly correlated with phylogeny.

Form vs. function

2B-PLS reveals no significant correlations between Procrustes coordinates (form) and standardized biomechanical coefficients (function), whereas MMR reveals significant but weak correlations between morphospace and function space (PC scores of form and function; Table S9). This indicates that multivariate correlation between form and function is either nonexistent or weak, based on the form and function metrics that we use as proxies. The least squares regression of PICs of form and function metrics reveals that there is no significant correlation between the single most important (most explanatory) PC values of form and function ($PC1_{\text{form}}$ vs. $PC1_{\text{function}}$) for all but one dataset, the correlation of which is extremely small (Figs. S23-25). Regressions of other form and function metrics ($PC2_{\text{form}}$ and $PC2_{\text{function}}$) against each other and PC1s are marginally significant but weak, with all r^2 values less than 0.44. This indicates that major patterns of variation in form and function are only weakly correlated.

Measures of functional disparity, calculated using the PC scores from the mechanical advantage analysis, indicate that carnivorous theropods have greater disparity than non-carnivorous taxa (significant only for sum of ranges, however), and rarefaction shows that this relationship holds at all sample sizes (Figs. S18-S20). Therefore, opposite to the relationship in form disparity, carnivores are more functionally diverse than non-carnivores.

Primary determinants of theropod skull shape

The series of MPVR reveals that two sources of variation, phylogeny and a combination of phylogeny and function, together explain about 71~85% of total variance in form

(morphospace variance) (Tables S10-S11). The phylogenetically structured functional variance is only 17~36%, whereas variance attributed to phylogeny alone is 49~60%. Further, the lack of significantly strong correlation between form and function (see above) indicates that any proportion of variance in form explained by function is almost entirely due to phylogenetic constraint rather than phylogenetically structured adaptive evolution. Therefore, based on these results, as well as the strong correlations between phylogeny and form but weak correlations between function and form, phylogeny is considered to be a greater determinant of theropod skull shape than biting function.

Discussion

Major patterns in theropod cranial shape

Theropod skulls vary greatly in length, depth, and in the size of the orbit, naris, and lateral temporal fenestra. The largest amount of variation, which is encapsulated by PC1 in the analyses that include oviraptorosaurs, involves skull length and snout depth, whereas there is also great variance in the size (depth and length) of the orbit and depth of the temporal (posterior) portion of the skull (encapsulated by PC2). Interestingly, the depth of the snout, a major component of PC1, is not necessarily associated with the depth of the posterior portion of the skull, which is a large component of PC2. This is intuitively reasonable, as these regions are under different biomechanical, functional, and developmental constraints.

Whereas snout depth is associated with the size of the naris and the antorbital fenestra (a sinus that probably lightened the skull: Witmer [1997]), posterior skull depth is closely tied to the size of the orbit, the configuration of the endocranial cavity, and the attachment area for jaw musculature (Holliday, 2009).

Based on the PCA with oviraptorosaurs included, most theropods cluster fairly closely together in cranial morphospace, in the vicinity of the origin (Fig. 2). The most significant

outliers are oviraptorosaurs, the bizarre toothless and crested theropods that are closely related to birds (Osmolska *et al.*, 2004). They occupy a highly positive region on PC1, reflecting their especially anteroposteriorly shortened skulls, and a relatively negative position on PC2, reflecting their large, circular orbits. Other distinctly placed taxa include the toothless ceratosaur *Limusaurus* (Xu *et al.*, 2009), which is among the most negatively-placed taxa on PC2 due to its enormous orbit and shallow cheek region, and the large-bodied carnivorous abelisaurids, which are positively positioned on PC1 due to their shortened skulls. In general, the morphospace occupation patterns show that oviraptorosaurs have an extreme cranial shape, and deviate most strongly from both the “typical” and the ancestral theropod morphology. This is reiterated by the fact that the major shape changes on PC1 and PC2 change dramatically between the PCAs that include and exclude oviraptorosaurs (see above).

When the PCAs are repeated after excluding oviraptorosaurs, it is now seen that large-bodied theropods, including distantly-related groups such as tyrannosaurids, abelisaurids, and allosauroids, preferentially occupy a highly positive region of PC1. In this dataset, PC1 largely summarizes variation in the depth of the orbit, cheek, and temporal region, and large-bodied taxa are positioned here due to their deep posterior skulls and narrow, keyhole-shaped orbits. The most positively placed taxon, the abelisaurid *Carnotaurus*, occupies an extreme position on PC1 due to its remarkably short and deep skull and constricted orbit (Bonaparte *et al.*, 1990). The toothless ceratosaur *Limusaurus* still occupies a unique position, this time in a highly positive region on PC2, due to its elongate skull and large orbit and shallow cheek region (which also contribute to PC2, although less extremely than to PC1). These observations indicate that, with oviraptorosaurs excluded, large-bodied theropods (especially abelisaurids) deviate most from the “typical” and ancestral theropod morphologies.

Theropod cranial shape and diet

Although the ancestral theropod was almost certainly carnivorous, more derived members of the clade developed a variety of dietary strategies, including omnivory, possible insectivory, and obligate herbivory (Barrett, 2005; Senter, 2005; Zanno *et al.*, 2009; Zanno & Makovicky, 2011). Our PCA results that include oviraptorosaurs show that non-carnivorous species have a greater disparity than carnivorous forms, and are also mostly positioned in separate regions of morphospace. There is no single “non-carnivorous” portion of morphospace, but rather each non-carnivorous clade occupies its own distinct swath. The non-carnivorous oviraptorosaurs, and to a lesser extent *Limusaurus*, are set well apart from carnivores, including their closest carnivorous relatives, and the non-carnivorous ornithomimosaur and alvarezsaurids (*Shuvuuia*) are positioned at the lower left hand corner of the morphospace, as they possess among the most negative scores on both PC1 and PC2. The single therizinosauroid exemplar, *Erlikosaurus*, is the only non-carnivore that is interspersed within a “carnivorous” region of morphospace. It is noteworthy that the various clades of non-carnivores mostly occupy different regions of morphospace (the exception being that ornithomimosaur and *Shuvuuia* are close together), indicating that different radiations of non-herbivorous taxa are associated with distinctly different cranial morphologies. In sum, these patterns suggest that the acquisition of non-carnivorous diets enabled theropods to explore different, and larger (due to their higher collective disparity), regions of morphospace, which is consistent with Zanno *et al.*'s (2009) hypothesis that dietary plasticity was an important driver of theropod morphological evolution.

This conclusion is tempered somewhat by the PCAs that exclude oviraptorosaurs. The collective disparity of non-carnivorous taxa is no longer greater than that of carnivores,

meaning that non-oviraptorosaurian non-carnivores did not exploit a greater swath of morphospace than carnivores. However, *Limusaurus* is still set apart from all other theropods due to its highly positive score on PC2, and the non-carnivorous ornithomimosaur and alvarezsaurids (*Shuvuuia*) are still positioned at the lower left hand corner of the morphospace. Furthermore, the therizinosauroid *Erlikosaurus* is still positioned within a “carnivorous” region of morphospace. These results indicate that the relative morphospace positions of other non-carnivorous taxa are insensitive to the inclusion or exclusion of oviraptorosaurs, and that some non-carnivorous clades did explore different (although perhaps not larger) regions of morphospace compared to carnivores. In other words, the distinct cranial morphology of non-carnivores is not entirely due to the highly aberrant nature of oviraptorosaurs, even if the overall higher disparity of non-carnivores relative to carnivores may be.

In contrast to non-carnivorous theropods, large-bodied theropods cluster together in morphospace, both when oviraptorosaurs are included and excluded. These taxa—tyrannosaurids, allosauroids, and the carnivorous ceratosaurs—overlap almost completely on PC2 when oviraptorosaurs are included and PC1 when oviraptorosaurs are excluded, as they all have small, ovoid eyes and deep cheeks. They do, however, exhibit some variation in skull length (PC1 when oviraptorosaurs are included, PC2 when excluded). Each group represents an independent acquisition of large body size, and each has a most recent non-large-bodied ancestor close to the root of the theropod tree, yet they converge on the same region of morphospace, contra to the overall pattern of strong phylogenetic signal in skull shape (i.e., non-convergence). This is not simply due to the fact that PC1 and PC2 are allometric (body size) axes, as there is almost always no significant relationship between PC scores and specimen size in the non-large-bodied taxa (see above). Furthermore, when oviraptorosaurs are included, the large-bodied taxa have significantly lower disparity than all other theropods

(although this relationship does not hold when oviraptorosaurs are excluded). In total, these patterns suggest that there is a limited morphological toolkit for building a large-bodied dinosaurian hyperpredator (although perhaps no more limited than for building a smaller carnivore, as large-bodied carnivores and smaller carnivores have indistinguishable disparity). Low disparity and morphological convergence have also been noted among mammalian hypercarnivores (those taxa that solely eat meat) (Holliday & Stepan, 2004), and may be more general evolutionary phenomena unique to large-bodied carnivores and/or taxa that solely consume meat.

Form, function, and phylogeny

Theropod skull form is strongly correlated with phylogeny but only weakly correlated with the measure of function that we utilise (mechanical advantage of the jaw muscles), and our statistical tests show that phylogeny explains a substantially greater amount of variance in skull shape than does function. In other words, closely related species are more similar in morphology than with distantly related species, and distances in morphospace are more congruent with phylogenetic distances than with distances in function space. Therefore, phylogeny is the primary determinant of broad patterns in theropod skull shape, and theropod cranial anatomy was apparently subject to strong phylogenetic constraint. It is important to keep in mind that our study is a broad-scale analysis that examines the range of skull shapes across Mesozoic non-avian theropods, rather than a focused analysis that looks at subtle differences between many individual species. Therefore, our results show that higher-level theropod phylogeny is the best correlate of large-scale variation in theropod skull shape, but it is possible that this correlation would be weaker at lower taxonomic levels (i.e., within individual theropod subclades). A disconnect between strong higher-level, but weak lower-level, correlations between phylogeny and shape has been noted in extant pinniped mammals

(Jones & Goswami, 2010), and whether this holds true for theropods awaits the compilation of larger morphometric datasets as more fossils are discovered.

Although our statistical tests show weak correlation between skull shape and function, we do not argue that function played no role in shaping theropod cranial anatomy. The function metric that we use, mechanical advantage, specifically quantifies the biting performance and efficiency of theropods (Westneat, 1994; Sakamoto, 2010). This is only one of numerous possible functional metrics, and other measures, such as skull strength, may exhibit stronger correlations with skull shape. Testing this proposition awaits further biomechanical studies of theropods, and it would be especially interesting to determine whether estimates of skull strength generated from finite element modeling (Rayfield, 2005, 2007) and beam theory (Henderson, 2002) correlate with broad-scale patterns in theropod skull shape. A previous study that noted a correlation between theropod orbit size (form) and skull strength generated from beam theory models (function) suggests that this may be the case (Henderson, 2002).

Furthermore, it is possible that we do not find a strong correlation between form and function because biting performance (and perhaps other function metrics) may not correlate with major sources of skull variation, such as variance in length, snout depth, and cheek depth, but rather correlate with other, more subtle features that are not captured by the morphometric analysis. As our morphometric study quantifies cranial shape using two-dimensional coordinates plotted only on the lateral surface of the skull, it is possible that future studies using different protocols (three-dimensional coordinates, landmarks on the dorsal and palatal surfaces, etc.) may find different results.

The evolution of skull shape in theropods

By plotting phylogeny into morphospace, with the position of internal nodes calculated using squared change parsimony, it is possible to examine broad patterns in theropod cranial evolution. The following description utilises the full morphospace with oviraptorosaurs (Fig. 2), as it contains the largest sample of theropod taxa, but similar (although slightly different) patterns are evident by examining the morphospace ordinated without oviraptorosaurs (Fig. 3). Interestingly, the common ancestors of theropods, tetanurans, coelurosaurs, and maniraptorans are all located fairly closely in morphospace. The common ancestor of all theropods had a long skull, shallow snout, and a horizontal naris (negative position PC1), and a large, circular orbit and shallow cheek region (quite negative position on PC2). Moving progressively up the tree, the tetanuran common ancestor had a similar skull length as the theropod ancestor (nearly identical score on PC1), but a smaller orbit and deeper cheek region (more positive position on PC2). Finally, the coelurosaurian and maniraptoran common ancestors had proportionally longer skulls and a larger orbit and shallower cheek region (reversal to more negative scores on PC2).

It is difficult to confidently assess the amount of evolution between sister taxa, because large jumps in morphospace may reflect either great bursts of cranial evolution or be a figment of missing data (most theropods do not preserve complete or near-complete skulls and could not be included in this study, but if included they may fill gaps between widely separated clades). With this in mind, two patterns appear to be robust.

First, although non-carnivorous taxa generally occupy distinct regions of morphospace, only half of them in the current study (the oviraptorosaurs and *Limusaurus*) are far separated from their closest carnivorous relatives. The other half, including ornithomimosaurids, alvarezsaurids, and therizinosauroids, are only marginally separated from their closest carnivorous relatives. In other words, branch lengths between these taxa and

their carnivorous relatives are on the same order of magnitude as branch lengths between carnivorous sister taxa (see Figures 2 and 3 for quantification of branch lengths). Therefore, although these taxa may have unusual skull morphologies that do not overlap with those of carnivorous taxa (hence their distinct positions in morphospace), it did not require great amounts (and perhaps rates) of evolution to acquire these. This supports the notion that phylogeny is a greater influence on skull shape than function, as even many dietarily aberrant clades are, at least based on branch lengths, morphologically similar to close relatives with different feeding habits. Dietary and ecological habits do play a supporting role in shaping skull morphology, however, as shown by the larger relative disparity of non-carnivorous taxa (with oviraptorosaurs included) and the mostly distinct positions of most herbivorous clades in morphospace (even if they are located near carnivorous relatives).

Second, distantly-related large-bodied theropods converge on the same region of morphospace (especially on PC2 when oviraptorosaurs are included and PC1 when excluded). Along with the observations about the high disparity and distinct morphospace positions of non-carnivores, this shows that although phylogeny is a major constraint on theropod skull form, function (especially relating to feeding ecology) still played a role in shaping theropod cranial evolution.

The relative importance of phylogeny, function, and other potential drivers of theropod skull shape should become clearer as morphometric techniques become more refined and especially as datasets expand with the discovery of new theropod taxa.

Unfortunately, many of our statistical comparisons are non-significant due to the overlap of large error bars, which is almost certainly a function of small sample sizes in many cases. Small sample sizes also preclude the use of some additional statistical techniques, such as Discriminant Function Analysis, to more confidently test whether non-carnivorous subclades inhabited distinct regions of morphospace (alvarezsaurids and therizinosauroids, for instance,

are only represented by a single taxon each in this analysis, because complete or near-complete skull material for these clades is so rare). The overriding hypothesis that we present in this paper, which our overall sample size of 36 taxa and cocktail of multivariate methods are adequate to address, is that phylogeny and not biting function better explains broad patterns in theropod skull shape. We look forward to additional tests of this hypothesis as more data become available, as well as similar studies of other clades. Only studies such as these can address a fundamental, but largely unsolved, question in the evolution of many groups: was phylogenetic constraint or functional adaptation more important in shaping morphology?

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Fig. 1. Theropod skull shape analyzed using geometric morphometrics. (a) Homologous landmarks plotted on all skulls in the study. (b) Major changes in skull shape (based on each landmark) on principal component (PC) axis 1 for the 26-taxon, 24-landmark analysis. (c) Major changes in skull shape based on principal component axis 2 for the same analysis. Skull depicted in (a) is the basal tetanuran *Monolophosaurus* (modified from Brusatte *et al.*, 2010b).

Fig. 2. Two-dimensional theropod skull shape morphospace, based on the first two PC axes generated by the 36-taxon, 13-landmark analysis. The phylogenetic tree is mapped into morphospace, with internal nodes placed according to a squared-change parsimony optimization. Four major nodes (most recent common ancestor of Theropoda, Tetanurae, Coelurosauria, and Maniraptora) are labeled. Major changes in skull shape along the two PC axes are depicted in Figure S7. Changes along PC1 (negative to positive) reflect an anteroposterior shortening of the skull, a dorsoventral deepening of the snout, and reorientation of the long axis of the naris from a horizontal to an oblique orientation. Changes along PC2 (negative to positive) reflect a reduction in the area of the orbit, the development of a proportionally taller and shorter orbit, and a deepening of the cheek region. Theropod silhouettes courtesy of Scott Hartman (<http://www.skeletaldrawing.com/>).

Fig. 3. Two-dimensional theropod skull shape morphospace, based on the first two PC axes generated by the 31-taxon, 13-landmark analysis (excluding oviraptorosaurs). The phylogenetic tree is mapped into morphospace, with internal nodes placed according to a squared-change parsimony optimization. Four major nodes (most recent common ancestor of Theropoda, Tetanurae, Coelurosauria, and Maniraptora) are labeled. Major changes in skull shape along the two PC axes are depicted in Figure S9. Changes along PC1 (negative to

positive) reflect a dorsoventral deepening of the snout, orbit, and temporal region, and anteroposterior constriction of the orbit. Changes along PC2 (negative to positive) largely reflect a proportionally longer skull and anteroposterior lengthening of the orbit, as well as some changes in the depth of the temporal portion of the skull. Theropod silhouettes courtesy of Scott Hartman (<http://www.skeletaldrawing.com/>).

Table 1. Comparisons of morphological disparity, based on four metrics (the sums and products of the ranges and variances on the first five PC axes from the morphometric analysis), in different categories of taxa. Comparisons are shown between carnivores and non-carnivores, as well as large-bodied carnivores vs. both smaller carnivores (all other carnivores) and all other theropods (small carnivores + non-carnivores). Disparity metrics are calculated twice, first using the 36-taxon/13-landmark analysis that includes oviraptorosaurs and secondly with the 31-taxon/13-landmark analysis that excludes oviraptorosaurs (denoted by “no ovi.” in the table). The two numerical values for each comparison indicate the disparity metric for the group in question. For example, in the first comparison, carnivores have a sum of ranges of 0.81 and non-carnivores 0.99. Significant comparisons are denoted by SIG and one marginally significant comparison (in which the error bars for both measures ever so slightly overlap) is denoted by MSIG. Please see the online supporting information for more details, an explanation of the statistical significance tests, and graphical plots of all disparity metrics and their associated error bars.

Comparison	Sum of Ranges	Prod of Ranges	Sum of Variances	Prod of Variances
Carnivore vs. non-carnivore	0.81/0.99	0.15/0.17	0.011/0.044 SIG	0.0018/0.0035 MSIG
Carnivore vs. non-carnivore (no ovi.)	0.79/0.56	0.15/0.11	0.012/0.015	0.0017/0.0023
Large carn. vs. small carn.	0.54/0.57	0.10/0.11	0.006/0.006	0.0012/0.0012
Large carn. vs. all others	0.54/1.06 SIG	0.10/0.18 SIG	0.006/0.029 SIG	0.0012/0.0026 SIG
Large carn. vs. small carn. (no ovi.)	0.56/0.54	0.11/0.10	0.0069/0.0069	0.0014/0.0011
Large carn. vs. all others (no ovi.)	0.56/0.73	0.11/0.14	0.0069/0.009	0.0014/0.0016