A peer-reviewed version of this preprint was published in PeerJ on 18 January 2016.

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Cranial ontogenetic variation in early saurischians and the role of heterochrony in the diversification of predatory dinosaurs

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Non-avian saurischian skulls underwent at least 165 million years of evolution and shapes varied from elongated skulls, such as in Coelophysis, to short and box-shaped skulls, such as in Camarasaurus. A number of factors have long been considered to drive skull shape, including phylogeny, dietary preferences and functional constraints. However, heterochrony is increasingly being recognized as a major factor in dinosaur evolution. In order to quantitatively analyse the impact of heterochrony on saurischian skull shape, we have analysed five ontogenetic trajectories using two-dimensional geometric morphometrics in a phylogenetic framework. This allowed for the evaluation of how heterochrony affected overall skull shape through both ontogenetic and phylogenetic trajectories and how it impacted modular changes within the skull. Using principal component analyses and multivariate regressions, it was possible to quantify different ontogenetic trajectories in light of heterochrony. The results recovered here indicate that taxa underwent a combination of local paedomorphosis and peramorphosis within the skull along individual ontogenies and phylogenies, but that either peramorphosis or paedomorphosis dominated when the skull was considered as a whole. We found that the hypothetical ancestor of Saurischia led to basal Sauropodomorpha mainly through paedomorphosis, and to Neotheropoda mainly through peramorphosis. Paedomorphosis then led from Orionides to Avetheropoda, indicating that the paedomorphic trend previously found in advanced coelurosaurians may extend back into the early evolution of Avetheropoda. Not only are changes in saurischian skull shape complex due to the large number of factors that affect shape, but heterochrony itself is complex, with a number of reversals throughout non-avian saurischian evolution. The sampling of ontogenetic trajectories is considerably lower than the sampling of adult species and the current study represents a first exploratory analysis. To better understand the impact of heterochrony on cranial evolution in saurischians, the data set we present must be expanded and complemented with further sampling from future fossil discoveries, especially of juvenile taxa.
Cranial ontogenetic variation in early saurischians and the role of heterochrony in the diversification of predatory dinosaurs

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Short title: Heterochrony in early saurischian skulls
Abstract

Non-avian saurischian skulls underwent at least 165 million years of evolution and shapes varied from elongated skulls, such as in *Coelophysis*, to short and box-shaped skulls, such as in *Camarasaurus*. A number of factors have long been considered to drive skull shape, including phylogeny, dietary preferences and functional constraints. However, heterochrony is increasingly being recognized as a major factor in dinosaur evolution. In order to quantitatively analyse the impact of heterochrony on saurischian skull shape, we have analysed five ontogenetic trajectories using two-dimensional geometric morphometrics in a phylogenetic framework. This allowed for the evaluation of how heterochrony affected overall skull shape through both ontogenetic and phylogenetic trajectories and how it impacted modular changes within the skull. Using principal component analyses and multivariate regressions, it was possible to quantify different ontogenetic trajectories in light of heterochrony. The results recovered here indicate that taxa underwent a combination of local paedomorphosis and peramorphosis within the skull along individual ontogenies and phylogenies, but that either peramorphosis or paedomorphosis dominated when the skull was considered as a whole. We found that the hypothetical ancestor of Saurischia led to basal Sauropodomorpha mainly through paedomorphosis, and to Neotheropoda mainly through peramorphosis. Paedomorphosis then led from Orionides to Avetheropoda, indicating that the paedomorphic trend previously found in advanced coelurosaurians may extend back into the early evolution of Avetheropoda. Not only are changes in saurischian skull shape complex due to the large number of factors that affect shape, but heterochrony itself is complex, with a number of reversals throughout non-avian saurischian evolution. The sampling of ontogenetic trajectories is considerably lower than the sampling of adult species and the current study represents a first exploratory analysis. To better understand the impact of heterochrony on
cranial evolution in saurischians, the data set we present must be expanded and complemented with further sampling from future fossil discoveries, especially of juvenile taxa.

Keywords
Dinosauria, Sauropodomorpha, Theropoda, skull shape, ontogeny, heterochrony, evolution, geometric morphometrics

Introduction
Heterochrony describes evolutionary changes due to shifts in the timing or rate of developmental processes in an organism relative to the respective processes in its ancestor (Alberch et al., 1979; McNamara, 1982, 2012; Reilly, Wiley & Meinhardt, 1997; Klingenberg, 1998; McNamara & McKinney, 2005). Heterochrony can lead to significant evolutionary changes in body plans within relatively short periods of time. Two major types of heterochronic processes are discerned: paedomorphosis and peramorphosis. Paedomorphosis occurs when the later ontogenetic stages of an organism retain characteristics from earlier ontogenetic stages of its ancestor, whereas a peramorphic organism is ontogenetically more developed than the later ontogenetic stages of its ancestor (Klingenberg, 1998). In practice, evidence for heterochronic events in evolution can be detected by comparing the ontogenetic trajectories of different taxa under the consideration of their phylogenetic interrelationships.

Documentation of heterochrony in the vertebrate fossil record is limited. Preserved fossil ontogenetic series are rare due to the fact that early juvenile specimens are either lacking or incomplete. Nevertheless, the role of heterochrony has been recognized and discussed for the
evolution of multiple fossil lineages that do preserve ontogenetic series (Gerber, Neige & Eble, 2007; Schoch, 2009, 2010, 2014; Bhullar, 2012; Forasiepi & Sánchez-Villagra, 2014; Ezcurra & Butler, 2015), including non-avian dinosaurs (e.g. Long & Mcnamara, 1997; Erickson et al., 2004; Guenther, 2009; Bhullar et al., 2012; Canale et al., 2014). For example, Long & McNamara (1997), Erickson et al. (2004) and Canale et al. (2014) hypothesized that the evolution of large body size in carcharodontosaurus and tyrannosaurs from medium-sized ancestors was the result of peramorphosis. Further, Bhullar et al. (2012) proposed that the skull shape of recent birds was the result of paedomorphic changes from both non-avian theropods and early birds, such as Archaeopteryx and Enantiornithes.

Shape diversity in non-avian dinosaurs has recently become a popular research venue, in which geometric morphometric methods have been applied on a regular basis (e.g. Bonnan, 2004; Chinnery, 2004; Campione & Evans, 2011; Hedrick & Dodson, 2013; Lautenschlager, 2014; Schwarz-Wings & Böhm, 2014; Maiorino et al., 2015). Skull shape diversity in saurischian dinosaurs has been studied in particular detail (e.g. Young & Larvan, 2010; Rauhut et al., 2011; Brusatte et al., 2012; Bhullar et al., 2012; Foth & Rauhut, 2013a,b), but usually in relation to functional constraints, dietary preferences, phylogenetic interrelationships, and macroevolutionary patterns. Geometric morphometrics is a powerful method to quantify both intraspecific (e.g. ontogeny, sexual dimorphism, polymorphism) and interspecific (e.g. systematics, macroevolution) shape variation on the basis of homologous landmarks or outlines (Corti, 1993; Rohlf & Marcus, 1993; Adams, Rohlf & Slice, 2004; Slice, 2007; Mitteroecker & Gunz, 2009; Zelditch, Swiderski & Sheets, 2012). As a result, geometric morphometrics has also been successfully applied to the study of heterochrony among various tetrapod groups (e.g.
The aim of the current study is to investigate the cranial shape diversity of saurischian dinosaurs by comparing the ontogenetic trajectories of different taxa from both qualitative and quantitative data, using two-dimensional geometric morphometrics (2D GM). Phylogenetic relationships of the taxa sampled in this study are taken into account and integrated into an ancestor-descendant framework to look for possible heterochronic processes in the cranial evolution of saurischians. However, due to the limited number of ontogenetic series known for sauropodomorphs, the current study focuses primarily on the early evolution of theropods. Therefore, this study is a first exploratory investigation of heterochrony in basal saurischians, which will need to be expanded and complemented with further sampling from future fossil discoveries.

Materials and Methods

Institutional Abbreviations

BMMS, Bürgermeister Müller Museum Solnhofen, Solnhofen, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, USA; GR, Ruth Hall Museum, Ghost Ranch, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, MCZ, Museum of Comparative Zoology, Harvard University, USA.

Taxon sampling
We sampled the crania of 35 saurischian dinosaur taxa (10 sauropodomorphs and 25 non-pennaraptoran theropods, see Table S3 in the Supplementary Information) on the basis of published reconstructions of adult (or advanced subadults) individuals in lateral view (with exception of the reconstructions of the basal tyrannosauroid *Dilong* [IVPP V14243] and the basal alvarezsauroid *Haplocheirus* [IVPP V15988], which were based on our personal observations). Large nasal crests of several theropods (e.g. *Ceratosaurus*, *Dilophosaurus*, *Guanlong*) were found to have an important impact on the ancestral shape reconstruction (see below) of Averostra, Avetheropoda, Coelurosauria and Tyrannosauroidea (see Fig. S5, Table S8, S9 in the Supplementary Information). Although cranial crests are a common structure within theropod dinosaurs (Molnar, 2005), reconstruction of moderately to strongly crested hypothetical ancestors within this study would necessarily be artificial due to the lack of intermediate crested forms and relatively small sample size of the available data set. As a result, *Ceratosaurus*, *Dilophosaurus* and *Guanlong* were not included in the main sample. 

*Monolophosaurus* was the only crested taxon included in the main data set because it possesses a rather moderately sized and simple nasal crest. ‘*Syntarsus’ kayentakatae*, which is often reconstructed with a pair of prominent nasal crests (Rowe, 1989; Tykoski, 1998), was analysed in this study without crests since this structure is probably artificial due to post-mortem displacement of the nasals (Ezcurra & Novas, 2005, 2007). As cranial crests usually represent external visual signal structures (Sampson, 1999; Padian & Horner, 2011; Hone, Naish & Cuthill, 2012), their evolutionary development was most likely sourced from regional peramorphic processes (see discussion on the evolution of horns and frills in Ceratopsia by Long...
We generated a second data set that includes crested taxa for comparison with the main data set (see below).

In our sample, five taxa preserve early ontogenetic stages allowing the reconstruction of both juvenile and adult skull shapes, which were used to reconstruct five simplified (i.e. including two stages) ontogenetic series. This sample includes the basal sauropodomorph *Massospondylus* (ontogenetic outgroup trajectory), the basal theropod *Coelophysis*, the megalosaurid *Dubreuillosaurus*, the allosauroid *Allosaurus*, and the basal coelurosaur *Tarbosaurus*. As the fossil record of juvenile dinosaur specimens with complete skull material is rare, the number of ontogenetic series is limited. To improve the sampling, previous studies have included reconstructions from multiple partial juvenile skulls or juveniles from closely related taxa (e.g. Bhullar et al., 2012). We implemented this approach in two cases: the reconstruction of the juvenile *Coelophysis* sample was based on three incomplete, somewhat taphonomically deformed individuals (MCZ 4326; GR 392; CM 31375); and *Sciurumimus* (BMMS BK 11) was used as the juvenile representative of megalosaurids (e.g. *Dubreuillosaurus*) (see Rauhut et al., 2012). In contrast to Bhullar et al. (2012), we did not include the ontogenetic series of *Byronosaurus*, Therizinosauridae (represented by a therizinosaurid embryo and the skull of *Erlikosaurus*) and *Compsognathus* in the data set because the postorbital region of the juvenile skulls of the former two taxa is crushed or incomplete (Bever & Norell, 2009; Kundrát et al., 2009), and the taxonomic referral of *Scipionyx* (as juvenile taxon) to the clade Compsognathidae (see Dal Sasso & Maganuco, 2011) is uncertain (see Rauhut et al., 2012).

**Two-dimensional Geometric Morphometrics (2D GM)**
We used 20 landmarks (LMs) and 51 semi-landmarks (semi-LMs) on our sample in order to accurately capture skull shape. The landmarks were collected using the software tpsDig2 (Rohlf, 2005) and were classified as either type 1 (points where two bone sutures meet) or type 2 (points of maximum curvature and extremities) (Bookstein, 1991) (see Fig. S1, Table S1 in the Supplementary Information for full description). Type 3 landmarks (points constructed between two homologous landmarks, which mainly define the shape of the skull or skull openings rather than the position of exact homologous points) were not used in our study. Semi-landmarks were used to capture the shape of skull openings and the overall skull outline by defining a number of points that are placed equidistantly along respective curves (Bookstein, 1991; Bookstein et al., 1999). The percent error for digitizing landmarks and semi-landmarks by hand was estimated for the skull reconstruction of the juvenile *Coelophysis* (with \( n = 10\) replications) using the method described by Singleton (2002). Landmark and semi-landmark error varies between 0.117 percent (LM 51 - most posterior point of the descending process of the maxilla contacting the nasal and/or the lacrimal) and 0.738 percent (LM 3 - contact between the maxilla and jugal along the ventral margin of the skull) with a mean of 0.283 percent. The error has no significant effect on the shape analyses (see Table S2 in the Supplementary Information).

The shape coordinates were then imported into the software package MorphoJ 1.05d (Klingenberg, 2011) and were superimposed using generalized Procrustes analysis (GPA). GPA rotates, translates and resizes all specimens accounting for all non-shape related differences between landmark configurations, leaving only shape information (Gower, 1975; Rohlf & Slice, 1990). Although semi-landmarks have fewer degrees of freedom than regular landmarks (and thus contain less shape information) (Bookstein, 1991), we treated landmarks and semi-
landmarks as equivalent for GPA (Zelditch, Swiderski & Sheets, 2012) and did not slide the
semi-landmarks. The sliding process created considerable artificial deformation on the
Procrustes shape in some taxa (see Fig. S2 in the Supplementary Information). However, due to
the equivalent weighting of landmarks and semi-landmarks, it should be kept in mind that the
shape information captured by the semi-landmarks strongly influences the results (Zelditch,
Swiderski & Sheets, 2012; see below). The generated Procrustes shapes were used to compare
juvenile and adult skull shapes to each other in each ontogenetic series to find ontogenetic
patterns between and within taxa.

The resulting Procrustes coordinates were subjected to an exploratory principal components
analysis (PCA) using the covariance matrix generated from Procrustes coordinates. PCA
simplifies descriptions of variation among individuals by creating new sets of variables that are
linear combinations of the original set such that the new sets are independent of one another and
have zero covariance. The principal components (PCs) describe successively smaller amounts of
total variance of the sample. This allows for a larger proportion of the variance to be described
using a smaller number of variables than the original data would have allowed (Zelditch,
Swiderski & Sheets, 2012). The different ontogenetic series were compared to each other by
calculating pairwise two-dimensional angles between different trajectories based on the PC
values of the first three axes, which are the significant principal components (significance
calculated using the broken stick method, see Jackson, 1993). PCs 1, 2 and 3 together contain
68% of the total shape variation. Each ontogenetic trajectory was described as a phenotypic
change vector, $\Delta \mathbf{\hat{y}}_i = \mathbf{\hat{y}}_j - \mathbf{\hat{y}}_k$, with two shape traits (PC 1 vs. PC 2 and PC 1 vs. PC 3), where $i$ is
a specific ontogeny between two fixed stages, juvenile ($j$) and adult ($k$) (Collyer & Adam, 2007).
The difference in direction (angle) between the ontogenetic phenotypic change vectors \( \Delta \mathbf{y}_a, \Delta \mathbf{y}_b \) was calculated using the dot product:

\[
\cos^{-1} \left( \Delta \mathbf{y}_a, \Delta \mathbf{y}_b \right) = \frac{\Delta \mathbf{y}_a \cdot \Delta \mathbf{y}_b}{|\Delta \mathbf{y}_a||\Delta \mathbf{y}_b|}.
\]

A multivariate regression of the Procrustes coordinates against log-transformed centroid sizes (= square root of the sum of the squared distances of each landmark to the centroid of the landmark configuration, Zelditch, Swiderski & Sheets, 2012) were used to test if overall skull shape variation is correlated to size and also to compare the different ontogenetic trajectories in terms of heterochrony (Piras et al., 2011; Bhullar et al., 2012; Zelditch, Swiderski & Sheets, 2012). As heterochrony is defined as the change in the timing or rate of developmental processes in ancestor-descendant relationships (Alberch et al., 1979; Klingenberg, 1998; McNamara, 2012), a direct comparison of ontogenetic trajectories from different species (as terminal taxa) can be problematic because it is hard to determine which trajectory would represent the ancestral and the descendant form, respectively. This is exacerbated when the supposed ancestral (terminal) species possesses an unknown, long evolutionary history resulting from a ghost lineage. This problem can be partially solved using a phylogenetic approach, in which the ancestor of two sister (terminal) taxa is represented by the hypothetical last common ancestor (Hennig, 1966). Therefore, we calculated hypothetical ancestral ontogenetic trajectories for Saurischia, Neotheropoda, Orionides and Avetheropoda using ancestral shape reconstructions as follows (see Fig. S3, S4 in the Supplementary Information). An informal supertree including all adult taxa was created based on recent phylogenetic analyses (see Fig. S3, S4 in the Supplementary Information): basal Sauropodomorpha (Cabreira et al., 2011), Coelophysoidea (Ezcurra & Novas, 2007), Ceratosauria (Pol & Rauhut, 2012), Tetanurae (Carrano, Benson & Sampson, 2012), and Coelurosauria (Turner et al., 2012; Loewen et al., 2013). The phylogenetic position...
of *Eoraptor* follows Martínez et al. (2011) and Martínez, Apaldetti & Abelin (2013). The position of *Adeopapposaurus* as sister taxon of *Massospondylus* follows Martínez (2009). The position of *Herrerasaurus* and *Tawa* at the base of Theropoda is based on Sues et al. (2011). *Zupaysaurus* was placed outside Coelophysoidea as one of the successive sister taxa of *Averostra* (Smith et al., 2007; Sues et al., 2011; Ezcurra, 2012). The supertree was time-calibrated using the stratigraphic age of each taxon (as mean of time interval) (see Table S3, S8 in the Supplementary Information). The assignment of branch lengths was performed in R (R Development Core Team, 2011) using the APE package (version 2.7-2; Paradis, Claude & Strimmer, 2004) and a protocol written by Graeme Lloyd (see http://www.graemetlloyd.com/methdpf.html) for adjusting zero branch lengths by sharing out the time equally between branches (see Brusatte et al., 2008; Brusatte, 2011), and adding an arbitrary length of 1 million years to the root. The time-calibrated supertree was imported into the software package Mesquite 2.72 (Maddison & Maddison, 2009). Subsequently, Procrustes coordinates and centroid sizes of the adult taxa were mapped onto the supertree as continuous characters using square change parsimony. This algorithm performs an ancestral state reconstruction by collating the sum of squared changes of continuous characters along all branches of a tree and estimates the most parsimonious ancestral states by minimizing the total sum of squared changes across the tree (Maddison, 1991). In the next step we tested if the continuous data contain a phylogenetic signal. We performed a permutation test in MorphoJ in which the topology was held constant and both the Procrustes shape data and the centroid size for each taxon were randomly permuted across the tree 10,000 times (Laurin, 2004; Klingenberg & Gidaszewski, 2010). The data contain a statistically significant phylogenetic signal if the squared length of the original supertree occurs in at least 95% of the randomly generated trees.
To obtain the ancestral ontogenetic trajectories, the protocol described above was repeated in a new nexus file containing the Procrustes shapes and centroid sizes of the juvenile taxa. As the juvenile data set is only represented by five taxa, the original supertree was pruned such that only these respective taxa remained, retaining the original time-calibration. Finally, the ancestral Procrustes shapes and centroid sizes of both juvenile and adult Saurischia, Neotheropoda, Orionides and Avetheropoda were exported and combined with the respective data from the ontogenetic trajectories of the terminal taxa. The ancestral Procrustes shape of Averostra was not considered because no ceratosaur juveniles have been published in detail so far (see Madsen & Welles, 2000). The new data set was loaded again into MorphoJ to perform a multivariate, pooled within-group regression of Procrustes shape against centroid size. Peramorphosis was inferred if the regression score of the descendant trajectory was higher than that of the respective ancestral one, whereas paedomorphosis resulted from a lower score. However, to test if the shape changes, and as a result the presence of heterochrony, of an ancestor-descendant relationship are statistically meaningful, we calculated the confidence interval (CI) of the regression scores of terminal and ancestral taxa (n = 69) and compared them with the differences of ancestral and descendant regression scores from the sub-sample containing the ontogenetic trajectories. Changes were considered significant if the differences between regression scores are at least 1.5 times higher than the CI value (see Cumming, Fidler & Vaux, 2007). The angles between ontogenetic trajectories were calculated based on Procrustes distances and centroid sizes (see above). To gain better insights into specific heterochronic changes, this procedure was repeated for the shape of several different skull regions, namely skull outline, external naris, maxilla,
antorbital fenestra, orbit, infratemporal fenestra, jugal-quadratojugal complex, postorbital, and skull roof, including the shape of the ventral process of the lacrimal.

In order to estimate the influence of the semi-landmarks (see above) on the shape data, a second data set was created that included only landmark data. The analyses on this data set (only for the overall skull shape) were performed as described above. Finally, the ancestral shape reconstructions calculated for the adult taxa were used to discuss the evolutionary changes within basal Sauropodomorpha and Theropoda with respect to the ontogenetic changes and heterochronic trends found in the different trajectories.

Results

General ontogenetic changes

The juveniles of the sauropodomorph *Massospondylus* and the theropods that were sampled here tend to have skulls with a short and abruptly tapering snout, short antorbital fenestra, large subcircular orbits, slender jugals, and dorsoventrally deep orbital and postorbital regions relative to the snout. In addition, the jaw joint is more anteriorly placed relative to the occiput, with exception of the juvenile specimen of *Allosaurus* sampled here. The general ontogenetic pattern includes an elongated and dorsoventrally deeper snout relative to the orbital and postorbital regions, and also a relative increase in size of the antorbital fenestra, which correlates with a relative decrease in size of the orbit. Finally, the jugal becomes more massive in all taxa, which is more pronounced in the large-bodied theropods *Allosaurus* and *Tarbosaurus* (Fig. 1). The relative elongation of the snout and antorbital fenestra were not observed in the *Allosaurus* or *Tarbosaurus* ontogenies, which is probably due to the fact that the juveniles sampled do not
represent the earliest ontogenetic stages (Loewen, 2009; Tsuihiji et al., 2011, see discussion).

However, the discovery of an isolated maxilla identified as a hatchling allosauroid might indicate that the snout of early *Allosaurus* juveniles was probably short and subsequently increased in relative length during early ontogeny (Rauhut & Fechner, 2005).

**Principal component analysis and phylogenetic correlation**

The first three principal components account for 68.0% of the total variation (PC 1: 30.8%; PC 2: 23.9%; PC 3: 13.3%), in which PC 2 and PC 3 contain the main allometric shape information (see Table S16 in the Supplementary Information). PC 1 describes the overall skull depth, size and anteroposterior position of the external naris, length of the premaxilla, size of the maxillary antorbital fossa, and position of the lacrimal and postorbital in the anteroposterior axis (affecting the size of the antorbital fenestra, orbit and infratemporal fenestra). The dorsoventral dimension of the orbit is affected by the relative depth of the entire orbital and postorbital regions, while that of the infratemporal fenestra is affected by the relative position of the jugal-quadratojugal bar. The variation in the depth of the skull also affects the position of the jaw joint in the dorsoventral axis.

PC 2 describes the length of the snout caused by variation in the length of the maxilla and inclination and anteroposterior position of the lacrimal. The inclination of the lacrimal affects the size of the antorbital fenestra, while both position and inclination affect the anteroposterior dimension of the orbit. PC 2 also accounts for the length and the dorsoventral position of the external naris and size of the upper temporal region.
PC 3 describes the length of the premaxilla, posterior extension of the external naris,
dorsoventral height of the maxilla, and anteroposterior dimension of the ventral process of the
lacrimal (which affects the shape of the antorbital fenestra and orbit). The shape of the orbit is
further affected by the anteroposterior dimension of the jugal-postorbital bar. Further variation
captured by PC 3 is related to the shape of the skull roof in the orbital and postorbital regions,
dorsoventral height of the infratemporal fenestra, and position of the jaw joint in the
anterodorsal-posteroventral axis.

The permutation tests recovered that both Procrustes shapes (tree length weighted
by branch lengths = 0.5108, p < 0.0001) and centroid size (tree length weighted
by branch lengths = 8.3598, p = 0.0005) are correlated with phylogeny. The phylogenetic signal
remains when semi-landmarks are excluded (tree length weighted
by branch lengths = 0.5341, p < 0.0001) and when crested taxa are included (tree length
weighted by branch lengths = 0.5482, p < 0.0001) in the sample.

Ontogenetic trajectories in the principal component morphospace

The ontogenetic trajectory of *Allosaurus* is mainly explained by shape variation captured by PC
1. The ontogenetic trajectory of *Coelophysis* is mainly explained by the shape variation captured
by PCs 1 and 2, and that of *Tarbosaurus* is mainly explained by the shape variation captured by
PCs 1 and 3. The ontogenetic trajectory of *Coelophysis* is in the opposite direction along PC 1
compared to the trajectories of *Allosaurus* and *Tarbosaurus*. The ontogenetic trajectories of
*Massospondylus* and the megalosaurid taxon are mainly influenced by the shape variation
captured by PCs 2 and 3, in which the ontogenetic trajectory of *Massospondylus* is directed in
the opposite direction along PC 3 to that of the megalosaurid taxon and *Tarbosaurus* (Fig. 2, Table S4 in the Supplementary Information).

It should be noted that the directions of the ontogenetic trajectories do not change when crested taxa are included in the data set (PC 1: 28.6 %; PC 2: 22.7 %; PC 3: 13.0 %; see Fig. S6, Table S10, S11, S16, see Supplementary Information for results when crested taxa are included). By contrast, the exclusion of semi-landmarks from the data set leads to five differently directed ontogenetic trajectories (PC 1: 28.4 %; PC 2: 20.0 %; PC 3: 15.6 %). Excluding semi-landmarks, the ontogenetic trajectory of the megalosaurid taxon is explained approximately equally by the first three PCs, that of *Allosaurus* is mainly captured by PC 1 and 2, and that of *Tarbosaurus* is explained by PCs 1 and 3. The ontogenetic trajectories of *Massospondylus* and *Coelophysis* are mainly explained by shape variation captured by PCs 2 and 3, in which the ontogenetic trajectory of *Massospondylus* along PC 3 is directed opposite to that of *Coelophysis*, *Tarbosaurus* and the megalosaurid taxon (see Fig. S7, Table S12, S13 in the Supplementary Information with results excluding semi-landmarks). Semi-landmark curves include important shape information and their exclusion leads to missing informative data (e.g. skull outline) and as a result we will discuss it below in the context of a sensitivity analysis.

Based on the results of the original data set (i.e. including semi-landmarks), the general ontogenetic patterns described above are not completely uniform for all taxa (Figs. 1, 2). The ontogenetic elongation of the snout is primarily related to a relative increase in the length of the maxilla (PCs 1, 2). In *Massospondylus* and the megalosaurid taxon the ontogenetic elongation of the snout is further affected by the relative increase of the length of the premaxilla (PC 3). The
relative increase in snout depth results mainly from a ventral expansion of the maxilla, which is more prominent in *Allosaurus* and *Tarbosaurus* than in other taxa (PCs 1, 3). In the megalosaurid taxon and *Allosaurus*, maxillary deepening occurs together with a dorsoventral expansion of the nasal (PC 1). Additionally, dorsoventral expansion of the premaxilla is observed in *Allosaurus* and *Tarbosaurus* (PC 1). The relative elongation of the snout in *Massospondylus*, the megalosaurid taxon and *Coelophysis* correlates with a relative increase in the anteroposterior length of the antorbital fenestra, caused by a posterior shift of the lacrimal and elongation of the maxilla (PCs 1, 2). Additionally, in *Coelophysis* the anterior border of the antorbital fenestra extends anteriorly (PC 1). In both *Massospondylus* and the megalosaurid taxon, the antorbital fenestra is shifted posteriorly during ontogeny (PC 2). The megalosaurid taxon shows a further dorsal expansion of the antorbital fenestra (PC 3), not seen in the latter two taxa. Although no relative size changes could be observed in the antorbital fenestrae of *Allosaurus* and *Tarbosaurus*, the antorbital fenestra of *Allosaurus* shifts posterodorsally during ontogeny, whereas that of *Tarbosaurus* shifts ventrally. In most trajectories, the most anterior point of the antorbital fossa shifts posteriorly during ontogeny (PCs 1–3), but a relative decrease in the length of the maxillary antorbital fossa is present in *Allosaurus* and *Tarbosaurus* (PC 1). In the megalosaurid taxon, the anterior margin of the antorbital fossa shifts ventrally, whereas in *Coelophysis* it shifts anteriorly (PC 1), which correlates with the anterior extension of the antorbital fenestra in this taxon (see above). As mentioned above, the orbit decreases in relative size in all taxa during ontogeny (PCs 1–3). In *Coelophysis* and *Massospondylus* this is related to a relative shift of the lacrimal posteriorly (PCs 1, 2). In the megalosaurid taxon, *Allosaurus* and *Tarbosaurus* the relative size reduction is correlated with a change in orbital shape from subcircular to oval. In the megalosaurid taxon these changes are linked to a posterior shift of the
391 lacrimal (PC 2) and anterior shift of the postorbital and ascending process of the jugal (PC 3), which is correlated with an anterior extension of the infratemporal fenestra. In Allosaurus, the ontogenetic changes of the orbit are related to the posterior extension of the lacrimal and anterior shift of the postorbital and ascending process of the jugal (PC 1). Additionally, the orbit of Allosaurus is shifted slightly dorsally. In Tarbosaurus, these changes result from an anterior extension of both the postorbital and ascending process of the jugal (PC 3). The orbit of Tarbosaurus becomes posteriorly constricted by an anterior shift of the ventral process of the postorbital, forming a suborbital process.

In addition to these more general ontogenetic modifications, the different trajectories of individual taxa show specific shape changes (Fig. 1):

a) In Massospondylus the external naris becomes larger and expands dorsally. The postorbital also becomes relatively more robust. The infratemporal fenestra decreases in relative size. The jaw joint moves anteroventrally.

b) In Coelophysis the external naris becomes smaller and shifts anteriorly. The notch of the alveolar margin between the premaxilla and maxilla decreases in relative size during ontogeny, while the alveolar margin of the premaxilla becomes more aligned with that of the maxilla. The descending process of the lacrimal becomes more slender anteroposteriorly. The postorbital becomes more gracile in its relative shape. The infratemporal fenestra increases in relative size. The jaw joint moves posterodorsally.

c) In the megalosaurid taxon, the external naris becomes relatively larger and expands posteriorly. The lacrimal is inclined strongly backwards and the postorbital becomes
relatively more robust. The infratemporal fenestra increases in its relative size. The jaw joint moves posteriorly.

d) In *Allosaurus* the external naris does not change in relative size, but shifts ventrally. The descending process of the lacrimal becomes more massive anteroposteriorly. The lacrimal develops a prominent dorsal horn through ontogeny. In contrast to previous taxa, the postorbital region of *Allosaurus* increases dorsoventrally such that the postorbital, quadratojugal and squamosal become more robust. The ventral shift of the jugal leads to the formation of a wide angle between the ventral margins of the maxilla and jugal. Due to its posteroventral expansion, the postorbital affects the overall shape of the infratemporal fenestra. However, the infratemporal fenestra does not decrease in its relative size, but shifts anteroventrally. The jaw joint moves anteroventrally.

e) In *Tarbosaurus* the external naris does not change in relative size, but shifts dorsally. As in *Allosaurus*, the descending process of the lacrimal becomes more massive. The same is true for the postorbital region, which increases in depth dorsoventrally. This change is correlated with the development of a more robust postorbital, quadratojugal and squamosal. The jaw joint moves posteroventrally.

**Main heterochronic changes**

Based on the multivariate, pooled within-group regression, peramorphic skulls tend to be more elongated, with long and slender snouts that have a rounded anterior end, and possess anteroposteriorly long antorbital fenestrae, oval orbits and a post-rostrum only slightly dorsoventrally higher than the snout. The maxilla increases in its relative length, but also expands ventrally. The ascending process of the maxilla, the anterior and ascending processes of
the jugal, and postorbital become more massive. Paedomorphic shape trends are opposite to
these peramorphic trends. All heterochronic processes are summarized in Figs. 2–7, Table 1, and
Table S6 and S7 in the Supplementary Information.

When compared to the hypothetical ancestor of Saurischia, the overall skull shape of
*Massospondylus* results from paedomorphosis primarily affecting the shape of the skull outline,
antorbital fenestra, orbit and skull roof. By contrast, the shapes of the external naris and
infratemporal fenestra of *Massospondylus* are peramorphic.

The evolutionary changes of overall skull shape that occurred from the hypothetical ancestor of
Saurischia to that of Neotheropoda are due to peramorphosis, which primarily affects the shape
of the skull outline, maxilla, antorbital fenestra, infratemporal fenestra and skull roof. Compared
to the hypothetical neotheropod ancestor, the skull of *Coelophysis* was found to be non-
significantly peramorphic. On the regional level, significant peramorphic shape changes found in
the external naris, antorbital fenestra and the skull roof. By contrast, significant shape changes
found in the orbit, postorbital, infratemporal fenestra, and jugal-quadratojugal complex are
influenced by paedomorphosis.

Between the hypothetical ancestors of Neotheropoda and Orionides (the hypothetical ancestor of
Averostra was not considered here) no significant shape changes could be observed for overall
skull shape. However, regional peramorphic changes are expressed significantly in the shape of
the external naris, maxilla, orbit, jugal-quadratojugal complex and postorbital. In comparison to
the hypothetical ancestor of Orionides, the skull of the megalosaurid taxon is peramorphic,
affecting all skull regions on a significant level except of antorbital fenestra and infratemporal fenestra.

Interestingly, the evolutionary changes in the overall skull shape that occurred from the hypothetical ancestor of Orionides to that of Avetheropoda are paedomorphic, affecting the shape of the skull outline, the external naris and the skull roof on a significant level.

Compared to the hypothetical ancestor of Avetheropoda, the overall skull shape of *Allosaurus* is peramorphic, but not on a significant level. On the regional level, *Allosaurus* shows significant changes related to peramorphosis in the maxilla, the orbit, the postorbital and the jugal-quadratojugal region. By contrast, the shape changes in the skull outline and external naris, which were found to be significant, are affected by paedomorphosis. The skull shape of *Tarbosaurus* was found to be non-significantly paedomorphic compared to the hypothetical ancestor of Avetheropoda. Regionally, significant paedomorphic changes are expressed in the shape of the skull outline, antorbital fenestra and skull roof. By contrast, the significant shapes found in the external naris, orbit, postorbital and jugal-quadratojugal complex are classified as peramorphic.

Peramorphosis found in the ontogenetic series is generally correlated with an increase in centroid size. Paedomorphosis observed in the hypothetical ancestor of Avetheropoda matches a decrease in centroid size, but not in *Massospondylus*. 
When semi-landmarks are excluded from the data set, most of the heterochronic trends found in
the sensitivity analysis are very similar to those described in the original analysis (see Fig. S7,
Table S14, S15, S16, see Supplementary Information for results excluding semi-landmarks).
However, contrasting with the main analysis, the evolutionary changes in the skull of
*Massospondylus* are not significant with respect to the hypothetical ancestor of Saurischia, the
skull of the hypothetical ancestor of Orionides is significantly peramorphic with respect to that of
Neotheropoda, and the skull shape of *Tarbosaurus* is peramorphic compared to that of the
hypothetical ancestor of Avetheropoda, but not significantly.

**Discussion**

Previous workers have hypothesized that skull shape diversity in theropods was driven by
phylogenetic interrelationships, dietary preferences (Brusatte et al., 2012; Foth & Rauhut,
2013a), functional constraints (Henderson, 2002; Foth & Rauhut, 2013a), and also heterochrony
(Long & McNamara, 1997; Bhullar et al., 2012). The current study supports a strong influence
of heterochrony on the cranial evolution of saurischian dinosaurs, which is indicated by different
trajectories of morphological changes between the respective ontogenetic series. These changes
are retained regardless of whether or not semi-landmarks or crested taxa are included in the
sample. By comparing the ontogenetic trajectories in a hypothetical ancestor-descendant
sequence, a complex pattern of heterochronic events is present within both the overall skull and
different skull regions. The early evolution of sauropodomorphs is primarily affected by
paedomorphosis, while shape changes in basal theropods is driven by peramorphosis. However,
in more derived tetanurans (i.e. Avetheropoda, Coelurosauria) skull shape is predominantly
affected by paedomorphosis (see also Bhullar et al., 2012). When comparing different skull
regions with each other, it becomes clear that often both pera- and paedomorphic changes are modularly constrained, but one overall trend (either paedomorphosis or peramorphosis) is dominant for the entire skull.

Evolutionary changes in the skull shape of Sauropodomorpha

Based on the regression analysis of ontogenetic trajectories it is possible to determine which shape changes are related to paedomorphosis and which are related to peramorphosis (see above). This can be used to explain particular shape changes found between hypothetical ancestors and terminal taxa in the ancestral shape reconstruction analyses of the main sample (i.e. continuous character mapping of the Procrustes shapes) in terms of heterochrony.

Comparing the skull shape of the hypothetical ancestor of Saurischia to that of Sauropodomorpha indicates an initial paedomorphosis in the evolution of the latter group, which is depicted by a decrease in the relative length of the preorbital region and an increase in the relative orbital size and depth of the postorbital region. However, the skull of the hypothetical ancestor of Massopoda is peramorphic with respect to that of Sauropodomorpha (but paedomorphic with respect to that of Saurischia, see above) due to a relative increase in length and depth of both the premaxilla and maxilla, as it was previously hypothesized by Long & McNamara (1997). The orbit size slightly decreases and becomes more oval, which was established as a peramorphic trend. Additionally, the jugal region becomes more massive.

However, in Eusauropoda the snouts become more aberrant due to a dorsal shift of the external naris, posterodorsal extension of the premaxilla, elongation of the ascending process of the maxilla and modification of the postorbital region, affecting the relative size of the jugal and postorbital, which become more gracile (Wilson & Sereno, 1998; Rauhut et al., 2011). While the
shape changes in the snout and the shift of the naris were diagnosed as peramorphic (Long & McNamara, 1997), one can assume on the basis of the current observations that the increase of gracility in the postorbital region of derived sauropods may result from modular paedomorphosis. However, this needs to be quantitatively analysed and is beyond the scope of the present study.

Evolutionary changes in the skull shape of Theropoda

The initial evolutionary changes in the skull shape of Theropoda were driven by peramorphic events, as is observed in the hypothetical ancestor of Neotheropoda and the megalosaurid taxon. These changes include the elongation of the snout, increase in length of the antorbital fenestra, and trends to a relatively smaller orbit and a more robust post-rostral region. In comparison to the ancestral reconstruction of Averostra, the skull of the hypothetical ancestor of Ceratosauria seems to be mainly the result of paedomorphosis, resulting in a shorter and deeper snout. The shape of the orbital and postorbital regions of *Limusaurus* (enlarged subcircular orbit and gracile jugal and postorbital) is paedomorphic with respect to the hypothetical ancestor of Averostra, while the respective regions in Late Cretaceous abelisaurids (e.g. *Carnotaurus* and *Majungasaurus*) are peramorphic (oval orbit, massive jugal and postorbital). The skull of the hypothetical ancestor of Avetheropoda is paedomorphic with respect to that of Orionides. This trend extends to the hypothetical ancestor of Coelurosauria, Maniraptoriformes and Maniraptora, leading to a shorter, more tapering snout in lateral view, smaller antorbital fenestra, enlarged subcircular orbit, and more gracile postrostral region, resembling the skull shape of the juvenile megalosaurid *Sciurumimus*. This finding may indicate that the paedomorphic trend hypothesized for Eumaniraptora (Bhullar et al., 2012) probably reaches back into the early evolution of
Avetheropoda, and that basal coelurosaurs in fact represent “miniaturized” tetanurans,
conserving juvenile characters in adult individuals. In contrast to this paedomorphic trend and to
the results of regression analyses (see above), the ancestral shape reconstruction reveals that the
skulls of allosauroids and tyrannosaurids become secondary more robust in relation to their
respective ancestors, supporting convergent peramorphosis in both lineages (see Long &
McNamara, 1997, Canale et al., 2014). This discrepancy to the regression results is probably
linked to the incomplete sampling of ontogenetic trajectories in the regression analyses (see
below). The heterochronic trends found in the current study are summarized in Fig. 8.

**General comments on saurischian heterochrony**

The cranial heterochronic events described here seem to be correlated with major trends
observed in the evolution of body size in theropods and sauropodomorphs (Sander et al., 2010;
Irmis, 2011; Dececchi & Larsson, 2013; Benson et al., 2014; Lee et al., 2014). As body size
evolution itself is driven by heterochrony (Erickson et al., 2004; Sander et al., 2004; McNamara,
2012), this correlation may indicate that the skull shape of theropods and sauropodomorphs is
additionally influenced by body size evolution (i.e. heterochronic events in body size evolution
can affect heterochrony in the cranium, but this correlation is not universal, see Therrien &
Henderson, 2007; Bhullar et al., 2012), which is additionally indicated by the rough correlation
found between heterochrony and centroid size.

Peramorphic trends in the cranial shape of Saurischia lead to skulls with an elongated snout,
proportionally small and oval orbit, and robust postorbital region. On the other hand,
paedomorphic trends tend to lead to skulls with short and deep snouts, enlarged subcircular
orbits and more gracile postorbital regions. These major differences in shape would clearly affect dietary preferences and functional constraints. The robust morphology of the postorbital region and the oval orbit in peramorphic skulls was previously discussed in relation to the generation of higher bite forces (Henderson, 2002; Foth & Rauhut, 2013a). However, these functional constraints go hand in hand with a decrease in cranial disparity (Brusatte et al., 2012).

Paedomorphic changes in the orbital and postorbital regions were discussed in relation to visual elaboration and brain enlargement (Bhullar et al., 2012), and may have played an important role for nocturnal activity (Schmitz & Motani, 2011) or the evolution of flight within Paraves (Balanoff et al., 2013). On the other hand, large and circular orbits might simply correlate with reduced mechanical stresses during biting (Henderson, 2002), which have been suggested to also influence size and shape of the external naris, antorbital fenestra and infratemporal fenestra (Witmer, 1997; Witzel & Preuschoft, 2005; Witzel et al., 2011).

Both ontogenetic and phylogenetic variations in snout shape are likely related to dietary preferences (Brusatte et al. 2012; Foth & Rauhut 2013), in which the shape of premaxillae and maxillae partly determines the number and size of teeth (Henderson & Weishampel, 2002). Various examples of ontogenetic changes in the morphology and number of teeth are documented in Saurischia, including the basal sauropodomorph Massospondylus, coelophysoids (Colbert, 1989), basal tetanurans (Rauhut & Fechner, 2005; Rauhut et al., 2012), Tyrannosauridae (Carr, 1999; Tsuihiji et al., 2011) and Maniraptora (Kundrát et al., 2008; Bever & Norell, 2009). Based on these observations the evolutionary increase in the number of teeth has been interpreted as peramorphic (Bever & Norell, 2009). Tooth morphology, however, was found to be a stronger indicator of diet than the shape of the snout itself (see Smith, 1993;
Barrett, 2000; Barrett, Butler & Nesbitt, 2011; Zanno & Makovicky, 2011; Foth & Rauhut, 2013a; Hendrickx & Mateus, 2014). In this context, Rauhut et al. (2012) hypothesised based on the similarities in the dentition of the juvenile megalosaurid *Sciurumimus*, adult compsognathids (Stromer, 1934; Currie & Chen, 2001; Peyer, 2006) and adult dromaeosaurids (Xu & Wu, 2001; Norell et al., 2006), that strongly recurved crowns with reduced or no mesial serrations may be paedomorphic in the latter two taxa. This heterochrony probably results from the decrease of body size observed in coelurosaur (see above) and indicate an evolutionary shift of dietary preferences to smaller prey (see also Zanno & Makovicky, 2011).

**Limitations**

As is common in vertebrate paleontology, the current study has a limited sample size when compared with extant neontological data sets (Brown & Vavrek, 2015). The current results are necessarily preliminary and must be viewed with some caution especially since the sampling of ontogenetic trajectories is considerably lower than the sampling of adult species. Furthermore, trajectories are constructed using a single juvenile and adult specimen, with no intermediate forms. The poor sample of juveniles is a result of rarity and poor preservation in the fossil record, which seems to be due to a number of factors, including preferred hunting of juveniles by predators (Hone & Rauhut, 2010) and a smaller likelihood of preservation, discovery, and collection because juveniles have smaller body sizes and more fragile bones than adults (Brown et al., 2013). Another issue affecting our results is that the juvenile individuals sampled here are all of different early ontogenetic stages. The juvenile of *Massospondylus* still represents an embryo, which is close to hatching (Reisz et al., 2010); the megalosaurid taxon (i.e. *Sciurumimus albersdoerferi*) is an early juvenile and its exact age could not be determined (Rauhut et al.,...
2012); the age of the *Coelophysis* juvenile reconstructed is approximately one year old
(estimated by Colbert, 1990; Rinehart et al., 2009); the juvenile *Tarbosaurus* specimen is two to
three years old (Tsuihiji et al., 2011); and the juvenile *Allosaurus* is likely five to seven years old
(estimated on the basis of Bybee, Lee & Lamm, 2006; Loewen, 2009). Thus, it cannot be ruled
out that the different ontogenetic stages of the juvenile specimens and the small number of
individuals for each ontogenetic series have affected the progression of the calculated trajectories
(and thus the angles between the trajectories) (see Cardini & Elton, 2007), including that of the
hypothetical ancestors. Furthermore, due to small sample sizes, the statistical power of our
analyses is generally low (see Cumming, Fidler & Vaux, 2007), limiting the explanatory power
of our results. On the other hand, Brown & Vavrek (2015) recently demonstrated that the overall
inference of allometry can be relatively robust against small sample sizes in both paleontological
and neontological data sets, meaning that the current results probably still show a true, albeit
statistically not well supported, signal. Due to this statistical uncertainty, further classification of
heterochronic subtypes (e.g. neoteny or hypermorphosis) was avoided.

The (non-significant) paedomorphic trends found for *Tarbosaurus* in relation to the hypothetical
ancestor of Avetheropoda illustrates the limitations of our analyses because this result is
seemingly contradictory to previous hypotheses and the ancestral shape reconstruction, which
proposed peramorphosis as the main driver of skull evolution in large-bodied tyrannosaurids (see
above, Long & McNamara, 1997, Bhullar et al., 2012). However, this result is most likely
related to the small sample size of ontogenetic trajectories as skulls with elongated and slender
snouts are considered to be peramorphic on the basis of the regression analyses. The hypothetical
inclusion of more ontogenetic trajectories of large-bodied theropods would probably change this
result in favour of a trend towards a deeper snout. Furthermore, large-bodied tyrannosaurids like
*Tarbosaurus* descended from small-bodied coelurosaurian ancestors (Xu *et al*., 2004, 2006;
Brusatte *et al*., 2010; Rauhut *et al*., 2010; Benson *et al*., 2014), which means that the
hypothetical inclusion of an ontogenetic trajectory of a small-bodied basal coelurosaur (e.g.
*Compsognathus, Dilong, Haplocheirus*) and a respective hypothetical ancestor of Coelurosauria
would probably change the current results, leading to a secondary peramorphic trend in Late
Cretaceous tyrannosauroids, as previously recovered. Thus, this result is very likely an artefact of
incomplete sampling.

**Conclusions**

The importance of heterochrony in non-avian dinosaur skull evolution is a relatively new
concept. This is the first study to quantitatively assess the impact of skull heterochrony across
early saurischian evolution. We analysed hypothetical ontogenetic trajectories of Saurischia,
Neotheropoda, Orionides, and Avetheropoda using ontogenetic trajectories of *Massospondylus,*
*Coelophysis,* a megalosaurid taxon, *Allosaurus,* and *Tarbosaurus.* General peramorphic skulls
include more elongate and slender snouts, elongate antorbital fenestrae, oval orbits,
dorsoventrally shallower post-rostral regions, and more massive maxillae, jugals, and
postorbitals. Paedomorphic skulls show the opposite features. The shape changes from the
hypothetical ancestor of Saurischia to *Massospondylus* were paedomorphic, while those from the
hypothetical ancestor of Saurischia to Neotheropoda were peramorphic. Avetheropoda shows
paedomorphic changes compared to Orionides, indicating that the paedomorphic trend
hypothesised for Eumaniraptora may reach back into the early evolution of Avetheropoda.
Different skull regions often show different trends: one region of the skull would be generally
peramorphic and another region would be predominantly paedomorphic, both along individual ontogenies and through phylogeny. We stress the importance of looking at morphometric data from different vantages to better elucidate trends. Though our data showed minimal differences between our crested-taxa and non-crested taxa data sets and semi-landmark and no semi-landmark data sets, it is important to fully evaluate all possible sources of trends, especially when working with a small data set. Our study is hampered by the preservation of the fossil record (mainly the poor sample of juvenile specimens) and more finds will help to elucidate evolutionary patterns related to heterochrony. With a larger number of taxa comprising juvenile and adult stages it will be possible to further test heterochronic hypotheses within Saurischia, and eliminate artefacts related to sample size. Future studies may also examine ontogenetic histories of individual taxa that have reasonably complete ontogenetic samples, such as *Coelophysis*, to evaluate which factors (dietary preference, heterochrony, etc.) drive shape change in individual taxa. A larger number of studies using geometric morphometrics for individual taxa as well as a more complete sampling within Saurischia are necessary to more completely assess the importance of heterochronic processes in both sauropodomorph and theropod skull shape. However, this study demonstrates that heterochrony played a large part in non-avian saurischian skull evolution.

Acknowledgements:

We thank Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, München), Miriam Zelditch (University of Michigan), Johannes Knebel (Ludwig Maximilians University, München) and Eduardo Ascarrunz (University of Fribourg) for discussion, and Michel Laurin (Sorbonne Universités, Paris) for critical comments on an earlier version of the
manuscript. We further thank Matthew Lamanna (Carnegie Museum of Natural History, Pittsburgh), Alex Downs (Ruth Hall Museum, Ghost Ranch), David Gillette (Museum of Northern Arizona, Flagstaff) and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) for access to collections. CF is supported by a DFG grant to Oliver Rauhut (RA 1012/12-1) and a postdoctoral fellowship of the DAAD German Academic Exchange Service (No. 9154678), BPH is supported by a Benjamin Franklin Fellowship at the University of Pennsylvania, MDE is supported by a grant of the DFG Emmy Noether Programme to Richard J. Butler (BU 2587/3-1).

References


Loewen MA. 2009. *Variation in the Late Jurassic theropod dinosaur Allosaurus: ontogenetic, functional, and taxonomic implications*. University of Utah, Salt Lake City.


Rohlf FJ. 2005. tpsDig, digitize landmarks and outlines, version 2.05.


**Figure 1** Ontogenetic changes in saurischian dinosaurs. (a) General ontogenetic pattern in Saurischia exemplified for *Coelophysis* (adult specimen modified after Rauhut, 2003). (b-f) Specific ontogenetic changes in saurischian dinosaurs visualized as wireframes of Procrustes shapes. (b) *Massospondylus*. (c) *Coelophysis*. (d) Megalosaurid taxon. (e) *Allosaurus*. (f) *Tarbosaurus*. Grey dashed lines represent the juvenile stage and black solid lines represent the adult stage.
Figure 2 PCA and regression analysis of the main sample. (a) Ontogenetic trajectories of terminal taxa for PC 1 versus PC 2. (b) Ontogenetic trajectories of terminal taxa for PC 1 against PC 3. Theropod taxa are shown as black dots, while sauropodomorph taxa are shown as grey dots. (c) Regression analysis against log-transformed skull centroid size (LogCS) showing the ontogenetic trajectories of saurischian dinosaurs based on the overall skull Procrustes shapes of terminal taxa (solid lines) and hypothetical ancestors (dashed lines).
Figure 3 Regression analyses for the skull outline and the external naris. Ontogenetic trajectories of terminal taxa (solid lines) and hypothetical ancestors (dashed lines) against log-transformed skull centroid size (LogCS). (a) Shape of the skull outline. (b) Shape of the external naris.
Figure 4 Regression analyses for the maxilla and antorbital fenestra. Ontogenetic trajectories of terminal taxa (solid lines) and hypothetical ancestors (dashed lines) against log-transformed skull centroid size (LogCS). (a) Shape of the maxilla. (b) Shape of the antorbital fenestra.
Figure 5 Regression analyses for the orbit and infratemporal fenestra. Ontogenetic trajectories of terminal taxa (solid lines) and hypothetical ancestors (dashed lines) against log-transformed skull centroid size (LogCS). (a) Shape of the orbit. (b) Shape of the infratemporal fenestra.
Figure 6 Regression analyses for jugal-quadratojugal region and postorbital. Ontogenetic trajectories of terminal taxa (solid lines) and hypothetical ancestors (dashed lines) against log-transformed skull centroid size (LogCS). (a) Shape of the jugal-quadratojugal region. (b) Shape of the postorbital.
Figure 7 **Regression analyses for the skull roof.** Ontogenetic trajectories of terminal taxa (solid lines) and hypothetical ancestors (dashed lines) against log-transformed skull centroid size (LogCS).
Fig 8 Simplified phylogeny of Saurischia showing the main heterochronic trends of the overall skull shape and single skull regions. Peramorphosis is colored in green and paedomorphosis in yellow. Shape of the hypothetical ancestors based on the continuous character mapping of the Procrustes shapes of the adult terminal taxa from the original data set. Blue skulls represent ancestral skull shapes for which ontogeny could not be analysed.
Heterochronic trends of the skull outline are visualized by the colour of the dots representing the positions of the landmarks and semi-landmarks. Grey skull regions and grey dashed branches represent evolutionary shape changes of skull regions that are not significantly different from the respective ancestor. Black dashed branches show hypothetical heterochronic trends (see discussion).
Table 1 Overview of heterochronies in saurischian overall skull shape and specific skull regions based on the regression analyses. The table shows the differences of Procrustes distances (ΔPD) between ancestor-descendent relationships of adult species. Positive values = peramorphic trends; negative values = paedomorphic trends; values in brackets = non-significant trends; AOF, antorbital fenestra; ITF, infratemporal fenestra; JU, jugal; QU, quadratojugal.

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<th>Overall skull</th>
<th>Skull outline</th>
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<th>Maxilla</th>
<th>AOF</th>
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<td>Orionides-Avetheropoda</td>
<td>-0.0299**</td>
<td>-0.0217**</td>
<td>-0.0736**</td>
<td>(-0.0318)</td>
<td>(-0.0181)</td>
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<tr>
<td>Avetheropoda-Allosaurus</td>
<td>(0.0153)</td>
<td>-0.0280**</td>
<td>-0.1067**</td>
<td>0.0445*</td>
<td>(-0.0296)</td>
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<tr>
<td>Avetheropoda-Tarbosaurus</td>
<td>(-0.0145)</td>
<td>-0.0260**</td>
<td>0.4429*</td>
<td>-0.0066</td>
<td>-0.0748**</td>
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<tr>
<td>95 % CIs</td>
<td>0.01497</td>
<td>0.01271</td>
<td>0.03776</td>
<td>0.02723</td>
<td>0.02938</td>
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<tr>
<td>Significance levels (p=0.05)</td>
<td>0.02246</td>
<td>0.01907</td>
<td>0.05663</td>
<td>0.04085</td>
<td>0.04407</td>
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<table>
<thead>
<tr>
<th></th>
<th>Orbit</th>
<th>ITF</th>
<th>JU-QJ region</th>
<th>Postorbital</th>
<th>Skull roof</th>
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</thead>
<tbody>
<tr>
<td>Saurischia-Massospondylus</td>
<td>-0.0780**</td>
<td>0.1328*</td>
<td>(-0.0029)</td>
<td>(0.0440)</td>
<td>-0.0425**</td>
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<tr>
<td>Saurischia-Neotheropoda</td>
<td>(0.0422)</td>
<td>0.1053*</td>
<td>(-0.0084)</td>
<td>(0.0004)</td>
<td>0.0976*</td>
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<tr>
<td>Neotheropoda-Coelophysis</td>
<td>-0.0689**</td>
<td>-0.1231**</td>
<td>-0.1827**</td>
<td>-0.0980**</td>
<td>(0.0436)</td>
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<tr>
<td>Neotheropoda-Orionides</td>
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<td>(-0.0119)</td>
<td>0.0427*</td>
<td>0.0960*</td>
<td>0.0129*</td>
</tr>
<tr>
<td>Orionides-megalosaurid taxon</td>
<td>0.1681*</td>
<td>(0.0261)</td>
<td>0.0621*</td>
<td>0.0730*</td>
<td>0.0622*</td>
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<tr>
<td>Orionides-Avetheropoda</td>
<td>(-0.0183)</td>
<td>(-0.0111)</td>
<td>(-0.0143)</td>
<td>(-0.0431)</td>
<td>-0.0397**</td>
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<tr>
<td>Avetheropoda-Allosaurus</td>
<td>0.1176*</td>
<td>(0.0248)</td>
<td>0.0741*</td>
<td>0.1193*</td>
<td>(0.0088)</td>
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<tr>
<td>Avetheropoda-Tarbosaurus</td>
<td>0.1122*</td>
<td>(-0.0257)</td>
<td>0.0445*</td>
<td>0.2097*</td>
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<tr>
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<td>0.03044</td>
<td>0.02146</td>
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